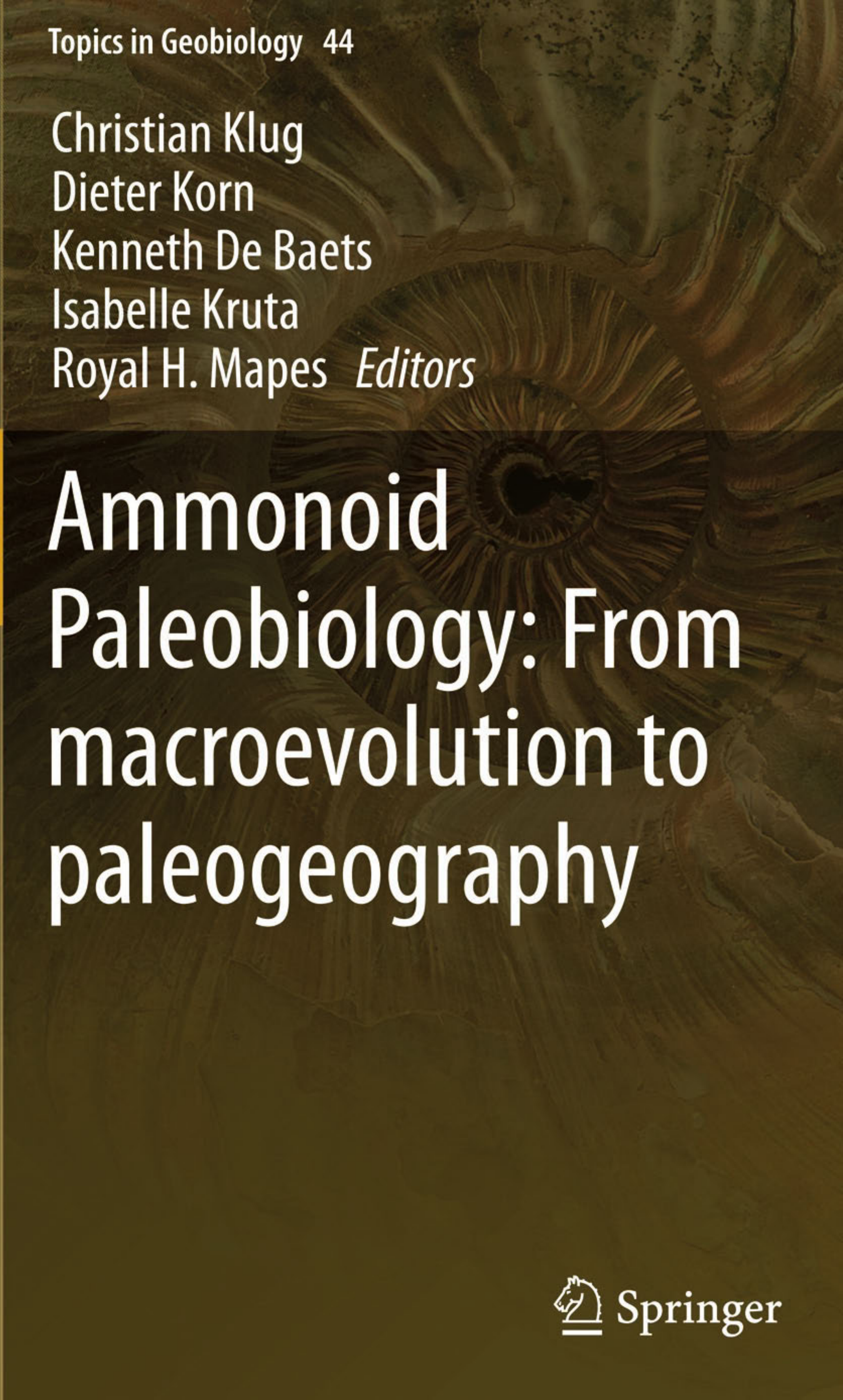

Topics in Geobiology 44

Christian Klug
Dieter Korn
Kenneth De Baets
Isabelle Kruta
Royal H. Mapes *Editors*

Ammonoid Paleobiology: From macroevolution to paleogeography

Springer

Topics in Geobiology

Volume 44

The **Topics in Geobiology** series covers the broad discipline of geobiology that is devoted to documenting life history of the Earth. A critical theme inherent in addressing this issue and one that is at the heart of the series is the interplay between the history of life and the changing environment. The series aims for high quality, scholarly volumes of original research as well as broad reviews.

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Theme-based volumes, such as predator-prey relationships, biomineralization, paleobiogeography, and approaches to high-resolution stratigraphy, cover specific topics and how important elements are manifested in a wide range of organisms and how those dynamics have changed through the evolutionary history of life.

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Metabactrites fuchsi De Baets et al. 2013, PWL2010/5251-LSmiddle Kaub Formation, Bundenbach (Hunsrück, Germany). This is one of the most plesiomorphic and oldest ammonoids known. Image by courtesy of Markus Poschmann (Mainz, GDKE).

Christian Klug • Dieter Korn • Kenneth De Baets
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Editors
Christian Klug
Paläontologisches Institut und Museum
University of Zurich
Zurich
Switzerland

Isabelle Kruta
Division of Paleontology
American Museum of Natural History
New York
USA

Dieter Korn
Leibniz-Institut für Evolutions-
und Biodiversitätsforschung
Museum für Naturkunde
Berlin
Germany

Royal H. Mapes
North Carolina Museum of Natural Science
Raleigh
USA

Kenneth De Baets
GeoZentrum Nordbayern
Friedrich-Alexander-Universität Erlangen
Erlangen
Germany

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Dedication

Image courtesy W. Gerber (Tübingen)
To the memory of Adolf (“Dolf”) Seilacher

(24. February 1925 to 26. April 2014)

There are paleontologists, who have published hundreds of articles, but there is hardly anybody who stimulated ammonoid paleobiological research as much with insightful and innovative articles as Dolf Seilacher. Also, he published the possibly most widely cited phrase on ammonoids:

“Ammonites are for paleontologists what Drosophila is in genetics. The structural complexity of their shells, the complete ontogenetic protocol and a long and rather perfect fossil record make them the most suitable invertebrate group for macroevolutionary studies.”

Seilacher (1989, p. 67)

Dolf Seilacher died peacefully on April 26th 2014 at the age of 89, short before the completion of this book. In order to acknowledge his scientific input and stimulation of research on ammonoids, we dedicate this book to his memory.

His main contributions to the field were probably the balloon-model for simple septa, the tie-point-model for complex septa, the Cartesian diver model, the use of epizoa to constrain ammonoid ecology and his works on ammonoid taphonomy and paleobiology. Below, we provide a list of his papers on ammonoids, which included ammonoid data.

Christian Klug, Dieter Korn, Kenneth De Baets,
Isabelle Kruta, Royal H. Mapes

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Foreword to the First Edition: Ammonoids Do It All

Ammonoids are *the* quintessential fossils, seemingly covering all the major themes of paleontology. Method and theory of stratigraphic correlation using fossils? Albert Oppel, whose concepts of zonation were explicated and applied by W. J. Arkell exhaustively in his monumental works on the Jurassic System, immediately spring to mind-works based virtually exclusively on the stratigraphic distributions of ammonoid species. Evolution? W. Waagen leaps to mind, applying the term "mutation" to his ammonoid lineages, and thus introducing the word to the scientific literature well before geneticists co-opted "mutation" for their own, starkly different, use.

Extinction? Cretaceous heteromorphs were type examples of "racial senescence" -if now wholly discredited, nonetheless an important part of earlier discourse on what is one of the most compelling issues that paleobiology brings to general biological theory. I was myself stunned, when compiling data on the end-Cretaceous mass extinction in the late 1960s for a seminar conducted by Norman D. Newell, to find that the scaphitids-far from dwindling to a precious few as Cretaceous time was running out-were actually in the midst of an evolutionary radiation, an expansion of diversity cut abruptly short by whatever it was that disrupted things so badly 65 million years ago.

Indeed, though of course much remains to be learned about ammonoid phylogeny, every chart that I have seen published in the last 30 years showing the basic outlines of ammonoid evolution against the backdrop of SilurianCretaceous geologic time constitutes a stark object lesson on the resonance between evolution and extinction. The theme of early "experimentation" shows up amidst Devonian ammonoid diversity: the clymeniids constitute an arch example, with their siphuncle on the opposite side of the body from what proved to be the "normal" ammonoid condition-an experiment that failed to survive the late Devonian biotic crisis. thus forever depleting ammonoid morphological diversity. And are the goniatites, ceratites, and ammonites mere grades, as nearly everyone suspected back in the parallel-evolution-mad 1960s? Or are they, as now seems evident, genealogically coherent, monophyletic clades that represent radiations consequent to major biotic crises of the Permo-Triassic and Triassic-Jurassic boundaries? That grade-like patterns can come from evolutionary radiations following severe extinction bottlenecks is an aspect of evolutionary theory yet to be fully expounded. And it is the ammonoids that show such patterns best.

Biostratigraphy, evolution, extinction-not to mention biogeography, paleoecology, and functional morphology: of all major taxa in the fossil record, the ammonoids arguably do it best. But there is something more to them, a certain allure that makes them deserved rivals of trilobites as the most ardently desired and sought -after relics of the deep past. Ammonoids are at once exotic yet familiarly organic. Though nearly always simply the empty shells of long-dead animals, they nonetheless seem complete. They are almost always beautiful-and sometimes even colorful. It's probably the (nearly always planispiral) logarithmic spiral that, in spite of its mathematical precision, nonetheless casts an aura of intrigue and mystery to what is otherwise just another fossil. A few years back I published a lavishly illustrated book on fossils, using photographs of many of the finest specimens of all taxa from the rich paleontological collections of the American Museum of Natural History. And though I had skulls of a male and female Tertiary artiodactyl on the front cover, it is the photo on the back-of a pretty little pyritized specimen of the Jurassic ammonoid *Hecticoceras-that* attracted the most attention, and that has been subsequently reproduced over and over again.

I can only conclude that, over and above the prodigious intellectual contributions that continue to come from contemplation of these marvelous animals (as this present volume amply demonstrates), ammonoids also have that certain *je ne sais quoi* that will always keep them at the forefront of the paleontological realm. Ammonoids really do seem to have it all.

The American Museum of Natural History
New York, New York

Niles Eldredge

Foreword to the New Edition

This two-volume work is a testament to the abiding interest and human fascination with ammonites. As Niles Eldredge wrote in the forward to our 1996 book "Ammonoid Paleobiology" (fondly referred to as the Red Book), ammonites are "the quintessential fossils." They have contributed to ideas about biostratigraphy, paleoecology, paleobiology, paleoenvironment, paleobiogeography, paleogeography, paleoceanography, evolution, phylogeny, and ontogeny. All of these themes are treated in the present book. The past two decades have witnessed an explosion of new information about ammonites: early life history, evolution of the buccal mass, feeding habits, soft-tissue preservation, radiation- and extinction-patterns, shell microstructure, sutures and pseudosutures, cameral membranes, mode of life, phylogeny, and habitats. Many of these discoveries have benefitted from the application of new technologies such as isotopic analysis, organic geochemistry, geographic information systems, geometric morphometrics, computerized tomography, and synchrotron imaging. They have also relied on more traditional techniques such as scanning electron microscopy and electron dispersive analysis, which continue to furnish an abundance of data. Fortunately, too, our field is constantly being re-energized by the discovery of new fossil finds that shed light on old questions and raise new ones. Given all these advances in our knowledge, this book is a comprehensive and timely "state of the art" compilation. Moreover, it also points the way for future studies to further enhance our understanding of this endlessly fascinating group of organisms.

Neil H. Landman, Kazushige Tanabe, and Richard Arnold Davis, Editors of the 1996 book "Ammonoid Paleobiology" (the original three musketeers).

Preface

Imagine you belong to any religion and your chief deity asks you: "Could you imagine editing the new sacred book?" This is the feeling you have as an ammonoid worker, when you are offered to take care of the new edition of 'Ammonoid Paleobiology'. Not only for us, who had the honor and burden of this gigantic task, 'Ammonoid Paleobiology' represented a comparably important book since we consulted it so often in order to better understand these organisms, which went extinct 65 million years ago.

Although many of the early ammonoid researchers of the nineteenth century have spent thoughts on the ammonoid organism and its mode of life, most of the major contributions to modern ammonoid paleobiology appeared roughly in the past half century. Looking at the scientific output of these decades, it appears like the first edition of "Ammonoid paleobiology" was a product of something like a golden age of ammonoid research. The two decades preceding its publication saw the first five international symposiums "Cephalopods—Present and Past" and many important articles by colleagues such as John Callomon, Antonio Checa, John A. Chamberlain, Larissa Doguzhaeva, Jean-Louis Dommergues, Jean Guex, Roger H. Hewitt, Michael House, David K Jacobs, Jim Kennedy, Cyprian Kulicki, Neil Landman, Ulrich Lehmann, Harry Mutvei, Takashi Okamoto, Bruce Saunders, Yasunari Shigeta, Kazushige Tanabe, Henri Tintant, Jost Wiedmann, Peter D. Ward. Gerd Westermann, Yuri Zakharov (incomplete list!) contributed essential data and interpretations, but they also stimulated further research in this field. Unfortunately, many important cephalopod workers and good colleagues have died in the last two decades. In 2014 alone, for example, Fabrizio Cecca, Adolf Seilacher, Helmut Hölder, Gerd Westermann, and Hiromichi Hirano passed away.

Due to fundamental changes in the structure of scientific communities including the dubious judgment of the value of scientific work by impact factors and citation rates, cephalopod research has changed as well. Additionally, the community of ammonoid researchers appears to have started shrinking. Nevertheless, the past decades still saw thousands of interesting contributions on representatives of this fantastic clade. And still, we have a lot of work ahead of us prior to becoming able to respond to all questions regarding ammonoid paleobiology.

So what is new? In terms of content, we have restructured the former into a two-volume work with the main parts shell, ontogeny, anatomy, habit and habitats, macroevolution, paleobiogeography, ammonoids through time, fluctuations in ammonoid diversity, and taphonomy. Most of these parts are subdivided into chapters. The great amount of 41 chapters reflects the panel of ammonoid workers present nowadays in academia, junior and senior scientists from many countries and a higher percentage of female authors compared to the previous edition. We aimed at being as up-to-date as possible, which had the consequence that some chapters also present unpublished specimens, data and results. We also included two chapters on the geochemistry of ammonoid shells, a field that still offers vast possibilities for new research. This is also reflected in the slightly different views presented therein.

Furthermore, we added an introductory chapter for the definition of terms and with a recommendation for the description of new ammonoid taxa. We emphasized the next challenges in ammonoid research such as reconstructing ammonoid phylogeny, understanding their intraspecific variability or reconstructing the soft parts. Studying intraspecific variability has been widely neglected, but it offers a wealth of possible implications for life histories, ontogeny, reproduction and, most importantly, for evolution. In this context, another challenge is establishing a phylogeny for ammonoids, and thus, one part comprising five chapters is dedicated to ammonoid macroevolution. In our eyes, paleontological data yield the essential information for research on evolution. As pointed out already by Seilacher and Eldredge, ammonoids are of particular interest due to their accretionary shell, which has a good fossilization potential and hold a record of their life history, their high evolutionary rates, their wide geographic distribution, high taxonomic diversity and morphological disparity as well as their well-constrained stratigraphic (i.e., temporal) framework. In the case of ammonoids, however, countless homoplasies occurred throughout their evolution, thus hampering attempts to reconstruct ammonoid phylogeny. Nevertheless, a sound phylogenetic model for the ammonoid clade should be one of the central tasks in ammonoid research because the knowledge of ammonoid phylogeny is still patchy. Furthermore, although some quantitative approaches have been pioneered with ammonoids (e.g., Raup's morphospace, Okamoto's growing tube model), such methods are still too little used in many studies on ammonoid paleobiology and evolution; many studies restrict themselves to narrative discussions or qualitative assessments. For this reason, the application of several quantitative and statistical methods to study many aspects of ammonoid like biostratigraphy, biogeography, intraspecific variability, evolutionary trends, etc. are explained and demonstrated in several of the chapters of these two volumes, in the hope these methods will be used more widely in the ammonoid community.

Finally, we added new information obtained from tomographic data obtained both from computer tomography and grinding tomography. The field of virtual paleontology has just started to deliver ammonoid data, which are of special interest in the studies of shell morphology, ontogeny, buoyancy, mode of life, and ultimately evolution.

These two volumes would have been impossible without our wonderful authors, and especially the help of Neil Landman as well as Kazushige Tanabe. Additionally, we greatly appreciate the support of the army of reviewers, who are listed and thanked in the corresponding chapters. Naturally, our partners and families have been affected more or less from the additional time consumed by the preparation of the volumes, we apologize for that and thank them for all their patience, inspiration, and support.

Christian Klug, Dieter Korn,
Kenneth De Baets, Isabelle Kruta,
and Royal H. Mapes

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Contributors

Marco Balini Dipartimento di Scienze della Terra “A. Desio”, Milano, Italy

Arnaud Brayard UMR CNRS 6282 Biogéosciences, Université de Bourgogne, Dijon, France

Morgane Brosse Paläontologisches Institut und Museum, Universität Zürich, Zürich, Switzerland

Hugo Bucher Paläontologisches Institut und Museum, Universität Zürich, Zürich, Switzerland

Luc Bulot Aix-Marseille Université, Marseille, France

Kenneth De Baets GeoZentrum Nordbayern, Friedrich-Alexander-Universität Erlangen-Nürnberg, Erlangen, Germany

Gilles Escarguel UMR CNRS 5276, Laboratoire de Géologie de Lyon: Terre, Planètes, Environnement, Université Claude Bernard Lyon 1, Villeurbanne Cedex, France

Camille Frau 9bis Chemin des Poissonniers, La Ciotat, France

Dirk Fuchs Earth and Planetary System Science, Department of Natural History Sciences, Hokkaido University, Sapporo, Japan

Stijn Goolaerts Department of Paleontology, OD Earth & History of Life, Royal Belgian Institute of Natural Sciences (IRSNB-KBIN), Brussels, Belgium

Neal S. Gupta Lab for Terrestrial Environments, Bryant University, Smithfield, RI, USA
Geophysical Laboratory, Carnegie Institution of Washington, Washington, DC, USA

Christina Ifrim Institut für Geowissenschaften, Ruprecht-Karls-Universität, Heidelberg, Germany

John W.M. Jagt Natuurhistorisch Museum Maastricht, Maastricht, The Netherlands

Elena A. Jagt-Yazykova Zakład Paleobiologii, Uniwersytet Opolski, Opole, Poland

St. Petersburg State University (SPbGU), St. Petersburg, Russia

James F. Jenks West Jordan, Utah, USA

Christian Klug Paläontologisches Institut und Museum, Zürich, Switzerland

Dieter Korn Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany

Björn Kröger Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland

Neil H. Landman Division of Paleontology (Invertebrates), American Museum of Natural History New York, New York, NY, USA

Jens Lehmann Geowissenschaftliche Sammlung, Universität Bremen, Bremen, Germany

Louise M. Longridge Earth, Ocean and Atmospheric Sciences, University of British Columbia, Vancouver, BC, Canada

Marcin Machalski Instytut Paleobiologii, Polska Akademia Nauk, Warsaw, Poland

Maximiliano Meier Paläontologisches Institut und Museum, Universität Zürich, Zürich, Switzerland

Claude Monnet UMR CNRS 8217 Géosystèmes, UFR des Sciences de la Terre (SN5), Université de Lille 1, Villeneuve d'Ascq cedex, France

Pascal Neige Laboratoire Biogéosciences, University of Burgundy, CNRS, Dijon, France

Isabelle Rouget Laboratoire CR2P, Sorbonne Universités, UPMC-Univ Paris 06, MNHN, CNRS, Paris, France

Günter Schweigert Staatliches Museum für Naturkunde, Stuttgart, Germany

Paul L. Smith Earth, Ocean and Atmospheric Sciences, University of British Columbia, Vancouver, BC, Canada

Jakob Vinther Schools of Earth and Biological Sciences, University of Bristol, Bristol, UK

Sonny A. Walton Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany

Ryoji Wani Faculty of Environment and Information Sciences, Yokohama National University, Yokohama, Japan

Peter Ward Sprigg Institute of Geobiology, University of Adelaide, Adelaide, Australia

Margaret M. Yacobucci Department of Geology, Bowling Green State University, Bowling Green, OH, USA

Part I
Macroevolution

Chapter 1
Ancestry, Origin and Early Evolution of Ammonoids

Christian Klug, Björn Kröger, Jakob Vinther, Dirk Fuchs and Kenneth De Baets

1.1 Introduction

The phylogeny of most of the major cephalopod clades has been reconstructed with some confidence using morphological, developmental and molecular data in the last decades and some general macroevolutionary patterns are beginning to crystalize (e.g., Dzik 1981, 1984; Woodruff et al. 1987; Engeser 1996; Young et al. 1998; Peterson et al. 2004; Kröger 2005; Bergmann et al. 2006; Strugnell et al. 2006; Strugnell and Nishiguchi 2007; Bizikov 2008; Shigeno et al. 2008, 2010; Kröger et al. 2011; Warnke et al. 2011). Undoubtedly, the sister group of cephalopods lies within the Mollusca, although the sister group of cephalopods is under debate. Nevertheless, it appears like the monoplacophorans are the best candidate as extant

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C. Klug (✉)
Paläontologisches Institut und Museum, University of Zurich, Karl Schmid-Strasse 6,
8006 Zurich, Switzerland
e-mail: chklug@pim.uzh.ch

B. Kröger
Finnish Museum of Natural History, University of Helsinki, 44 (Jyrängöntie 2), 00014 Helsinki,
Finland
e-mail: bjorn.kroger@helsinki.fi

J. Vinther
Schools of Earth and Biological Sciences, University of Bristol, Woodland Road, BS8 1UG,
Bristol, UK
e-mail: jakob.vinther@bristol.ac.uk

D. Fuchs
Earth and Planetary System Science, Department of Natural History Sciences, Hokkaido
University, Sapporo, Japan
e-mail: dfuchs@mail.sci.hokudai.ac.jp

K. De Baets
GeoZentrum Nordbayern, Fachgruppe PaläoUmwelt, Universität Erlangen, Loewenichstr. 28,
91054 Erlangen, Germany
e-mail: kenneth.debaets@fau.de

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sister group (Kröger et al. 2011 and references therein). In contrast to earlier views, the oldest generally accepted cephalopod fossil is *Plectronoceras cambria* Walcott, 1905 from the middle Late Cambrian (Glaessner 1976; Dzik 1981; Kröger 2007; Mutvei et al. 2007; Landing and Kröger 2009; Mazurek and Zatoń 2011; Kröger et al. 2011). It possessed a small (<2 cm) simple breviconic (short conical) shell with a subventral ('posterior' *sensu* Kröger 2007) siphuncle and about ten septa (Webers and Yochelson 1989). Still in the Late Cambrian, the early cephalopods underwent an explosive radiation that continued and intensified in the Ordovician (Kröger 2007). An important clade of cephalopods, the Orthocerida from which all living cephalopods and the Ammonoidea are derived at the end of the Silurian, originated already in the Early Ordovician (Kröger et al. 2011).

The transition from the Orthocerida via the Bactritida to the Ammonoidea has been documented in detail recently (Kröger and Mapes 2007). According to fossil evidence, the Bactritida had originated already in the earliest Emsian. This phylogenetic event was followed by the origin and radiation of ammonoids in a geologically abbreviated amount of time (Erben 1960, 1964a, b, 1965, 1966; Becker and House 1994; House 1996; Klug et al. 2008; Kröger 2008b; De Baets et al. 2010, 2013b; Frey et al. 2014).

In this chapter, we will discuss the origin of cephalopods and ammonoids as well as their respective Bauplans. Important evolutionary events and morphological innovations around these originations are also listed.

1.2 Phylogenetic Position of the Ammonoids in the Cephalopod Tree

Most cephalopod workers agree on the Cambrian origin of cephalopods, that they were ectocochleate (externally shelled) and that the shell was chambered (Dzik 1981, 1984; Holland 1987; Engeser 1996; Shigeno et al. 2008, 2010; Kröger et al. 2011). There is also a wide agreement that the cephalopods evolved in one way or the other from a group of monoplacophorans (Yochelson et al. 1973; Pojeta 1980; Dzik 1981; Kröger 2007; Webers and Yochelson 1989). By contrast, Brock and Paterson (2004) as well as Peel (1991) sought for the origin of cephalopods in the Helcionellida. Dzik (1981, 2010) thought that possibly, the cephalopods root in the Circothecidae (Hyolithida), although this hypothesis was rejected by Landing and Kröger (2012). Thus the origin of cephalopods among Cambrian molluscs is still not settled firmly.

Pojeta (1980) suggested that the snorkel-like process of the curved shell of the monoplacophoran Yochelcionellidae might have evolved into the plectronocerid siphuncle. Dzik (1981) hypothesized that the first cephalopods might have taken off from the sediment by secreting a salt-depleted and thus lighter liquid in the apex. This hypothesis is indirectly corroborated by the fact that the water is osmotically removed from newly formed chambers in nautilids (Ward 1979). Subsequently, the phragmocone evolved by a beginning alternation of liquid- and shell-secretion. The final physiological step in the phragmocone evolution was according to Dzik (1981) the increasing chamber pressure produced by the ionic pump, thus allowing gas diffusion.

In accordance with Kröger et al. (2011), we favor the hypothesis that the close ancestors of cephalopods resemble Cambrian monoplacophorans (Fig. 1.1) like *Knightoconus* (Yochelson et al. 1973; Webers and Yochelson 1989; Dzik 2010) or hecionellids like *Tannuella* (Brock and Paterson 2004). Thus, their shells were probably slightly curved, high and conical. However, more research on middle and late Cambrian fossil mollusks is necessary to reliably solve this question.

An additional controversial hypothesis was introduced by Smith and Caron (2010) with a redescription of *Nectocaris* from the Burgess Shale (Smith 2013). This form looks superficially like a derived coleoid cephalopod with its lateral fins, stalked eyes and a funnel-like structure attached to the head. The profound implication was that the fossil record of cephalopods might be severely biased and

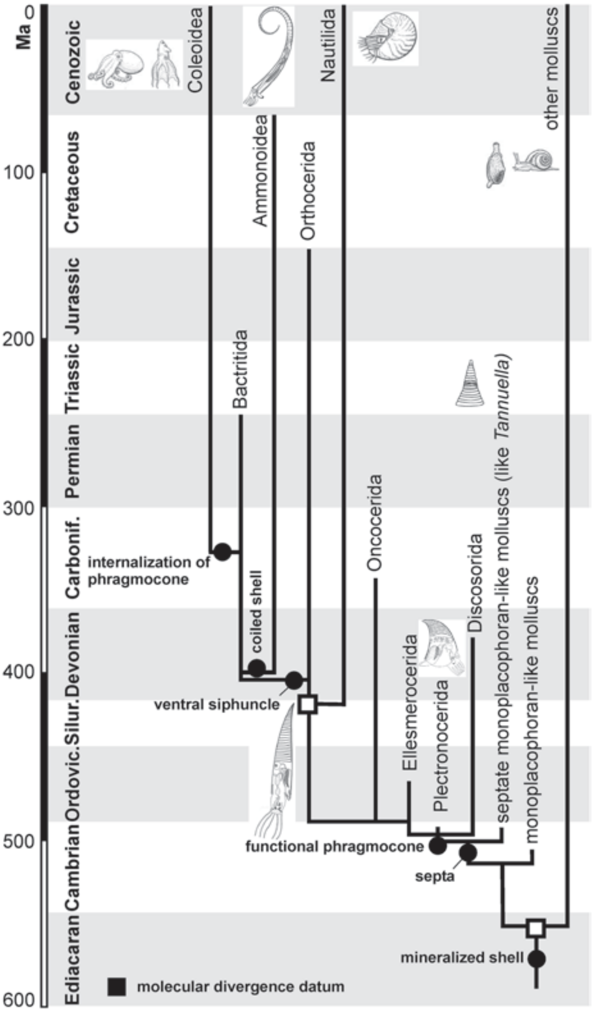

Fig. 1.1 Cephalopod phylogeny (modified after Kröger et al. 2011)

that the ancestral cephalopod might have resembled a coleoid. The interpretation was quickly taken under scrutiny (Mazurek and Zaton 2011; Kröger et al. 2011; Runnegar 2011) and criticized for several incongruences, which rejected the presumed primary homologies. Among those, they listed a closed funnel, which is attached to the head in an organism with a straight gut. Embryology demonstrates that the funnel evolves from the posterior part of the embryo and attains its position adjacent to the head by dorsal folding of the body (Kröger et al. 2011). Furthermore, the funnel is attached to the mantle, while the structure in *Nectocaris* is attached to the head. Thus, this is more likely a case of superficial convergence. There is no single unequivocal molluskan feature in *Nectocaris*, and it therefore seems more reasonable to interpret this taxon as a yet unknown lophotrochozoan of unclear systematic affinity, which developed a mode of life possibly convergent with modern squids (Kröger et al. 2011; Runnegar 2011).

1.2.1 The Cephalopod Bauplan

Since no fossilized soft parts of plectronocerids or ellesmerocerids are known so far, all ideas on the cephalopod Bauplan are based on empirical evidence from the shell and its soft tissue imprints (Kröger 2007) as well as inferences from the phylogenetic context (Fig. 1.2). In the following, we present the autapomorphies of the cephalopod Bauplan (Table 1.1) and shortly discuss the (sometimes weak) evidence for each character state. The list is based on that of the Hypothetical Ancestral Siphonopodean Cephalopod (HASC) of Engeser (1990a, 1996), which is modified here to define the last common ancestor (an orthocerid) of the crown group of cephalopods.

1. Chambered shell with straight to slightly cyrtoconic phragmocone for buoyancy control (see preceding paragraphs).
2. One arm crown, probably with ten arms: Since ten arms represent the ancestral state of coleoids (e.g., Fuchs 2006; Kröger et al. 2011) and nautilids have ten arm buds in early embryonic developmental stages (Shigeno et al. 2008, 2010), it appears reasonable to infer this state also for the shared ancestor of coleoids and nautilids, i.e., some Paleozoic orthocerids. It is difficult to assess the number of arms in older forms, and since orthocerids diversified in the early Ordovician it is not yet possible to conlusively reconstruct the number of arms in the majority of Palaeozoic forms, although from the above data, ten arms appears to be likely. In any case, a gastropod-like foot as proposed by Bandel (1982) and Teichert (1948) appears unlikely. Mehl (1984) reported the possible imprints of ten arms in *Michelinoceras* from the Silurian of Bolivia, but this imprint might as well be something else.
3. Hyponome: There is no direct fossil evidence yet for the presence or absence of a hyponome (and several other organs listed below) in early cephalopods. From the extant phylogenetic bracket (Witmer 1995), we can extrapolate that the hyponome was present in the common ancestor of Nautilida and Coleoidea. There is some indication for the presence of a hyponomic sinus in the ellesmero-

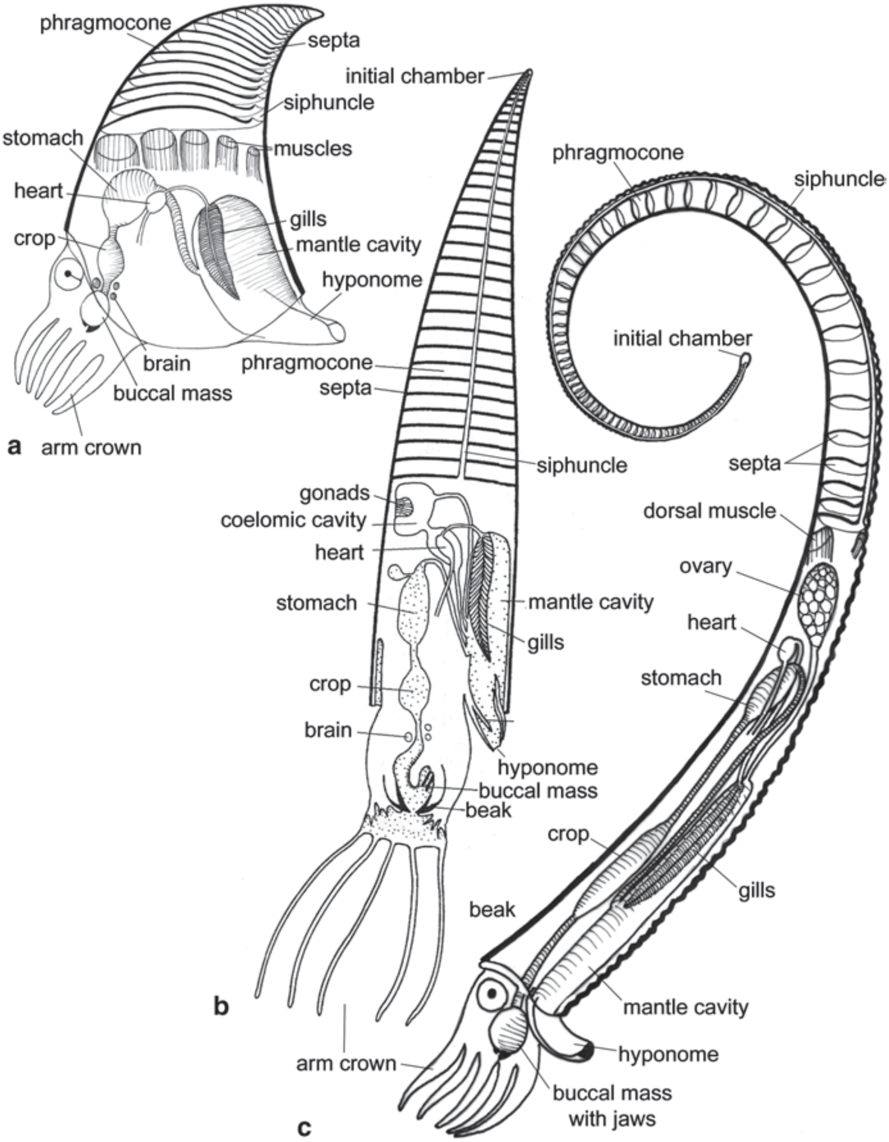

Fig. 1.2 Hypothesized Bauplan of **a** an ancestral cephalopod like *Plectronoceras* (based on Kröger 2007), **b** the HASC, modified after Engeser (1996) and **c** an ancestral ammonoid like *Metabactrites fuchsi* (De Baets et al. 2013b)

cerids (Kröger 2007) as well as in forms that diverged from orthocerids in the Early Ordovician. However, fossil evidence for the homologization of the hyponomic sinus between plectronocerids and ellesmerocerids on the one side and the condition in crown cephalopods on the other side is ridden with some level of uncertainty. Nautilids have a unfused hyponome. It is derived from posterior

Table 1.1 Autapomorphies (in **bold**) and plesiomorphies (in regular) of the Cephalopoda, the Siphonopodean Cephalopoda (HASC), the Bactritida and the Ammonoidea, using data from Engeser (1990a, 1996). Character states, which are hypothesized based on the extant phylogenetic bracket or extrapolations are marked in grey

Trait	Cephalopoda	HASC	Bactritida	Ammonoidea
Phragmocone	**Present**	Present	Present	Present
Siphuncle	**Subventral, narrow**	Central, narrow	**Ventral**, narrow	Ventral, narrow
Shell shape	Cyrtoconic	Orthoconic	Orthoconic	**Crioconic**
Cross section	Subcircular	Circular	**Slightly compressed**	**Compressed**
Initial chamber	Unknown	**Ovoid, small**	Ovoid, Small	Ovoid, Small
Initial shaft angle	**Wide**	Wide	**Narrow**	Narrow
Suture line	**Straight**	Straight	**Ventral lobe**	Ventral + **lateral lobes**
Muscle attachment	**Circular, serial**	Circular	**Dorsal concentration**	Dorsal concentration
Hyponomic sinus	**Deep**	Shallow or absent	**Moderately deep**	**Deep**
Arm crown	**10 Arms**	10 Arms	10 Arms	10 Arms
Hyponome	**Present**	Present	Present	Present
Jaws	No Real Jaws	**Present**	Present	Present
Internal fertilization	**Present**	Present	Present	Present
Copulatory organs	**Present**	Present	Present	Present
Brain	**Present**	Present	Present	Present
Direct development	**Present**	Present	Present	Present
Large embryo	**Present**	Present	Present	Present
Large coelomic cavity	**Present**	Present	Present	Present
Carnivorous life style	**Present**	Present	Present	Present
Crop	**Present**	Present	Present	Present
Nidamental glands	**Present**	Present	Present	Present
Pericardial glands	**Present**	Present	Present	Present
Needham's sac	**Present**	Present	Present	Present
Crystalline style	**Present**	Present	Present	Present
Partially closed blood circulatory system	**Present**	Present	Present	Present

mantle folds in the embryo. These folds are not fused in nautilids; this condition was likely the plesiomorphic condition for the crown cephalopod ancestor.

4. Jaws: Unclear. There is no fossil evidence for cephalopod jaws older than Late Devonian (e.g., Woodward 1885; Clausen 1969). Hence, it is the question whether this is a taphonomic problem or whether the cephalopod jaw evolved

only in the orthocerids and their phylogenetic successors (see HASC; Engeser 1996) or convergently in the Nautilida and the Bactritida plus their descendants. This was already discussed shortly by Kröger et al. (2011). Presence of at least jaw-like structures appears likely, because such possibly homologous structures are also present in scaphopods, monoplacophorans (the supposed sister-group of cephalopods) and some gastropods (Boletzky 2007). Remarkably, the upper and lower jaws are fused in early ontogenetic stages of some coleoids. It is still conceivable that the cephalopod jaw as it is known from the crown groups evolved only in the Middle Paleozoic orthocerids and not in the Early Paleozoic groups. These formed perhaps part of the adaptive radiation of crown cephalopods in the Devonian as part of the Devonian Nekton Revolution (Klug et al. 2010) and the sudden diversity of jawed vertebrates, which they were in an escalatory arms race with. Some authors (e.g., Dzik 1981) have considered fossils like *Aptychopsis* to function as both jaws and operculum in Silurian cephalopods, but there is some indication that these can be treated as opercula (Turek 1978; Holland et al. 1978; Holland 1987 and references therein) or that they are homologous with later cephalopod beaks.

5. Internal fertilization and copulatory organs: The presence is inferred from the extant phylogenetic bracket (same line of reasoning as for the hyponome).
6. Brain: The presence is inferred from the extant phylogenetic bracket (same line of reasoning as for the hyponome).
7. Direct development of a yolk-rich egg: Although direct evidence is missing, the record of embryonic and post-embryonic ontogeny in the shell lacks evidence for true larval stages, thus supporting direct development.
8. Moderately large embryonic conch (compared with other molluscs, especially monoplacophorans): There is good evidence for this from the preserved embryonic shells of several early Paleozoic cephalopod groups (and also monoplacophorans), although these are not known yet from plectronocerids.
9. Relatively large coelomic cavity (compared with other molluscs): Same line of reasoning as for the hyponome.
10. Carnivorous life style: The presence is inferred from the extant phylogenetic bracket (same line of reasoning as for the hyponome); at least some injuries on shelled organisms (Brett and Walker 2002 and references therein) and coprolite contents point to a predatory mode of life (Botting and Muir 2012 and references therein) of Ordovician cephalopods, but these are usually based on the circular argument that extant and therefore fossil ones were carnivorous.
11. Crop: The presence is inferred from the extant phylogenetic bracket (same line of reasoning as for the hyponome).
12. Nidamental glands: The presence is inferred from the extant phylogenetic bracket (same line of reasoning as for the hyponome).
13. Pericardial glands: The presence is inferred from the extant phylogenetic bracket (same line of reasoning as for the hyponome).
14. Needham's sac: The presence is inferred from the extant phylogenetic bracket (same line of reasoning as for the hyponome).
15. Crystalline style: The presence is inferred from the extant phylogenetic bracket (same line of reasoning as for the hyponome).

16. Partially closed blood circulatory system: The presence is inferred from the extant phylogenetic bracket (same line of reasoning as for the hyponome).

In his contribution on the phylogenetic position of ammonoids, Engeser (1990a, 1996) introduced his model of the Hypothetical Ancestral Siphonopodean Cephalopod (HASC). HASC (modified in Fig. 1.2) is his model of the shared ancestor of crowngroup (i.e. Recent) cephalopods, which are all Coleoidea and Nautilida of today. In Table 1.1, give an overview over characters of Engeser's compilation are listed with some minor modifications, namely the number of arms.

In his chapter on the phylogenetic position of ammonoids, Engeser (1996) also listed the plesiomorphies supposedly present in the HASC.

1. Marine habitat. Most cephalopod fossils so far have been found in marine rocks and such from other deposits were probably reworked.
2. Radula (possibly with nine teeth in a row, four marginalia). Comment by Engeser (1996): "Campitius titanicus *from the Lower Cambrian of the Westgard Pass area, California, is a large isolated radula with 13 elements per row* (Firby and Durham 1974). *Although its former "owner" is unknown, it demonstrates that a group of molluscs with this character lived in the Early Cambrian seas. This radula might have belonged to a stem lineage representative of the Cephalopoda.*" Radulae have become known from Ordovician orthoconic nautiloids (Gabott 1999) and the Silurian orthoceratid *Michelinoceras* (Mehl 1984), but the exact morphology of the radula as well as the number of teeth can not be confidently reconstructed from these finds due to their poor preservation (Nixon 1988; Gabott 1999; Kruta et al. 2014).
3. Two gills in a pallial cavity, one pair of kidneys, and a heart with one pair of auricles. Although others have argued that paired pathologies in shell structures might indicate that ammonoids are tetrabranchiate cephalopods like the Nautilida as opposed to all other living cephalopods (e.g., De Baets et al. 2011, p. 172), direct evidence for two or four gills from externally shelled cephalopod fossils is missing still.
4. One pair of retractor muscles: Kröger (2007) studied the muscle attachment features of the Ellesmerocerida. Potentially, the situation was more complicated in the earliest cephalopods, perhaps including the HASC with multiple paired muscle scars.
5. Simple pinhole eyes: Fossil evidence is missing. Extant Nautilida have pinhole eyes which could well represent the plesiomorphic condition for cephalopods as the outgroup has less complex photoreceptor organs. However, the pinhole camera eye (as suggested by a novel molecular study: Ogura et al. 2013) might be a specialization of the Nautilida just like the great number of arms (Shigeno et al. 2008, 2010; Sasaki et al. 2010). Ammonoids are stem coleoids and are thus situated on a lineage that evolved camera type eyes. Ocular sinuses suggest that many shelled cephalopods had eyes and eye capsules might even be preserved in rare cases in derived Cretaceous ammonoids (Klug et al. 2012), but these results are inconclusive as to whether the eye was a camera or a pinhole type.
6. A single, high, conical shell with periostracum, prismatic, and nacreous layers; shell covering the visceral mass; mineralized parts of the shell consisting of aragonite.

7. A pair of statocysts. No support from the fossil record so far, but is justified based on phylogenetic bracketing.
8. Body bilaterally symmetrical.
9. Sexes separate and of roughly equal size.
10. Salivary glands. No support from the fossil record so far.
11. Two oviducts, two spermiducts. No support from the fossil record so far.
12. (?) r-selected reproductive strategy: The embryonic shells of plectronocerids are still unknown. Taking the small size of plectronocerids into account and the smallest known shell diameter of plectronocerid fossils (Kröger 2007), the number of offspring was potentially not very high, possibly tens to hundreds, following the reasoning for more derived cephalopods in De Baets et al. (2013a). In the orthocerids as well as the bactritids, this was probably still the case (De Baets et al. 2012, 2015b). It appears like the reproductive rates rose significantly in the Ammonoidea and some Coleoidea, but it was low in the Actinocerida, Endocerida as well as the Nautilida. Therefore, the survivorship curves of HASC-like cephalopods were probably intermediate, i.e. a moderate number of offspring combined with a moderate number of individuals that managed to achieve sexual maturity and succeeded with reproduction.
13. (?) Planktic early life phase. The small adult size (ca. 5 mm) of *Plectronoceras*, relatively great shell thickness, and numerous septa speak against a planktic early life stage (Landing and Kröger 2012). The apex of *Plectronoceras* is still unknown, but the apices of all plectronocerid descendants (with the exception of Orthoceratida) are *Nautilus*-like, cap-shaped, and have high initial angles of expansion, so that a cap shaped apical shell must be assumed for *Plectronoceras* based on the similarity of the general conch form with that of ellesmerocerids, primitive discosorids, and other descendants of plectronocerids. The small size of embryonic shells in at least some orthocerids, bactritoids and ammonoids as well as their facies distribution suggests a planktonic early life phase of these forms with small, spherical initial chambers (Kröger et al. 2009; Mapes and Nützel 2009; De Baets et al. 2012, 2015b). The oldest known spherical (orthocerid) cephalopod protoconchs occur in the Early Ordovician (Tremadocian) from *Bactroceras* (compare Evans 2005; Kröger 2006; Kröger and Evans 2011; Landing and Kröger 2012).
14. (?) Blood pigment consisting of hemocyanin. *Nautilus* diverged from other extant cephalopods around the Siluro-Devonian (Bergmann et al. 2006; Kröger et al. 2011), so that it might have been present at least since then in cephalopods.

1.2.2 Position of the Bactritida and Ammonoidea

As mentioned above, coleoids and ammonoids are derived from the Bactritida which root in the Orthocerida in the latest Silurian or earliest Devonian. The orthocerids form a long branch down to the earliest Ordovician (Dzik 1984; Kröger 2007, 2008a; Kröger and Mapes 2007; Kröger et al. 2011; Kröger and Lefebvre

2012). With respect to synapomorphies of Orthocerida and Bactritida, one can list the small subspherical to ovoid initial chamber, the straight to slightly bent conical shell and the narrow siphuncle (Fig. 1.3).

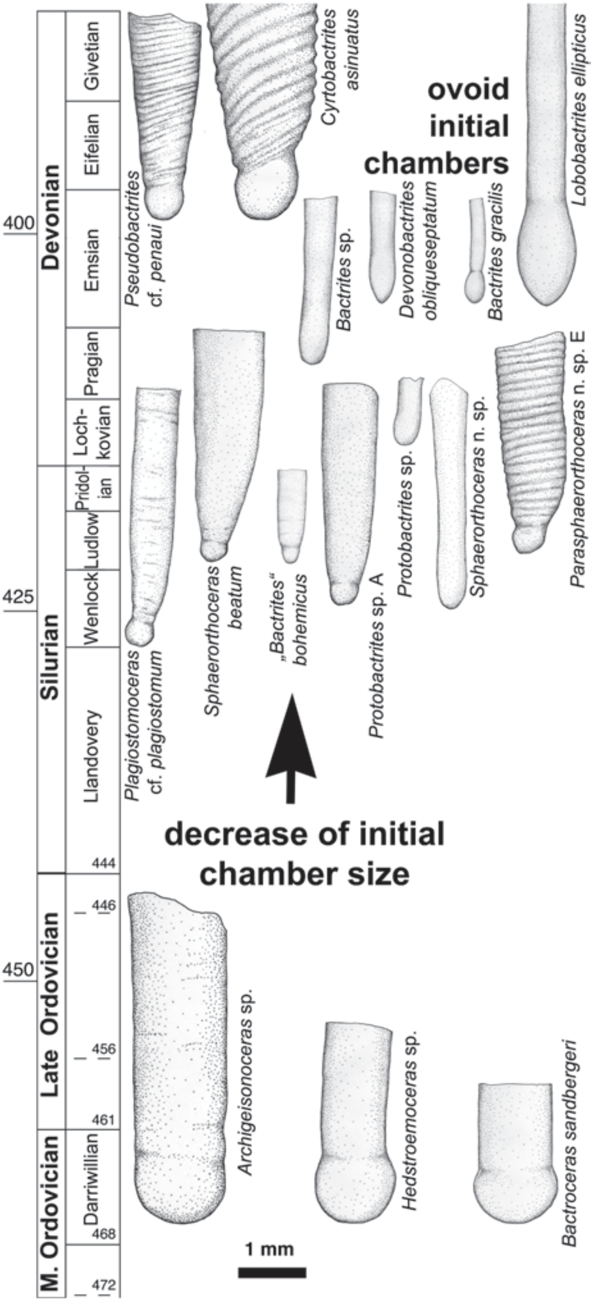

Fig. 1.3 Occurrences of embryonic shells of orthocerids and bactritids in the Paleozoic (modified after Kröger and Mapes 2007)

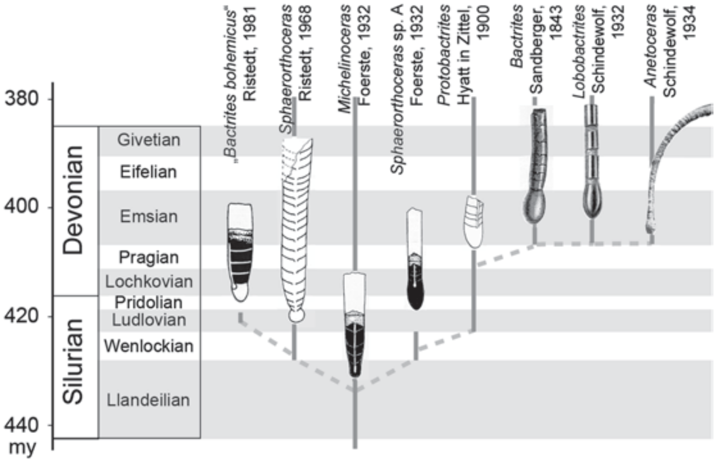

Fig. 1.4 Morphological changes of the embryonic shell around the origin of bactritids and ammonoids (modified after Kröger and Mapes 2007)

In the course of the Silurian and Early Devonian, a ventral shift of the siphuncle occurred in two orthocerid lineages (Fig. 1.4), one of them leading to the Bactritida (Kröger and Mapes 2007). These lineages differ in the shape of their initial chamber (subspherical vs. ovoid) and shaft (high vs. low apical angle). This phylogenetic hypothesis of Kröger and Mapes (2007) opposed that of Ristedt (1968). The two hypotheses mainly differ in the interpretation of the homeomorph evolution of a ventral siphuncle (Kröger and Mapes 2007) and of a narrow initial shaft (Ristedt 1968). Both character states persist into the early Ammonoidea.

As in other animal groups, the similarities between the newly evolved group and the sister group are strong close to the bifurcation. This caused a complicated pattern of apomorphic and plesiomorphic characters in both groups (compare the much discussed origins of arthropod stemgroups in the Cambrian). For instance, this is reflected in the contradicting character states in the intensely disputed genus *Pseudobactrites* (= *Bojobactrites* of Horny 1956; Erben 1960; De Baets et al. 2013b), which has *"a transversally ornamented shaft with a high angle of expansion adapical to the initial chamber"* (Kröger and Mapes 2007: p. 325). It is unclear whether this checker pattern of character state distribution originated from phenotypic plasticity, intraspecific variability (compare De Baets et al. 2015a), some kind of homoplasy (Monnet et al. 2015) or still something different.

In any case, there is not much doubt that the lineage from *Devonobactrites* via *Bactrites* to *Lobobactrites* led ultimately to the first ammonoids (Erben 1964a, b, 1966; Dzik 1984; Klug 2001b; Klug and Korn 2004; Kröger and Mapes 2007; Klug et al. 2008a, b; De Baets et al. 2009; De Baets et al. 2013a, b, 2015b). This is also not contradicted by stratigraphy (De Baets et al. 2013b, p. 27) as the earliest known *Devonobactrites* (Kröger 2008a) and *Lobobactrites* are found below the earliest ammonoid finds in the early Emsian of Australia (compare Teichert 1948; Mawson 1987) and Morocco (Kröger 2008b). Further morphological changes occurred at the transitions from the Bacritida to the Ammonoidea (Erben 1966; De Baets et al. 2013b). With the translocation of the hyponome to the venter, the suture line began to undulate. This induced the formation of the external lobe. The ventralization of the hyponome possibly caused a slight dorsoventral imbalance which might have initiated in one way or the other the increasing curvature of the shell (or vice versa), the lateral compression of the shell cross section, the formation of lateral lobes in the suture line (caused by the compressed section) and the tilting of the aperture (and thus growth lines) with a deepening of the hyponomic sinus. These apomorphies are opposed by the plesiomorphic shape of the initial chamber and the narrow shaft.

1.3 Origin of the Ammonoidea

The most recent phylogenetic reconstructions of the origin of ammonoids and their bactritid ancestors were published by Kröger and Mapes (2007) as well as Kröger et al. (2011). De Baets et al. (2012, 2013a, b) discussed developmental, reproductional and morphological changes around the origin of ammonoids and their early evolution. The stratigraphic order of ammonoids and their direct ancestors could now be stratigraphically corroborated (Kröger and Mapes 2007; De Baets et al. 2013b).

Irrespective of the phylogenetic relationships, the question for the main apomorphies of ammonoids arises. Classically, ammonoids have been separated from their bactritid ancestors by the presence of at least one full whorl (e.g., House 1988). This character, however, appears somewhat arbitrary, although coiling undoubtedly represents an important character in this context (e.g., Kröger 2005).

The systematic positions and levels of Bactritida, Coleoidea and Ammonoidea need to be critically revised. The phylogenetic position of some curved bactritoids like *Pseudobactrites* (Kröger and Mapes 2007; showing also some similarities to *Cyrtobactrites*, which might indicate closer affinity or convergence) as well as *Kokenia* (Turek and Marek 1986) are still debated (compare Erben 1966; Turek and Marek 1986; Kröger and Mapes 2007; De Baets et al. 2013b for a review). The oldest stratigraphic occurrences of these genera are all younger than the earliest ammonoids (Klug 2001b). In combination with their morphology, this might indicate that *Kokenia* and potentially even *Cyrtobactrites* and *Pseudobactrites* represent independent lineages of coiled bactritoids, only resembling the transitional morphology (Erben 1966; Klug 2001b; De Baets et al. 2013b). This would indicate iterative coiling trends in bactritoids around the origin of ammonoids (see also Kröger 2005). Therefore, only the earliest coiled Anetoceratinae and closely related more derived ammonoids (excluding bactritoids and *Kokenia*) would be included in the Ammonoidea until better preserved material becomes known and the bactritoid/ammonoid transition can be further refined. The bactritoids as currently defined are a paraphyletic group with a rather conservative morphology, which also gave rise to coleoids.

1.3.1 Ammonoid Bauplan and the HASC

Although often used as a model for reconstructing the Ammonoidea Bauplan, Extant Cephalopoda should be used with caution. *Nautilus* has a superficial resemblance with ammonoids because of the external shell, but was determined as a poor model for the appearance of ammonoids (Jacobs and Landman 1993; Ritterbush et al. 2014). Indeed, not many features (pinhole eye, 90 arms, large embryonic shell, hood etc.) appear to have developed specifically in the lineage leading up to extant *Nautilus* (Shigeno et al. 2008, 2010; Sasaki et al. 2010; Ogura et al. 2013), potentially all after their separation from the Orthocerida (Kröger et al. 2011). Coleoids, which are more closely related to ammonoids, are not necessarily a better model for ammonoid anatomy considering their evolution since their separation over 400 Ma ago (Kröger et al. 2011). Even if the extremely limited information from soft-tissue preservation of Mesozoic ammonoids is included (Klug and Lehmann 2015 Ritterbush et al. 2014), no further details can be added to the bauplan of ammonoids. Consequently, it appears like the differences between the bauplan of ammonoids and those of the Bactritida and the HASC (as shown in Table 1.1) are actually not very big and limited to a few autapomorphies or slight differences in character states.

The limit between derived Bactritida such as *Lobobactrites* and *Cyrtobactrites* on the one side and the first Ammonoidea (Anetoceratinae) such as *Metabactrites, Ivoites, Anetoceras* (senior synonym of *Ruanites*; De Baets et al. 2009) and *Erbenoceras* on the other side is additionally blurred by intraspecific variability (De Baets et al. 2013a, b, c, 2015a), incomplete preservation (De Baets et al. 2013b, c), as well as homoplasies (see Monnet et al. 2015 for a discussion of this phenomenon). Thus, only the crioconic coiling comprising at least one whorl is a trait that separates the early ammonoids from their bactritid ancestors. Less distinct characters of early ammonoids are the more strongly sinuous sutures with external and lateral lobes, the laterally compressed whorls and the distinct hyponomic sinus. However, all of the latter characters are also known to some degree from a few bactritids such as *Lobobactrites*, *Cyrtobactrites* (Erben 1964a, b, 1966; Dzik 1984; Klug 2001b; Kröger 2005, 2008b; Klug et al. 2008a).

Hardly anything is known with respect to the jaws or soft parts of early ammonoids (Korn and Klug 2003). Similarly, only very poor traces of soft tissue attachment structures have become known (Kröger et al. 2005; Klug et al. 2008a, b). Klug et al. (2008a, b) described an early ammonoid ("*Metabactrites ernsti*", now considered to be belong to *Ivoites*: De Baets et al. 2013b, p. 35) from the early Emsian (Devonian) of Morocco, which displays spirally arranged lines in the dorsal part of the shell, crossing from the mural parts of the last septa onto the body chamber wall. These track bands witness the anteriorward translocation of a soft tissue attachment site, possibly of dorsally located muscles. It is unclear whether these dorsal muscles are homologous to the cephalic retractor muscles of the Nautilida or not. Additionally, some Early and Middle Devonian ammonoids display linear imprints on the septa and in the plain of symmetry of the body chamber. According to Klug et al. (2008b), these imprints may represent imprints of arteries of the septal mantle and another artery (see also Polizzotto et al. 2015).

There is no direct evidence for the presence of a hood similar to that of extant *Nautilus*, but both the absence or presence of a hood or a homologues structure has been suggested based on circumstantial evidence (compare Keupp 2000; Lehmann et al 2015; Ritterbush et al. 2014). Although extant coleoids do not have a hood like *Nautilus*, they do have a homologous structure in their early embryonic development (compare Shigeno et al. 2008).

1.3.2 Early Evolution of Ammonoids

1.3.2.1 Morphological Changes

The Early Devonian was a time, in which several new cephalopod clades of high systematic ranks emerged such as the Bactritida, the Nautilida and the Ammonoidea (Erben 1964a, b, 1966; Klug 2001b; Kröger and Mapes 2007; Kröger 2008b; De Baets et al. 2009, 2010, 2013b). In addition to these important clades, several less diverse ones evolved and within the Ammonoidea, the radiation went on at a high pace, at least as far as shell morphology is concerned (e.g., House 1996; Korn 2001; Korn and Klug 2003; Monnet et al. 2011; De Baets et al. 2012). This is also shown by the co-occurrence of openly coiled to tightly coiled ammonoids within the same beds (De Baets et al. 2010, 2013b).

It appears like the increase in coiling was the most important character complex in the early evolution of ammonoids (Figs. 1.5, 1.6.). This holds true for the initial chamber and the shaft included in the ammonitella (Erben 1960, 1964a, 1966; Bogoslovsky 1969; Klug and Korn 2004; Kröger 2005; Klug et al. 2008; De Baets et al. 2012, 2013a, b), for the juvenile shell and the neanoconch until the adult shell (Klug and Korn 2004; Kröger 2005; De Baets et al. 2012, 2013a, b). This evolutionary trend in the increase in coiling is only rarely reversed; extreme examples for evolutionary trends towards looser coiling are the Mesozoic groups of heteromorph ammonites (Cecca 1997; Guex 2006; Monnet et al. 2015). As pointed out by House (1996) and De Baets et al. (2012), these reversions usually do not include the embryonic shell (compare De Baets et al. 2015). Once, the fully coiled embryonic shell had evolved, the umbilical window was closed and the initial chamber had also evolved a coiled longitudinal axis, no loosely coiled embryonic shell appeared again later in earth history. The only exception that occurred repeatedly is a certain variation in size of the initial chamber and the embryonic shell, although the overlying trend is towards a size decrease (De Baets et al. 2015). According to De Baets et al. (2012), this size decrease of the ammonoid embryo lead to higher reproductive rates (and low survivorship numbers), because simultaneously, the ratio from embryo size to body chamber volume decreased (compare House 1996). This latter hypothesis of an evolutionary trend towards higher reproductive rates actually coincides with a number of morphological changes, which will be listed below. Naturally, this is only one hypothesis out of several, which are also summarized below.

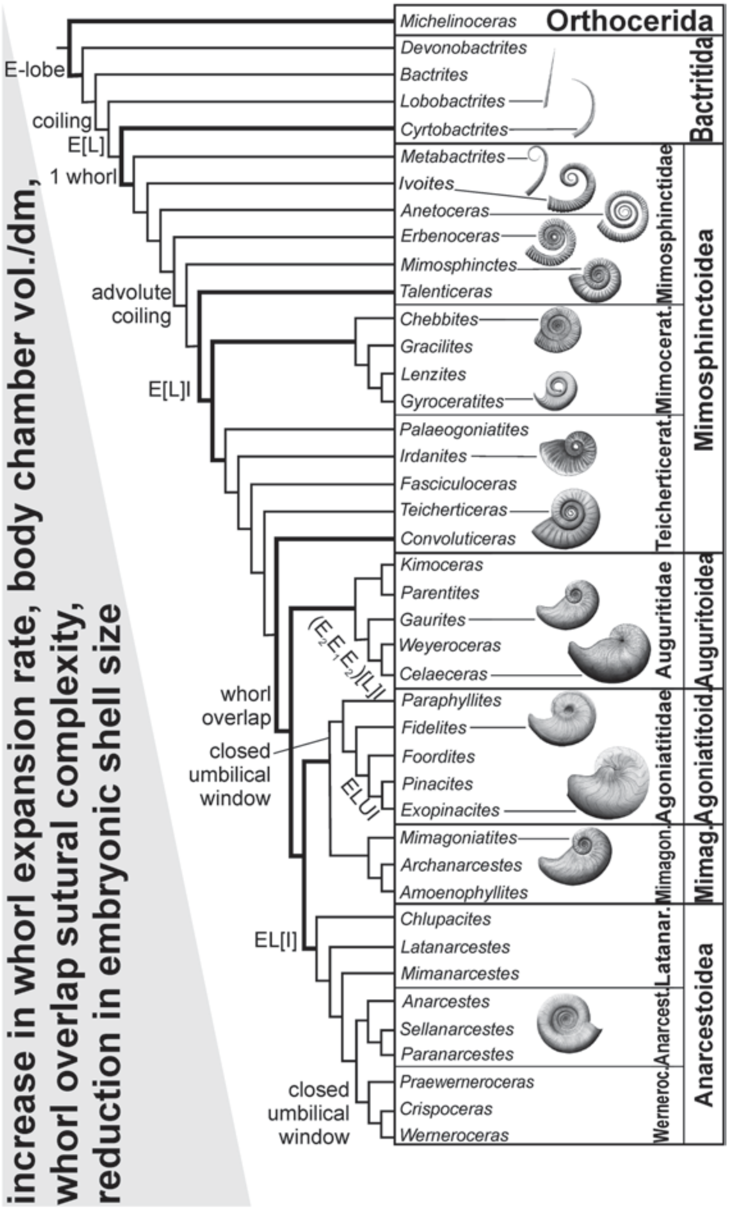

Fig. 1.5 Phylogeny of Emsian and Eifelian cephalopods, mainly based on Korn (2001) and Klug (2001b); compare Korn and Klug (2003)

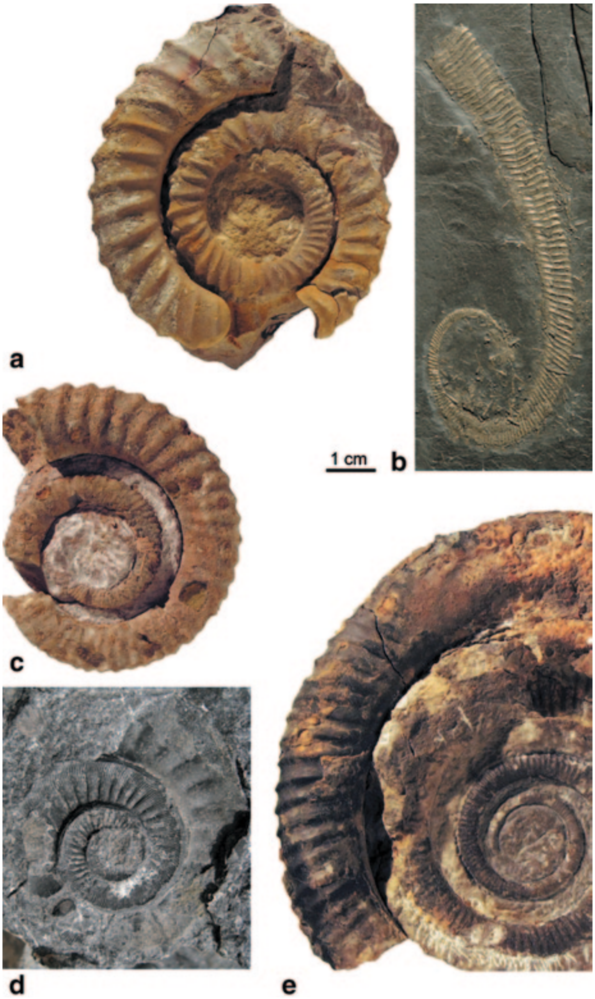

Fig. 1.6 Some ammonoids from the early Emsian, to illustrate morphological change early in ammonoid phylogeny. **a** *Erbenoceras solitarium*, GPIT 29789, Ouidane Chebbi, Morocco. **b** *Metabactrites fuchsi*, PWL2010/5251-LS, Bundenbach (Germany). **c** *Erbenoceras* cf. *solitarium*, GPIT 29806, Ouidane Chebbi, Morocco, note the wider space between the whorls. **d** *Mimosphinctes rudicostatus*, PIMUZ *28985*, Kodzha Kurganm Gorge, Zeravshan, Uzbekistan. **e** *Anetoceras obliquecostatum*, PIMUZ 29637, Achguig, Morocco

In the previous paragraph, we stressed that one of the major morphological changes of the ammonoid shell during the Devonian was the degree of shell coiling. Coiling of ammonoids (e.g., Raup 1967) can be quantified in various ways using several ratios and measurements, which have been discussed in Chap. 1.1 of this volume (Klug et al. 2015). Many of these parameters and ratios underwent profound evolutionary changes already in the Early Devonian, i.e. shortly after the origin of ammonoids. In the following, we list the main evolutionary changes that occurred in the post-embryonic shell already within the Emsian (Early Devonian):

1. Whorl expansion rate increase from around 1.5 to values above 2.0 with extreme values exceeding 4.0 (e.g., in *Mimagoniatites* and *Rherisites*; Klug 2001a, b).
2. Decrease of the umbilical width index from around 0.7 (e.g., in *Anetoceras, Borivites* or *Erbenoceras*) to 0.2 (e.g., in *Celaeceras* or *Weyeroceras*; Chlupáč

and Turek 1983; Bogoslovsky 1984; Klug 2001a, b; Klug and Korn 2002; Monnet et al. 2011; De Baets et al. 2013b).

3. Increase of the whorl height index from around 0.2 (e.g., in *Anetoceras* or *Erbenoceras*) to 0.5 (e.g., in *Celaeceras* or *Weyeroceras*; Klug 2001a, b; De Baets et al. 2010).
4. Increase in the ratio body chamber volume to diameter (Klug 2001a).
5. Initial decrease in the strength of ornamentation (De Baets et al. 2013b).
6. Increase in sutural complexity (Wiedmann and Kullmann 1980; García-Ruíz et al. 1990; Boyajian and Lutz 1992; Saunders and Work 1996; Daniel et al. 1997; Saunders et al. 1999; Gildner 2003; Ubukata et al. 2014).

These evolutionary changes have been discussed to differing degrees by various authors (Erben 1964a, 1965, 1966; Bogoslovsky 1969; Kutscher 1969; House 1988; Kröger 2005; Korn 2001; Korn and Klug 2002, 2003, 2012; De Baets et al. 2009, 2012, 2013b). It was Korn (2001), who first analyzed these morphological changes using cladistics. His study on the phylogeny of Early and Middle Devonian ammonoids is still unrivalled. According to his work, these morphological changes were more or less unidirectional, at least in the Early Devonian. Reversals in the morphological evolution did occur in single parameters, but in most cases, the changes occurred in the way listed above (Figs. 1.5, 1.6).

1.3.2.2 Potential Consequences for the Mode of Life

Considering the morphological changes listed above, a number of hypotheses have been proposed to explain these, some of which are linked with each other:

1. Saturation of the demersal habitat and increasing predatory pressure by the explosive radiation of gnathostome fish (Kröger 2005; Klug 2007; Klug et al. 2010): As documented by Klug et al. (2010), the Early Devonian was a time, where demersal animals decreased in relative diversity while nektonic forms began to diversify. They explained this by a saturation of habitats on and near the sea-floor in combination by the increasing amount of nektonic predators among the jawed fish. This predatory pressure induced an escalatory feedback.
2. Increase in swimming speed and maneuverability (Klug 2001a; Korn and Klug 2003; Klug et al. 2008a, b; Monnet et al. 2011; De Baets et al. 2013b; Frey et al. 2014; Naglik et al. 2015): The changes in conch morphology of early ammonoids occurred simultaneously and convergently (or even in parallel) in various clades (Korn and Klug 2003; Kröger 2005; Monnet et al. 2011, 2015). This supports the hypothesis that the evolutionary tendency towards tighter coiling was ecologically driven. In any case, the change in coiling altered the *syn vivo* shell orientation in such way that the aperture became horizontally aligned with the center of mass, enabling the ammonoids of reasonably high swimming speeds (Saunders and Shapiro 1986; Klug 2001a; Klug et al. 2008a; Hoffmann et al. 2015; Naglik et al. 2015).

3. Increase in reproductive rates (Klug 2001a, 2007; De Baets et al. 2012, 2013b, 2015): The temporal correlation of the reduction of embryo size and the increase of both the absolute body chamber volume and the body chamber volume-diameter ratio suggests that the reproductive rates increased by several orders of magnitude presuming a constant relative size of the gonads (from possibly about 100 in Emsian *Erbenoceras* to about 100,000 in Frasnian *Manticoceras*; De Baets et al. 2012).

Independent of the likelihood, plausibility or correctness of these hypotheses, it has to be taken into account that many of the morphological changes of the ammonoid shell (e.g., degree of coiling, whorl expansion rate, sutural complexity, umbilical width…) that occurred during the Early Devonian started near a left wall. It is therefore unclear if one or more of these ecological changes and selection for certain character states to deal with them in the best possible way was driving these changes in coiling. Alternatively, the hypothesis might be valid that these evolutionary changes occurred during a random walk of the ammonoid subclades, affected by left wall-effects; in the latter case, the three ecological explanations listed above were just side-effects or wrong. Nevertheless, the synchronicity of the mentioned evolutionary innovations and changes among the ammonoids with each other on the one hand and with macroecological events on the other hand provides some support for these three hypotheses which might have worked in concert.

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Chapter 2
Evolutionary Trends of Triassic Ammonoids

Claude Monnet, Arnaud Brayard and Morgane Brosse

2.1 Introduction

This chapter is a review of the major evolutionary trends of Triassic ammonoids. During this period (ca. 252.2–201.3 Ma), global biota recovered, diversified and modernized after the end-Permian mass extinction, which was the most severe mass extinction of the Phanerozoic (Raup 1979; Raup and Sepkoski 1982; Hallam and Wignall 1997; Erwin 2006). Therefore, the Triassic is a key time interval for both Earth and Life history showing successive major biotic and abiotic events (see review of Ogg 2012). Ammonoids are well-known and have been used to date and correlate Triassic marine strata since the late nineteenth century (Mojsisovics et al. 1895). Their abundance and widespread distribution reflect that they constitute an appropriate group in the construction of the Triassic timescale (Tozer 1984; Balini et al. 2010; Jenks et al. 2015). Besides, all of the Triassic substages are currently defined by ammonoid bioevents. Triassic ammonoids are geographically widespread and their most important and complete records are in the Canadian Arctic (especially Ellesmere and Axel Heiberg islands), British Columbia, the western USA Basin (mainly Utah, Nevada, Idaho), the Germanic Basin, Western Tethys (the Alps from Italy to Turkey), Transcaucasia (Iran), Salt Range (Pakistan), Spiti (Himalayas), Tibet, South China (Guangxi and Guizhou provinces), and eastern Siberia (Balini

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C. Monnet (✉)
UMR CNRS 8217 Géosystèmes, UFR des Sciences de la Terre (SN5), Université de Lille, Avenue Paul Langevin, 59655 Villeneuve d'Ascq cedex, France
e-mail: claude.monnet@univ-lille1.fr

A. Brayard
UMR CNRS 6282 Biogéosciences, Université de Bourgogne, 6 boulevard Gabriel, 21000 Dijon, France
e-mail: arnaud.brayard@u-bourgogne.fr

M. Brosse
Paläontologisches Institut und Museum, Universität Zürich, Karl-Schmid Strasse 4, CH-8006 Zürich, Switzerland
e-mail: morgane.brosse@pim.uzh.ch

C. Klug et al. (eds.), *Ammonoid Paleobiology: From macroevolution to paleogeography,* Topics in Geobiology 44, DOI 10.1007/978-94-017-9633-0_2

et al. 2010). Despite this long history of biostratigraphic research and key evolutionary steps, the evolution of Triassic ammonoids still remains poorly studied. Nevertheless, during the last few decades, several publications have addressed this topic, especially in the context of the recovery after the end-Permian mass extinction (e.g., McGowan 2004; Brayard et al. 2009; Brühwiler et al. 2010; Brosse et al. 2013; Korn et al. 2013a).

The Triassic is a key interval in the evolutionary history of ammonoids and can be labeled as the "ceratite" world since it is characterized by the flourishing and the dominance of the Ceratitida with their typical suture line indented on the lobes only. Indeed, only a few ammonoid species crossed the Permian/Triassic mass extinction leading to a quasi-monophyletic group during the Triassic (Kummel 1973; Spinosa et al. 1975; Tozer 1980; Brayard et al. 2006; McGowan and Smith 2007; but for a few ambiguous cases, see, e.g., Glenister and Furnish 1980; Becker and Kullmann 1996; Brayard et al. 2007a). Following the end-Permian mass extinction, this time interval was one of the most interesting in the evolution of the Ammonoidea with an impressive succession of radiations and crises (Tozer 1980, 1982; Dagys 1988; Brayard et al. 2009; Balini et al. 2010; Brayard and Bucher 2015) and with the first experiment in heteromorphic coiling in the Late Triassic (e.g., Wiedmann 1973; Shevyrev 2005). The resulting impressive Triassic ammonoid record consists of three orders (Prolecanitida, Ceratitida, Phylloceratida), about 80 families, about 700 valid genera and an estimated 5000 valid species (Tozer 1980; Balini et al. 2010). A few Triassic ammonoid families (e.g., Sageceratidae, Sturiidae, Gymnitidae, Ptychitidae, Isculitidae, Cladiscitidae, Arcestidae, Sphingitidae and Joannitidae) consist of smooth, relatively long-ranging forms that are informally defined as "Leiostraca", whereas the majority of families belong to the group "Trachyostraca", which includes the ornamented, fast-developing and short-ranging forms. The Triassic ammonoids include a great variety of forms from evolute to involute, smooth to ribbed, tuberculated and spiny, and suture lines from ceratitic to ammonitic.

In biology and particularly in paleontology, evolutionary trends are a long standing theme. According to McNamara (2006), "*an evolutionary trend can be defined as a persistent, directional change in a character state, or set of character states, resulting in a significant change through time*" (see also Gould 1988; McNamara 1990; McShea 1994; Monnet et al. 2015). Commonly assumed examples of macroevolutionary trends include increasing adult body size (Cope's rule) throughout the Cenozoic within horses coupled with a reduction in digit number (MacFadden 1986, 1992; Gould and MacFadden 2004), an increase in shell size in the Foraminifera (Gould 1988; Norris 1991), increasing complexity of life forms from eukaryotic cells to complex multicellular vertebrates (Gould 1996; McShea 1996), as well as, among many other, increase in suture indentation of ammonoids (Boyajian and Lutz 1992; Saunders et al. 1999). Most of the evolutionary trends described in the fossil record are macroevolutionary and large-scale (or long-term) in the sense that they occurred over several million years and among or above the species level. Since the works of Gould (1988, 1990) and McShea (1994, 2000), two basic patterns of evolutionary trends have been recognized: these may be either 'passive' or 'driven' (the absence of a trend characterizes a third pattern: stasis) (Monnet et al. 2015). In a driven trend, not only the mean, but also the entire morphological range of an evolving lineage is shifted through time within its multidimensional morphological space. In a passive trend, the mean value of a character will increase and appear like a trend, but only because of a natural result of increase in variance (Gould 1988) constrained by a natural physiological/physical boundary in the morphological space of the studied organisms (so-called left-wall effect). For instance, if the species at the origin of a clade was small-sized, subsequent evolution could only be stasis or a shift towards larger sizes.

Large-scale macroevolutionary trends in fossils within their morphological space have usually been studied qualitatively or by the stratophenetic method (e.g., Raup and Crick 1981, 1982; Charlesworth 1984; Gingerich 1993; Roopnarine et al. 1999; Monnet et al. 2010), that is the distribution (or characteristic numbers of this distribution such as the mean) of some quantified morphological characters through successive stratigraphic strata or units (time slices). Recently, several authors developed quantitative methods to describe and assess statistically these trends: for details and example applications of these methods, see Monnet et al. (2011, 2015). With regard to quantified ammonoid shell characters, four of them commonly display long-term evolutionary trends through time: adult size, degree of involution (coiling), strength of ornamentation, and indentation of suture line (e.g., Haas 1942; Kennedy 1977, 1989; Bayer and McGhee 1984; Kennedy and Wright 1985; Dommergues 1990; Boyajian and Lutz 1992; Saunders et al. 1999; Guex 2003; Klug et al. 2005; Monnet et al. 2011, 2012; De Baets et al. 2012). Hence, the major goal of this chapter is to make a review of the rare studies analyzing the evolutionary trends of these ammonoid shell characters during the Triassic (for a review of processes generating evolutionary trends in ammonoids, see Monnet et al. 2011, 2015).

2.2 Adult Size

The most commonly observed evolutionary trends in the fossil record are probably those including adult body size, in particular the apparent frequency of size increase, which has been coined as Cope's rule (i.e. the widespread tendency of animal groups to evolve towards larger sizes). Different processes have been suggested to generate trends in body size evolution such as adaptiveness (or fitness), predator-prey relationships, energy intensiveness, life history strategies (r-K continuum), growth rates, external abiotic factors (e.g., temperature, food supply) (see Newell 1949; Stanley 1973; Vermeij 1987; McKinney 1990; Gould 1997; Jablonski 1997; Alroy 1998; Hone and Benton 2005; Novack-Gottshall and Lanier 2008). With regard to ammonoids, several authors have illustrated and discussed examples of increasing shell size (see Monnet et al. 2015 and references therein). However, very few studies focus on the Triassic (e.g., Klug et al. 2005; Monnet et al. 2012) and the sometimes large range of intraspecific variation of size at maturity is often overlooked (see De Baets et al. 2015). Several studies focusing on peculiar lineages have described evolutionary changes in adult shell size potentially compatible with

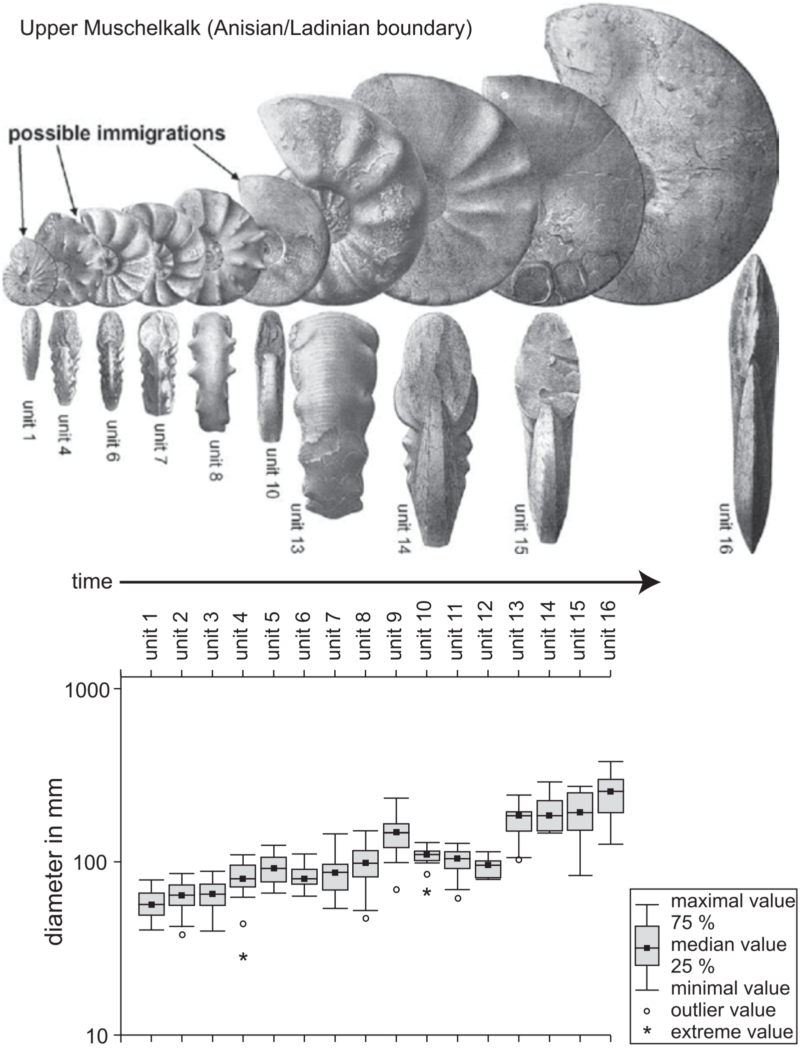

Fig. 2.1 Stratophenetic evolutionary trend of size increase of ammonoids during the deposition of the *Upper Muschelkalk* (Middle Triassic) of the Germanic Basin (modified after Klug et al. 2005)

Cope's rule. For instance, Klug et al. (2005) documented the stratophenetic evolution of Middle Triassic ammonoids from the German Muschelkalk for several morphological characters (Fig. 2.1). Interestingly, several of these (inclusive of adult shell diameter) show more or less regular changes in conch morphology through geological time, except for some intervals with abrupt and rather drastic transformations, which are synchronous with episodes of faunal immigrations.

The most recent and comprehensive study on adult ammonoid shell-size is from Dommergues et al. (2002) who documented in a large compendium (more than

1000 species) of Early Jurassic ammonoids that there are no statistically preponderant trends. This study highlighted that at a large taxonomic scale, there is no tendency in the evolution of conch size with a roughly equal number of cases of increase, decrease, and stasis. In contrast to Jurassic ammonoids, changes in shell size at a global scale have not yet been investigated for Triassic ammonoids. For Triassic ammonoids, only cases of size increase have been reported (see above). However, cases of conch size decrease are likely to have existed also in Triassic ammonoids. Indeed, Triassic ammonoids cover a large range of sizes (typically ranging between 5 to 500 mm), e.g., from the tiny *Paranannites dubius*, over the medium-sized *Rieppelites cimeganus*, to the large-sized *Churkites noblei* (Fig. 2.2). Therefore, evolutionary changes and trends in shell size can be expected within Triassic ammonoids, but a general study similar to that of Dommergues et al. (2002) still needs to be done in order to investigate dominance (or not) of one pattern among size changes of Triassic ammonoids. Guex (2001, 2006) argued that size decreases are more likely to be sudden and promoted by stressful abiotic events whereas size increases are more protracted during more stable environmental periods. Monnet et al. (2013) quantitatively described an example of this evolutionary hypothesis within the Triassic family Acrochordiceratidae. This family is characterized by a protracted morphological evolutionary trend during the early and middle Anisian (ca. 4 Myr) composed of classical increases in adult size, shell involution and suture indentation. This trend followed a sudden morphological change (e.g., drastic size reduction and uncoiling) at the Spathian/Anisian boundary between members of the family. This boundary is associated with several stressful environmental changes that may have triggered this evolutionary jump, which corresponds to a generalized morphological reset of long-term trends. This process differs from classic paedomorphic transformations since it is characterized by the reappearance of atavistic characters instead of paedomorphic characters (for further details, see Guex 2001, 2006).

Interestingly, ammonoids should have shown marked size decrease after the end-Permian mass extinction and during the successive Early Triassic oceanographic and climatic events (e.g., late Smithian; Brayard et al. 2006; Galfetti et al. 2007b; Romano et al. 2013). Indeed, a sharp size decrease of surviving taxa in the immediate aftermath of an extinction event is expected (the "Lilliput effect") and has been suggested for other mollusks (see e.g., Payne 2005; Twitchett 2007; but see Brayard et al. 2010). However, although analyses remain qualitative for that time, the Early Triassic apparently records the highest abundance of the largest ammonoid specimens of the Triassic (see Brayard et al. 2013). Furthermore, the evolution of ammonoids is more complex as illustrated by a size decrease prior to the end-Permian mass extinction in some regions like Iran (compare Korn et al. 2013b).

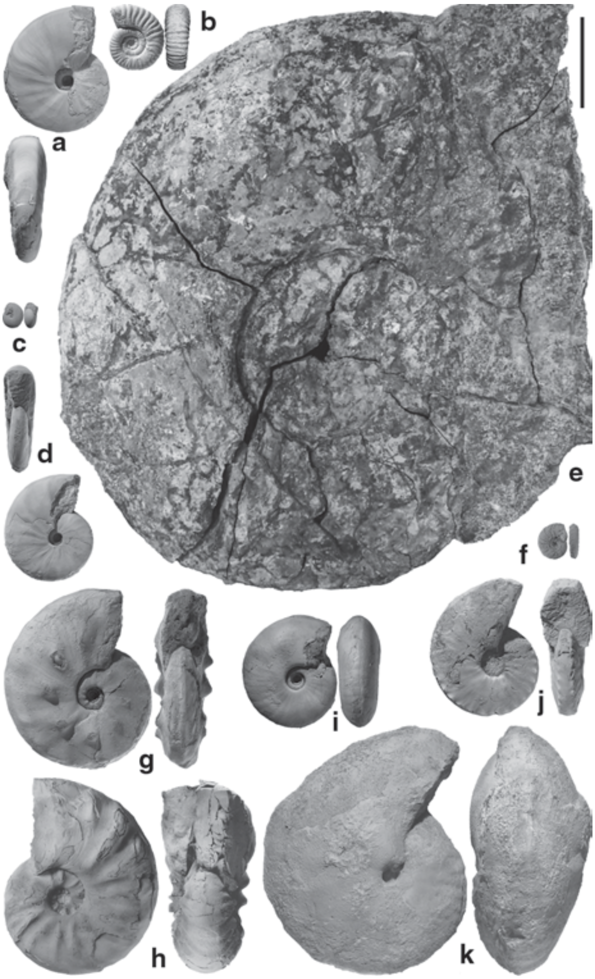

Fig. 2.2 The vast range of shell size in Triassic ammonoids. **a** *Billingsites cordeyi* (Anisian; after Monnet and Bucher 2005, pl. 7 Fig. 3). **b** *Paracrochordiceras americanum* (Anisian; after Bucher 2002, pl. 1 Figs. 1,2). **c** *Paranannites dubius* (Smithian; after Brayard and Bucher 2008, pl. 33 Fig. 13). **d** *Gymnotoceras mimetus* (Anisian; after Monnet and Bucher 2005, pl. 17 Fig. 1). **e** *Churkites noblei* (Smithian; after Brayard et al. 2013, Fig. 43a). **f** *Procurvoceratites pygmaeus* (Smithian; after Brayard and Bucher 2008, pl. 44 Fig. 4). **g** *Silberlingitoides cricki* (Anisian; after Monnet and Bucher 2005, pl. 26 Fig. 1). **h** *Acrochordiceras carolinae* (Anisian; after Monnet et al. 2010, text-Fig. 12). **i** *Paranannites ovum* (Smithian; after Brayard and Bucher 2008, pl. 34 Fig. 1). **j** *Rieppelites cimeganus* (Anisian; after Monnet et al. 2008, Fig. 11a, b). **k** *Globacrochordiceras transpacificum* (Spathian; after Monnet et al. 2013, Fig. 5). All specimens are at the same scale (scale bar = 5 cm)

2.3 Taxonomic Diversity

Fundamentally, paleontology focuses on past life and probably the most used synthesis of past changes have been the reconstruction of diversity curves. For paleontologists, diversity generally means taxonomic richness (i.e. the number of taxa present at a given time) and diversity trends have been studied since Phillips (1860). Reconstructing the trajectory of global diversity by compiling data from the fossil record has been a major research agenda for paleontologists for decades. The goal is to produce an accurate reconstruction of the pattern of global diversity that will ultimately allow understanding of the causes of diversity increases, decreases and transitions in the composition of the biota (Simpson and Kiessling 2010; Escarguel et al. 2011). Paleontologists attempt to document the history of biodiversity by tabulating fossil occurrences in large databases, especially for identifying large-scale evolutionary patterns (e.g., Raup and Sepkoski 1982; Sepkoski 1993; Alroy et al. 2008).

Ammonoids are well known for their high diversification and extinction rates and thus constitute a material of choice for diversity studies (Tozer 1980; House 1985; Page 1996). To build robust databases from which to extract reliable diversity patterns, a necessary prerequisite is having a homogeneous taxonomy complemented by up-to-date biostratigraphic data. During the last few decades (and still today), Triassic ammonoids have been thoroughly revised and documented, leading to more consistent taxonomic and biostratigraphic frameworks (see Jenks et al. 2015). This enabled Brayard et al. (2009) to provide a thorough quantitative analysis of ammonoid diversity trends during the entire Triassic, based on a database presently recording about 730 genera from 50 regions around the world. The major result of this study was that, although the ammonoids, which were abundant during the Permian, were nearly eradicated during the end-Permian mass extinction (only a few species survived), they recovered remarkably quickly taking only ~1 Myr after the extinction event (compared to the commonly suggested 10 million-year biotic recovery period for benthic organisms; Kirchner and Well 2000; Erwin 2006; but see e.g. Hofmann et al. 2011, 2014) and even had recovered to diversity levels higher than those seen in the Permian. For further details with regard to the recovery, see Brayard and Bucher (2015).

The diversity trends of Triassic ammonoids (Fig. 2.3) are characterized by four long-term successive diversity oscillations of declining magnitude, which are probably shaped by global climatic and oceanographic changes (Brayard et al. 2006; Galfetti et al. 2007b; Konstantinov 2008). As highlighted by Brayard et al. (2009), in the first oscillation, during the Olenekian, ammonoid generic diversity reached values (~110) higher than those for the Permian. This Early Triassic generic richness is unsurpassed during the Middle and Late Triassic, where diversity oscillated around an average value of ~70 sampled genera per time bin. This period also records a very rapid succession of new families and genera, echoed by the simultaneously high numbers and rates of origination and extinction. The Early/Middle Triassic transition was marked by a severe drop in ammonoid diversity, probably

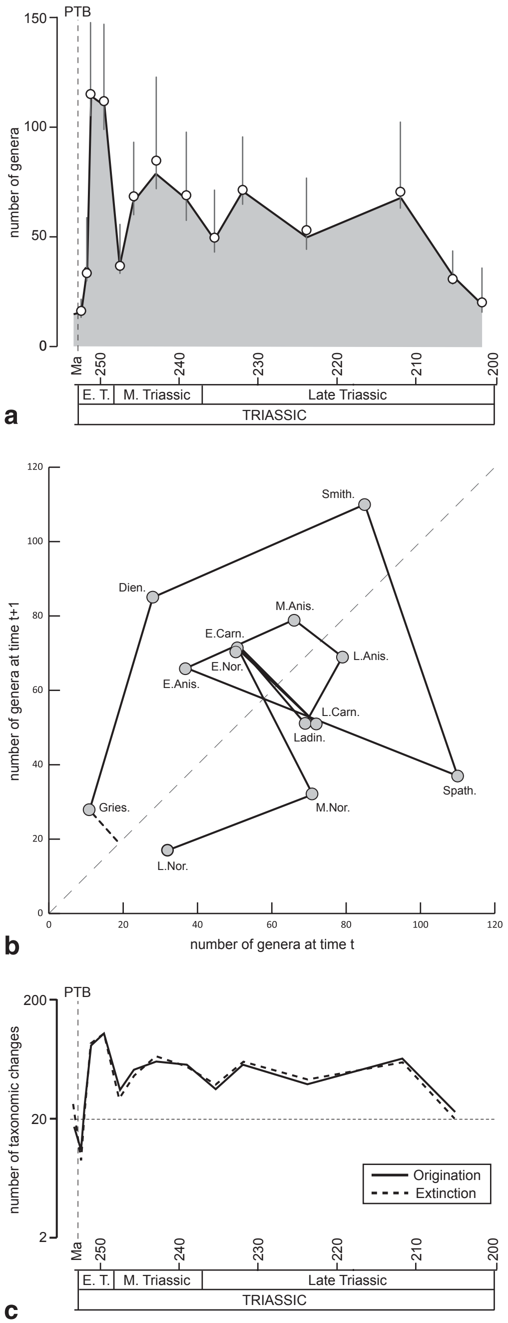

Fig. 2.3 Trends of taxonomic diversity of Triassic ammonoids (modified after Brayard et al. 2009). **a** Generic richness of Triassic ammonoids: black bold line: total generic richness (observed + inferred occurrences); large circles with vertical bars: mean Chao2 estimate of the overall generic richness with its 95 % confidence interval. Triassic ammonoids actually reached

triggered by a fall in global sea level (Embry 1997); this interval also impacted ammonoid evolutionary trends (see Monnet et al. 2013). Middle and Late Triassic generic and family richness remained lower than in the late Early Triassic; they also appeared less variable, possibly because oceanic geochemical conditions stabilized during that time (Payne et al. 2004; Galfetti et al. 2007a, b). From the early Anisian onward, three successive diversity cycles are evident: Early Anisian–Early Carnian, Early Carnian–Early Norian, and Early Norian–Rhaetian. The latter ends with a marked diversity decline before the Jurassic. Additional studies have explored the diversity of Triassic ammonoids but with lower time resolution, smaller datasets and/or more restricted geographic scope (e.g., Yang and Wang 2000; Konstantinov 2008; Brühwiler et al. 2010; Zakharov and Abnavi 2013).

There appears to be a close relationship between changes in ammonoid diversity and climate, as reflected by the correlation between cosmopolitan to latitudinally restricted distributions of genera on the one hand and sea surface temperature gradient on the other hand (Brayard et al. 2006, 2007b, 2015). Also, these long-term trends in diversity were marked by shorter, but important disturbances, such as a diversity drop at the Smithian/Spathian boundary (Tozer 1982; Dagys 1988; Brayard et al. 2006) concomitant with a major perturbation of the global carbon cycle (Payne et al. 2004; Galfetti et al. 2007a, b, c). This end-Smithian global event did not markedly delay the explosive recovery of ceratitid ammonoids, although it was the most important one within the entire Triassic. Other significant extinction events for ammonoids occurred at the Spathian/Anisian boundary, in the early Ladinian, and at the Carnian/Norian boundary (Brayard et al. 2009).

2.4 Morphological Disparity

2.4.1 Shell Geometry

Quantitative analyses on diversity trends of fossil groups have usually and fruitfully focused upon taxonomic diversity (see above). However, there are multiple facets/metrics of biodiversity (e.g., genetic, morphological, ecological, phylogenetic, functional, body size). One of these considers morphological variation (or disparity), which is the raw material of biological evolution (Foote 1993) and the primary material of fossilized organisms. Disparity-based analyses supply relevant insights into biological evolution by the establishment of phenotypic spaces and

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levels of diversity higher than in the Permian less than 1 million years after the PTB by an explosive and non-delayed diversification of the Ceratitida. Highest levels of diversity are reached in the Early Triassic, after which diversity slowly decreases, as well as the turnover rate, until the end of the Triassic. Note that the end-Smithian ammonoid extinction event discussed in the text is not illustrated here due to its short time duration. **b** Phase diagram of Triassic ammonoid diversity showing the rapid recovery of the Early Triassic, followed by a dynamic equilibrium during the Middle Triassic, and the final decrease of diversity in the Late Triassic. **c** Origination and extinction of Triassic ammonoid genera

Fig. 2.4 The vast range of shell geometry in Triassic ammonoids. **a** *Longobardites zsigmondyi* (Anisian; after Monnet and Bucher 2005, pl. 31 Fig. 13). **b** *Otoceras concavum* (Griesbachian; after Dagys and Ermakova 1996, pl. 2 Fig. 4; × 0.5). **c** *Gymnites* sp. indet. (Anisian; after Monnet

the comparison of occupied morphospace through time and taxonomy (e.g., Gould 1991; Foote 1993; Roy and Foote 1997). Morphological disparity is a quantitative estimate of the empirical distribution of taxa in a multidimensional space (morphospace), the axes of which represent measures of morphology (Roy and Foote 1997). Morphological disparity is not necessarily linked to taxonomic diversity, and is even a valuable complement in characterizing evolutionary patterns (Foote 1993; McGowan 2004; Villier and Korn 2004). The comparison between different aspects of diversity is often essential in understanding the processes underlying observed biodiversity patterns (Roy and Foote 1997). Qualitatively, Triassic ammonoids show a wide range of geometries, which vary from completely involute to completely evolute, from compressed to widely depressed, and with various shapes of the whorl section (Fig. 2.4).

The approach of morphological disparity has been fruitfully applied to ammonoids (e.g., Ward 1980; Saunders and Swan 1984; Swan and Saunders 1987; Dommergues et al. 1996; Saunders et al. 1999; Olóriz et al. 1999; Korn 2000; Neige et al. 2001; Zhang 2002; Villier and Korn 2004; Klug et al. 2005; Moyne and Neige 2007; Gerber et al. 2008; Korn et al. 2013a). The general geometry of the ammonoid shell has been usually quantified in two major approaches: (1) by traditional linear biometric measurements that enable the characterization of the shell geometry in an empirical morphospace, such as the degree of involution (often referred to as the coiling: U/D) and the ellipsoid of the whorl section (often referred to as the degree of compression: H/W); and (2) by using Raup's parameters that enable to characterize the shell geometry in a theoretical morphospace (Raup 1966, 1967), such as the whorl expansion rate, distance from the coiling axis and whorl shape. The latter approach is very interesting because it enables comparison of realized ammonoid morphologies in a theoretical morphospace (see review of McGhee 1999, 2007).

In contrast to Paleozoic ammonoids (references above), few studies have investigated trends in morphological disparity of Triassic ammonoids. They mainly focused on the Early Triassic or peculiar taxonomic groups (e.g., Klug et al. 2005; Monnet et al. 2012) or were subordinated to tentative paleoecological analyses (e.g., Ritterbush and Bottjer 2012; Brayard and Escarguel 2013). Villier and Korn (2004) analyzed the morphological disparity of Permian and Early Triassic ammonoids at

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and Bucher 2005, pl. 4 Fig. 5). d *Sageceras walteri* (Anisian; after Monnet and Bucher 2005, pl. 18 Fig. 5; × 0.75). **e** *Rieberites transiformis* (Anisian; after Monnet and Bucher 2005, pl. 24 Fig. 6). **f** *Rohillites sobolevi* (Smithian; after Brayard and Bucher 2008, pl. 20 Fig. 1). **g** *Gymnotoceras weitschati* (Anisian; after Monnet and Bucher 2005, pl. 16 Fig. 7; × 0.8). **h** *Tropigastrites louderbacki* (Anisian; after Monnet and Bucher 2005, pl. 30 Fig. 10). **i** *Dieneroceras tientungense* (Smithian; after Brayard and Bucher 2008, pl. 15 Fig. 5). **j** *Ptychites euglyphus* (Ladinian; after Monnet et al. 2014, pl. 8e, f; × 0.5). **k** *Nevadites hyatti* (Anisian; after Monnet et al. 2014, pl. 7o, p; × 0.4). **l** *Mesohimavatites columbianus* (Norian; after McLearn 1960, pl. 5 Fig. 6). **m** *Ptychites* sp. indet. (Anisian; after Monnet and Bucher 2005, pl. 23 Fig. 11). **n** *Ptychites* (Anisian; after Monnet et al. 2008, Fig. 14 g, i). **o** *Drepanites rutherfordi* (Norian; after Tozer 1994, pl. 128, Fig. 5). **p** *Proharpoceras carinatitabulatum* (Smithian; after Brayard et al. 2007a, Fig. 3w, x). **q** *Ussurites arthaberi* (Anisian; after Monnet and Bucher 2005, pl. 4 Fig. 11). **r** *Proarcestes bramantei* (Anisian; after Monnet and Bucher 2005, pl. 30 Fig. 7). **s** *Stikinoceras kerri* (Norian; after McLearn 1960, pl. 3 Fig. 2; × 2). **t** *Tropites crassicostatus* (Carnian; after Jenks et al. 2015, pl. 9e, f). All specimens are at the same scale (scale bar = 2 cm) unless stated otherwise the genus and stage ranks, and highlighted that the end-Permian mass extinction operated as a random, nonselective sorting of morphologies, which is consistent with a catastrophic cause (see also Korn et al. 2013a).

McGowan (2004, 2005) made the first comprehensive review on the entire Triassic (Fig. 2.5) and compared the taxonomic diversity and morphological disparity at the genus rank. This study highlighted that taxonomic and morphological metrics are decoupled during the Triassic. Indeed, the Dienerian (Early Triassic) records a decrease in disparity while taxonomic richness drastically increases at the same time; later on (Middle and Late Triassic), disparity weakly fluctuates compared to richness and often in opposition. This mismatch was explained by a combination of the loss of representatives of morphologically distinctive clades, followed by origination of many morphologically similar genera. Unfortunately, the chronostratigraphic resolution of the dataset used is restricted and the knowledge of the taxonomy and biostratigraphy of Triassic ammonoids has been largely expanded since then, especially in the Early Triassic (see Jenks et al. 2015), thus possibly making the results partly obsolete.

More recently, using an updated dataset, Brosse et al. (2013) re-explored the morphological disparity of (only) Early Triassic ammonoids. Although diversity and disparity curves are not strictly similar to that of McGowan (2004), such as the presence of the end-Smithian extinction event, their trends in diversity remain roughly comparable (compare Figs 2.3a and 2.5a). Interestingly, this study confirms that trends in disparity and richness were decoupled during the Griesbachian and Dienerian with persisting low disparity values in the Dienerian whereas richness increased (Fig. 2.6). Briefly, after the end-Permian mass extinction, the first marked disparity peak occurred early in the Smithian. The end-Smithian extinction had obvious consequences with a marked contraction of the previously occupied morphospace (Fig. 2.6). The Spathian corresponds to a second disparity peak with a morphospace analogous to the early-middle Smithian. However, Spathian superfamilies apparently occupied more restricted portions of the morphospace compared to the early-middle Smithian. Interestingly, Brosse et al. (2013) also showed that disparity evolved similarly at both regional and global scales, suggesting a global influence of abiotic factors.

Morphological diversification occurred early in the Smithian and a marked contraction of the morphospace took place during the end-Smithian extinction. Three macroevolutionary processes may be involved (Brosse et al. 2013): (1) a nonselective extinction at the Permian/Triassic boundary; (2) a Dienerian constrained radiation with several homeomorphic genera; (3) a potential deterministic extinction during the end-Smithian crisis. Sphaerocones were indeed the most affected by the Dienerian and end-Smithian extinction, but explanations remain elusive. On the one hand, this may be linked to widespread harsh conditions at those times. On the other hand, as the sphaerocones occurred episodically during the Early Triassic, this might be explained by a relaxing of ecological constraints or simply by convergent evolution. Besides, it has long been recognized that the Early Triassic ammonoid radiation is represented by numerous homeomorphic taxa (e.g., Kummel and Steele 1962).

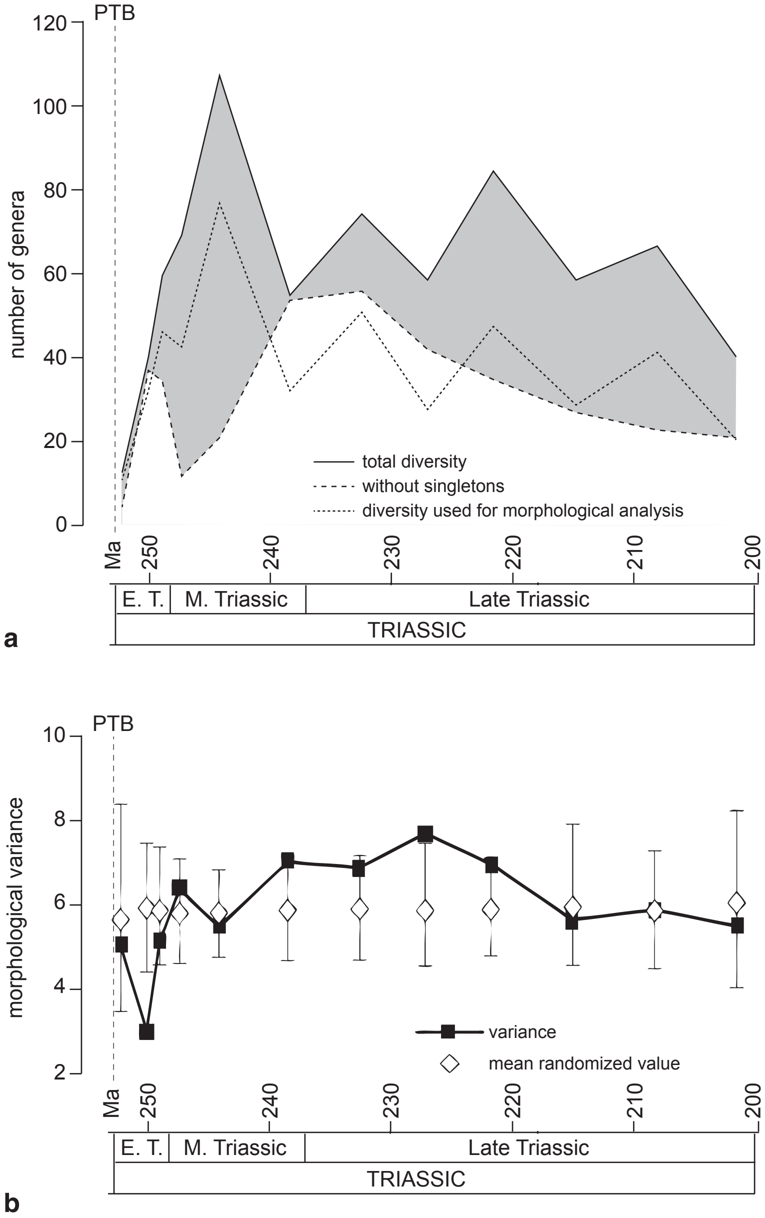

Fig. 2.5 Morphological disparity of Triassic ammonoids (modified after McGowan 2004). **a** Taxonomic diversity at the genus rank (total diversity and without singletons) and sampled diversity for analyzing morphological disparity (but compare with the more recent diversity curve of Brayard et al. 2009; Fig. 2.3). **b** Observed morphological disparity, as well as mean value and 90 % confidence interval for randomized samples

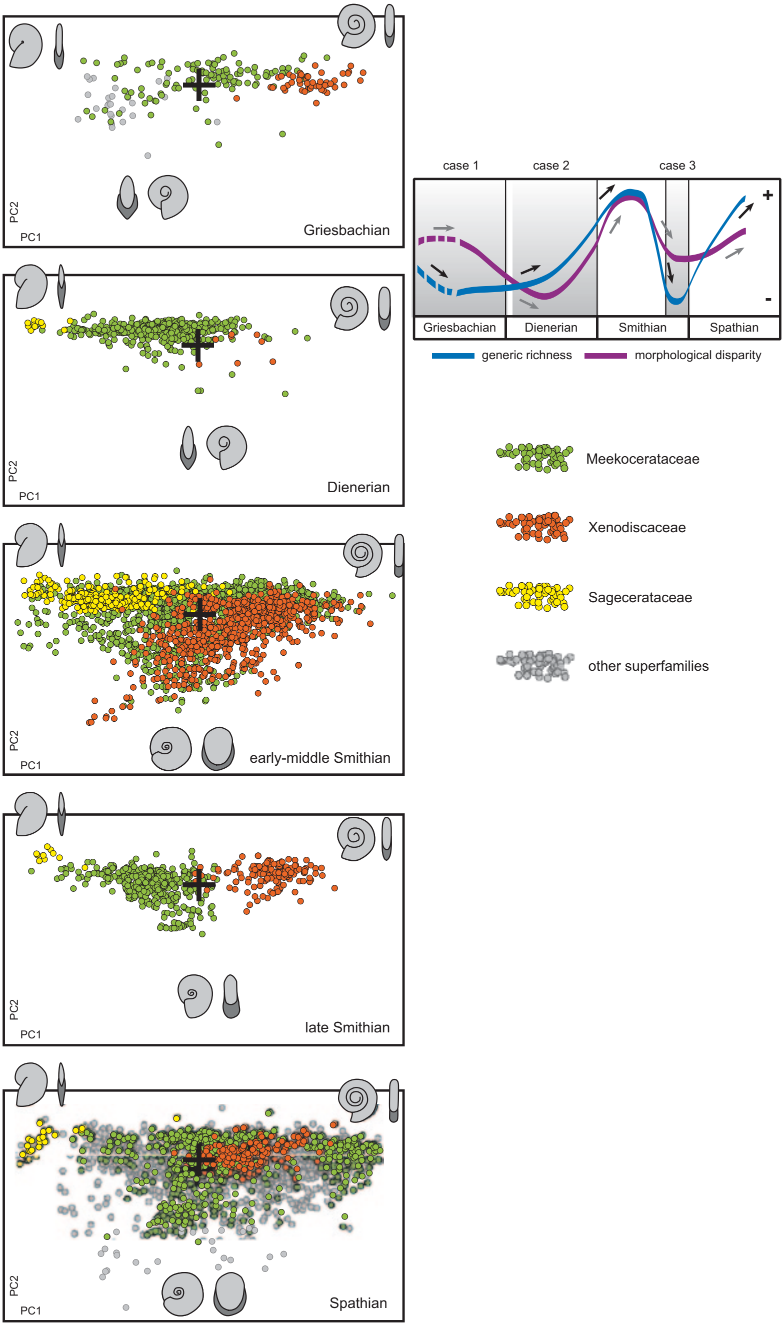

Fig. 2.6 Trends in morphological disparity of Early Triassic ammonoids (modified after Brosse et al. 2013). Superimposition of generic richness and disparity curves and evolution of the morphospace occupation, with the three main superfamilies highlighted, for each of the five studied time bins

Finally, although not quantified in the disparity curve of McGowan (2004; Fig. 2.5), a major event in shell geometry of ammonoids is the sudden appearance of tiny heteromorphic forms at the end of the Norian. These possess semi-evolute, completely straight or slightly curved, twisted or turriconic shells, with coarse ornamentation and a simple four-lobed suture (Fig. 2.4). According to the recent review of Shevyrev (2005), they are represented by one superfamily, three families, six genera, and about 30 species. Their geographic range is wide; they are documented in the Tethyan Realm (from Sicily to Timor) and along the Pacific coast (from Chukotka to the Molucca Islands, from the Yukon Territory and British Columbia to Chile and Argentina). Like all ceratitids, the Triassic heteromorphs disappeared at the Triassic/Jurassic boundary; by deriving from different lineages, heteromorphs reappeared in the Middle Jurassic and several times in the Cretaceous (Wiedmann 1969, 1973; Cecca 1997; Guex 2001, 2006).

2.4.2 Ornamentation

The ornamentation of ammonoids provides an important set of characters used to discriminate species. The interpretation of potential trends in ornamentation is currently complicated by a poor understanding of shell morphogenesis. For instance, convergent evolution of spines in marine mollusk shells have been interpreted as having repeatedly evolved as a defense in response to shell-crushing predators (e.g., Ward 1981; Vermeij 1987; Kröger 2005; Ifrim 2013). However, recent studies (Moulton et al. 2012; Chirat et al. 2013) have demonstrated that a large diversity of ornamentation and spine structures can be accounted for by small variations in control parameters of the mechanical interaction between the secreting mantle edge and the calcified shell edge, suggesting that convergent evolution of spines can also be understood through a generic morphogenetic process without such selective pressures. Interestingly, both shell ornamental simplification and diversification throughout the evolution of a clade have been frequently documented (e.g., Bayer and McGhee 1984, 1985; Kennedy and Wright 1985).

Although being of prime importance to discriminate between ammonoid species, shell ornamentation is poorly characterized from a quantitative point of view and also rarely investigated within Triassic ammonoids. Hence, not much is known about their evolutionary trends in ornamentation. Interestingly, Triassic ammonoids show a large range of variation in types and distribution of ornaments such as tubercles (nodes, spines, bullae), parabolic lines, megastriae, varices, constrictions, keels, strigations, and ribs (Fig. 2.7). Therefore, Triassic ammonoids can potentially have experienced evolutionary trends of their ornamentation. A recent case study is the stratophenetic analysis of the family Acrochordiceratidae by Monnet et al. (2012, 2013). Although this family is characterized by a protracted trend of size increase and involution increase, its ornamentation (quantified by its ribbing density) rather displays a phase of stasis without trend and always with a large intraspecific variation (compare De Baets et al. 2015).

Fig. 2.7 Ornamentation of Triassic ammonoids. If not stated otherwise, the images are from Monnet and Bucher (2005). **a** *Acrochordiceras carolinae* (Anisian; after Monnet et al. 2010). **b** *Dixieceras* lawsoni (Anisian). **c** *Brackites spinosus* (Anisian). **d** *Eutomoceras dunni* (Anisian). **e** *Rieppelites boletzkyi* (Anisian). **f** *Silberlingitoides cricki* (Anisian). **g** *Rieppelites boletzkyi* (Anisian). **h** *Proarcestes bramantei* (Anisian). **i** *Gymnotoceras blakei* (Anisian). **j** *Pseudaspenites layeriformis* (Smithian; after Brayard and Bucher 2008). **k** *Anasibirites multiformis* (Smithian; after Jenks et al. 2015). **l** *Chiratites retrospinosus* (Anisian). **m** *Euflemingites cirratus* (Smithian; after Jenks et al. 2007; scale bar = 4 cm). All specimens are at the same scale (scale bar = 5 cm) unless stated otherwise

2.4.3 Suture Line

During their long history, the ammonoids showed a remarkable variability in suture shape, from the subsinusoidal nautilitic forms, over goniatitic (smooth lobes and saddles) and ceratitic (smooth saddles but denticulate lobes), to true ammonitic morphotypes (both denticulate lobes and saddles; Fig. 2.8). As had been argued for shell geometry and ornamentation, the pattern of evolution and origin of these various morphotypes resulted from a combination of phylogenetic, functional, constructional, and contingent factors (Monnet et al. 2011, 2015). Different processes have been suggested to generate trends in the amount of suture indentation (frilling or "*complexity*") such as buttressing against hydrostatic pressure on the phragmocone, but without reaching a consensus (e.g., Westermann 1971; Kennedy and Cobban 1976; Olóriz and Palmqvist 1995; Saunders 1995; Daniel et al. 1997; Hassan et al. 2002; De Blasio 2008; Klug and Hoffmann 2015).

It is commonly assumed that the complexity of ammonoid septa generally increased through time at a very large scale (Kullmann and Wiedmann 1970), mainly as a passive trend since the clade originated with a very simple suture (Fig. 2.8; Boyajian and Lutz 1992; Saunders et al. 1999). The Triassic ammonoids have long been recognized to be mostly characterized by ceratitic sutures (Kennedy 1977). However, Triassic ammonoid sutures are absolutely not limited by this single pattern. As illustrated in Fig. 2.9, Triassic sutures are very diverse and cover the largest range among all ammonoid groups through time by ranging from goniatitic to ammonitic suture types (Fig. 2.8). Allen (2006) suggested that the general pattern of within-suture variance exhibited by the basal Triassic ammonoid sutures was unique with regard to Paleozoic taxa and may have been a key property to enable ammonoid sutures to evolve into the true ammonitic (fractal-like) forms characteristic of Mesozoic sutures. Several studies have described trends either in indentation increase (e.g., Monnet et al. 2012) or in indentation decrease (e.g., Urlichs and Mundlos 1985; Guex 2006). However, there is as of yet no comprehensive or quantitative study of all Triassic ammonoids with regard to evolutionary changes in suture patterns. Such a study could also have important implications for the use of the suture line in systematics, which has only little values in many Triassic ammonoids (e.g., Arctohungaritidae: Dagys 2001).

2.5 Conclusions

Triassic ammonoids cover a vast range of morphologies with regard to size, geometry (whorl shape and involution), ornamentation, and suture patterns. They represent a quasi-monophyletic clade and quickly recovered after the end-Permian extinction showing high evolutionary rates. Triassic ammonoids have been extensively studied for taxonomic and biostratigraphic purposes. However, only a few published cases at a reduced taxonomic and/or geographic scale attempted explicitly to decipher trends. Despite an excellent framework, studies for evolutionary trends in Triassic

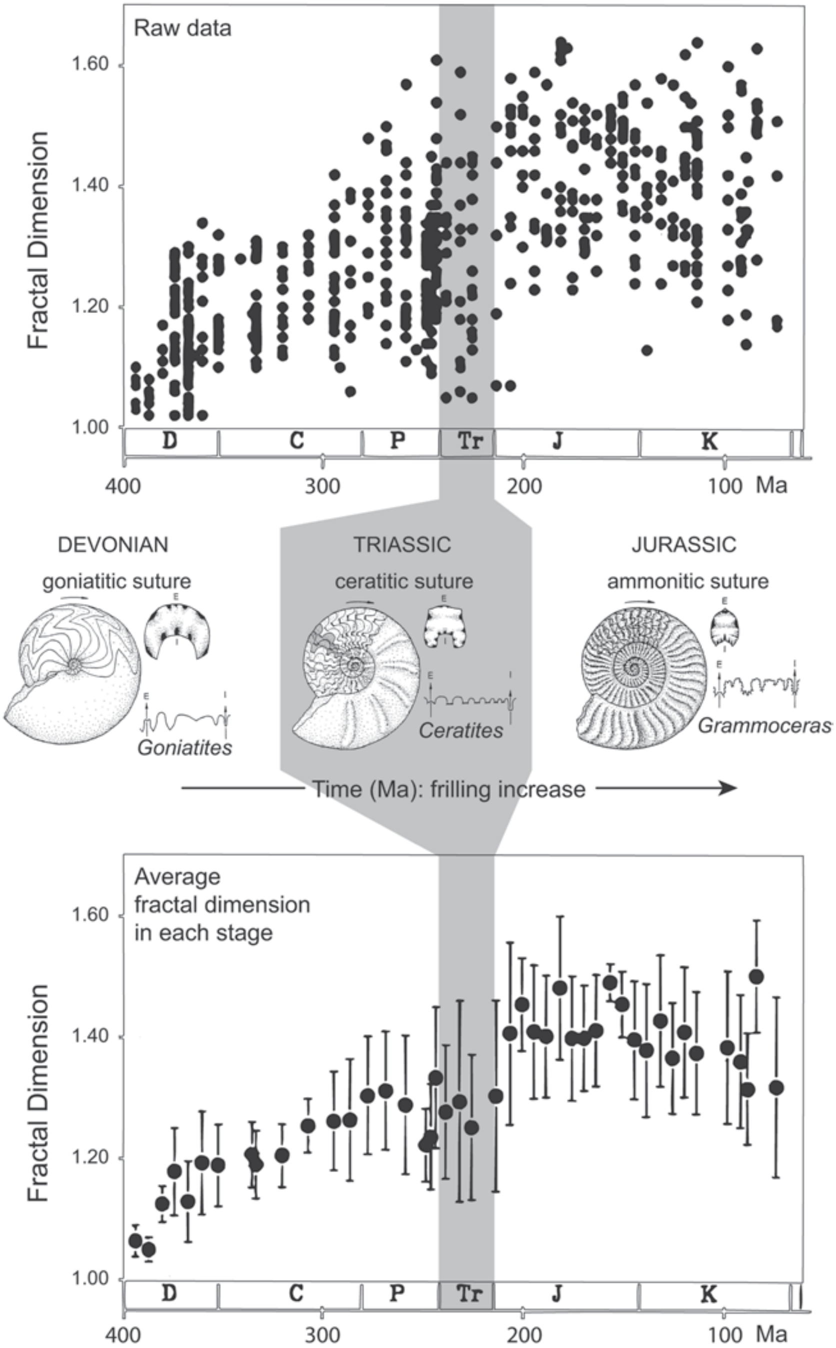

Fig. 2.8 Evolutionary trend in the fractal dimension of ammonoid suture throughout their entire history (modified after Boyajian and Lutz 1992) and illustration of the three major suture patterns (goniatitic, ceratitic, and ammonitic)

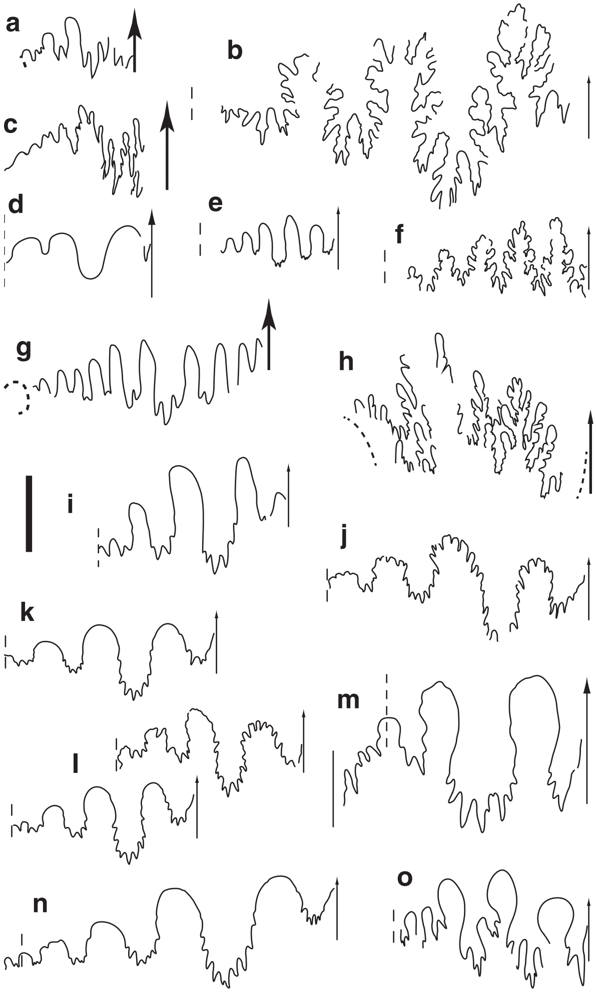

Fig. 2.9 The vast range of suture shapes in Triassic ammonoids. If not stated otherwise, the images are from Monnet and Bucher (2005). **a** *Xiaoqiaoceras involutus* (Smithian; after Brayard and Bucher 2008). **b** *Discoptychites megalodiscus* (Anisian). **c** *Lanceolites bicarinatus* (Smithian; after Brayard and Bucher 2008). **d** *Proavites hueffeli* (Anisian; after Monnet et al. 2008). **e** *Longobardites parvus* (Anisian). **f** *Proarcestes bramantei* (Anisian). **g** *Pseudosageceras multilobatum* (Smithian; after Brayard and Bucher 2008). **h** *Parussuria compressa* (Smithian; after Brayard et al. 2013, Fig. 57f). **i** *Pseudaspidites muthianus* (Smithian; after Brayard and Bucher 2008, pl. 10 Fig. 9). **j** Gymnotoceras *rotelliformis* (Anisian). **k** *Rieppelites boletzkyi* (Anisian). **l** *Billingsites* escargueli (Anisian). **m** *Globacrochordiceras transpacificum* (Anisian; after Monnet et al. 2013, Fig. 4b). **n** *Bulogites mojsvari* (Anisian). **o** *Ussurites arthaberi* (Anisian). All specimens are at the same scale (scale bar = 5 mm)

ammonoids are still rare and thus are poorly known. Improving the contribution of Triassic ammonoids to evolutionary biology now requires the construction of quantitative databases on the various morphological characters and reconstruction of Triassic ammonoid phylogeny. The latter is currently almost nonexistent, whereas phylogenetic reconstructions are crucial to explore trends at the lineage level. Ammonoids can still provide significant insights into evolutionary biology topics and are worth these efforts.

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Chapter 3
Evolutionary Trends within Jurassic Ammonoids

Pascal Neige and Isabelle Rouget

3.1 Introduction

Evolutionary trends have long been studied and discussed in evolutionary biology (e.g., Vrba 1983; McKinney 1990; McShea 1994, 2001; McNamara 2006; Gregory 2008). Such a trend may be defined as an identifiable pattern of a trait (e.g. body size, species richness, extinction rate) shifting in a given direction for a sufficiently long period of time to be detected. Traits that describe a trend may be expressed as "*state variables*" (McKinney 1990) and can be quantified using statistical point estimates (e.g. mean, maximum) or dispersion parameters (e.g. total variance). This concept of trends is central to evolutionary biology and can be studied at very different scales: from lineages to supraspecific clades (see McShea 2001 for a review).

It is common practice to divide trends into two kinds based on the nature of the dynamic underlying them (McShea 1994; Gregory 2008). The first kind, "*passive trends*", exemplifies evolutionary patterns where a boundary (e.g. a design limitation) constrains fluctuations of the state variable. Consequently the state variable will generally fluctuate in two directions (e.g. increase or decrease in size) so approaching the boundary. However, there can be no fluctuations beyond the boundary (e.g., it is impossible to be smaller than a given "*boundary size*"). Consequently, lineages within the clade tend to vary in two directions but the clade as a whole varies in one direction only (e.g. the clade expands in the direction of larger size but only because any shift beyond minimum size is impossible). The second kind, known as "*driven trends*", exemplifies evolutionary patterns where the state variable varies overall in one direction only and for most lineages

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P. Neige (✉)
Laboratoire Biogéosciences, University of Burgundy, CNRS,
6 boulevard Gabriel, F-21000 Dijon, France
e-mail: pascal.neige@u-bourgogne.fr

I. Rouget
Laboratoire CR2P, Sorbonne Universités, UPMC-Univ Paris 06, MNHN, CNRS,
4 place Jussieu, Case 104, 75252 Paris cedex 05, France
e-mail: isabelle.rouget@upmc.fr

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(e.g., the clade expands in the direction of larger size and the smallest specimens also tend to be larger). Even if successful, it is worth noting that this terminology ("*passive*" vs. "*driven*") does not imply any direct understanding of causes: passive does not mean random change any more than driven means adaptive change (McShea 1994; Wang 2001; and see Gregory 2008 for a synthesis). Therefore, a major problem in paleontology is to discover the causes generating the trends. As Gregory (2008) put it, trends are real phenomena and their underlying causes are rarely simple.

Obviously, before a trend can be identified and so before any attempt can be made to decipher the causes that trigger it, traits must first be quantified and then their fluctuations over time computed. This involves collating a robust bank of data and exploring it statistically. Such exploration is far from straightforward: different statistical parameters (e.g. mean, median, maximum) might reveal different patterns, as may studies at different scales (subclades vs entire clade). Even the first part of the agenda (constructing the database) is subject to difficulties: in the case of speciose clades, the number of species may be difficult to ascertain and the patterns observed may be skewed by various kinds of bias. For example, in a study based on Jurassic ammonoids, Nardin et al. (2005) show that the ratio between morphological disparity and species number tends to decline over historical time (i.e. the time over which the clade has been studied by paleontologists). This is attributed to the tendency of paleontologists to describe and name extreme forms before intermediate ones. Other biases such as the non-random geographic distribution of outcrops may affect the patterns observed (e.g. McGowan and Smith 2008; Vilhena and Smith 2013). However, in spite of bias, the fossil record provides a unique opportunity to study evolutionary trends extensively for different periods of time.

In this context, Jurassic ammonoids may be considered as a primary model. They benefit from a good fossil record (compared to other fossils), and they have been studied intensively for more than 200 years, yielding a comprehensive set of data in terms of geographic and stratigraphic species distribution. It is no surprise, then, to find an extensive literature about the evolutionary patterns of Jurassic ammonoids over time. Historically (and oversimplifying), scholars of Jurassic ammonoids focused first on evolutionary trends of lineages until the late twentieth century, and since then have favored broader sampling (i.e. macroevolutionary scale). In this paper we will focus largely on the latter. In a first part, we will review papers that explicitly attempt to reconstruct evolutionary patterns (thus potentially discovering trends) for Jurassic ammonoids. We exclude paleobiogeographic explorations of the type studied by Cecca et al. (2005) which are discussed elsewhere in this book. The second part will explore large-scale taxonomic patterns based on our own compilation of data published by various authors. Finally, we discuss limitations encountered in the study of evolutionary trends within Jurassic ammonoids.

3.2 The Jurassic System

Today, we consider that the Jurassic system encompasses more than 56 myr (Gradstein et al. 2012) from 201.3 Ma (base of its first stage: the Hettangian) to 145 Ma (top of its last stage: the Tithonian). The onset of the Jurassic was historically based on the large faunal turnovers brought about by the end-Triassic mass extinction (one of the five biggest Phanerozoic mass extinctions, Hallam and Wignall 1997). This mass extinction largely affects ammonoids: just three genera (*Choristoceras, Rhacophyllites*, *Eopsiloceras*) cross the Triassic/Jurassic boundary, and quickly become extinct (Yin et al. 2007; Smith et al. 2014). The Lower Jurassic limit is now formally recognized by a GSSP (Global boundary Stratotype Section and Point) located in the Karwendel Mountains, Austria (Hillebrandt et al. 2013; and see Ogg and Hinnov 2012a for a complete GSSP synthesis within the Jurassic), and the correlation event is the First Apparition Datum (FAD) of the ammonite *Psiloceras spelae*. The end of the Jurassic (i.e. the Jurassic/Cretaceous boundary) has generated dozens of debates and thousands of pages of publications. Today, its formal limit is still not fixed, and no GSSP is recognized yet. However, a possible correlation event for this limit may be the FAD of the ammonite *Berriasella jacobi* (Ogg and Hinnov 2012b).

The Jurassic system is subdivided into 11 stages. Their durations are far from equal: the Hettangian and the Bajocian are estimated to have lasted 2.0 myr whereas the Toarcian is estimated to span 8.6 myr. Ogg and Hinnov (2012a, p. 763) provide the most recent synthesis of the Jurassic Time Scale using different methods and data and recognize that "*the primary reference scales for most stage boundaries and other events in Jurassic stratigraphy are the ammonite zones […]*". These 11 stages form three large subdivisions (Lower, Middle, Upper) which together make up the complete Jurassic System. It is worth saying that studies of the Jurassic ammonoids have historically generated a tremendous number of concepts and results in various scientific fields such as biostratigraphy, paleogeography, paleoclimatology, sequence stratigraphy, and macroevolution. Celebrated geologists and paleontologists who contributed to this eighteenth- and nineteenth-century Jurassic "*epic*" include Alexander von Humboldt, who first recognized the Jurassic in 1795 when speaking of the "*Jura Kalkstein*" during a geological trip through southern France, western Germany, and northern Italy (and see Humboldt 1799); Alexandre Brongniart, who coined the name "*Terrains Jurassiques*" (1829); Leopold von Buch, who established the three-fold subdivision of the Jurassic (1839); Alcide d'Orbigny, who largely developed the idea of stages ("*étages*") within mostly ammonoid-based Jurassic subdivisions (1852), and Albert Oppel, who developed the concept of biostratigraphic zone (1856–1858). More recently, Arkell (1956) synthesized what is known of the Jurassic in his *Jurassic Geology of the World*.

Besides the lower limit extinction of the Jurassic (first-order end Triassic mass extinction), several biotic events occurred during the Jurassic (Hallam and Wignall 1997). One such event was the Mesozoic Marine Revolution (Vermeij 1977). This revolution saw the restructuring of shallow marine benthic communities mainly during the Jurassic and the Cretaceous. A particularly interesting event was the second-order extinction event at the Pliensbachian/Toarcian boundary: the so-called "*Early Toarcian Crisis*", which largely affected marine faunas and microflora (see Dera et al. 2010 for a review). This appears to have been a multi-stage event and to have given rise to a rapid recovery for ammonoids (Dera et al. 2010). Finally, a second-order crisis, but less marked, occurred at the very end of the Jurassic (the "*Tithonian event*", Hallam and Wignall 1997). Although less marked among ammonoids than previously thought (Sepkoski 1992; Hallam and Wignall 1997), this event has been recognized recently on a disparity-based approach which focuses on southern German ammonoids (Simon et al. 2010).

3.3 A Review of Macroevolutionary Patterns and Evolutionary Trends within Jurassic Ammonoids

Historically, identifying evolutionary trends was mainly process-oriented up to the last decades of the twentieth century (Rouget et al. 2004). As with many other groups, the first ammonoid evolutionary trends described in the literature were based on accepted laws which depend on the author's concept of evolution, such as the biogenetic law (Waagen 1869; Hyatt 1889, 1897) or the irreversibility of evolution (Dollo 1922). The repeated occurrence of similar morphologies (including coiling, shell shape, and ornamentation) has long been known and led to the successful concept of iterative evolution (Salfeld 1913; Spath 1930). This concept postulates that evolution gave rise to a repetition of trends in distinct lineages at different times. This case of parallel evolution in a chronological sequence prevailed among ammonite workers during the first part of the twentieth century and has never been totally abandoned (Bayer and McGhee 1984; Landman et al. 1991). This concept was strikingly linked to the acceptance of the anagenetic process that impels all evolutionary trends. This was still the case in the 1980s when the study of heterochrony reappeared in evolutionary studies after being pioneered by such scholars as Schindewolf (1936). Ammonites were a highly suitable clade for such studies and provided many relevant examples of heterochronic trends: the so-called paedo- or peramorphocline (see Dommergues et al. 1989 and Dommergues 1990 for a large scope within Jurassic ammonites). These trends were mainly oriented by an anagenetic hypothesis, involving a low taxonomic rank level analysis (genus, species). In this context, Raup and Crick (1981), following Brinkmann (1929), published probably the most widely reported example of trend analysis within Jurassic ammonoids. Based on a biometric study of phyletic evolution in the Callovian genus *Kosmoceras* (including its four subgenera) through 14 m of the Peterborough section (lower half of the Oxford Clay Formation), they showed that some characters (e.g. adult shell diameter) display a non-random evolution (i.e. fewer reversals of a given state variable through time than would be predicted from a null hypothesis based on a random walk). They concluded that "*it is reasonable to interpret the low number of runs as indication of sustained trends in* Zugokosmoceras *[one of the subgenera* *of* Kosmoceras*] evolution*", and explained this trend as a non-random operation of natural selection. It is worth noting that trends in this example are far from systematic (depending on characters and/or sampling strategy along the studied section).

More recently, authors have described evolutionary patterns through time but without making assumptions about evolutionary processes. For example, House (1989) explores ammonoid taxonomic diversity fluctuations from the Devonian to the end of the Cretaceous by computing a large database at the family level. He relates the different fluctuation events (mainly extinctions) to sea-level fluctuations. In the same way, contemporary studies explore evolutionary patterns at very different taxonomic levels (from species to families), and generally—and contrary to the period when heterochronies were fashionable—do not focus on a single or a limited number of lineages. This corresponds to a macroevolutionary approach, and the traits explored are as different as body size, taxonomic richness, and morphologic disparity. Among these evolutionary patterns, trends may stand out.

We focus here on papers explicitly attempting to reconstruct evolutionary patterns for Jurassic ammonoids. However, this synthesis does not take into account all published papers dealing with Jurassic ammonoids. For example, Wiedmann and Kullmann (1981) focus on ammonoid suture trends throughout their evolutionary history. Therefore data for the Jurassic are very scarce and do not represent a pattern within the Jurassic period. On the same way, Boyajian and Lutz (1992) demonstrated that both the mean and range of suture complexity increased over the stratigraphic range of the Ammonoidea (from the Devonian to the end of the Cretaceous). However, no particular trends seem to occur for the Jurassic period. Similarly, Parent et al. (2010) explore size-shape relationships at the Mesozoic scale. Figure 3.1 shows a selective sample of published studies exploring macroevolutionary patterns of Jurassic ammonoids. These studies focus on different traits: body size, taxonomic richness (at the species, genus, or family levels), and shell morphology. Surprisingly, most of these studies make no attempt to find evolutionary trends, only a few of them doing so explicitly.

For example, Guex (2001) claims—in a study based on Toarcian ammonite lineages—that trends during ecologically stable periods are characterized by shell coiling change from evolute to involute, and those during episodes of stress are characterized by a reverse shell coiling change. O'Dogherty et al. (2006), exploring ammonoid taxonomic fluctuations within the southern Iberian paleomargin, claim that trends during ecologically stable periods also show the development of more complex ornamentation. In another example, Navarro et al. (2005) report that the trend toward more compressed forms of shell occur during the initial colonization of the Arctic Basin by the Cardioceratidae at the end of the Bajocian. This observation was based on a quantification of morphological disparity. Dommergues et al. (2002) explore shell size patterns of ammonoids through the Early Jurassic ammonite radiation using a database of 1236 ammonite species representing all known Early Jurassic faunas. Shell size patterns are studied for the entire period and then at the biozone scale for the first four stages of the Jurassic (28 myr), during which ammonites recovered from the crisis at the Triassic/Jurassic (T/J) boundary. They do not identify any global trend, but a sustained increase in size disparity at the beginning of the Early

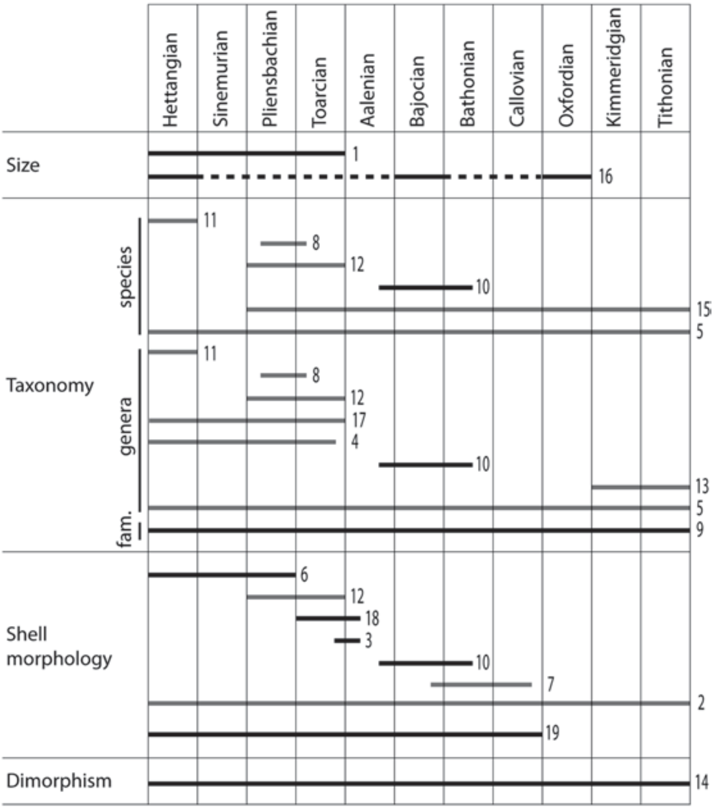

Fig. 3.1 Sample of published studies exploring macroevolutionary patterns of Jurassic ammonoids for different traits. *Black lines* represent worldwide studies. *Grey lines* represent geographically limited studies (geography or paleogeography named here in brackets according to original names of cited papers). (*1* Dommergues et al. (2002), *2* Simon et al. (2010): Southern Germany, *3* Neige et al. (2001), *4* Hallam and Wignall (1997): Great Britain, *5* Sandoval et al. (2001): Betic Cordillera, data used partially by O'Dogherty et al. (2006), *6* Dommergues et al. (1996), *7* Navarro et al. (2005): Arctic, *8* Macchioni and Cecca (2002): Western Tethyan areas, *9* House (1989), *10* Moyne and Neige (2007), *11* Guex et al. (2012): NW European and Pacific realms, *12* Dera et al. (2010): NW Tethyan and Arctic domains, *13* Rogov (2012): Northern Hemisphere, *14* Davis et al. (1996), *15* Ruban (2007): Caucasus, *16* Stanley (1973), *17* Ziegler (1981): Southern Germany, *18* Guex (2001), *19* Smith et al. (2014))

Jurassic radiation: during the Hettangian up to the base of the Sinemurian (Fig. 3.2). They interpret this pattern as a passive evolutionary trend: ammonites at the beginning of the radiation were initially medium-sized and so amenable to changes in size in both directions (toward smaller and larger extremes) thus finally engendering a passive increase in size disparity. They also note that the minimum value of the coefficient of variation describing shell size disparity occurs during the Early Toarcian Crisis (Tenuicostatum zone), followed by an increase of size disparity during the Toarcian stage. However, in a global analysis of ammonoids during the recovery of the Lower Jurassic following the end-Triassic mass extinction, Dommergues

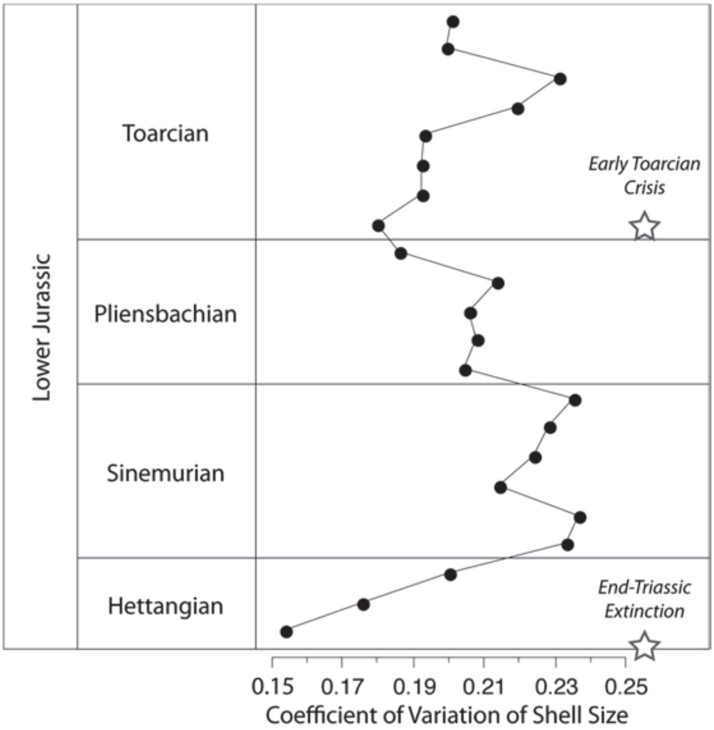

Fig. 3.2 Coefficient of variation in ammonite shell size throughout the Early Jurassic (one point per standard ammonite biozone). *Stars* indicate extinction events (modified from Dommergues et al. 2002)

et al. (1996) conclude that their disparity-based study of shell shape reveals a fairly homogeneous distribution with no significant trend. In a review paper, Davis et al. (1996) analysed dimorphism within ammonoids. A section of this paper focuses on patterns of dimorphism through time in the Jurassic, using a qualitative approach. For this period of time, dubious cases of sexual dimorphism appear as soon as the Hettangian, and obvious cases during the Toarcian among the Hildoceratinae (but see Davis et al. 1996 for a general discussion about sexual dimorphism recognition within ammonoids). After the Lower Jurassic, sexual dimorphism becomes a common ammonoid feature of nearly all Middle and Late Jurassic ammonoids.

3.4 Global Diversity Pattern

In this part, we begin a very preliminary exploration of Jurassic ammonoid macroevolutionary patterns. For that purpose, we constitute a database based on four publications offering a complete overview of Jurassic ammonoid evolution. These are the publications of four "primary" authors: Arkell (1957), Tintant et al. (1975), Donovan et al. (1981), and Page (1996). Note that House (1989) who explored macroevolutionary patterns of the complete ammonoid clade (from the Devonian to the end of the Cretaceous) used data from Donovan et al. (1981) for the Jurassic. We admit that more recent data exist for different ammonoid groups, but the four publications used here synthesize the evolution of ammonoids during the Jurassic in a homogeneous way. As far as we know, no other publications are available covering the entire Jurassic and considering all ammonoid clades.

For our purpose, we simply report here FADs and LADs (Last Apparition Datum) of the different families during the Jurassic, given by these primary authors. Their data are available at stage level. A complementary and more precise compilation at the biozone level has been constituted based on the publication of Tintant et al. (1975). Others do not give sufficient temporal details. The biozone framework—based on ammonoids—used by Tintant et al. (1975) is episodically different from the chronozone scheme used nowadays (Page 2003), but we consider that these differences do not flaw the results. Our database may be biased in considering that some families are paraphyletic (Rouget et al. 2004). The use of paraphyletic groups for macroevolutionary studies is subject to debate (Sepkoski and Kendrick 1993). In our case, we assume that family level is a good proxy for scrutinizing Jurassic ammonoid biodiversity. This choice and its consequences will be discussed at the end of this study. The timeline used to represent the data is the last chronostratigraphical chart (Gradstein et al. 2012). Although numerical ages and stages duration are of different reliability during the Jurassic, this chart provide a relevant framework to characterize diversity pattern through time.

Spindle diagrams (number of taxa within each time bin) within ammonoid families for the four publications display very similar patterns (Fig. 3.3). First, we observe an increase in diversity from the beginning of the Jurassic up to the end of the Pliensbachian. This covers the recovery phase after the End-Triassic mass extinction and the continuation of the Early Jurassic Radiation phase. The Pliensbachian/Toarcian boundary is marked by a decrease in family numbers, corresponding to the Early Toarcian Crisis (second-order extinction event). After the Toarcian, we observe a new diversification phase, known as the Middle Jurassic Radiation: for Arkell (1957) and Page (2003) the maximum number of families is achieved during the Bajocian, whereas for Tintant et al. (1975) and Donovan et al. (1981) it is during the Callovian. Despite these slight differences, all the four spindle diagrams show a stable and less diverse Upper Jurassic.

Looking at this pattern at a finer time scale (i.e. biozone scale) offers a complementary view (Fig. 3.4). The Early Jurassic radiation is well marked. However, contrary to the preceding graphs (Fig. 3.3) it may be observed that the radiation reaches its peak at the beginning of the Pliensbachian. This difference is a simple effect of the temporal slicing used (stages vs biozones), the latter being more precise. The Early Toarcian Crisis appears less marked than previously. The Middle Jurassic radiation displays two successive phases: first is a marked upturn in diversity from the beginning of the Aalenian up to the end of the Bajocian then comes a more or less stable period up until the end of the Callovian. These two radiations (Early and Middle Jurassic) unfold in a very comparable duration of about 10 myr. They

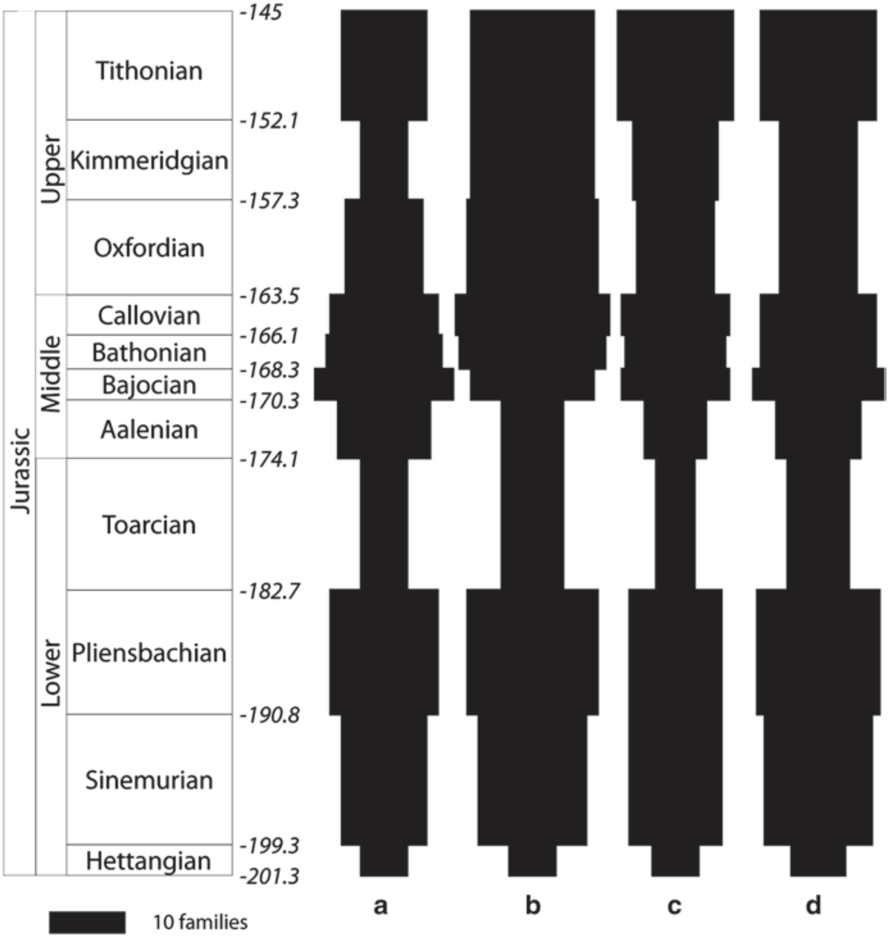

Fig. 3.3 Spindle diagrams for Jurassic ammonoids (number of families) according to four primary authors, at the stage level: **a** Arkell et al. (1957). **b** Tintant et al. (1975). **c** Donovan et al. (1981). **d** Page (1996). Numerical ages (Ma) from GTS2012, see Ogg and Hinnov (2012a)

consist in a sustainable increase in taxonomic diversity, which could be considered as a trend. Both the Early Jurassic and Middle Jurassic radiations observed in the present analysis concern drastic and profound changes in ammonoid diversity (i.e. changes in dominant clades), which has also been documented by cladistic and macroevolutionary studies (see Dommergues et al. 1996, 2001; Moyne and Neige 2004, 2007; Neige et al. 2013).

These two radiations are not temporally related in the same way to their preceding extinctions (Fig. 3.4b): the Early Jurassic Radiation immediately follows the first-order End-Triassic Extinction, whereas the Middle Jurassic Radiation is delayed relative to the second-order Early Toarcian Crisis. This is observed at the taxonomic scale of the family. At the species level, Dera et al. (2010) demonstrated

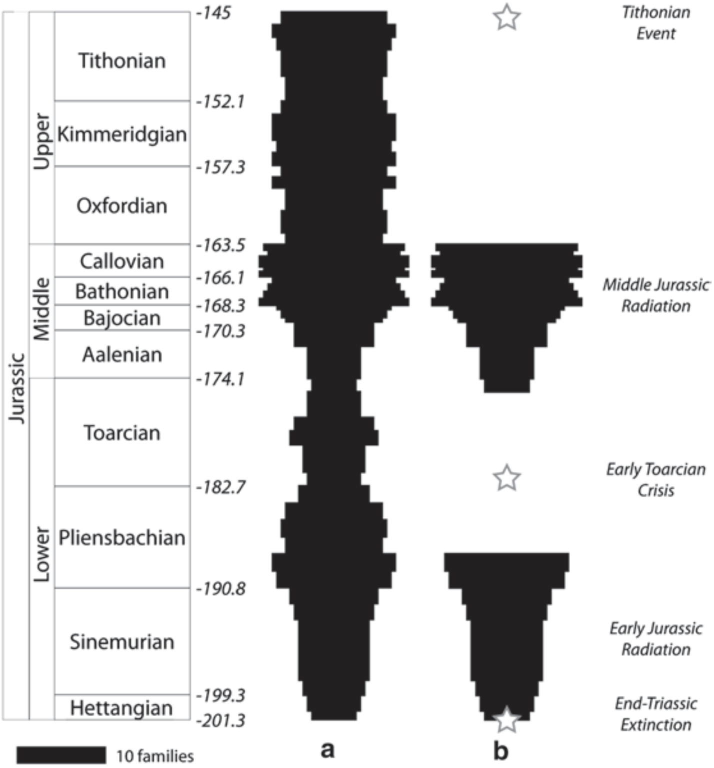

Fig. 3.4 **a** Spindle diagrams for Jurassic ammonoids (number of families) according to Tintant et al. (1975), at the biozone level, and main macroevolutionary events. Numerical ages (Ma) from GTS2012, see Ogg and Hinnov 2012a **b** Same but showing only evolutionary radiations (*stars* indicate extinction events)

a large and rapid recovery for ammonoids during the Toarcian, immediately after the Early Toarcian Crisis. In a recent paper, Neige et al. (2013) survey all main ammonoid clades during the Toarcian and Early Aalenian stages, using both taxonomic and disparity-based approaches. Results show that (1) one clade (the 'hammatoceratids', which engendered the Middle Jurassic radiation) has a fossil record that begins with low diversity and disparity but is superseded by a sustained radiation pattern, and (2) the rapid recovery after the crisis during the Toarcian is mainly due to clades that will rapidly become extinct. Therefore, the Middle Jurassic radiation is not strictly a consequence of the Early Toarcian Crisis. Even if first members of the root clade (the 'hammatoceratids') of the Middle Jurassic radiation are known just after this event, this clade radiates during the complete Toarcian stage to finally permit the Middle Jurassic radiation displaying the emergence of new clades (classified in different taxa: sonniniids, haploceratids, strigoceratids or stephanoceratids, perisphinctoids, see Moyne and Neige (2004) for a cladistics analysis of the Middle Jurassic radiation).

3.5 Conclusions and Prospects

Ultimately, this analysis of evolutionary trends within Jurassic ammonoids, exemplifies several main points:

- Jurassic ammonoids have been extensively studied and the evolutionary pattern of this clade is largely exemplified both at a global and local geographic scale;
- Searches for evolutionary trends within Jurassic ammonoids are not common within the literature;
- Only a few published cases at a large taxonomic and/or geographic scale attempt explicitly to decipher trends. These concern—for example—shell shape (i.e. evolute to involute, depressed to compressed), and adult shell size disparity;
- As far as we know, only Raup and Crick (1981), following Brinkmann (1929), attempted a statistical analysis of trends for Jurassic ammonoids but at a very local geographic scale (one section), and for a very short span of time (infra Callovian stage). They found few cases of trends and hypothesized that natural selection played a role;
- At the family level—and based on the analysis of four previously published synthetic papers about Jurassic ammonoids as a whole—we observe two trends in the context of increasing diversity for periods of time circa 10 myr: the Early Jurassic and the Middle Jurassic radiations;
- Observed at the family level, the Early Jurassic Radiation immediately follows the first-order End-Triassic Extinction, whereas the Middle Jurassic Radiation is largely delayed with respect to the second-order Early Toarcian Crisis.

Examples of demonstrated (or at least observed) evolutionary trends within Jurassic ammonoids are surprisingly few compared to the tremendous number of papers on Jurassic ammonoids. As previously stated, ammonoids, and particularly those from the Jurassic, offer a range of advantages for such a demonstration (good fossil record, fine chronostratigraphic framework, etc.). However, we must confess that this very good knowledge is drowned in confused high-rank taxonomic and phylogenetic frameworks. These taxonomic and phylogenetic uncertainties act as limiting factors when attempting to decipher evolutionary trends. For instance, in the present study, the four primary published papers that examine Jurassic ammonoids as a whole are based on the recognition of families that are mostly paraphyletic (Donovan 1994; Rouget et al. 2004; Neige et al. 2007 for explorations of taxonomic and phylogenetic practices among ammonoid and cephalopod scholars). This may lead to artificial patterns (e.g., pseudoextinctions). In this context, obtaining robust (i.e. character based) phylogenies is crucial to exploring trends at the lineage level. We attempted here to summarize these phylogenetic relationships among main ammonoid groups by a postulated phylogeny (Fig. 3.5). This phylogeny has not been obtained using a parsimony-based approach, but may be viewed as a summary of Jurassic ammonoid scholars point of views (and more precisely: Donovan et al. 1981; Guex 1995; House 1989; Page 1996; Moyne and Neige 2004; Tintant et al. 1975). To avoid any taxonomic confusion we used informal names

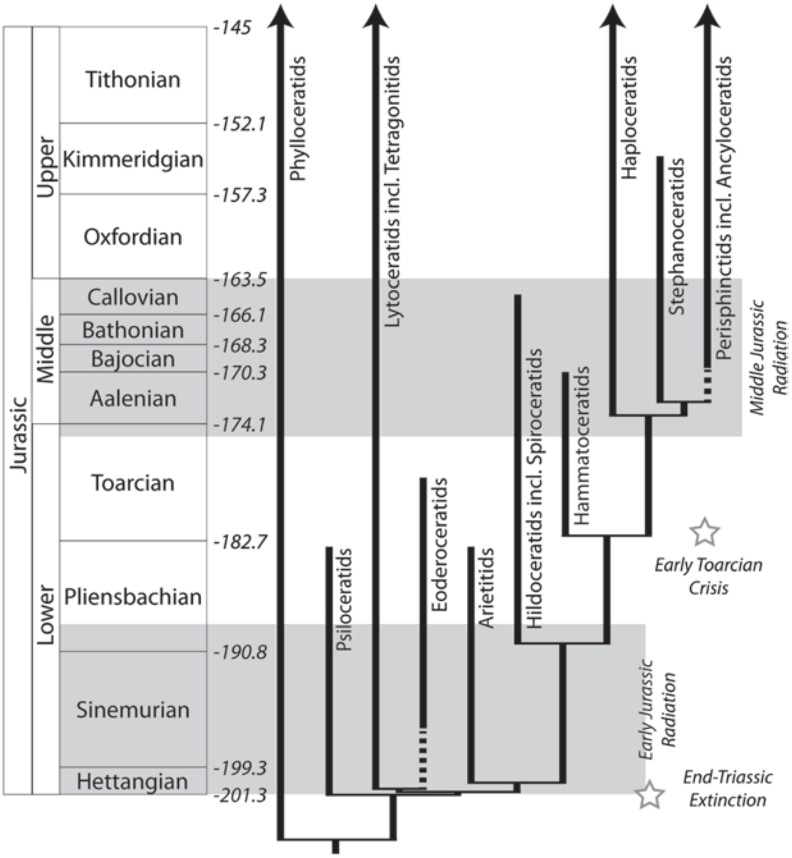

Fig. 3.5 Postulated phylogeny of Jurassic ammonoids assuming various sources of data (e.g., Donovan et al. 1981; Guex 1995; House 1989; Page 1996; Moyne and Neige 2004; Tintant et al. 1975). *Dotted lines* are supposed ghost lineages. (Note that informal names have been preferred to formal ones to avoid any taxonomic confusion)

(e.g. Psiloceratids instead of Psiloceratoidea). This phylogenetic tree can thus be considered as a first step toward a more formal (i.e. parsimony-based) one. It is not a surprise that the two radiation events (Lower and Middle Jurassic) appear in the phylogeny (Fig. 3.5, grey zones): Early Jurassic radiation is marked by the more or less synchronous emergence and diversification of numerous new clades (e.g. Psiloceratids, Eoderoceratids, Arietitids), whereas Middle Jurassic radiation is due the diversification of Hammatoceratids followed by the synchronous emergence of three clades (Haploceratids, Stephanoceratids and Perisphinctids). Increasing phylogenetic resolution among Jurassic ammonoids (i.e. obtaining good phylogenies for the each clade figured on Fig. 3.5) will definitely permits a better study of evolutionary trends. A second limiting factor when exploring evolutionary trends is to assign paleoecological conditions to ammonoids. The relationship between ammonoid shell shapes and their environment has long been discussed (see Westermann

1996 for an extensive review of arguments), the main debate being whether ammonoid habitats strongly influence their shapes compared to other factors such as phylogenetic inheritance, morphogenetic constraints, or developmental pathways. Increasing our knowledge of ammonoid habitat conditions would help greatly in interpreting evolutionary trends once established. In particular, this would permit fine interpretations between shell shapes and abiotic parameters such as sea-level changes, salinity, and temperatures. All in all, we believe that greater knowledge of the phylogeny and paleoecological conditions of Jurassic ammonoids would certainly give renewed impetus to evolutionary trend studies, and would reaffirm their value as a model in evolutionary paleontology.

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Chapter 4
Buckman's Rules of Covariation

Claude Monnet, Kenneth De Baets and Margaret M. Yacobucci

4.1 Introduction

Many ammonoid taxa have long been known to show a huge degree of morphological variation of their conch (for reviews, see Kennedy and Cobban 1976; De Baets et al. 2015). Morphological variability is an important subject in evolutionary studies because genetic variation and thus its morphological reflection is one of the driving factors of evolution. To some extent, intraspecific morphological variability reflects the evolvability of species and their evolutionary dynamics by promoting diversification and by protecting against extinction (West-Eberhard 1989, 2003; Wagner and Altenberg 1996; Sniegowski and Murphy 2006; Kolbe et al. 2011). High levels of morphological variability have been attributed to various ecological and developmental mechanisms, including selection for ecological generalists in an unstable environment (Simpson 1944; Parsons 1987; but see Sheldon 1993), adaptation to a variable hydrodynamic regime (Jacobs et al. 1994), inherent developmental plasticity (Yacobucci 1999), and the lack of competitors (Erwin et al. 1987; Valentine 1995). Variations in ammonoid shell forms have been rarely studied in this context, but see Yacobucci (2004b).

This very broad range of shell shapes of many ammonoid species continues to present a challenge for delimiting and distinguishing species, which becomes even more important when it concerns taxa widely used in biostratigraphy (e.g., Reeside

C. Monnet (✉)
UMR CNRS 8217 Géosystèmes, UFR des Sciences de la Terre (SN5), Université de Lille 1, Avenue Paul Langevin, Villeneuve d'Ascq cedex 59655, France
e-mail: claude.monnet@univ-lille1.fr

K. De Baets
GeoZentrum Nordbayern, Fachgruppe PaläoUmwelt, Friedrich-Alexander-Universität Erlangen-Nürnberg, Loewenichstraße 28, Erlangen 91054, Germany
e-mail: kenneth.debaets@fau.de

M. M. Yacobucci
Department of Geology, Bowling Green State University, Bowling Green, OH 43403, USA
e-mail: mmyacob@bgsu.edu

C. Klug et al. (eds.), *Ammonoid Paleobiology: From macroevolution to paleogeography,*
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and Cobban 1960; Kennedy and Cobban 1976; Dzik 1985). However, whatever the causes of morphological variation of ammonoid shells are, these morphologies were not randomly distributed. The ammonoid shell, which grew by accretion, consists of a roughly conic, chambered, calcified conch, usually coiled (more or less regularly), which may bear ornamentation consisting of ribs, tubercles, spines, or keels. Numerous characters can be used to describe the ammonoid shell (e.g., Arkell et al. 1957; Dommergues et al. 1996; Korn 2010; Klug et al. 2015a); its morphology can be separated into three major sets of characters, which are the geometry of the shell tube (including whorl shape and degree of involution), its ornamentation, and the suture shape. These three categories all display strong patterns of covariation, which were first described over a century ago (e.g., Buckman 1892; Jayet 1929; Haas 1946) and more recently have been used to characterize the intraspecific variation of ammonoids.

In his study on Bajocian (Middle Jurassic) ammonoids from Dorset (England), Buckman (1892) noted the following observation on the genera *Sonninia* and *Amaltheus*: "*roughly speaking inclusion and compression of whorls correlate with the amount of ornament—the most ornate species being the most evolute, and having almost circular whorls*" (Buckman 1892, p. 313). Later, Westermann (1966) restudied the material of Buckman. He took measurements of shell characters to quantitatively evaluate the descriptive observation of Buckman (1892). He was thus able to confirm the phenomenon, which he called "*Buckman*'*s first law of covariation*": "*covariation between ornament on the one hand and the whorl section and coiling [involute/evolute] on the other*" (Westermann 1966, p. 305). He also described another relationship between ornament and suture frilling: compressed variants normally have more elongated and finely frilled suture lines ("*Buckman's second law of covariation*"; Westermann 1966). Note that these morphological patterns will be referred to here as rules (and not laws), because a law usually describes a true, absolute and unchanging relationship among interacting elements, whereas a rule describes a frequently documented pattern (with known exceptions) in the interactions of organisms and their environments, particularly in biology (e.g., Cope's rule, Bergmann's rule).

This chapter aims to illustrate these patterns of covariation in the ammonoid conch and then review the various explanations for the origin of this constrained morphological variation. For a discussion of intraspecific variation of ammonoids more generally, see De Baets et al. (2015).

4.2 Rules of Covariation

4.2.1 First Rule—The More Evolute, The More Depressed, The More Ornamented

Buckman's first rule of covariation was coined by Westermann (1966) for the interdependence between shell geometry (involution of the shell and shape of the whorl section) and the coarseness of shell ornamentation. In other words, the more evolute, the more depressed and the more ornamented the ammonoid shell is (Fig. 4.1). As initially defined, this pattern of covariation holds within a species (i.e., intraspecific variation) of ammonoids. Indeed, many authors have characterized a species as a variable species ranging from compressed forms that have dense, fine ribs and small, sharp tubercles to more robust forms that have fewer but more robust ribs and more rounded tubercles (e.g., the classic example of the Cenomanian *Acanthoceras*; Kennedy and Hancock 1970; Wright and Kennedy 1987).

This pattern of covariation of some shell characters has been documented in very different taxonomic groups and time periods: Devonian agoniatitins (De Baets et al. 2013), Triassic tropitids (Silberling 1959, 1962; Tozer 1971), Spathian sibiritids and dinaritids (Dagys et al. 1999; Weitschat 2008), Anisian beyrichitins, ceratitins and arctohungaritids (Silberling and Nichols 1982; Dagys and Weitschat 1993; Dagys 2001; Monnet and Bucher 2005), Jurassic cardioceratids (Callomon 1985; Wright 2012), Toarcian hildoceratids (Morard and Guex 2003), Aalenian leioceratins (Bayer 1972; Bayer and McGhee 1984; Chandler and Callomon 2009), Oxfordian-Kimmeridgian perisphinctids (Atrops and Melendez 1993), Barremian gassendiceratins (Bert et al. 2013), Aptian deshayesitids (Martin 2003), Cretaceous hoplitids (Reeside and Cobban 1960; Kennedy and Cobban 1976; Reyment and Kennedy 1998), Albian mortoniceratines (Jayet 1929), Late Cretaceous acanthoceratoids (Kennedy and Hancock 1970; Kennedy and Wright 1985; Wright and Kennedy 1984, 1987, 1990; Courville and Thierry 1993), Cenomanian schloenbachiids (Wilmsen and Mosavinia 2011), Turonian collignoniceratids (Tanabe 1993; Kennedy et al. 2001), and many others (review in De Baets et al. 2015). Although abundantly described, this pattern of covariation is rarely assessed quantitatively, even though such an approach could be used to evaluate species delimitations and investigate the evolution of intraspecific variation.

The covariation pattern involves the conch geometry (shape and coiling) and the shell ornamentation (robustness and density). The ammonoid shell geometry can be quantified by using the classical linear measurements usually supplied with systematic descriptions of ammonoid species: D, shell diameter; H, whorl height; U, umbilical diameter; W, whorl width (Klug et al. 2015). Conch geometry can be approximated with the following ratios: degree of compression of whorl section (ratio H/W; ellipsoid of whorl shell aperture), and degree of involution (ratio U/D; amount of overlap between successive whorls). These ratios provide a relative metric, which allow shells of different absolute size to be compared. Note, though, that these ratios are known to change through ontogeny.

The ornamentation of the ammonoid shell is an important diagnostic character, which has frequently been interpreted incorrectly because of the lack of recognition of the intraspecific covariation of shell characters. Ornamental characters may be relatively diverse but are described mostly as qualitative characters. The degree of ornamentation can be approximated by the density of these ornaments and by their thickness. The former (often available in the literature) can be expressed as the number of (ventral) ribs (and/or tubercles) per whorl or demi-whorl at a distinct diameter (R/D). The latter (more rarely available in the literature) can be characterized by the difference of height and width of the whorl section (H and W) measured

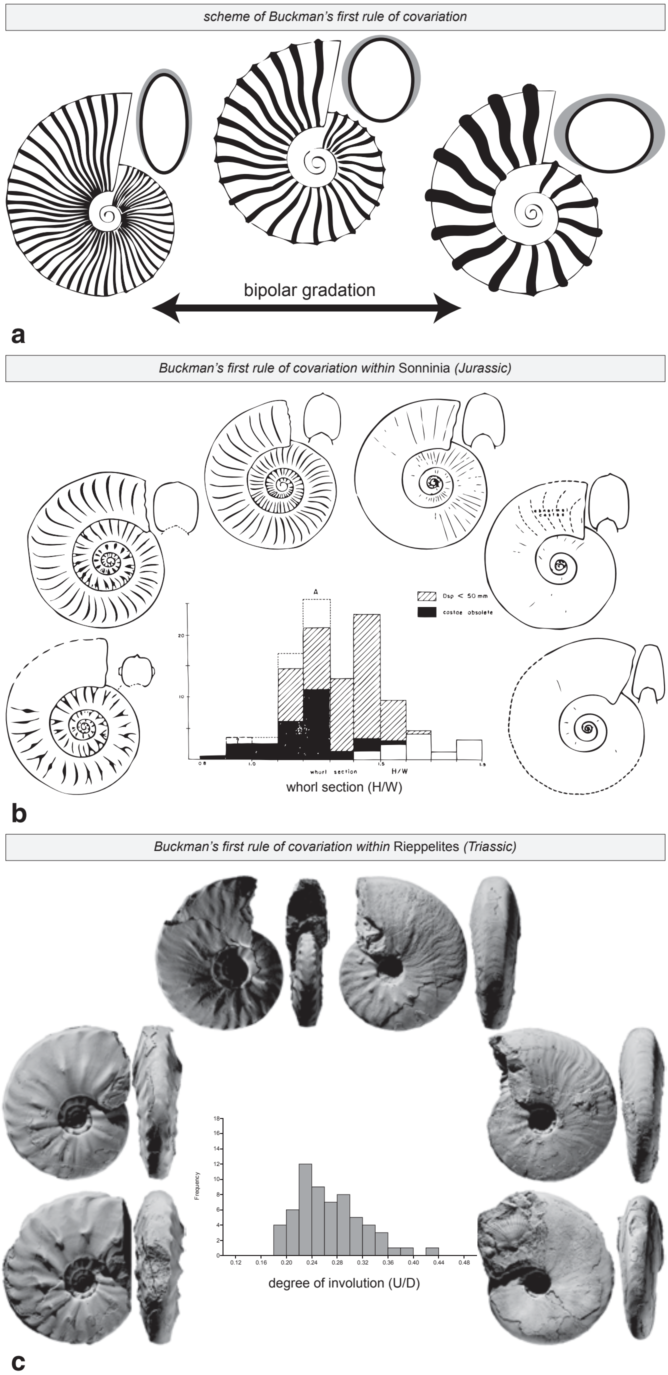

Fig. 4.1 Buckman's first rule of covariation: the more evolute, the more depressed, the more ornamented the ammonoid shell is. **a** Scheme of Buckman's first rule of covariation (modified

exactly on top of a rib and between two consecutive ribs (RH and RW, respectively; Hammer and Bucher 2005). Note that ribbing density and strength of ornamentation are mostly negatively correlated (Bert 2013; De Baets et al. 2015).

Buckman's first rule of covariation is thus the statement of a regular relationship between three characters: negative correlation between whorl compression and strength of ornamentation as well as negative correlation between whorl involution and strength of ornamentation. This kind of correlation can be evaluated by means of standard linear regression models for each pair of characters. Here, quantitative analyses have been performed using the software PAST (Hammer et al. 2001) and the statistical environment R (http://www.r-project.org/). These analyses and their graphical outputs are standard (e.g., Davis 2002; Hammer and Harper 2006; for a detailed application see Bert 2013). Figure 4.2 illustrates this pattern of covariation for the ammonoid species *Acrochordiceras carolinae* from the Anisian of Nevada (dataset from Monnet et al. 2010). The linear regression analysis of the covariation pattern for this species (146 specimens from a single bed) indicates that the three character sets are significantly correlated (*p* value lower than 1 %). Whorl section (H/W) and degree of involution (U/D) are more strongly correlated ($r=0.59$), whereas density of ornamentation (R/D) is less correlated with the two other characters ($r=0.25$).

4.2.2 Second Rule—The More Compressed, The More Frilled

In his monographic study, Buckman (1892) also stated that in *Sonninia*, the complexity of the suture line increases in proportion to the decrease of ribbing intensity (i.e., negative correlation between suture complexity and strength of ornamentation). However, he neither illustrated nor quantified this relationship. Furthermore, this correlation had already been suggested by previous authors (for a review, see De Baets et al. 2015). Westermann (1966) referred to this covariation pattern as Buckman's second rule of covariation. Based on the first rule, a relationship between the complexity of the suture pattern and the geometry of the whorl section can be derived: the more compressed the whorl section, the more frilled the suture line (i.e. positive correlation between suture indentation and whorl compression). Contrary to the first rule, which is abundantly recognized in large samples, the second rule may not necessarily hold in all these cases (e.g., Dagys et al. 1999; Dagys 2001) or may be muted by larger constraints on suture pattern than shell shape (e.g., in *Neogastroplites* species: Yacobucci and Manship 2011).

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after Bert 2013): intraspecific variation of a species grades from a gracile morph (higher and *tight* whorl section, thin ornamentation and close umbilicus) to a robust morph (*lower and broad* whorl section, strong ornamentation and wide umbilicus). **b** Intergrading morphological series of *Sonninia adicra* (Bajocian) illustrating the covariation pattern between ornamentation robustness and whorl section (modified after Westermann 1966). **c** Intergrading morphological series of *Rieppelites boletzkyi* (Anisian) illustrating the covariation pattern between ornamentation robustness and degree of involution (modified after Monnet and Bucher 2005)

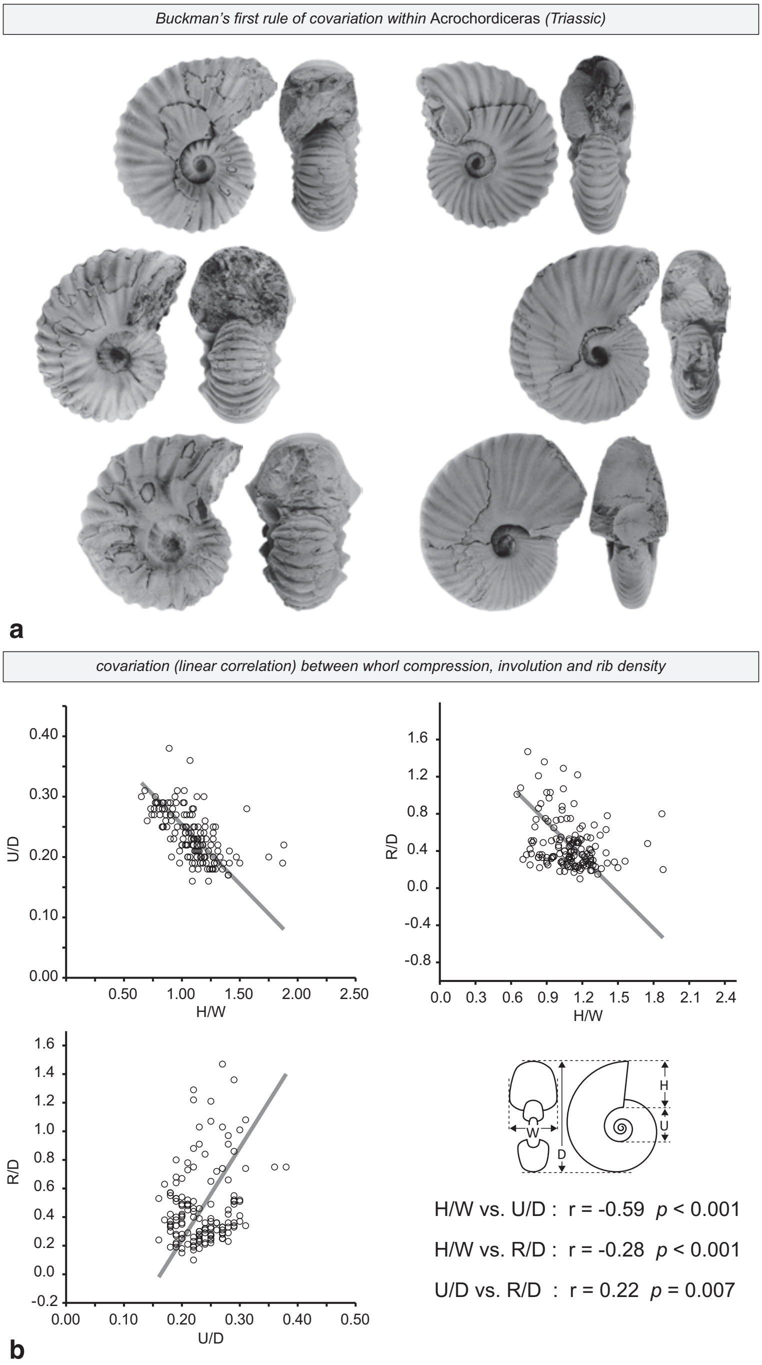

Fig. 4.2 Buckman's first rule of covariation within *Acrochordiceras carolinae* (Anisian) for 146 specimens from the same stratigraphic bed. **a** Intergrading morphological series illustrating the

The suture line (imprint of septa on the conch) has been variously quantified: by simple indices such as the number of lobes (e.g., Batt 1991; Saunders et al. 1999) or by more complex indices such as fractal indices (e.g., Garcia-Ruiz et al. 1990; Boyajian and Lutz 1992; Pérez-Claros 2005; Pérez-Claros et al. 2002, 2007), by Fourier analysis (Gildner 2003; Allen 2006; Ubukata et al. 2014), by geospatial information systems (Manship 2004; Yacobucci and Manship 2011), or by Eigenshape analysis (Ubukata et al. 2010). Despite all these tools, the correlation between whorl shape, coiling and suture indentation has rarely been quantified within species. The reality of this second rule thus remains to be completely investigated. Nevertheless, shell shape and coiling are well known to have a conspicuous effect on suture pattern (Westermann 1971, 1975; Seilacher 1988; Checa and García-Ruiz 1996; Olóriz et al. 1997; Klug and Hoffmann 2015).

Note that the two rules can be merged into a single covariation pattern: the more evolute the shell, the more depressed, the more ornamented, and the less frilled is the suture. However, since the second rule is rarely tested, it is not yet known if this extended rule always holds. Finally, two additional types of covariation have been proposed. Hammer and Bucher (2006) added a potential additional rule: negative correlation between septal spacing and whorl compression (Fig. 4.3). Because of the lack of additional descriptions and datasets corroborating this latter rule, it will not be discussed further in the present study. Interestingly, Bert (2013) also described intraspecific patterns of covariation within *Gassendiceras* (Barremian), not only between two morphs like Buckman's rules of covariation, but between three morphotypes. In addition to the two classic poles usually recognized (a robust pole with thick section, evolute shell and strong ornamentation *versus* a slender pole with narrower section, involute shell and weaker ornamentation), Bert added a third morphological pole with thick section and less robust ornamentation. Additional cases are discussed by De Baets et al. (2015).

4.3 Impact of These Rules on Ammonoid Systematics

Since only hard tissues are typically fossilized for ammonoids, paleontologists necessarily define morphological species and do not have access to the interbreeding criterion of biological species (i.e., a set of interbreeding individuals reproductively isolated from other populations; e.g., Mayr 1963, 1969). Two major and opposite approaches have been used to define fossil morphospecies (for reviews on ammonoids, see Tozer 1971; Dzik 1985, 1990; Chandler and Callomon 2009; De Baets et al. 2015). The first concept ("*typological approach*") puts emphasis on every (even slight) difference in morphological characters; such an approach leads to the multiplication of species (oversplitting) and is encouraged by the concept of the

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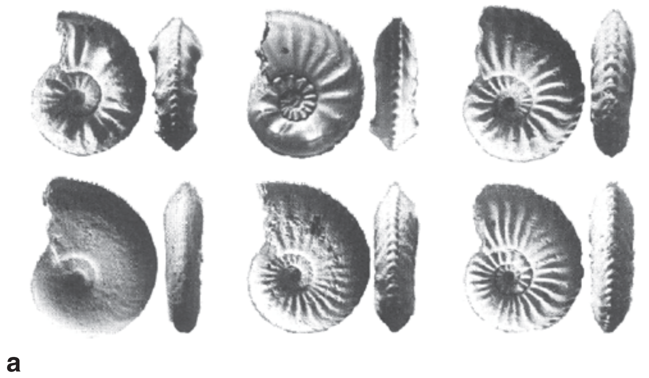
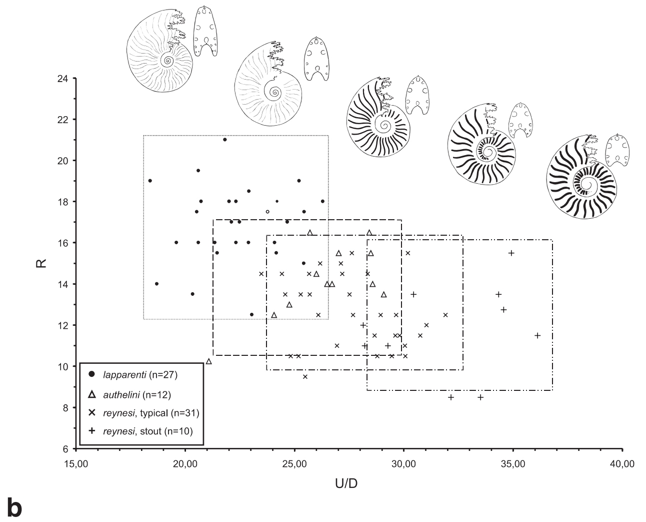
covariation pattern between ornamentation robustness, whorl section, and degree of involution. (Modified after Monnet et al. 2010). **b** Pairwise linear fitting (reduced major axis) of the three character sets (ornamentation is here evaluated by means of rib density)

Buckman's first rule of covariation within Amaltheus *(Triassic)*



covariation (linear correlation) between whorl compression, involution and rib density



covariation between septal spacing, involution, and ornamentation

Fig. 4.3 Buckman's first rules of covariation within *Amaltheus margaritatus* (Pliensbachian). **a** Intergrading morphological series illustrating the covariation pattern between ornamentation

holotype as well as by the utility of ammonoid species as stratigraphic markers. However, many living species are known to not have such a narrow morphological variation. The second concept (population approach) takes the present-day biological species' structure into account by allowing a certain degree of morphological variation. The notion of species as an array of intergrades separated from another series of organisms between which intermediates are absent or at least rare has been formally known at least since Dobzhansky (1937). It is worth noting that it has been demonstrated that in a single interbreeding population, the quantitative, morphological characters are variable and their frequencies often follow a statistically normal distribution (e.g., Mayr 1942; Sokal and Rohlf 1995; Templeton 2006). Hence, a set of specimens showing a continuous inter-gradation of characters fitting a normal (or at least continuous and unimodal) distribution should be interpretable as variants of a single species (De Baets et al. 2015). The recognition of Buckman's rules of covariation can then serve as an aid to discriminate between ammonoid morphospecies, which may correspond to biospecies (although some discrepancies between reproductive isolation and distribution of morphological characters may inevitably occur, such as in sibling/cryptic species; e.g., Mayr 1948; Knowlton 1993; Boyle and Rodhouse 2005). Note that the criterion of normal distribution of the intergrading character states can be relaxed because it is not always strictly normal within living biospecies and because fossil populations often are biased by several geological and taphonomic processes (e.g., temporal and vertical mixing/averaging, transport; Bush et al. 2002; Kidwell and Holland 2002; Hunt 2004; review in De Baets et al. 2015).

Ammonoids, perhaps more than any other group, have suffered from taxonomic splitting (Tozer 1971; Kennedy and Cobban 1976), and authors have frequently divided intergrading populations into a whole range of typological species and even genera, which belong to what can now be regarded as a single variable species (e.g., Buckman 1892 and Westermann 1966). This problem results from the truly remarkable intraspecific variation seen among many ammonite groups (De Baets et al. 2014). Note that in some groups, end-member variants may show an extreme morphological distance and, in the absence of sufficiently large samples, may be attributed to different species or genera (e.g., taxonomic discussion in Monnet et al. 2010, p. 972; De Baets et al. 2013). The two extreme forms can be very different in their morphological proportions, but are always linked by (more frequent) intermediate forms (Weitschat 2008; De Baets et al. 2015). It is therefore critical to assess intraspecific variation from large assemblages. Recognition of this variation has led to significant simplification of the nomenclature in several cases (e.g., Reeside and Cobban 1960; Kennedy and Cobban 1976; Silberling and Nichols 1982; Wright and Kennedy 1984, 1987, 1990; Hohenegger and Tatzreiter 1992; Atrops and Melendez 1993; Weitschat 2008; Monnet et al. 2010; Bert 2013). Neglecting the population

robustness, whorl compression, and degree of involution (modified after Guex et al. 2003). **b** Scatter plot illustrating covariation of rib density and degree of involution (modified after Morard and Guex 2003). **c** Illustration of the covariation between septal density and whorl compression (modified after Hammer and Bucher 2006) concept can lead to erroneous ecological and biostratigraphic interpretations (Dagys and Weitschat 1993) as well as overestimated values of past taxonomic richness. As a consequence, ammonoid workers have to accept that a single specimen may not necessarily be sufficient for unequivocal species identification and/ or description. This evaluation also requires that the studied assemblages are derived from a single bed in order to minimize the mixing of forms that evolved through time or that lived in different environmental settings (see Kidwell and Holland 2002). In the face of this large variation in ammonoid forms, developing species definitions is often challenging.

It is worth noting that Buckman's rules of covariation of the ammonoid shell are defined for a single species from a single sample and for regularly coiled (monomorphic) planispiral ammonoids. The systematic context for the original studies was an attempt to reduce the number of named species by recognizing that the observed range of fossil forms was, in fact, due to intraspecific variation rather than species-level differences. For instance, based on a careful re-study of *Sonninia* from the Jurassic of Dorset, which Buckman (1892) split in 64 typological species, Westermann (1966) clearly documented the pattern of covariation between the geometry of shell tube and strength of the ornamentation, and recognized a single (highly) variable species. Although a large degree of intraspecific variation in *Sonninia* is still accepted, Westermann (1966) lumped together specimens from various stratigraphic levels (e.g., Callomon 1985; Sandoval and Chandler 2000; Dietze et al. 2005) and this stratigraphic "lumping" should be avoided at the risk of synonymizing species with temporal anagenetic changes (compare Monnet et al. 2010 and Dzik 1990). Another relevant case has been described by Dagys and Weitschat (1993), who documented a case of marked intraspecific variation in a large sample of 600 specimens of *Czekanowskites rieberi* from a single concretion of Anisian age (Middle Triassic) from Arctic Siberia. Morphologically, specimens of *C. rieberi* grade from keeled, narrowly umbilicate, smooth suboxycones to widely umbilicate subcadicones with bullate, straight ribs. Dagys and Weitschat (1993) illustrated that this variation has a roughly normal distribution, which suggests that all specimens belong to a single population (for another example, see Bert 2013). Fig. 4.4 displays an example of the covariation pattern and normality of the quantitative parameters for the shells of *Acrochordiceras carolinae* from the Anisian of Nevada (dataset from Monnet et al. 2010).

A recent example of the impact of Buckman's rules of covariation on ammonoid taxonomic nomenclature has been described by Monnet et al. (2010). Based on bed-by-bed ammonoid collections in north-west Nevada, this study revised the species of *Acrochordiceras*, which is one of the most important genera of both Tethyan and North American ammonoid faunas of the Anisian (Middle Triassic). However, there was a profusion of species in the literature included in *Acrochordiceras*, mainly because of the typological taxonomic concept, which is often based on small samples and usually characterized by slight morphological differences such as a more compressed shell, coarser ribbing, or absence of tuberculation. A careful examination of these co-occurring "species" erected applying the classical typological concept reveals the presence of intermediate forms among them, thus suggesting the existence

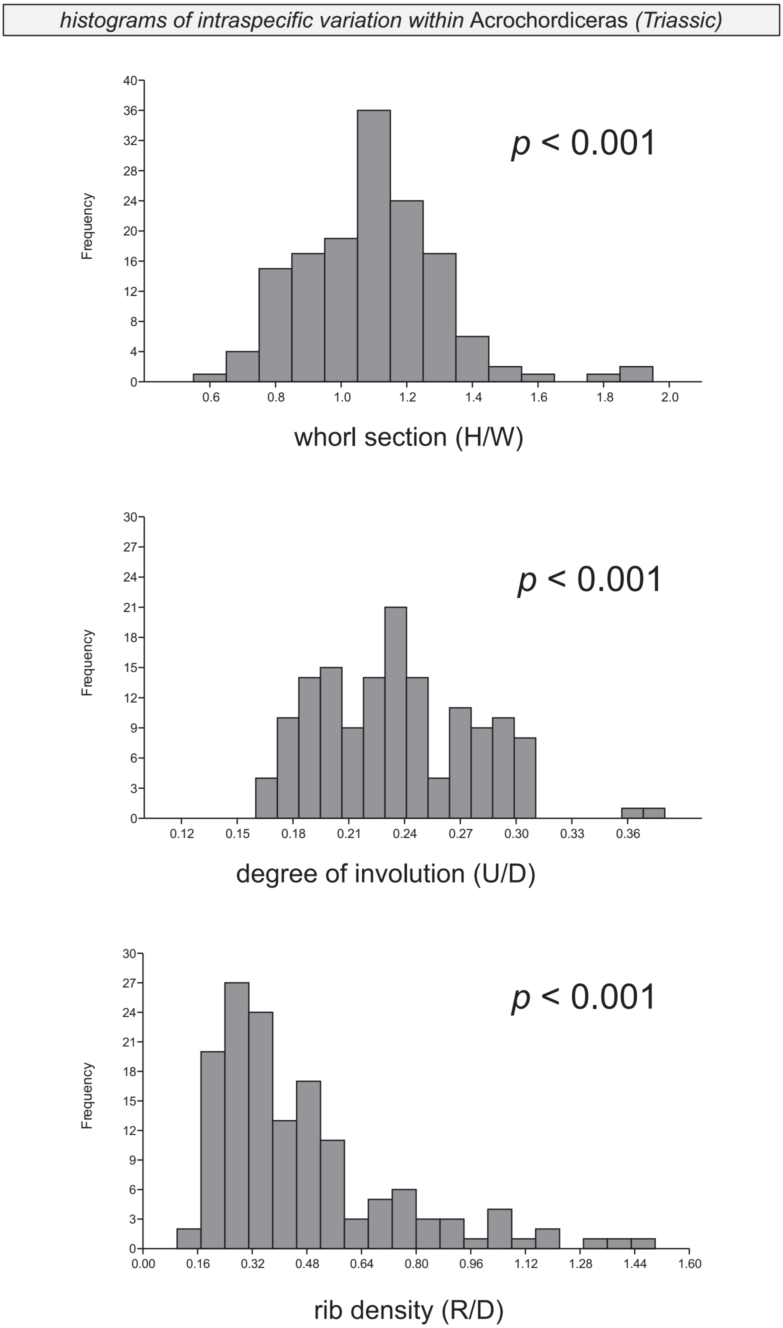


Fig. 4.4 Distribution of some characters (whorl section, coiling, and ornamentation) for 146 specimens from the same stratigraphic bed of *Acrochordiceras carolinae* (Anisian). All characters display a normal distribution with *p* values significantly lower than 1 % (Shapiro–Wilk test)

of only one highly variable species. This pattern is illustrated in Fig. 4.5a, which compares the distribution of the degree of coiling (U/D) for various sizes of *Acrochordiceras carolinae* from north-west Nevada, with inclusion of values for the holotype of other synonymized species (for more details, see Monnet et al. 2010). The figure shows that *A. carolinae* has a wide range of intraspecific variation with a continuous unimodal distribution and that each old typological "species" falls within this variation. Hence, the wide range of morphological variation exhibited by acrochordiceratids illustrates Buckman's first rule of covariation well.

When additional material is acquired through more sampling with better preserved and better stratigraphically controlled material, the revision of ammonoid species accounting for intraspecific variation usually significantly decreases species richness of ammonoid genera (Kennedy and Cobban 1976; De Baets et al. 2015). Study of additional specimens more rarely leads to the erection of additional species or the re-establishment of older ones based on previously overlooked differences in ontogeny or morphology (e.g., *Rieppelites cimeganus* in Monnet et al. 2008; *Sonninia* in De Baets et al. 2015). Therefore, the history of species taxonomy for an ammonoid genus usually is characterized by an initial rapid increase in taxonomic richness as a result of taxonomic oversplitting related to a strict typological approach, followed by a plateau with the accumulation of data, and then a decline in diversity when a better numerical grasp on intraspecific variation and finer stratigraphic resolution is achieved. The taxonomic history of the genus *Acrochordiceras* illustrates this pattern well (Fig. 4.5b). Note also that the confusion between dimorphism and continuous intraspecific variation is not uncommon, particularly when only a small sample is available (e.g., Dzik 1990; Monnet et al. 2010). Nevertheless, continuous intraspecific variation does not rule out dimorphism (see e.g., Wright and Kennedy 1984 for an example of dimorphic species in *Mantelliceras* for which each dimorph follows Buckman's rule of covariation; further discussion in De Baets et al. 2015; Klug et al. 2015b).

4.4 Causes of Covariation

Buckman's rules of covariation involve three sets of characters: shell shape, ornamentation, and suture patterns. What mechanism could produce such consistent and pervasive covariation across the ammonoid body plan? A helpful way to think about constraints on form was provided by Seilacher (1970) in what has come to be known as "*Seilacher's Triangle*" (Gould 2002). The three corners of the triangle represent three categories of constraint that limit the types of forms organisms take: (1) historical/phylogenetic, (2) functional/adaptive, and (3) constructional/morphogenetic. In reality, all three types of constraint are likely to influence the anatomical forms of organisms and entangling these in fossil samples is not straightforward. Given the pervasiveness of Buckman's covariation across a variety of ammonoid clades, phylogenetic constraints are not likely to explain the phenomenon. Several authors, though, have attempted to explain Buckman's rules in terms of either functional or constructional constraints.

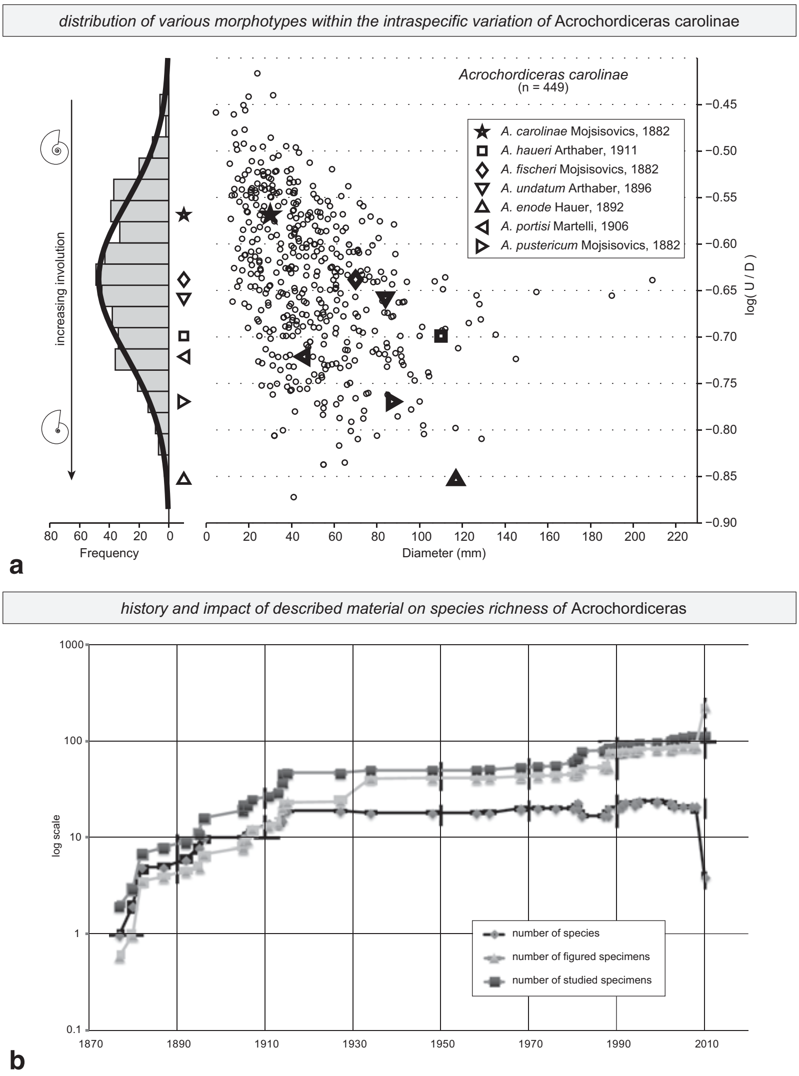


Fig. 4.5 Impact of Buckman's rules of covariation on ammonoid taxonomic nomenclature. **a** Distribution of degree of coiling (U/D) for *Acrochordiceras carolinae* Mojsisovics, 1882 in the middle Anisian from northwest Nevada (modified after Monnet et al. 2010). This diagram shows the normal distribution of U/D and the position of each species synonymized with *A. carolinae*, thus illustrating the continuous range of degree of coiling for all of the old typological species. *D* shell diameter, *U* umbilical diameter. **b** Numbers of species, figured specimens and studied specimens of the genus *Acrochordiceras* through time in the literature (unpublished data exhaustively compiling all publications with taxonomic descriptions of the genus)

4.4.1 Adaptive and Environmental Constraints

The various forms of the ammonoid shell have been largely interpreted in terms of functional needs (e.g., Dietl 1978; Jacobs 1992; Jacobs et al. 1994; Jacobs and Chamberlain 1996; Hewitt 1996; Westermann 1996; Klug and Korn 2004; Saunders et al. 2004, 2008; Klug et al. 2008), mostly in order to reconstruct the modes of life and habitats of this extinct group (e.g., Kennedy and Cobban 1976; Westermann 1996; Westermann and Tsujita 1999; Ritterbush and Bottjer 2012; Ritterbush et al. 2014). Although parts of these adaptive interpretations remain debated, the ammonoid shell has defense properties and is undoubtedly a buoyancy apparatus, which, along with shell shape, structure, and ornamentation, impose hydrodynamic limits on the animal's swimming abilities (e.g., Saunders and Shapiro 1986; Elmi 1993; Jacobs 1992; Jacobs and Chamberlain 1996; Seki et al. 2000; De Blasio 2008; Ifrim 2013). The sometimes extreme intraspecific variation and covariation of characters of ammonoids challenge current and past ideas about a close correlation between mode of life and shell morphology in ammonoids (Dagys and Weitschat 1993; Dagys et al. 1999; reviewed in De Baets et al. 2015).

Checa et al. (1997) argued that the usual morphological covariation observed within ammonoid species (involution–whorl section–ornamentation) might result from a selection pressure to maintain a similar hydrodynamic performance among the morphotypes. Indeed, based on calculation of the center of gravity for a population of *Czekanowskites rieberi*, which illustrates Buckman's first rule of covariation well (Dagys and Weitschat 1993), Checa et al. (1997) demonstrated that, despite the extreme morphological variation, hydrostatic (orientation) and hydrodynamic (stability) properties of the population remained within narrow limits. Hence, covariation may be a way of regulating the major hydrostatic parameters at population and ontogenetic levels, thus supporting this functional interpretation of shell shape (Hammer and Bucher 2006). Kawabe (2003) documented for Cenomanian ammonoids that compressed forms tend to inhabit high-energy sandy inner shelf environments and depressed forms tend to occur in low-energy offshore mud facies, but external shell ornamentation does not necessarily vary according to lithofacies differences. A similar pattern has also been documented by Landman and Waage (1993a) for Maastrichtian *Scaphites* and by Jacobs et al. (1994) for Turonian *Scaphites whitfieldi*, which shows a similar correlation between nearshore–offshore environments and whorl shape compression (additional examples are discussed in De Baets et al. 2015). Hence, Buckman's rules of covariation may result from an ecophenotypic response to habitats with different energy. However, some authors reported the exactly opposite pattern, with more depressed and heavily ornamented forms in shallower water, thus questioning this functional interpretation (Fig. 4.6; Wilmsen and Mosavinia 2011). Batt (1989) showed that the distribution of various morphotypes of Cenomanian ammonoids in the Western Interior partially reflects environmental gradients (e.g., water depth), especially among different lineages. Furthermore, size (ontogenetic stage) probably plays an important role in controlling the amplitude of these adaptive constraints, which may be reduced at small sizes.

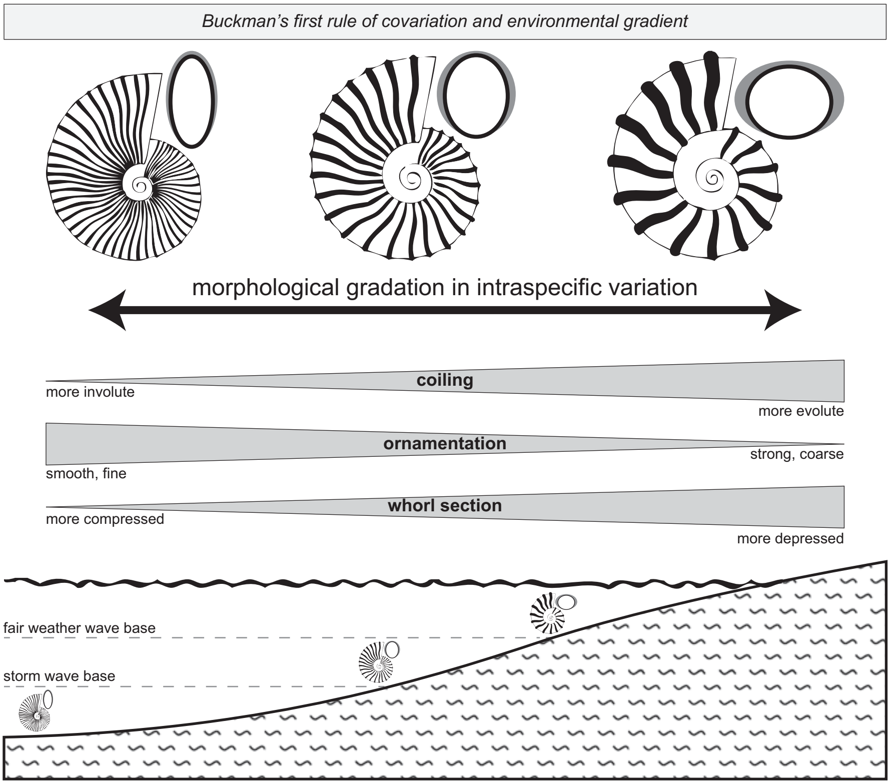


Fig. 4.6 Buckman's rules of covariation and ecophenotypism. Ammonoid intraspecific variation of its shell morphology is often reported to be ordered along a paleoenvironmental gradient (especially water depth as reflected by proximal–distal facies): strongly tuberculate, depressed forms reflect comparatively shallow, nearshore environments with higher water energy and predation pressure, whereas compressed, weakly ornamented morphs are forms of open (and deeper) marine waters. (See, e.g., Wilmsen and Mosavinia 2011; but compare with Bayer and McGhee 1984 and Jacobs et al. 1994 who reported the exact opposite pattern)

In contrast to the previous interpretations, Westermann (1966) and Reyment (1988) argued against any adaptive cause of this intraspecific covariation pattern. They maintained that the occurrence of such a large morphological variation within a single species and its abundant presence in distantly related groups through time and space is unlikely to reflect ecophenotypism. Paleogeographic differences also do not seem to impact the covariation patterns: e.g., the low paleolatitude *Acrochordiceras* and the high paleolatitude *Czekanowskites* (Anisian) show similar patterns of covariation (Dagys and Weitschat 1993; Monnet et al. 2010).

The covariation between suture indentation and shell ornamentation may also reflect functional constraints, in this case resulting from the role of suture complexity in stiffening the phragmocone (the more indented the suture, the more resistant the shell to hydrostatic pressure; Westermann 1966). However, the function of the septal folding is still the subject of much debate and several hypotheses have been proposed (Klug and Hoffmann 2015), so the hypothesis about shell stiffening might prove to be invalid.

With regard to the covariation between septal spacing and whorl compression, Hammer and Bucher (2006) explained it in terms of hydrostatic properties. They calculated that, under equal lengthening of the body chamber during growth, the buoyancy of compressed forms is more affected. Hence, this covariation pattern can be explained by function: in order to retain neutral buoyancy, the more compressed forms must construct septa more often than the depressed morphs. However, given the often very variable septal spacing of sutures within species (e.g., Paul 2011), this covariation requires additional studies to be further tested. Kraft et al. (2008) documented cases of non-mature septal crowding in Carboniferous ammonoids and suggested that close septal spacing can be interpreted as a response to adverse ecological conditions, which caused growth deceleration.

4.4.2 Constructional and Developmental Constraints

With regard to the first rule of covariation (the more evolute, the more depressed, the more ornamented), several authors have argued for morphogenetic explanations. Westermann (1966) stressed that the correlation between H/W and U/D is logical, at least partially, because whorl height (H) is part of the diameter (D) (Sokal and Sneath 1963). Hence, the fact that evolute whorls are much more rounded than involute whorls in part due to a single varying dorso-ventral growth vector. Westermann (1966) also tentatively proposed that the amplitude (robustness) of shell ornamentation (ribs, spines) is a function of the growth rate for whorl width (W) and thus varies with whorl roundness (H/W). Westermann (1966) supposed that the mantle margin secreting the shell tended to more intense rhythmic lateral contraction in depressed forms than in compressed ones.

Guex et al. (2003) simulated the covariation pattern by a reaction/diffusion model of ammonoid morphogenesis, in which morphogens concentrate in shell regions of high curvature such as on the flanks of a depressed shell. The aim of this model is to fit the following observation: "*the most salient ornamentation is present where the whorls are most curved, shells with slight angular bulges often being spinose or carinate and flat ones being almost smooth*" (Guex et al. 2003). Although this model is an interesting attempt to better understand shell morphogenesis, it remains speculative. Indeed, this model makes a large number of assumptions about the nature of the underlying pattern formation system of shell morphogenesis (discussion in Hammer and Bucher 2006), which remain to be corroborated by physiological studies. Even if these reaction/diffusion models are able to reproduce color patterns of mollusks (e.g., Meinhardt 1995; Boettiger et al. 2009), it is not yet demonstrated that it upholds for shell morphogenesis as well. Additionally, this model does not yet explain the covariation of ribbing density with whorl compression and degree of involution. Other researchers (Checa 1987, 1994; Checa and Westermann 1989) argued for the opposite causal link for constructional constraints that could explain

Buckman's first rule, noting that the formation of more robust ribs during shell growth could cause the shell to automatically become more inflated and depressed.

Hammer and Bucher (2005) suggested that the first rule of covariation is "*simply*" a statement of proportionality that needs no special explanation. They assumed that robustness of ornamentation is proportional to the amount of soft parts: "*if the shell is depressed* (*compressed dorsoventrally*)*, the diameter of the soft parts is small in the dorsoventral direction, and the ventral ribbing correspondingly small*". Hence, size of lateral and ventral ornamentation correlates with the proportions of the aperture (width and height). This explanation of Buckman's rule highlights simple mechanical constraints on the construction of ammonoid ornamentation. While morphogenetic pre-patterns can probably be translated into pigmentation patterns more or less directly (Fowler et al. 1992; Meinhardt 1995; Hammer and Bucher 1999; Boettiger et al. 2009), ribbing and other three-dimensional shell features involve growth, folding, and stretching of tissues, implying strong developmental constraints in terms of growth rates, mechanics, and geometry. The ratios of proportionality can vary across species (some species have stronger lateral ribs relative to shell width than others) and thus weaken the interspecific correlation between ornamentation and whorl shape (Hammer and Bucher 2005). Whatever the model, the covariation involving rib density can be explained by a domain effect if it is considered as a secondary consequence of ornamentation robustness and controlled by reaction/diffusion processes: thicker ribs tend to imply fewer ribs in the same space (Hammer and Bucher 1999).

Buckman's second rule of covariation (more compressed shell, more frilled sutures) can also be explained as a case of constructional constraint. Although the function of septal folding is subject of much debate, it has been suggested that septal formation behaves like "*viscously fingering*" liquids (Checa and Garcia-Ruiz 1996). According to this model, the degree of suture indentation depends on the space and shape available for the suture during its formation ("*domain effect*"): with equal mantle length secreting the septum, the more compressed the shell, the less space is available for the mantle, and the more constrained the suture shape will be. This domain effect on suture pattern has also been invoked to explain the evolutionary trends in suture complexity coupled with trends in involution and size increase (e.g., Monnet et al. 2011, 2015). This effect is also illustrated by increasing indentation of suture line during ontogeny (e.g., Swinnerton and Trueman 1917; Wiedmann 1966a, 1966b; Korn and Klug 2003; Pérez-Claros et al. 2007).

Hammer and Bucher (2006) argued that whorl shape and suture indentation covariation results from a heterochronic process. Because most ammonoids have rather circular whorls and simple sutures early in ontogeny, late in ontogeny the more depressed forms can be regarded as retaining their juvenile shape and suture (paedomorphosis) compared to the more compressed forms. However, this interpretation may not always hold, especially with regard to cadiconic forms in which sutures also increase their indentation, thus corroborating the domain effect hypothesis (see above). Nevertheless, Buckman's second rule of covariation may reflect intraspecific variation in development which is well known to vary within ammonoid species (e.g., Dommergues et al. 1986; Meister 1988; Courville and Crônier

2003). Similarly, Bert et al. (2013) also argued that heterochronic variation can explain the covariation between whorl compression and ornamentation coarseness, since this covariation is reflected in the ontogenetic changes of studied species (see also Courville and Crônier 2003; compare De Baets et al. 2015).

Yacobucci (2004a) studied the correlation between the variation of shell shape and of ornamentation (rib thickness and spacing). With respect to Buckman's first rule of covariation, one can expect that species with variable shell shapes would also have variable patterns of ornamentation. However, her study documented a different pattern in Cenomanian acanthoceratids of the Western Interior: groups with especially large shape variation are not those with the most intense variation in ornamentation. Hence, ammonoid shell morphogenesis is complex with some character sets more constrained than others, probably due to a different impact of developmental, constructional, environmental, and functional processes.

In conclusion, the causes of Buckman's rules of covariation for the ammonoid shell are still debated. Constructional and adaptive constraints are not mutually exclusive: both can contribute to the fabrics of structured intraspecific variation for ammonoid shells (Seilacher 1970). The recurrence of particular combinations of morphology, which are commonly regarded as strong arguments for functional constraints, can also represent "*fabricational noise*" (Seilacher 1970, 1973). Additional studies are required to test quantitatively the various hypotheses (e.g., the proportionality hypothesis of Hammer and Bucher 2005 is so far confirmed only by a single dataset). Additional insights may be found in comparative studies on the morphogenesis of living mollusks as well as from theoretical models of shell morphogenesis (e.g., Urdy et al. 2010a, 2010b; Moulton et al. 2012; Chirat et al. 2013; Moulton et al. 2015).

4.5 Extent of Buckman's Rules of Covariation

Buckman's rules of covariation appear to be a pervasive pattern of the intraspecific variation of monomophic Mesozoic ammonoids to varying degrees. A number of questions still remain to be investigated: Does each component of the covarying character set equally contribute to the global covariation pattern? Is the degree of covariance constant during growth? Is the degree of covariance constant through time during anagenetic changes? Do dimorphic pairs show similar covariance? Does the covariation pattern apply equally within different taxonomic groups? Does the extent of covariation vary through time and phylogeny? Does it change with environmental factors and, if so, which ones? Is it related to environmental instability, developmental flexibility, or competition (Yacobucci 2004b)?

With regard to the relative contribution of each character set into the global covariation pattern, no comparative study has yet been conducted to our knowledge. Nevertheless, as can been seen with the examples of *Acrochordiceras* and *Amaltheus* (Figs. 4.2 and 4.3), pair components of the extended rule (the more evolute, the more depressed, the more coarsely ornamented, the less densely ornamented, the less frilled the sutures, and the less densely septate) are not equally correlated, as shown by the various values of the linear correlation coefficient. Since these pair components (e.g., involution/whorl compression, or suture frilling/whorl compression) can be explained by different causes, not only are these different contributions expected, but their detailed investigation can help decipher which explanations best fit observed patterns and consequently are the most likely explanations for Buckman's rules of covariation.

Very little is known about ontogenetic patterns of covariation (De Baets et al. 2015). Since intraspecific variation of ammonoids is frequently documented to be higher in juvenile stages, one can question whether Buckman's rules of covariation uphold with the same amplitude throughout ontogeny. For instance, some covarying patterns are revealed only late in ontogeny (Monnet et al. 2010: variation of ribbing density for *Acrochordiceras* drastically decreases through ontogeny and is weakly correlated early in ontogeny). Investigating the relative proportion of covarying components through growth may help us to find the best explanation for this covariation. Understanding covariation through growth patterns may also yield insights into shell morphogenesis (e.g., Urdy et al. 2010a, 2010b; Chirat et al. 2013), such as which parameters contribute in which proportion to covariation.

With regard to the phylogenetic imprint on covariation patterns, studies have clearly focused on Mesozoic planispirally coiled ammonoids. Intraspecific variation and covariation has only rarely been quantitatively studied in Paleozoic ammonoids (Nettleship and Mapes 1993; Kaplan 1999; Korn and Vöhringer 2004; Ebbighausen and Korn 2007; Korn and Klug 2007; De Baets et al. 2013). On the one hand, Kaplan (1999) found significant covariance only in clades within the Medlicottiaceae and the Clymeniina for Paleozoic ammonoids, while on the other hand, the lack of reports of Buckman's rules from Paleozoic ammonoids is related to the rarity of studies and certainly need not reflect the true absence of covariation. According to Swan and Saunders (1987), Buckman's first rule also applies to Paleozoic ammonoids, but they discussed the correlation mostly above the species level and not in the context of intraspecific variation. Several authors reported two or more discrete morphs in Carboniferous ammonoids (e.g., McCaleb and Furnish 1964; Furnish and Knapp 1966) ranging from a more openly coiled group with a more compressed whorl section and more prominent ribbing to a less openly coiled group with a less compressed and/or less prominent ornamentation. In most cases, intergradational forms between the two or three categories were found and larger intraspecific variation exists in juvenile than in adult forms (Davis et al. 1996), which might speak for a more continuous range of intraspecific variation and covariation (for alternative interpretations, see Davis et al. 1996; Stephen et al. 2002 and De Baets et al. 2015).

Concerning covariation patterns within heteromorphic species, few studies are available and their results vary. It has often been stated that heteromorph ammonoids have a higher degree of intraspecific variation than normally coiled ammonoids (e.g., Wiedmann 1969; Dietl 1978; Ropolo 1995; Kakabadze 2004 and references therein). The phenomenon has only rarely been quantified (Urreta and Riccardi 1988; Landman and Waage 1993b; Tsujino et al. 2003; De Baets et al. 2013; Knauss and Yacobucci 2014). This might be partially related to fragmentary preservation and problems of dealing with the unconventional shell morphology (e.g., classic Raup parameters cannot be used in some of these forms). Note that *Scaphites* is here not considered as a heteromorphic ammonoid as it only uncoils at the end of ontogeny, but see Landman et al. (2010) for a review of intraspecific variation in *Scaphites* conforming to the first rule of covariation. Nevertheless, Delanoy (1997) documented that *Heteroceras emerici* (Barremian) varies between two poles interconnected by intermediates: from heterocone (large turricone and no planispiral part of the shell before the shaft) to colchicone (small turricone preceding a substantial planispiral portion before the shaft). The first pole is associated with a rather robust ornamentation and the latter pole with a rather slender ornamentation, thus illustrating a covariation between strength of ornamentation and coiling. A similar variation is also known in *Imerites* (Barremian; Bert et al. 2011). In contrast, Ropolo (1995) described *Crioceratites shibaniae* (Hauterivian) with a very variable coiling grading continuously from the criocone morphology to the tripartite morphology (coil, shaft, and hook), but without changing the ornamentation, which is very stable from one morphotype to another. Interestingly, Urreta and Riccardi (1988) reported covariation of whorl shape and ribbing in several species of the heteromorph *Labeceras* (Albian) "*with the more depressed specimens having stronger and fewer ribs and incipient tubercles on the hook's inner margin*". Bert et al. (2013) reported similar covariation between whorl compression and ornamentation coarseness within *Gassendiceras* (Barremian). Finally, De Baets et al. (2013) described a continuous variation between more coarsely ribbed, more loosely coiled forms with a more compressed whorl section and less coarsely ribbed, but less coiled forms with a more depressed whorl section in the openly to advolutely coiled *Erbenoceras solitarium* (Devonian). De Baets et al. (2013) reported a negative correlation between coiling and ribbing, such that more loosely coiled variants had a more densely spaced, finer ribbing, as opposed to Mesozoic coiled ammonoids where the relationship is reversed (denser, finer ribbing for more coiled variants). Therefore, it is not possible in the present state of knowledge to generalize a single rule of covariation patterns of ammonoids. They can partially follow some of Buckman's rules or completely diverge from them.

Apparently, Buckman's rules of covariation are valid in most ammonoid groups with regularly coiled shells throughout their long evolutionary history and as such should result from inherent constructional properties and/or common selection pressures. It is worth noting that even with sufficiently large collections, not all species follow these covariation rules, even if they coexisted (e.g., Brayard et al. 2013; Monnet and Bucher 2005; De Baets et al. 2015). The phylogenetic imprint of the strength of Buckman's rules of covariation in ammonoids thus remains to be investigated (e.g., do phylogenetically closely related species share similar proportions of covarying characters).

Another question in evolutionary biology pertains to whether intraspecific variation can lead to interspecific differentiation (West-Eberhard 1989, 2003, 2005), because anatomical variations within populations increase the range of ecologically relevant variation that can fuel speciation (Schluter 2000, 2001; Butler et al. 2007; Nosil 2012), especially by means of heterochrony (Spicer et al. 2011; Tills et al. 2011). In this context, Yacobucci (2004a) described a Buckman-like pattern of covariation within a Late Cretaceous clade of acanthoceratid ammonites. Entire genera could be categorized as compressed, involute, and lightly ornamented (e.g., *Metoicoceras*, *Neocardioceras*) while other, closely related genera were depressed, involute, and more heavily ornamented (e.g., *Acanthoceras*, *Plesiacanthoceras*). Similarly, within a genus, different species showed either a more compressed morph (e.g., *Metoicoceras praecox*) or a more depressed morph (e.g., *Metoicoceras geslinianum*), along with the corresponding coiling and ornamentation. Therefore, Buckman's rules of covariation may uphold (compare Swan and Saunders 1987; Yacobucci 2004a; Moulton et al. 2015), but additional datasets and studies are required to better understand this phenomenon. Particularly, such studies may help to determine whether patterns of covariation are constrained by phylogenetic heritage.

4.6 Conclusions

Ammonoids have long been known to show a large intraspecific variation of their shell morphology. This phenomenon is often, but not systematically, considerably structured and characterized by a typical covariation of characters: species can be characterized by a continuous unimodal intergradation of morphotypes following the overall rule 'the more evolute, the more depressed, the more coarsely ornamented, and the less frilled the sutures'. These covariation patterns have been labeled as Buckman's rules of covariation. Although this covariation has been abundantly documented in ammonoids of almost all geological periods and taxonomic groups, coexisting species still can have different intraspecific patterns (reviewed in De Baets et al. 2014). Competitive, but not mutually exclusive, hypotheses explain this pattern (especially adaptive vs. constructional constraints). As noted by Bert (2013), it appears that Buckman's rules of covariation are not the only covariation patterns of intraspecific variation of ammonoids, although these rules may be more common. Nevertheless, Buckman's rules of covariation and ammonoid morphogenesis are not yet fully understood (Yacobucci 2004a, 2004b). Documenting the existence of Buckman-like covariation patterns among various related groups of ammonoid species and genera will help us better understand the underlying cause(s) of these correlations. Therefore, construction of datasets (especially for ornamentation and suture) and their quantitative analyses is the next important step in order to investigate and test the various still unresolved questions about covariation rules of the ammonoid shell.

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Chapter 5
Evolutionary Patterns of Ammonoids: Phenotypic Trends, Convergence, and Parallel Evolution

Claude Monnet, Christian Klug and Kenneth De Baets

5.1 Introduction

Ammonoids are characterized by high evolutionary rates. Because taxa evolved and became extinct rapidly, ammonoids are extremely useful tools for dating strata. For instance, due to their high turnover rates, ammonoid species can often enable the construction of biozones spanning less than 100,000 years duration (see e.g., House 1985; Monnet et al. 2015a). In addition to this outstanding time marker property, ammonoids also can provide significant insights into evolutionary biology. They have repeatedly been proven valuable study objects to develop or test evolutionary hypotheses and to investigate patterns of biodiversity (e.g., Schindewolf 1933, 1940, 1950; Kennedy 1977, 1989; Kennedy and Wright 1985; Landman 1988; Korn 1995, 2003; House 1996; Saunders et al. 1999; Guex 2001, 2003, 2006; Korn and Klug 2003; Gerber et al. 2008; Neige et al. 2009; Brayard et al. 2009; Monnet et al. 2011; De Baets et al. 2012; Korn et al. 2013a). Seilacher (1988, p. 67) correctly summarized this fact in his famous phrase stating that ammonoids "*are for paleontologists what* Drosophila *is in genetics*". This is the result of exceptional properties such as their high abundance, widespread occurrence, high evolutionary rates, high taxonomic diversity and morphological disparity, usually well-known stratigraphic framework (e.g., Stanley 1979; Sepkoski 1998; Foote and Sepkoski 1999), and their

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C. Monnet (✉)
UMR CNRS 8217 Géosystèmes, UFR des Sciences de la Terre (SN5), Université de Lille,
Avenue Paul Langevin, 59655 Villeneuve d'Ascq cedex, France
e-mail: claude.monnet@univ-lille1.fr

C. Klug
Paläontologisches Institut und Museum, Universität Zürich, Karl-Schmid Strasse 4, 8006 Zürich,
Switzerland
e-mail: chklug@pim.uzh.ch

K. De Baets
GeoZentrum Nordbayern, Fachgruppe PaläoUmwelt, Friedrich-Alexander-Universität Erlangen-Nürnberg, Loewenichstraße 28, 91054 Erlangen, Germany
e-mail: kenneth.debaets@fau.de

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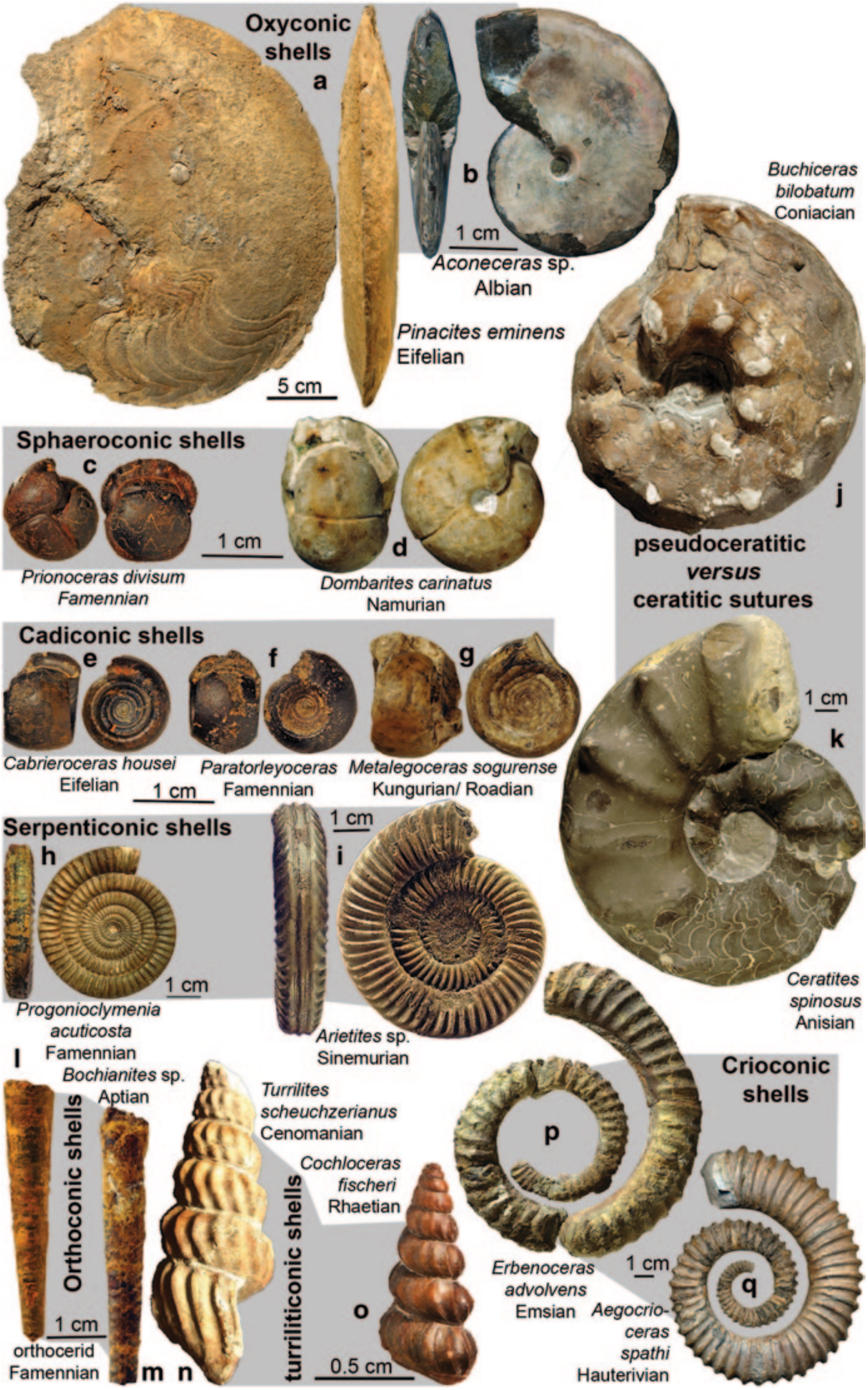

Fig. 5.1 Some cases of convergence in shell form and suture line course. **a** *Pinacites eminens*, PIMUZ 31078, Eifelian, Jebel El Mrakib, Morocco. **b** *Aconeceras* sp., Albian, Mahajanga,

accretionary mode of shell growth that recorded the complete development (ontogeny) of the animals from the embryonic and juvenile stages to adulthood. In the fossil record, ammonoids are well-known to display major evolutionary patterns in shell morphology. They often evolved homeomorphic lineages and experienced numerous long-term (often several million years) morphological evolutionary trends, many of which were iterative or even parallel over time. This review will focus on these two points.

Homeomorphy has been recognized frequently among ammonoids (e.g., Schindewolf 1933, 1940; Haas 1942; Reyment 1955; Kennedy and Cobban 1976; Kennedy 1977; Wright and Kennedy 1979; Bayer and McGhee 1984; Kennedy and Wright 1985; Hewitt 1989; Page 1996; Bujtor 2010). Homeomorphy can be defined as the result of the evolution of close morphological similarities between species that are not closely related, or as the recurrence of phenotypic similarity within unrelated clades that evolved independently (Neville 1962; Lauder 1981; Wake 1991; Sanderson and Hufford 1996; Hall 2007; Futuyma 2009; McGhee 2011). It is generally thought to result from adaptation to similar modes of life or similar functions in different organisms or parts of organisms (but not always; see e.g., Reyment 1955). Homeomorphy can be the outcome of convergent evolution (McGhee 2011) when animals exploit similar habitats/ecological niches in similar ways and thus likely arrive at morphologically similar solutions independently. The wings of birds, bats and pterosaurs are a classic example of homeomorphy, having evolved independently in three separate lineages from joint ancestors lacking this character as a means of achieving the functional requirements of flight. In order to determine the common origin, homology of the homeomorphic organs has to be examined.

Among animals with an external shell, convergent evolution leading to homeomorphic taxa has always been common and thus has been abundantly documented (e.g., Rudwick 1965; Horne 2005). For ammonoids, which are limited to a tubular external shell with finite limits of variation in coiling, ornament and suture imposed by constructional constraints, evolutionary convergence is widespread (Fig. 5.1). In the most extreme cases, Mesozoic forms developed "atavistic" shell shapes reminiscent of Paleozoic ammonoids. Some examples (out of countless) are the shell shapes or suture lines of Triassic Arcestina resembling Paleozoic Goniatitina

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Madagascar. **c** *Prionoceras lamellosum*, PIMUZ 31072, middle Famennian, Madene El Mrakib, Morocco. **d** *Dombarites carinatus*, PIMUZ 31075, Namurian, Aktubinsk, Kazakhstan. **e** *Cabrieroceras housei*, PIMUZ 31076, late Eifelian, Oued Chebbi, Morocco. **f** *Paratorelyoceras globosum*, PIMUZ 31077, early Famennian, Oued Chebbi, Morocco. **g** *Metalegoceras sogurense*, PIMUZ 31084, Kungurian/Roadian, Aktubinsk, Kazakhstan. **h** *Progonioclymenia acuticosta*, Famennian, South Urals, Orenburgskaya Obl., Russia. **i** *Arietites* sp., Sinemurian, Mögglingen, Germany (Staatliches Museum für Naturkunde Stuttgart). **j** *Buchiceras bilobatum*, Coniacian, Peru. **k** *Ceratites spinosus*, Anisian, Garnberg (Muschelkalkmuseum, Ingelfingen, col. H. Hagdorn). **l** Orthocerida gen. et sp. indet., PIMUZ 31074, Late Famennian, Lambidia, Morocco. **m** *Bochianites* sp., PIMUZ 31073, Albian, Anges, France. **n** *Turrilites scheuchzerianus*, Cenomanian, Pas de Calais, France (col. H. Chatelier, France). **o** *Cochloceras fischeri*, Rhaetian, Sandling, Austria (col. H. Keupp, Berlin, MAm-1131). **p** *Erbenoceras advolvens*, GPIT 1849–2002, early Emsian, Gart El Anz, Morocco. **q** *Aegocrioceras spathi*, Hauterivian, Resse, Germany. All specimens at the Palaeontological Institute and Museum of the University of Zurich if not mentioned otherwise. Images: i and p: W. Gerber (Tübingen), n: H. Chatelier (France), o: H. Keupp (Berlin), q: R. Hoffmann (Bochum)

(Page 1996), or members of the Cretaceous Flickiidae with a simplified suture line and shell form similar to some Devonian Anarcestina (Wright and Kennedy 1979). These morphological similarities are no evidence for phylogenetic relationships but of convergent evolution. In some cases, ammonoids have developed very similar morphologies in most aspects generally accepted to be of diagnostic, taxonomic value that can lead to erroneous phylogenetic inferences or classification when not taking into account the stratigraphic gap separating these taxa. The situation is even more precarious when these forms co-occur or follow each other closely in time and where homeomorphic characters might be used to infer phylogenetic relationships.

Among ammonoids, examples of long-term morphological evolutionary trends are numerous (e.g., Haas 1942; Guex 1973, 1981, 1992, 2001, 2006; Kennedy 1977; Thierry 1982; Bayer and McGhee 1984, 1985; Kennedy and Wright 1985; Dommergues et al. 1989; Dommergues 1990; Neige et al. 1997; Korn and Klug 2003; Klug et al. 2005; Monnet et al. 2011, 2013; De Baets et al. 2012). These long-term phenotypic evolutionary trends are persistent and directed changes of morphological characters through significant periods of geological time (often several million years) within a monophyletic group (e.g., Gould 1988, 1990). Furthermore, these repeated trends can be independent, but often are organized in convergent, iterative and parallel patterns over time (Haas 1942; Guex 2001, 2003). Last but not least, all these patterns can contribute in a major way to the understanding of homeomorphic characters in ammonoid shells.

Parallel evolution (e.g., Serb and Eernisse 2008) can be defined as the independent evolution of similar biological traits in at least two different lineages having similar phenotypic trajectories driven by common (developmental) constraints. Parallel evolution is often confused with convergence (Webb 1994) since both can result in taxa with highly similar characters, but the two concepts remain distinct (Serb and Eernisse 2008) even if there may be a continuum between parallelism and convergence (Gould 2002; Donoghue 2005). On the one hand, superficially similar features are formed by different developmental pathways in convergence. On the other hand, parallel evolution is thought to involve similar developmental modifications that evolved independently (often in closely related organisms). Parallel evolution is a moderately common phenomenon in extinct and extant lineages (e.g., Averoff and Patel 1997) and often assumed to be the product of adaptation by means of natural selection. The literature on ammonoid evolution contains several references to parallel evolution or "parallelism" (parallelism is sometimes used in a slightly different meaning: Monnet et al. 2011), but many of these studies are spurious because they do not account for dimorphism and intraspecific variability and they rely only on qualitative description (Kennedy 1977). However, there are now convincing examples based on data for which their taxonomy, stratigraphy and phylogeny have been revised by quantitative methods (e.g., Meister 1993; Monnet et al. 2011).

Homeomorphic character states can evolve convergently or in parallel. They are major patterns of phenotypic evolution. Such examples of homoplasy (Lankester 1870) present opportunities to discover the foundations of morphological traits and determine processes and mechanisms of evolution (Wake et al. 2011). Furthermore, understanding what is driving the high degree of homeomorphy within ammonoids is of great importance for taxonomy (e.g., Hewitt 1989; Webb 1994) and phylogeny as it might result in a high degree of homoplasy (Wake 1991; Yacobucci 2012). Understanding the long-term morphological trends is also of prime importance as they are at least partially responsible for the high degree of homeomorphism among ammonoids and may provide significant insights into evolutionary constraints operating on the ammonoid shell. However, the processes behind these common evolutionary patterns are still not well understood. As noted by Kennedy and Wright (1985, p. 142), the evolution of Cretaceous ammonoids shows "*repeated patterns that reflect the selection of features whose adaptive significance in most cases escapes the observer*". For ammonoids, this situation may partly arise from two major sources of noise. First, the phylogeny of ammonoids at the species rank is only rarely reconstructed by means of state-of-the-art, recent phylogenetic methods (Neige et al. 2009; Yacobucci 2012) and consequently prevent the valuable use of ammonoids in evolutionary studies despite having a huge potential. Second, studies on ammonoid evolution are very often carried out using qualitative/descriptive approaches without real quantification and statistical testing. However, these phenotypic evolutionary patterns can only be confidently assessed by novel quantitative and statistical methods. The major aim of this chapter is to review some of these methods and their application to ammonoids, which reflect the potential of ammonoids for providing insights into evolutionary patterns and processes.

5.2 Macroevolutionary Trends

5.2.1 Definition

> *One of the crowning achievements of paleontology, and of surpassing importance in the development of evolutionary theory, has been the discovery of innumerable graded morphological series of fossils showing progressive change as we ascend the geological scale of time. Many of the evolutionary modifications follow simple patterns, or trends, which recur again and again in related, or even unrelated stocks.* (Newell 1949, p. 103)

One of the intriguing outcomes of biological evolution (as described by Newell above) is the frequent occurrence of long-term evolutionary trends. These patterns are persistent and directed changes of morphological characters through significant periods of geological time within a monophyletic group (Fig. 5.2; Simpson 1953; Gould 1988, 1990; McKinney 1990; McShea 1994; McNamara 2006). The fossil record displays numerous examples of lineages persistently evolving during several million years toward greater "*complexity*" and/or toward larger body size (Cope 1887, 1896; Depéret 1909; Matthew 1926; Newell 1949; Simpson 1953; Rensch 1959; Stanley 1973; Hallam 1975; Kennedy and Wright 1985; Fisher 1986; MacFadden 1986, 1992, 2005; Gould 1988, 1990, 1996, 1997; Jablonski 1987, 1997; McShea 1991, 1994, 1996; Boyajian and Lutz 1992; Valentine et al. 1994; Kaiser and Boucot 1996; Wagner 1996; Trammer and Kaim 1997; Alroy 1998, 2000;

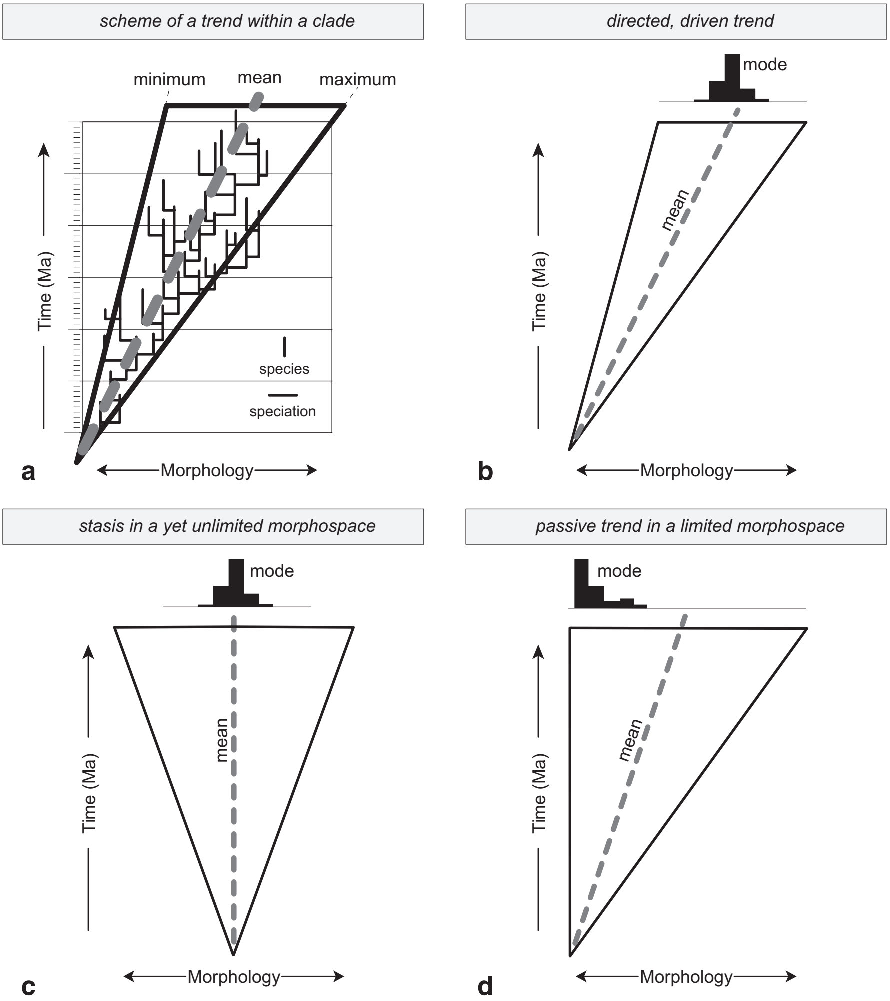

Fig. 5.2 Schemes of long-term phenotypic macroevolutionary trends of a lineage through time (modified after McShea 1994). **a** The vagaries of the morphology (origination and extinction of species) of a clade through time are mainly characterized by its mean and range in its phenotypic space. **b** A long-term trend is characterized by a protracted shift of the entire range and mean morphology of the studied group. **c** Absence of changes in this morphological mean illustrates stasis. **d** A seemingly driven trend may occur in a phenotypic space limited by physical/constructional boundaries, but in this case the most abundant forms still remain similar to the root of the clade (compare with b)

Saunders et al. 1999; Adami et al. 2000; Wang 2001; Gould and MacFadden 2004; Guex 2006; Hunt and Roy 2006; Adamowicz et al. 2008; Novack-Gottshall and Lanier 2008; McGhee 2011). Such trends occur in almost all metazoan groups and probably reflect a pervasive pattern of evolution. This sustained directionality of morphological evolution is one of the oldest and most important aspects of evolution, and is therefore an important research program in paleobiology (McNamara 1990). The occurrence, generality and causes of long-term evolutionary trends have been intensively studied and debated, and have significant implications for an overall understanding of patterns and processes of evolution.

5.2.2 *Phenotypic Trends in Ammonoid Shell Characters*

Ammonoids are characterized by a septate, univalved, usually coiled shell, basically conic, with or without an external sculptured ornamentation. This shell can be described by multiple qualitative (for a list of ammonoid characters, see e.g., Arkell et al. 1957; Dommergues et al. 2002; Korn 2010) and quantitative characters, some of which will be illustrated here (for their definition, see Monnet et al. 2011 and Klug et al. 2015b). Among quantified ammonoid shell characters, there are four that commonly display long-term evolutionary trends through time: adult body size, degree of involution (coiling), strength (or spacing) of ornamentation, and indentation of suture line (Kennedy 1977; Kennedy and Wright 1985; Dommergues 1990; Saunders 1995; Saunders and Work 1996; Saunders et al. 1999; Guex 2001, 2006; Korn and Klug 2003; Klug and Korn 2004; Monnet et al. 2011 and references therein). The general tendency for body size to increase during the evolution of a group of animals is known as Cope's rule (Rensch 1948) or as the law of phyletic increase in size (Depéret 1909). With regard to ammonoids, several authors have illustrated and discussed examples of increasing shell size (Stanley 1973; Hallam 1975; Thierry 1982; Kennedy and Wright 1985; Guex 2003; Dommergues et al. 2002; Monnet et al. 2011, 2012; De Baets et al. 2012). For instance, Hallam (1975) described Cope's rule in some Jurassic ammonoid families but he focused only on maximum shell size, whereas Dommergues et al. (2002) documented no preponderant trends (but without phylogenetic data) in an almost exhaustive compendium (more than 1000 species) of Early Jurassic ammonoids. Furthermore, trends of decreasing shell size might also occur (Korn 1995b).

Another repeatedly documented evolutionary trend within ammonoids is that from an openly umbilicate ancestral group (evolute) toward a descendant group with a smaller or closed umbilicus (involute; Fig. 5.3a). Such trends have been documented already by Hyatt (1889) for Liassic arietitids. This pattern has even been documented in the earliest history of ammonoids: during the Early Devonian, ammonoids showed a progressive coiling from straight orthocerids via curved bactritoids to coiled ammonoids (Erben 1966; Wiedmann 1966; Klug 2001; Klug and Korn 2004; De Baets et al. 2009, 2012, 2013b). This increasing shell involution (protracted closure of the umbilicus by increasing overlap of the whorls) is also the most commonly described long-term morphological trend among more derived ammonoids (e.g., Hyatt 1889; Schindewolf 1940; Haas 1942; Guex 1973, 1981, 1992; Bayer and McGhee 1984, 1985; Dommergues 1990; De Baets et al. 2009, 2012; Klug et al. 2010, 2015a; Monnet et al. 2010, 2012, 2013; see also Monnet et al. 2011 and references therein). Note that uncoiling of ammonoids has also been documented repeatedly (e.g., Wiedmann 1969; Cecca 1997).

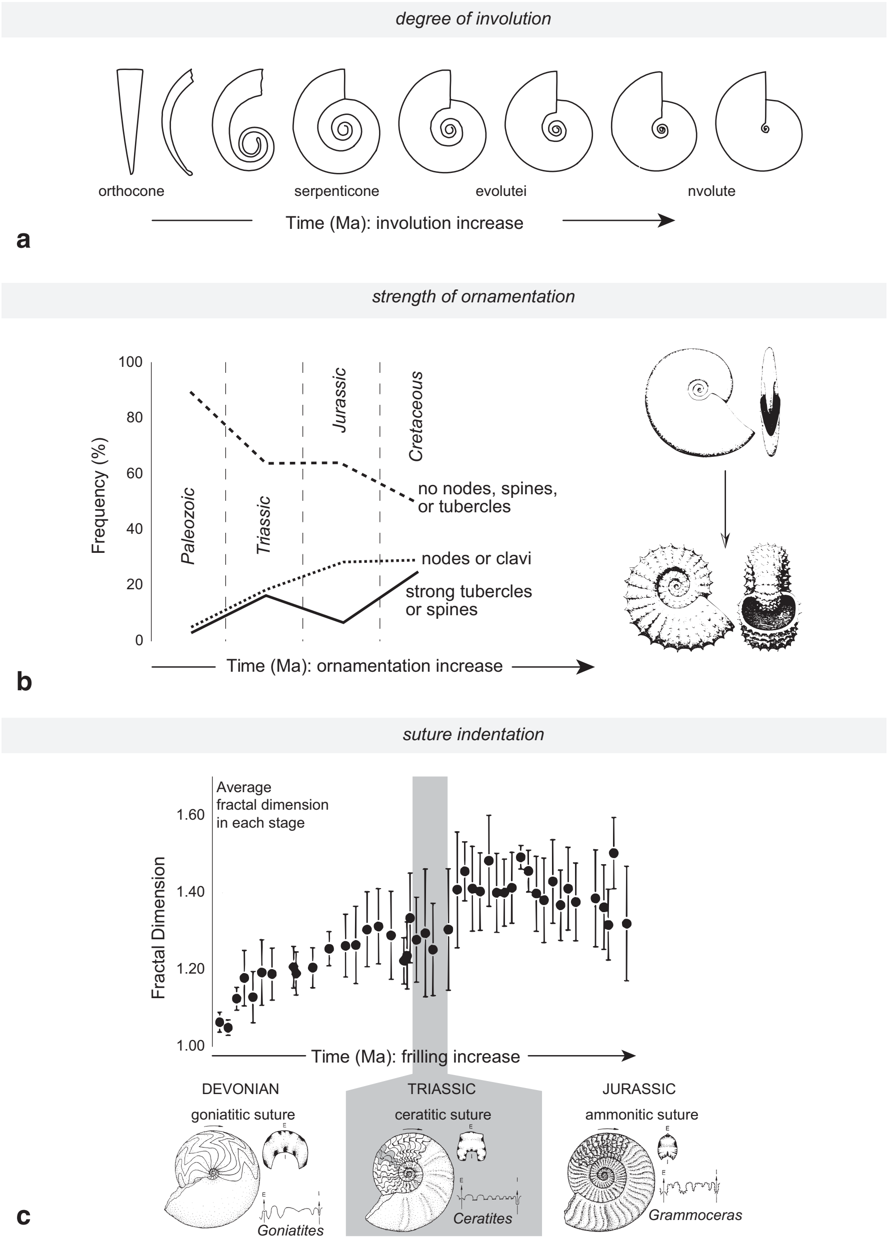

Fig. 5.3 Global long-term evolutionary trends of the ammonoid conch. **a** Scheme of the initial trend in the degree of involution within Devonian early ammonoids (modified after Wiedmann 1966). **b** Scheme of the trend toward more ornamented shells (modified after Ward 1981). **c** Scheme of the trend toward greater complexity of the suture line (modified after Boyajian and Lutz 1992)

With regard to shell ornamentation, various authors (Ward 1981, 1996; Vermeij 1987; Westerman 1996) showed that the whole ammonoid clade reveals a trend toward more ornamented forms (Fig. 5.3b). Although the authors interpreted this pattern as a response to the evolution of increasing numbers of shell crushing predators, the qualitative data of Ward (1981) suggest a passive trend constrained by a left-wall effect. For instance, convergent evolution of spines in marine mollusk shells have classically been interpreted as having repeatedly evolved as a defense in response to shell-crushing predators (e.g., Vermeij 1987; Kröger 2005; Ifrim 2013), but other interpretations are also available (see Ifrim 2013). Recent studies (Moulton et al. 2012, 2015; Chirat et al. 2013) have demonstrated that a large diversity of ornamentation and spine structures can be accounted for through small variations in control parameters of the mechanical interaction between the secreting mantle edge and the calcified shell edge, which suggests that convergent evolution of spines can also be understood through a generic morphogenetic process without selective pressures. By contrast, simplification of shell ornament through the evolution of a clade was also frequently observed at a lower taxonomic scale (e.g., Bayer and McGhee 1984, 1985; Kenney and Wright 1985).

Finally, ammonoid evolution is also characterized by an overall increase in the intensity of indentation of adult sutures (= frilling or "complexity") (Fig. 5.3c): from agoniatitic (smooth lobes and saddles), via goniatitic (smooth lobes, pointed saddles), to ceratitic (smooth saddles, denticulate lobes), and to ammonitic (frilled lobes and saddles). This increasing suture indentation has been quantified by fractal or Fourier analyses by several authors (e.g., García-Ruiz et al. 1990; Boyajian and Lutz 1992; Saunders and Work 1996, 1997; Saunders et al. 1999; Pérez-Claros et al. 2002, 2007). For instance, Saunders et al. (1999) documented a bias in the direction of speciation toward more indented sutures (within 475 ancestor/descendant pairs; descendants were more than twice as likely to be more complex than their ancestors). They also noted that mass extinctions acted in opposition to this long-term trend by eliminating more indented forms and thus resetting the trend (which might be linked with the elimination of extreme morphologies like oxycones and cadicones, which tend to have more sutural elements). Interestingly, this role of lineage sorting by means of increased extinction rates of particular morphologies has also been emphasized either as resetting trends (Guex 2001, 2006) or as strengthening trends (De Baets et al. 2012). At lower taxonomic ranks and shorter time intervals, evolutionary trends in suture indentation are also common and include not only patterns of increasing indentation, but also decreasing indentation and smoothing of sutures (see e.g., Kennedy and Wright 1985; Checa 1987). In addition, this statement holds for every character (size, ornamentation, coiling, and suture): both increasing and decreasing trends have been documented (see review of Kennedy and Wright 1985).

Interestingly, the morphological trends described above often happened simultaneously. This lead to a particular evolutionary pattern characterized by lineages originating with small, ornamented, evolute and depressed forms, which more or less progressively changed and ended with large, smooth, involute and compressed shells (Fig. 5.4a; e.g., Silberling and Nichols 1980; Bayer and McGhee 1984,

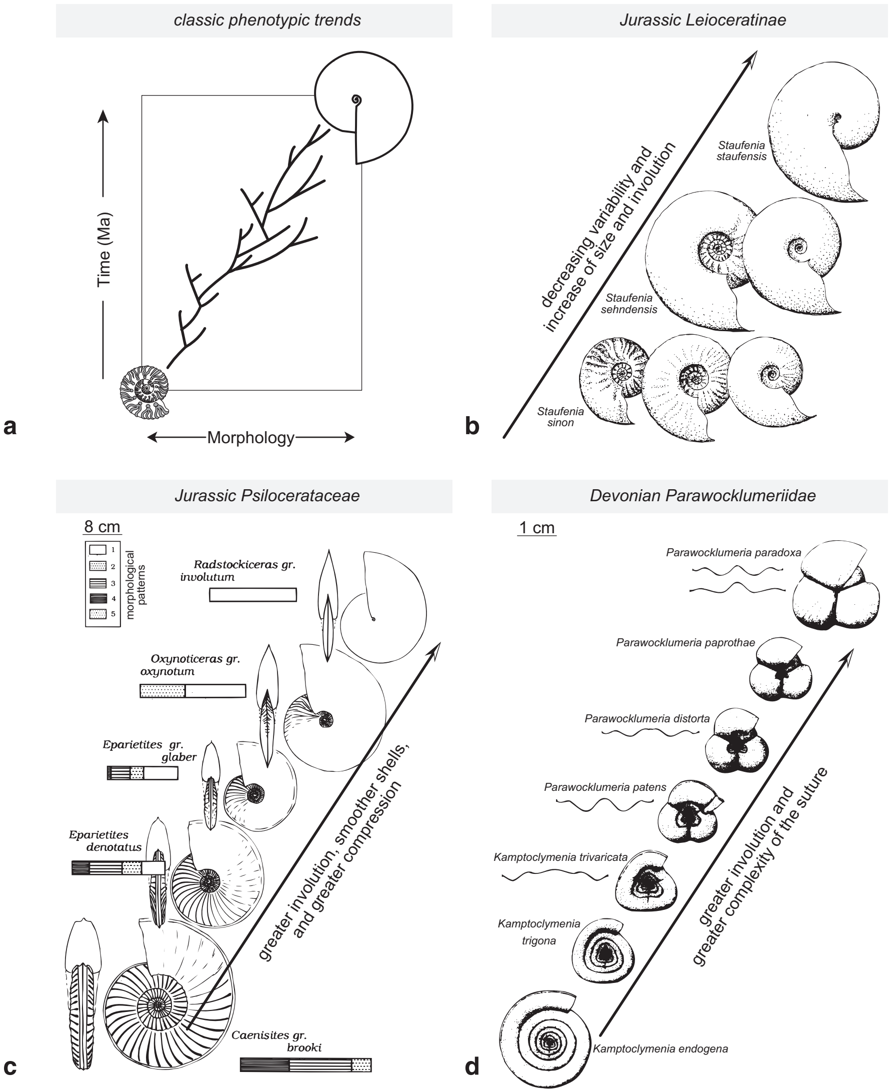

Fig. 5.4 Examples of long-term phenotypic evolutionary trends of the ammonoid shell within lineages. **a** Scheme of the most frequently described ammonoid trend: it starts with more evolute, more depressed, and more ornamented shells and evolves toward more involute, more compressed, and smoother shells. **b** Morphological trend of *Staufenia* during the Jurassic of Germany (modified after Bayer and McGhee 1985). **c** Peramorphic trend of Psiloceratacea (modified after Dommergues 1990). **d** Devonian transition from *Kamptoclymenia* to *Parawocklumeria* in the Rhenish Massif (modified after Korn 1995a)

1985; Klinger and Kennedy 1984; Guex 2001, 2003, 2006; Monnet et al. 2012). Figure 5.4b–d reports examples of such phenotypic trends. These trends are also recognized to occur successively several times within a clade leading to a repetitive pattern of similar trends ("*evolutionary cycles*" of Haas 1942). The frequency, combination and proportion of these morphological trends within the evolution of ammonoids remain however to be investigated. Moreover, Kennedy and Wright (1985) recognized that Late Cretaceous ammonoids experienced almost all combinations of trends and it is not yet clear if one pattern predominates or not.

5.3 Univariate Phenotypic Trends in Ammonoids

5.3.1 Classic Descriptive Stratophenetics

Evolutionary changes of the ammonoid shell through time are classically investigated by means of a stratophenetic approach (Gingerich 1979, 1993; Raup and Crick 1981, 1982; Bookstein 1988; Roopnarine et al. 1999) regardless of its phylogenetic interpretation. It usually includes a graphic illustration of the morphological range of a character through successive time slices such as beds or biozones (e.g., Raup and Crick 1981; Thierry 1982; Bayer and McGhee 1984; Kennedy and Wright 1985; Dommergues et al. 1989; Dommergues 1990; Klug et al. 2005; Monnet et al. 2011, 2012; De Baets et al. 2012). Patterns of phenotypic evolution of quantitative characters are usually examined separately by means of bivariate plots depicting their quantile distribution (or descriptive statistics such as mean, minimum, maximum, median and/or quartiles). These plots enable an empirical evaluation of the presence or absence of directed evolutionary changes (trends) for each character.

A recent example of morphological trends of the ammonoid shell investigated by a classic stratophenetic approach has been published by Monnet et al. (2012). Therein, details of the long-term phenotypic evolution of Acrochordiceratidae during the Anisian (Middle Triassic) were analyzed. Morphological changes of the acrochordiceratid shell were quantified based on large collections (more than 700 specimens) from Nevada (USA). This study showed (Fig. 5.5a) that the monophyletic clade of Acrochordiceratidae (i) underwent a significant increase (possibly with several steps) of its adult shell diameter (i.e. Cope's rule), (ii) showed an evolute to involute evolutionary trend (i.e. an increase of the degree of shell involution), and (iii) experienced a qualitative increase of indentation of its suture line. The protracted changes in shell morphology of the Acrochordiceratidae are robust and non-random (Monnet et al. 2012). They can be interpreted as being constrained by the persistent, common selection pressure on this mostly anagenetic lineage with relatively moderate evolutionary rates during an ecologically stable period (Fig. 5.5c). As discussed by Monnet et al. (2011), such trends of morphological evolution in the ammonoid shell may suggest that their morphology is mainly controlled by adaptive and constructional constraints. Interestingly, not all quantified characters showed trends such as whorl shape compression and ribbing density (Fig. 5.5b).

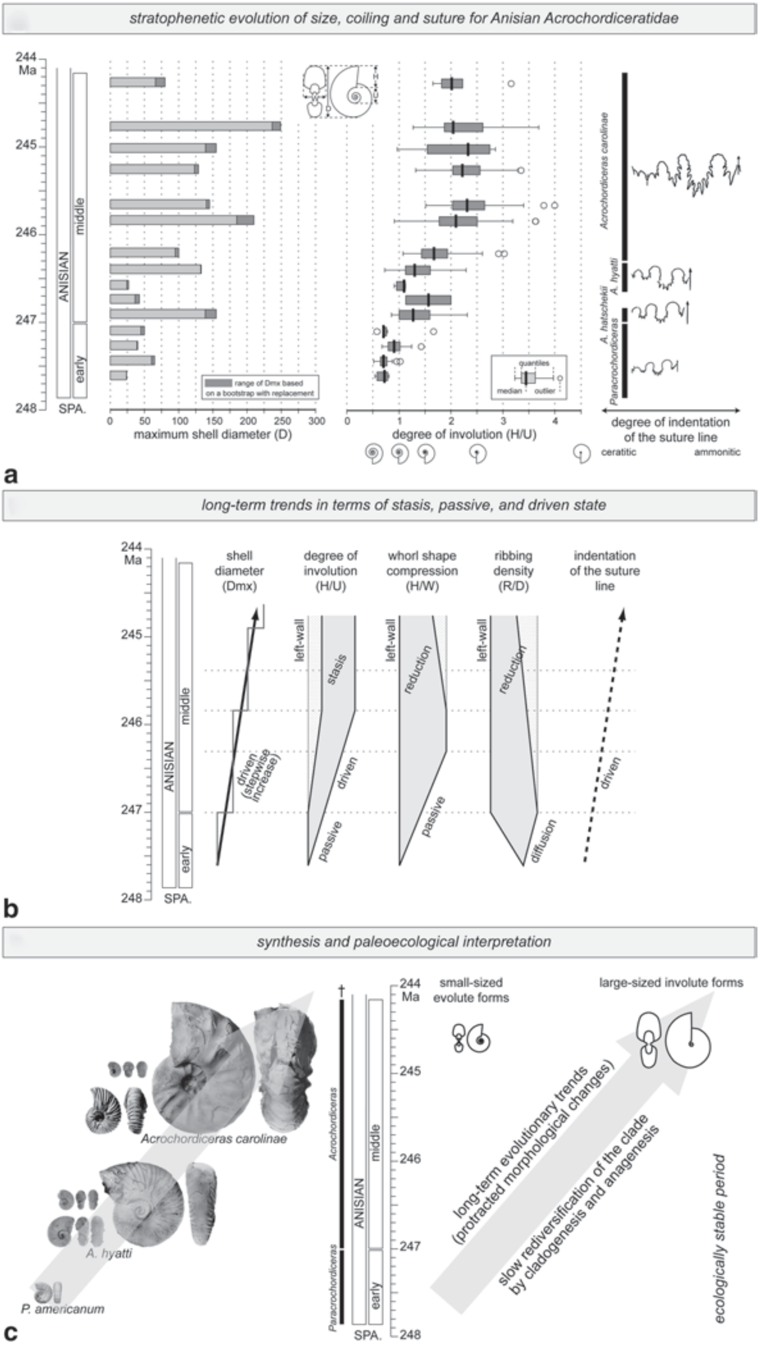

Fig. 5.5 Evolution of maximum shell diameter, degree of involution and suture shape for Acrochordiceratidae during the Anisian (Middle Triassic) (modified after Monnet et al. 2012). **a** Stratophenetic patterns of some conch characters showing a trend of their mean. **b** The corresponding

5.3.2 Passive and Driven Trends and Lineage Sorting

The ammonoid literature is rich in descriptions of phenotypic trends through time (references in 5.3.1). However, a crucial question is whether these evolutionary trajectories are robust and not just random fluctuations in phenotypic space. Indeed, the classic stratophenetic approach is a subjective graphic approach, which impedes distinguishing random fluctuations from persistent trends (e.g., Roopnarine et al. 1999; Hunt 2006). The method has been criticized because it lacks a means of evaluating the robustness of the documented pattern. This is not always straightforward in fossil organisms due to, e.g., low sample size combined with large variation in fossil groups (De Baets et al. 2015). The absence of quantitative methods adapted to the study of the incomplete and time-averaged fossil record lead in the past to biased descriptive studies. In addition, Gould (1988, 1990) pointed out two major common misinterpretations of stratophenetic trends: (i) biases may result from the systematic search of gradual evolution between species by arbitrary picking out only part of a clade and ignoring the entire complex phylogenetic tree ("*anagenesis faith*"); (ii) other biases may arise from a focus on extreme values (maximum) instead of accounting for the entire variance. Furthermore, Raup et al. (1973) showed that trends can be simulated even if both direction and frequency of speciation and extinction are allowed to vary randomly. To overcome such problems, several approaches have been developed and/or used during the past decades for evaluating trends, especially for stratophenetic data and with or without a phylogenetic framework.

One major advance in the understanding of trends came with the recognition of the "*left-wall effect*" (Stanley 1973; Gould 1988; McShea 1994). Indeed, many patterns could arise via (random) fluctuations from a fixed boundary, as when a clade originates near a minimum viable morphology (Fig. 5.1d); in this case, the mean of the studied lineage can increase because change in one direction is blocked by a boundary in some region of the morphological space. For instance, the coiling of ammonoids is bounded on one side by "*straight conch*" and on the other side by "*fully occluded umbilicus*". Such boundary-limited trends were referred to as "*passive*" in opposition to "*active*" trends, which display a shift of the entire range of the morphology (McShea 1994; see also discussion of Alroy 2000). Note that "*passive*" is not identical with "*random*", because a passive trend can still result from different processes acting independently and heterogeneously (McShea 1994). Since such passive trends arise owing to the topography of the adaptive landscape (Kaplan 2008; Pigliucci 2008), it is useful to identify them in order to avoid overinterpretation (usually adaptive) of the patterns and help discriminate the limiting effects of structural constraints from natural selection (Gould 1988).

Long-term phenotypic changes can arise by means of a wide range of mechanisms, and different dynamics can operate simultaneously, in opposition or in concert, at different levels (Stanley 1973; Vrba and Gould 1986; Gould 1988, 2002;

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patterns in terms of long-term trends (stasis, left-wall effect, directed shift) showing that some characters have very different evolutionary patterns. **c** Interpretation of the typical documented pattern (illustrated ammonoids are at the same scale)

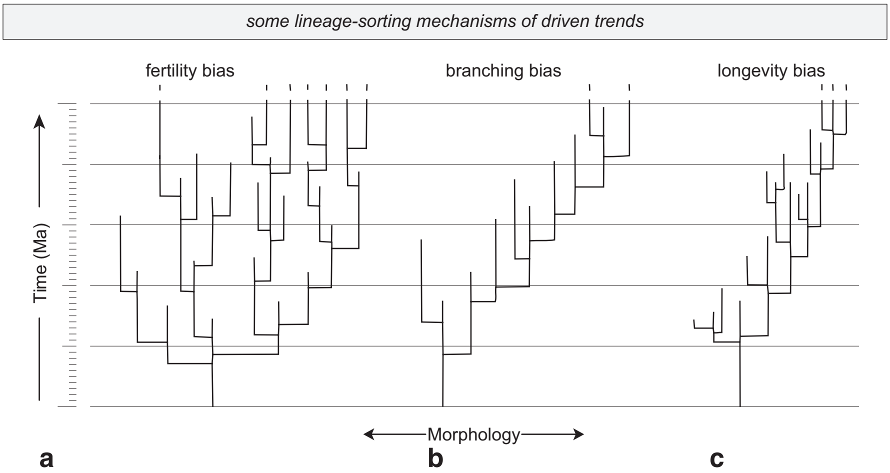

Fig. 5.6 Some lineage-sorting mechanisms leading to phenotypic patterns of among-species, driven trends (modified after Gould 1988). **a** The trend results from a higher speciation rate of a part of the morphospace of the studied lineage. **b** The trend is triggered by a preferred direction of speciation. **c** The trend is induced by longer persistence of species from a particular part of the morphospace

McNamara 1990; McShea 1994; Foote and Miller 2007). For instance, a trend may be underlain by transformation of its constituent species, by preferential origination of new species, by random speciation followed by differential survival or proliferation in the direction of the trend, or by any combination of these very different processes (Stanley 1973; Gould 1988; Jablonski 2007). For example, Gould (1988) showed that one process or the combination of several processes might cause a driven process (Fig. 5.6): (i) a bias in the direction of speciation ("*branching bias*": is the number of speciation events equally distributed among decreasing and increasing phenotypic changes?); (ii) a bias in the magnitude of speciation ("*fertility bias*": are speciation rates similar throughout the morphospace?); (iii) a bias in the amount of extinction ("*longevity bias*": do species located in a particular part of the morphospace survive longer?).

Evolutionary trends can also result from mechanisms acting at different hierarchical levels, leading to the concept of "*lineage sorting*" (Vrba and Gould 1986): (i) trends can be driven by organism-level traits (within-lineage sorting) such as body size or habitat preferences that can also be translated into patterns of among-species evolution (Vrba 1980, 1983, 1984); or (ii) trends can be driven by emergent properties at the species level (among-lineage sorting) such as geographic range, speciation rates, or longevity (Stanley 1979; Gould 2002). From a methodological viewpoint, several authors discussed several tests to discriminate passive and driven trends, globally for a clade (Gould 1988; McShea 1994; Wagner 1996; Wang 2001, 2005), mainly by focusing on the biases listed above. Alroy (2000) also proposed additional approaches to analyze phenotypic macroevolutionary trends. However, none of these tests have been applied to ammonoids.

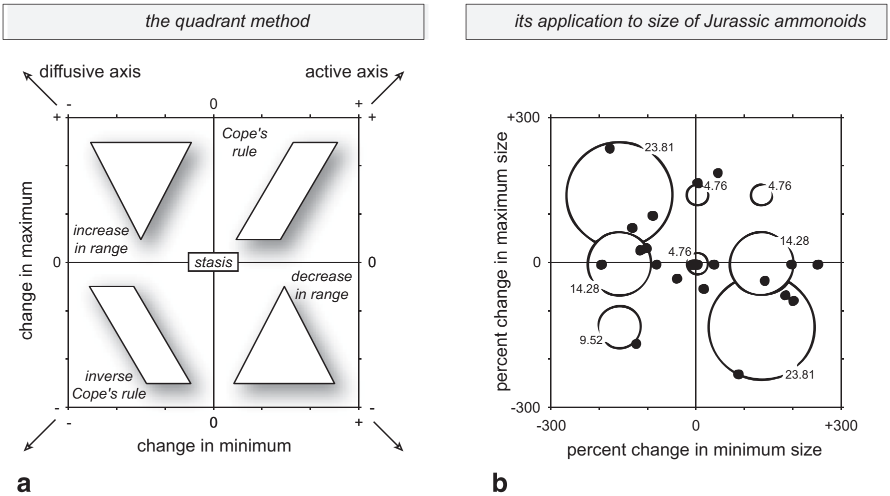

Fig. 5.7 The quadrant method and its application to quantify the relative proportion of passive and driven trends within a linage. **a** The quadrant method of Jablonski (1997) reports phenotypic changes between pairs of successive stratigraphic intervals or phylogenetic data in terms of changes in variance. The top right quadrant corresponds to an increase in the studied morphology, the bottom left quadrant to a decrease, the top left quadrant to an increase in range, and the bottom right quadrant to a decrease in range. **b** Styles of size change in Early Jurassic ammonoids (black circles are the difference between two successive sets of biozones; circle diameter is proportional to frequency in the corresponding quadrant) (modified after Dommergues et al. 2002)

Another major approach to quantify the relative proportion of passive and driven trends within a lineage is that of Jablonski (1997; see also Trammer and Kaim 1999). He proposed the "*quadrant*" method as a graphic approach to evaluate the relative proportion of evolutionary changes between the minimum and maximum of the range of a character (Fig. 5.7a). This approach thus focuses on changes in variance (*sensu* Gould 1988) and can accommodate stratophenetic series or for phylogenetic sequences. In this approach, a graph reports and synthesizes the complete series within a clade of the differences of morphological values of some characters either between an ancestor and its descendant or between two successive stratigraphic intervals. The four quadrants represented four possible trends in character evolution. This enables the comparison of the relative proportion of increases, stases, and decreases within the studied clade and thus evaluates if one macroevolutionary pattern dominates or not. By accounting for the changes at the lower and upper phenotypic bounds, these analyses essentially correspond to the test based on "the behavior of the minimum" for distinguishing passive from active (directional) trends. Jablonski (1997) applied the method to evaluate Cope's rule within Cretaceous mollusks and found no support for a predominance of body size increase. For ammonoids, Dommergues et al. (2002) applied the method also to evaluate the pervasiveness of Cope's rule in the Jurassic. Their study highlighted the absence of sustained trends for shell size and even emphasizes the predominance of random fluctuations in shell size (Fig. 5.7b).

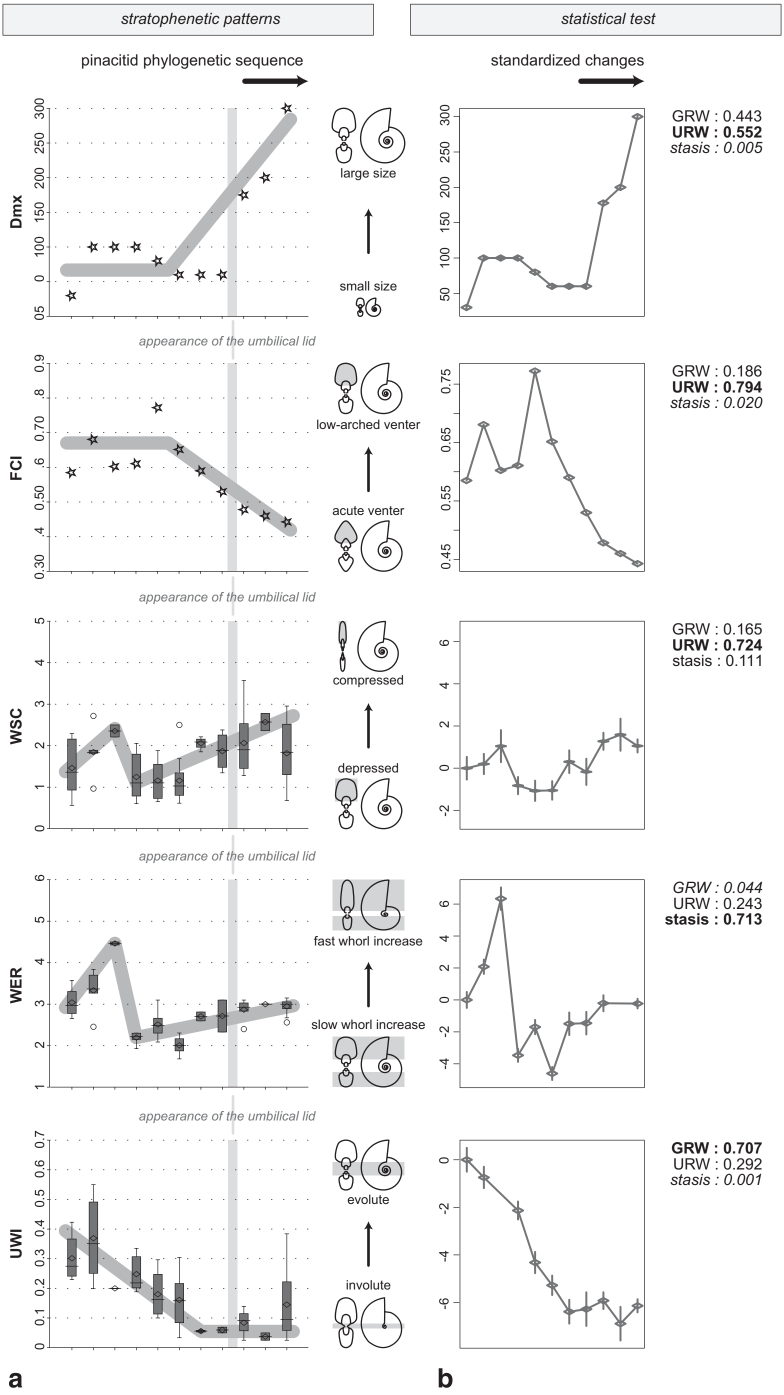

Fig. 5.8 Phenotypic trajectory analysis of univariate shell characters of Devonian ammonoids (modified after Monnet et al. 2011). **a** Stratophenetic patterns of some conch parameters and

5.3.3 Random Walks and Univariate Phenotypic Trajectory Analysis

Previously described approaches aim to describe and quantify the relative phenotypic changes of a lineage through time and phylogeny, usually at the species rank. However, trends in evolutionary series can be produced randomly (Raup and Gould 1974; Raup and Crick 1981; Bookstein 1987, 1988; Raup 1997; Roopnarine et al. 1999; Sheets and Mitchell 2001). Hence, previously empirically identified evolutionary trends must be tested statistically before examining the discrimination of patterns and processes of macroevolutionary trends. For this purpose, several methods exist, which are based on random walk models, to test and characterize observed trends and to distinguish the three modes of evolutionary change commonly considered in paleontological studies: directional change (GRW, general random walk), random walk (URW, unbiased random walk), and stasis (Gingerich 1993; Roopnarine 2001; Sheets and Mitchell 2001; Hunt 2006). The evolutionary changes of each character can be evaluated by means of the maximum likelihood method of Hunt (2004, 2006, 2007) and Hunt et al. (2008). The method performs well even when evolutionary sequences are incompletely sampled, which is likely for empirical sequences of fossils (Hunt 2006). It has been implemented as a package (“paleoTS”; Hunt 2006) in the freely available statistical and scientific environment R (http://www.r-project.org/). The method evaluates the maximum likelihood of producing the observed trends for the three evolutionary modes (GRW, URW, stasis). The relative support of each of these three models is assessed using statistical means such as Akaike weights (Anderson et al. 2000; Hunt 2004, 2006; Hunt et al. 2008). Methods to study phenotypic evolution and evolutionary trends in a phylogenetic framework have also been developed (e.g., Hunt and Carrano 2010).

For ammonoids, a recent application of random walk methods is the study of Monnet et al. (2011). Therein, the evolution of two lineages of Early to Middle Devonian age (405–395 Ma) was investigated. Eight quantitative shell characters were analyzed (Monnet et al. 2011; Klug et al. 2015b). The stratophenetic evolution of some of these shell characters for the lineage that includes the Pinacitidae is shown in Fig. 5.8a. Within this lineage, the maximum adult shell size (Dmx), the number of lobes of the suture (NLb), their relative depth of the lateral lobe (OLb), as well as the acuteness of the venter (FCI) increased simultaneously, especially among the more derived species. The umbilical width index (UWI) and the imprint zone rate (IZR) also display trends but these occur only among the more primitive species. Evolutionary changes of whorl shape compression (WSC) and whorl expansion rate (WER) display different, slightly more complex evolutionary patterns: a quick increase in the most primitive species, an abrupt reset and then a slight increase in the most derived species, giving the trend a sigmoid course.

sketch of the impact on the ammonoid shell. Boxes represent the inter-quartile range of individual values for each character and species. **b** Statistical assessment of the same macroevolutionary trends by means of the random walk method of Hunt (2006). Akaike values of the three tested evolutionary modes (GRW—directional trend, URW—random walk, and stasis) are reported and significant when greater than a half unit

This ammonoid lineage thus displays empirical morphological evolutionary trends of some shell characters. The statistical evaluation of the three evolutionary modes (directional trend, random walk, stasis) by means of the method of Hunt (2006) is illustrated in Fig. 5.8b. Among the three tested evolutionary patterns, the studied quantitative characters are mainly characterized by random trends and/or stasis (Akaike weights > 0.5). The only well-supported directional trend is for UWI (increasing degree of involution). Two other shell characters may display possible directed trends (Dmx, NLb), which have negligible values for stasis and moderate values for random walks. Thus, the studied ammonoid lineage displays directed trends for UWI with certainty, and probably for Dmx and NLb, while all other characters remain devoid of directional trends. In other words, through time and phylogeny, pinacitids acquired larger, more involute and oxyconic shells and more complex sutures. With the appearance of the umbilical lid (an extension of the lateral shell wall covering the umbilicus), the trends toward greater involution (decreasing UWI) leveled off (Fig. 5.8a). This leveling off corresponds to a "left-wall effect", i.e. the trend cannot go further once the umbilicus is closed, because this marks a constructional boundary (successive whorls completely overlap). Given the variety of patterns illustrated by the various quantitative shell characters studied, this example illustrates the necessity to test statistically for the likelihood of the three evolutionary modes. This prerequisite test is crucial to avoid over-interpretation of the evolutionary patterns and their suspected causes. Studies of phenotypic evolution of ammonoid shells can thus greatly benefit from these recent quantitative approaches (see chap. 5.5).

5.4 Multivariate Phenotypic Trends in Ammonoids

Investigating morphological macroevolution of a lineage through time by focusing on a single character (univariate) enables one to distinguish two major patterns: either stasis (absence of significant changes), or trend (directional or random walk; Fig. 5.9a). Based on these two primary patterns of morphological evolution, a series of additional patterns can be distinguished based on the relative evolution among multiple trends (multivariate): convergence, divergence, and parallel evolution (Fig. 5.9b). In a phenotypic space, convergence and divergence describe that the youngest forms are closest and farthest from the oldest forms, respectively; magnitude, shape, and direction of this change do not have to be similar. Parallel evolution is defined as the independent evolution of similar biological traits in at least two different lineages having similar magnitude, shape, and direction of their phenotypic trajectories. Cases of convergence and divergence are frequent but the concepts are broad. Demonstrated cases of parallel evolution are less frequent but concern a more precise pattern. Assessing quantitatively the significance and robustness of any of these evolutionary patterns is a difficult task, for which two statistical methods became available recently. The difficulty is to model and compare curves (evolutionary trajectories) within a multidimensional space constituted by the studied morphological characters (morphospace). These two methods were applied to ammonoids to test for parallel evolution.

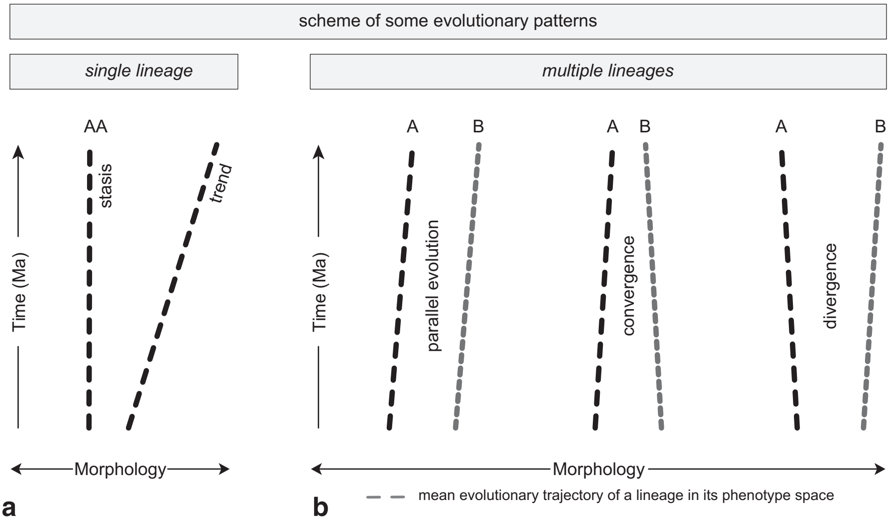

Fig. 5.9 Scheme of some macroevolutionary patterns of a lineage in its morphological space. **a** Accounting for a single character enables distinction of stasis and directed/random trend. **b** Accounting for multiple characters enables distinction of convergence, divergence, and parallel evolution

The relative evolution of a subset of characters within a morphological space can be evaluated by a method developed by Adams and Collyer (2009) for comparing evolutionary trajectories of phenotypic change (see also Collyer and Adams 2013). According to this method, the phenotypic evolution of a lineage is defined as a trajectory across a set of evolutionary levels in a multivariate morphological space. Attributes of these trajectories (magnitude, direction and shape) are quantified and statistically compared across pairs of taxa by means of a residual randomization permutation method (Collyer and Adams 2007, 2013; Adams and Collyer 2009), and a summary statistic is used to determine the extent to which patterns of phenotypic evolution are concordant. This method is very powerful since it can be used to evaluate various evolutionary patterns. One constraint is that it currently requires the same number of comparable evolutionary levels (e.g., the same number of species) between the two compared lineages. Within this method, parallel evolution of two lineages can be defined by a similar origin in the morphological space, and by similar magnitude and direction of their evolutionary trajectories.

A second method to test parallel evolution of two lineages has been proposed by Monnet et al. (2011). It follows an approach proposed by Mitteroecker et al. (2005) for comparing ontogenetic trajectories. This method is a permutation test based on within-lineage multivariate regression of the characters hypothesized to be involved in the parallel evolution. If the two lineages evolved in parallel, then their phylogenetic trajectories are identical in the morphological space defined by the subset of characters involved. This hypothesis is tested by comparing the summed squared distances of a linear total least square regression for each lineage separately between the two original lineages and for random series of two lineages obtained

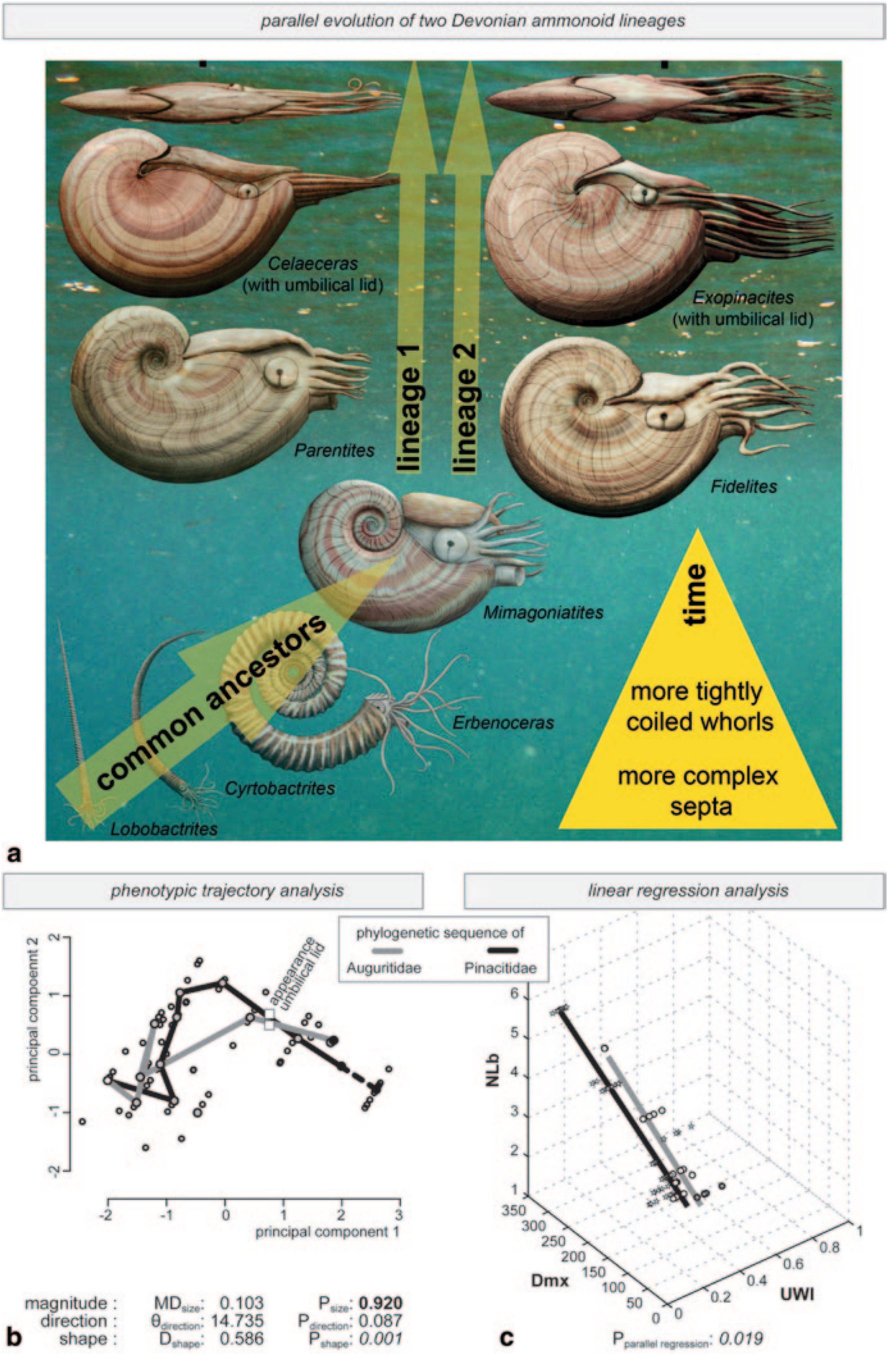

Fig. 5.10 Parallel evolution of two Devonian ammonoid families (Auguritidae and Pinacitidae) during the most intense phase of the "Devonian Nekton Revolution" (modified after Monnet et al. 2011). **a** Illustration of this parallel evolution with reconstructions of the loosely coiled ancestors

by permutation of species. If the two studied lineages evolved in parallel, the original test statistic should not be an outlier in the permutation distribution of summed squared distances (Mitteroecker et al. 2005; Monnet et al. 2011). In other words, the affiliation of permuting specimens does not increase the residuals of the multivariate regressions and this is possible only if specimens of both families are close together in the studied morphological space. The major constraint of this method is that it assumes a linear trajectory of the evolution of studied lineages in the phenotypic space, but evolutionary steps are not required to be comparable and of the same quantity as opposed to the first method (Adams and Collyer 2009).

For ammonoids, the multivariate phenotypic trajectory analysis and permutation test were applied by Monnet et al. (2011) for the first time by investigating the evolution of eight shell characters for two Devonian lineages (Auguritidae, Pinacitidae). This period was a time of major changes in the marine ecosystems with the major diversification of several important nektonic groups such as jawed fishes and ammonoids (Klug et al. 2010). In time and through phylogenetic order of appearance, both lineages display morphological directed trends toward more involute coiling, larger adult body size, more sutural elements, and the development of an umbilical lid in the most derived taxa (Figs. 5.8, 5.10a).

The hypothesis of parallel evolution of the quantified characters under consideration has been tested by the two previously described permutation methods based on the character subset including UWI, Dmx and NLb (Fig. 5.10b). These three characters were selected because they were previously demonstrated to follow directed trends and not just random walks (see above; Fig. 5.8). Using the phenotypic trajectory analysis approach of Adams and Collyer (2009), it appears that there are no significant differences in the magnitude ($\mathrm{MD}_{\mathrm{size}}=0.103$, $P_{size}=0.920$) and in the direction ($\theta_{\mathrm{dir}}=14.735$, $P_{dir}=0.087$) of phenotypic evolution between the two lineages (Fig. 5.10b). However, there are significant differences in the shape of the two evolutionary trajectories ($\mathrm{D}_{\mathrm{shape}}=0.586$, $P_{shape}=0.001$). This difference is, however, expected because the taxa in each lineage are not truly equivalent and do not necessarily represent the same evolutionary steps. Using the linear regression approach of Monnet et al. (2011), it appears that the hypothesis of parallel trajectories of the two studied lineages cannot be rejected ($p=0.019$), but the value is low (Fig. 5.10c). Hence, it appears likely that auguritids and pinacitids evolved in parallel with respect to increasing involution, adult size, suture indentation and construction of an umbilical lid.

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and two representatives of the two lineages under consideration. **b** Statistical evaluation of the parallel evolution by means of the trajectory approach of Adams and Collyer (2009). Plot of the first and second principal components estimated from the correlation matrix for auguritids and pinacitids based on the three standardized characters UWI, Dmx, and NLb. There are no significant differences in magnitude and direction of the trajectories, but they are different in shape. **c** Statistical evaluation of the parallel evolution by means of the regression approach of Monnet et al. (2011). The phylogenetic trajectory of each lineage is fitted by a linear total least square regression. The *p*-value of the test is low, but the hypothesis of parallel trajectories could not be rejected by the permutation test

5.5 Discussion

5.5.1 Adaptation (Functional Constraints)

Among the documented morphological evolutionary trends of ammonoids, the trends of increasing involution, increased adult shell diameter, and increased suture indentation are the most frequent. In the context of the neo-Darwinian theory of evolution, all these phenotypic trends have been and still can be interpreted as reflecting increasing adaptation of shell morphology to environmental factors and/or inter-/intra-specific competition. The various forms of the ammonoid shell have thus been interpreted in terms of functional needs, mostly in order to reconstruct the modes of life and habitats of this extinct group (see e.g., Kennedy and Cobban 1976; Westermann 1996; Westermann and Tsujita 1999; Ritterbush and Bottjer 2012; Lukeneder 2015). Opposite trends also have been documented for each shell character (see above).

With regard to increasing adult body size, several advantages have been enumerated, such as increased defense against predation, increased food competition, increased success in mating and reproduction, increased individual longevity, and better energy use (e.g., Newell 1949; Kurten 1953; Simpson 1953; Rensch 1959; Gould 1966; Stanley 1973; Brown and Maurer 1986; Hone and Benton 2005; Korn and Klug 2007; Monnet et al. 2011; De Baets et al. 2012). Hence, trends toward larger shell diameter have traditionally been interpreted to reflect persistent adaptive selection within long-ranging lineages. Trends toward smaller size, often interpreted by paedomorphosis, are also documented (e.g., Wright and Kennedy 1979; Kennedy and Wright 1985; Korn 1995b; Korn et al. 2013b).

With regard to trends of increasing involution, their abundance and recurrence among numerous and distantly related ammonoid clades suggest that it may have an adaptive significance due to functional constraints (Dietl 1973, 1978; Westermann 1996; Klug and Korn 2004; Saunders et al. 2004, 2008). Although hydrodynamic capabilities of these extinct animals are impossible to measure, it appears reasonable to assume that they were no enduring high-speed swimmers (Chamberlain 1980; Jacobs 1992). This interpretation is corroborated by mechanical experiments on shell models and analytical calculations of shell hydrodynamics (Chamberlain 1976, 1980; Saunders and Shapiro 1986; Elmi 1991, 1993; Jacobs 1992; Jacobs and Chamberlain 1996; Seki et al. 2000; De Blasio 2008; Naglik et al. 2015), as well as by analogy with recent nautilids (the only extant cephalopod with a chambered external shell; Ward 1988; Jacobs and Landman 1993). It has been widely demonstrated that, for shells with oxyconic shell shapes (involute and compressed), the energy consumption for swimming is the lowest and potential maximal swimming speed is the highest (decreasing drag, increasing streamlining, etc.; Schmidt 1930; Raup 1967; Chamberlain 1976, 1980; Chamberlain and Westermann 1976; Jacobs 1992; Jacobs and Chamberlain 1996; Hassan et al. 2002; Klug and Korn 2004; Klug et al. 2008; Naglik et al. 2015). Increased involution of the shell therefore appears to represent an adaptation toward improved hydrodynamic properties of the shell

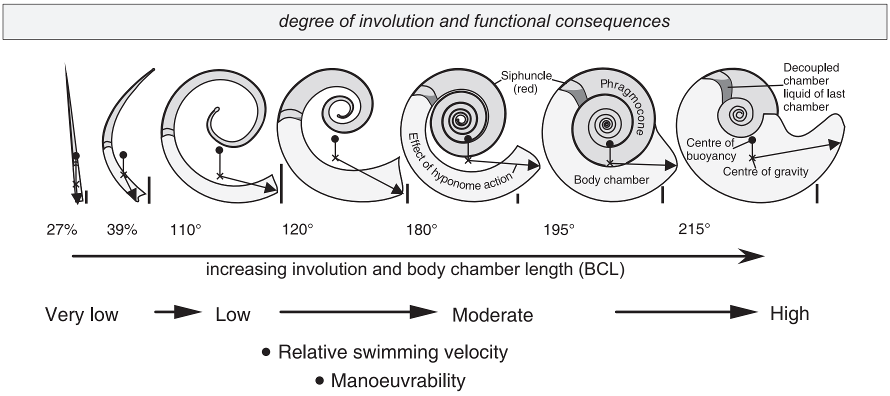

Fig. 5.11 Degree of involution of the ammonoid conch and functional interpretation. Phylogenetic change in orientation of the conchs and swimming velocity of Bactritida and primitive Ammonoidea during the Devonian (modified after Klug and Korn 2004; Klug et al. 2008). Outlines of the conchs with body chamber lengths (BCL), orientation of the aperture (OA), and relative swimming speed. Centre of gravity is indicated by a cross and the centre of buoyancy by a circle

(Fig. 5.11; but for alternative interpretations including sea-level changes and predatory pressure, see, e.g., Bayer and McGhee 1984, 1985; McGhee et al. 1991; Neige et al. 1997; Olóriz et al. 1997, 1999; Kröger 2005; Wilmsen and Mosavinia 2011). For example, the gradual shift during the Devonian from marine communities dominated by organisms with openly-coiled shells to communities dominated by tightly coiled shells in distantly related organisms (e.g., nautilids, ammonoids, gastropods) was probably caused by predatory selective forces (Nützel and Frýda 2003; Kröger 2005; Klug et al. 2010), assuming that open coiling makes shells weak and vulnerable to attack and force but also, they are simply larger (this selection pressure is also linked with swimming abilities).

With regard to trends of increasing suture frilling, the function of septal folding is subject of much debate (e.g., Kennedy and Cobban 1976; Saunders 1995; Hewitt and Westermann 1997; Daniel et al. 1997; Westermann and Tsujita 1999; Lewy 2002; Checa 2003; Klug and Hoffmann 2015). The classic morpho-functional interpretation is that increasing suture frilling reduces the risk of implosion by providing buttressing against hydrostatic pressure on the phragmocone (Pfaff 1911; Westermann 1971, 1975; Hewitt and Westermann 1986, 1997; Seilacher 1988; Jacobs 1990; Hewitt 1996; Daniel et al. 1997; Hassan et al. 2002; De Blasio 2008). By contrast, available quantitative analyses of the ammonoid fossil record reveal no correlation between suture frilling and supposed water depths (Olóriz and Palmqvist 1995; Olóriz et al. 1997, 1999). The evidence for paleobathymetric reconstruction is, however, commonly poor, thus making the hypothesis of depth-controlled suture frilling difficult to test. Ammonoids were mostly epipelagic organisms inhabiting the uppermost part of the marine water column (<300 m; Westermann 1996; Westermann and Tsujita 1999; Lukeneder 2015). Wells (1999) even thought that this payed a role in their extinction, because nautilids (simple septa) can sustain pressures in depths up to 700 m (e.g., Ward 1988; Dunstan et al. 2011). In any case, septum shape has also a strong developmental component (suture frilling increases through growth and is significantly correlated with the space available; Klug and Hoffmann 2015).

5.5.2 Iterative Evolution and Evolutionary Jumps

Numerous examples of morphological long-term trends have been described in the literature within ammonoid cephalopods (see above). These repeated trends in phenotypic traits are commonly regarded as evidence of adaptation under common selection pressures (Simpson 1953; Endler 1986; Schluter 2000), therefore illustrating natural selection's major role in shaping morphological evolution and repeatability of evolutionary processes.

In this context, repetitive sedimentary sequences reflecting cyclic environmental changes (e.g., sea level, climate) have been suggested as a major trigger of morphological evolutionary trends of the ammonoid shell by means of similar morpho-functional adaptive responses. For instance, Bayer and McGhee (1984, 1985) studied the morphological evolution of several ammonoid lineages during the Jurassic and they identified *"iterative repetition of identical evolutionary courses"* in the ammonite faunas (Fig. 5.4b). They argued that these iterative morphological changes were in response to cyclic changes in the physical marine environment: "*similar environments were inhabited by ammonite faunas of similar morphology, and moreover, similar directional changes in the physical environment are mirrored by similar morphological changes in the ammonite faunas*" (Bayer and McGhee 1984). Both endemic forms, which evolved *in situ* and migrant forms from the Tethyan realm were equally affected. The phenomenon of iterative evolution in ammonoids is well known and several authors noted that these morphological sequences are repeated in groups separated both in time and taxonomy (e.g., Schindewolf 1940, 1950; Haas 1942; Arkell et al. 1957; Wiedmann 1973; Kennedy and Cobban 1976). However, most discussions in the literature concern taxonomic and biostratigraphic consequences of the implied homeomorphies. This view of iterative evolution led to the concept that ammonoids repeatedly evolved from long-lived generalist lineages mainly inhabiting distal environments toward short-lived opportunistic lineages inhabiting shallower environments (e.g., Wiedmann 1973; Jacobs et al. 1994).

In contrast, Guex (1992, 2001, 2003, 2006) qualitatively examined these iterative patterns for Mesozoic ammonoids. He argued that during stable periods, ammonoid lineages experience classic long-term evolutionary trends of their shell (e.g., increase of shell size, involution, compression, as well as increase of suture frilling) and that during extinction periods, relatively tightly coiled ammonites can give rise to highly evolute forms or heteromorphs with simple ornamentation and almost ceratitic suture line. He dubbed this sudden evolutionary change, which is at variance with previous long-term changes, an "*evolutionary jump*". He pointed out that these evolutionary jumps are characterized by the appearance of forms, which are partly homeomorphic with remote ancestors of their own lineage and interpreted these newly evolved homeomorphic taxa as being atavistic. He called also this phenomenon "*proteromorphosis*" because it cannot be explained by normal paedomorphic transformations. Monnet et al. (2013) recently described such a potential evolutionary jump within a lineage of Triassic ammonoids. Guex (1992, 2001, 2006) also argued that episodes of strong environmental stress are at the origin of many new ammonoid lineages by promoting the abrupt appearance of significantly different forms by means of such evolutionary jumps.

The most extreme case of iterative evolution is probably the recurrent appearance of loosely coiled, uncoiled and trochospirally coiled heteromorph ammonoids, which have not only been linked to periods of environmental stress (Guex 2006), but also to advantageous trophic conditions (Nesis 1986; Cecca 1997) or sea-level changes (Keupp 2000). Such heteromorphic ammonoids were long seen as evolutionary dead ends and irreversible, phylogenetic end-forms (for a review, see Wiedmann 1969). Before this time, the belief in Dollo's law of irreversibility was deeply entrenched in the thoughts of natural scientists, stating that the re-evolution of any complex character like the coiled ammonoid shell was considered unlikely or impossible. Besides methodological problems with interpreting uncoiled as less complex than coiled shells (Urdy and Chirat 2006), there are additional reasons to see heteromorphic ammonoids as anything but evolutionary dead ends. Heteromorphs were highly successful (diverse and abundant) during some periods (Cretaceous), and diverse heteromorphic lineages gave rise to coiled representatives, which counter-act these ideas (e.g., Wiedman 1969; Cecca 1997; Bert and Bersac 2013). Contra-intuitively involute forms have also been seen as phylogenetic end-forms. For instance, this seems to be the case of the Devonian Auguritidae and Pinacitidae (Monnet et al. 2011), Triassic Sagecerataceae and Pinacocerataceae (Diener 1917; McGowan and Smith 2007; Korn 2012), and Jurassic Amaltheidae (Meister 1988), among others. However, some lineages with oxyconic forms have also successfully given rise to less coiled descendants.

The major characteristic of all these models of macroevolution of the ammonoid shell is that they rely on two widespread views among ammonitologists: (i) the ammonoid conch is shaped by its functional needs only and thus reflects environmental changes, and (ii) ammonoids evolved toward particular morphologies, which correspond to adaptive peaks in the ammonoid phenotypic landscape. By contrast, the widespread adaptive interpretations of the ammonoid conch are *ad hoc* explanations in many cases, partially because their behavior cannot be observed (e.g., swimming speeds, habitat depths, vertical movements; compare Ritterbush et al. 2014, Naglik et al. 2015). This is a common problem in paleontology (Ebbighausen and Korn 2013), strongly limiting the range and number of falsifiable hypotheses. In some cases, iterative intricate evolutionary patterns or morphological characteristics allow speculations with a certain degree of plausibility, which justifies their description and discussion.

Moreover, natural selection is one possible and important, although commonly over-rated, trigger and driver among several others in the fabric of evolutionary trends. Interestingly, evolutionary trends are never global and opposite patterns are also common: usually, they occur only in specific clades, while other coexisting clades still retain or evolve very different shell morphologies. For instance, crioconic, serpenticonic and platyconic forms coexisted with the highly involute auguritids and pinacitids (see Klug 2002; Korn and Klug 2003). Representatives with very complex and very simple suture lines were found together (e.g., *Beloceras* and *Archoceras*: Korn et al. 2013b; *Metoicoceras* and *Euomphaloceras*; Cobban et al. 1989). Micromorphic and large-sized ammonoids also co-occured (e.g., *Nannometoicoceras* and *Metoicoceras*; Kennedy 1989), and very involute and compressed forms coexisted with evolute and/or depressed forms (e.g., *Oxylongobardites*, *Tropigastrites* and *Proarcestes*; Monnet and Bucher 2005). Furthermore, quantitative analyses of the correlation between the supposed adaptive shell characters and environmental factors produced variable results (Bayer and McGhee 1985; Donovan 1985; Cariou and Hantzpergue 1988; Batt 1989; Jacobs et al. 1994; Westermann 1996; Neige et al. 1997; Olóriz et al. 1997, 1999, 2002; Westermann and Tsujita 1999; Vörös 2002; Kawabe 2003). But it must be acknowledged that environmental parameters (e.g., bathymetry, temperature) are usually difficult to assess and quantify in the past and in most cases, evidence for the ammonoids' actual habitats is weak because they might have lived anywhere in the water column above where they are found (De Baets et al. 2015) and their shells could easily be transported (Wani and Gupta 2015). Nevertheless, some indication of their habitat can be constrained by combining multiple lines of evidence (Ritterbush et al. 2014; Naglik et al. 2015), including predator–prey interactions (e.g., Keupp 2006; Kruta et al. 2011; Hoffmann and Keupp 2015; Tanabe et al. 2015) and stable isotopes of their shells (e.g., Lécuyer and Bucher 2006; Lukeneder et al. 2010; Lukeneder 2015). Interestingly, the co-occurrence in time of different evolutionary trends leading to very disparate co-existing morphologies may reflect the existence of multiple adaptive peaks in the ammonoid phenotypic landscape and/or that the triggers of these trends are not global and not only adaptive. The model of Guex (2001, 2006) assumed that trends are reset during periods of high environmental stress. This remains to be tested but enables us to ask about the distribution, influence and frequency of trends within/among space, time, taxonomy, and phylogeny, as well as the proportion of adaptation, covariation and chance generating these trends. Furthermore, rates of morphological change depend on the observed time interval, so that these first need to be quantified to speak about evolutionary jump as opposed to normal evolutionary trends.

5.5.3 Covariation (Constructional Constraints)

Evolution of shell shape driven by adaptation, although reasonable from a mechanical point of view, is certainly not the sole driving mechanism behind long-term evolutionary trends in ammonoids. To explain how certain organisms have evolved certain features, evolutionary biologists emphasized the role of constructional/developmental constraints on evolution (Williamson 1981; Alberch 1982; Charlesworth and Lande 1982; Holder 1983; Maynard-Smith et al. 1985; Raff 1987; Goldsmith 1990; Arnold 1992; Tabin 1992). Maynard-Smith et al. (1985, p. 266) defined a developmental constraint as "*a bias on the production of various phenotypes caused* *by the structure, character, composition, or dynamics of the developmental system*". Correlations between characters belong to the most common patterns attributed to developmental constraints. Such correlations may result from interactions between tissues during the development or the involvement of the same genes or developmental pathways in multiple morphogenetic processes. Although it is difficult to rule out selective (functional) constraints (adaptation), constructional, developmental and/or genetic constraints can also explain common evolutionary patterns (e.g., Morita 1993, 2003; Wagner and Erwin 2006).

In this context, it is here suggested that many of the described long-term morphological evolutionary trends of ammonoids can be explained, in part, by other constraints than selective ones. Indeed, some of the documented trends of the ammonoid shell can be produced by constructional constraints (Seilacher 1973; Urdy et al. 2010a, 2010b; Monnet et al. 2011) referred to as covariation. In other words, some morphological trends of specific characters of the ammonoid shell can result from trends in other traits because the way the shell is constructed (morphogenesis) involves the covariation (scaling, usually by means of allometric rules) of several shell characters. It is important to identify such aspects of covariation, because in this case, it is unnecessary to search for an adaptive explanation.

Covariation of shell characters is well known from ammonoids. For instance, the intraspecific variation of an ammonoid species is usually expressed by the following gradient: the more evolute the shell, the thicker the whorl shape (large whorl width to whorl height ratio), and the more robust the ornamentation. It is referred to as Buckman's first rule of covariation (e.g., Reeside and Cobban 1960; Westermann 1966; Dagys and Weitschat 1993; Morard and Guex 2003; Yacobucci 2004; Hammer and Bucher 2005; Monnet et al. 2010, 2015b; Bert and Bersac 2013; De Baets et al. 2013a, De Baets et al. 2015). This covariation pattern concerns intraspecific variability and differs from the type of covariation discussed below. Among phenotypic directed evolutionary trends of ammonoids, the concept that some of these trends can be due to scaling effects is discussed below for the two most frequent morphological trends: increasing involution and increasing suture indentation.

A striking pattern of ammonoid evolution is that trends of increasing adult shell diameter are commonly, but not systematically, associated with trends of increasing involution and increasing suture indentation. These trends in size are usually interpreted to exemplify Cope's rule. However, these trends concern the adult shell diameter, not the volume of the soft tissues. Soft tissues of ammonoid cephalopods are insufficiently known and consequently also their relation with conch size. Nevertheless, we can reasonably assume that their soft body scales with the volume of the body chamber (Arkell et al. 1957; Doguzhaeva and Mutvei 1991; De Baets et al. 2012, De Baets et al. 2015). Yet, from a morphogenetic point of view, what would happen if a studied ammonoid clade followed a size-increase of its soft body? It appears that increasing body size (volume of soft tissues in the body chamber) can be accommodated in several ways (Guex 2001, 2003): increasing arc length of the body chamber, increasing whorl width, or increasing whorl height, which can result in increasing shell diameter and/or involution (Fig. 5.12). We stress that several trends in ammonoid shell geometry can be explained by increasing adult body size

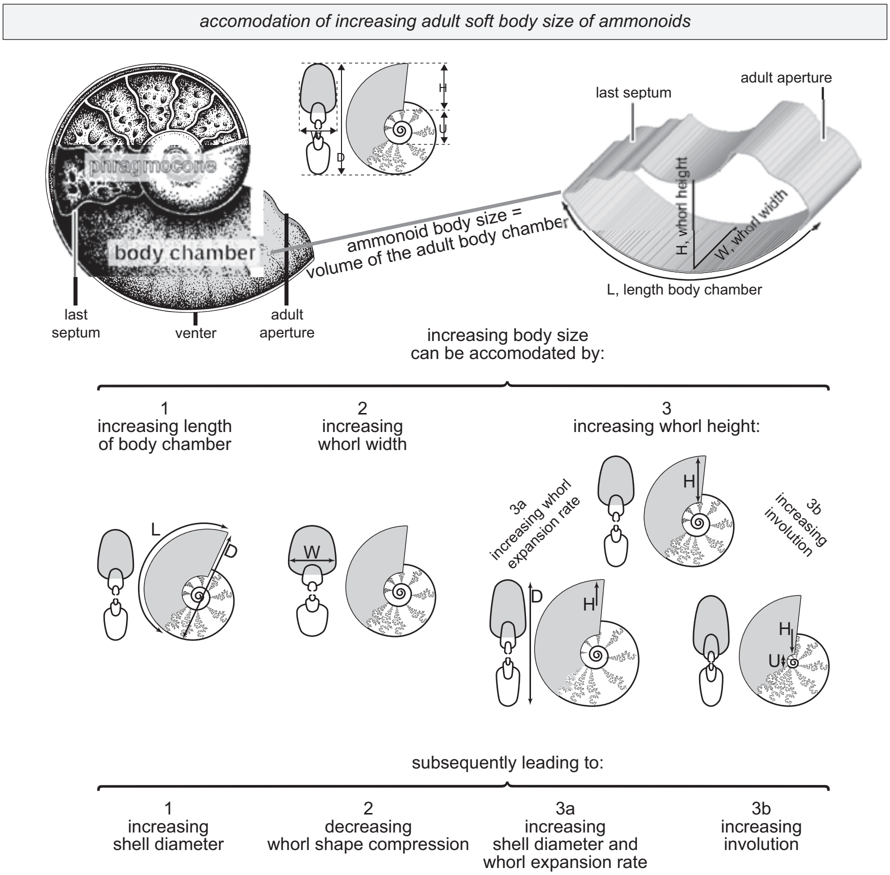

Fig. 5.12 Scheme illustrating the various ways that an increase of adult soft body size of ammonoids can be accommodated by the geometry of their external shell. Increase in ammonoid soft body size can be expressed in terms of three basic alternatives, which are not mutually exclusive and can be accumulated in various combinations and proportions: increasing arc length of body chamber, increasing whorl width, and increasing whorl height. These three accommodating changes can lead to four increasing phenotypic trends of shell geometry: in shell diameter, in whorl shape depression, in whorl expansion rate, and in involution (compare with Figs. 5.5, 5.8)

as an alternative to functional explanations (Guex 2003), because both changes in shell diameter and shell involution are two possible paths for ammonoids to accommodate soft body size increase. Although shell diameter is usually assumed to reflect body size, it does not suffice and even is not required to identify a case of body size increase for ammonoids. For example, increasing whorl width or increasing involution without changes in shell diameter still can be induced by an increasing adult body size (Fig. 5.12). Therefore, an evolutionary increase of ammonoid soft body size can indirectly trigger several trends in ammonoid geometry.

Bearing this distinction in mind is essential because morphological trends of the ammonoid shell are quite often interpreted by more or less *ad hoc* adaptive and morpho-functional explanations. With regard to trends of increasing involution, it may well result solely from an increase in body size, and not directly from a selection pressure on the coiling itself and its associated swimming advantage; increase in body size may itself be a swimming-related factor, because it provides the possibility for a larger volume of propulsive muscles and hydrodynamic properties change with body size as well (Naglik et al. 2015). Therefore, some conclusions on improved hydrodynamics of the shell may be speculative and represent secondary adaptations (Gould and Lewontin 1979; but see Levinton 2001). The role of hydrodynamic efficiency in ammonoid shell shape, argued by several authors, may have been overestimated (Weitschat and Bandel 1991). This is also supported by large intraspecific variability in shell shape in several ammonoid lineages (Dagys and Weitschat 1993; De Baets et al. 2015). With regard to trends of increasing suture indentation, it may also result from an increase in body size, and not directly from selection pressure on the suture frilling. Although knowledge of the morphogenesis of ammonoid septa remains incomplete (Klug and Hoffmann, 2015), septal patterns display similarities with structures that developed under a "*domain effect*" by a "*viscous fingering*" phenomenon (see also review of Checa and García-Ruiz 1996). In this morphogenetic model, details of the suture pattern depend on the space and shape available for the suture during its formation (septa are secreted after the surrounding shell). This is supported by the widely documented significant increase in suture indentation throughout ontogeny of the ammonoid shell (the number of suture elements increases with whorl height of the shell; e.g., Swinnerton and Trueman 1917; Erben 1966; Korn and Klug 2003; Pérez-Claros et al. 2007). In this context, as for involution, folding and fluting of the septal mantle are an additional means to accommodate body size increase (Guex 2003; compare Illert and Reverberi 1988). Interestingly, even if some trends in ammonoid shell geometry can be triggered by an increase of ammonoid soft body size and thus result from constructional constraints as stressed above, adaptive pressure can still operate indirectly: An increase in soft body size coupled with a constant shell diameter will induce a loss of buoyancy, which can be compensated in several ways (e.g., decrease of body chamber length or decrease of shell thickness, which both influence shell orientation). Hence, positive or negative adaptive feedback can enhance or minimize the impact of constructional constraints.

The comparison of these theoretical investigations with the previously described long-term evolution of Triassic acrochordiceratids and Devonian auguritids and pinacitids (Figs. 5.5, 5.8) is striking. The three lineages are characterized by directed trends toward increasing involution and suture indentation concomitant with increasing adult shell size (Monnet et al. 2011, 2012). Following the previous reasoning, it appears that these trends can be induced by covariation (constructional constraints) with evolutionary changes in soft body volume. They may be secondary trends and as such their interpretation in terms of adaptation should be cautious. Notably, these trends in the three studied ammonoid lineages are not associated with any trend in whorl shape compression whereas it is one of the possible ways of accommodating increased soft body volume (compare Figs. 5.5, 5.8, 5.12). This observation highlights the view that the relative influence of these different possible covariation patterns remain to be elucidated and investigated, as well as why certain evolutionary trajectories are favored or not (possibly by means of adaptive feedbacks induced by some constructional constraints). Therefore, it is stressed that long-term phenotypic trends in ammonoid shell form must be tested rigorously and conjointly. This remains to be done, but such an effort is crucial because it is not really possible to interpret the adaptive value of trends in ammonoid shell form without accounting for such possible constructional constraints. An additional problem is that there may be other constructional or even adaptive constraints that are not yet understood because of missing data, non-preservation or simply the historic aspect (i.e. behavior). In the case of the degree of septal frilling, it has to be understood that not all aspects of septal growth and construction are fully understood yet. This situation strongly limits the scientifically correct approaches to identify potential evolutionary drivers triggering the evolution of ammonoid septa.

In conclusion, from a theoretical point of view, long-term phenotypic evolutionary trends of the ammonoid shell can result from adaptation (selective constraints),from covariation (constructional constraints) or a combination of these and other factors. For instance, both increasing involution and suture indentation can just be scaling effect of within-lineage size-increase (if soft body volume is considered and not shell diameter); similarly, seeming simplification of sutures might have originated in size-reduction or changes in whorl cross section or development. The respective relative role of these non-mutually exclusive, possible drivers of evolutionary trends in shaping ammonoid evolution has not been investigated sufficiently yet. Furthermore, morphogenesis of the ammonoid shell (and other mollusk shells) is still insufficiently known. More and new information on mollusk shell morphogenesis could provide crucial insights on patterns and processes of mollusk evolution. In this context, it is not surprising that previous studies trying to evaluate the prevalence of Cope's rule or increasing complexity of life resulted in unclear and controversial results. Indeed, such studies have to differentiate between adaptive trends and covariation, be it driven by scaling effects or other factors.

5.5.4 Developmental Constraints and Heterochrony

Constraints on evolutionary trends are not limited to adaptive selection and constructional covariation. Naturally, there are also developmental and genetic constraints. The latter cannot be assessed in ammonoid cephalopods since it is an extinct group and DNA of that age is unknown, but these factors may have an important role. For instance, the repeated evolution of a shell character may speculatively result from the repetitive loss of the expression of regulatory Hox-genes (Averoff and Patel 1997; Prud'homme et al. 2006) or the repeated recruiting of developmental genes (Lindsey 1962; Colosimo et al. 2005). Sudies on extant shell-bearing mollusks such as gastropods are one of the only ways to provide clues about this kind of constraints on the evolution of ammonoids.

Major evolutionary changes in a trend are often constrained by morphological and functional trade-offs, with one structure improving at the expense of another.

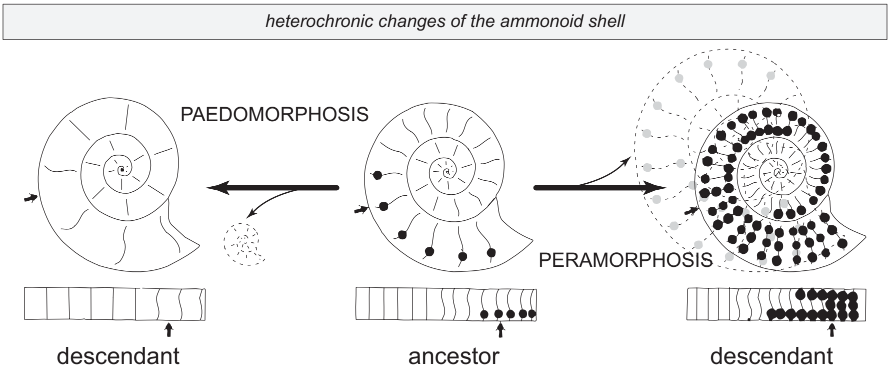

Fig. 5.13 Scheme illustrating the paedomorphosis and peramorphosis of an ancestral ammonoid with regard to the presence and number of rows of tubercles (modified after Landman and Geyssant 1993)

Many such trade-offs have a developmental basis and have arisen from heterochrony (McNamara 1997). Heterochrony (i.e. developmental change in the timing of events, leading to changes in size and shape) is a fundamental aspect of evolution, supported by a vast biological and paleontological literature. It has been argued that heterochrony plays an important role in evolutionary trends (McNamara 1982, 1990), including both anagenetic and cladogenetic trends, and both micro- and macro-evolutionary trends (McNamara and McKinney 2005). Briefly, heterochrony can be described in the form of paedomorphosis and peramorphosis that occur between an ancestor and its descendant: on the one hand, paedomorphosis can be observed when a descendent retains in its reproductive, adult stage the juvenile traits of its ancestor taxon, and on the other hand, peramorphosis is delayed maturation and extended periods of growth (Fig. 5.13). It must, however, be kept in mind that in fossil organisms like ammonoids only size and shape is available, while the duration (age) and the rate of growth are mostly unknown (Landman and Geyssant 1993; allometric heterochrony *sensu* McKinney 1988). A relationship between evolutionary trends and heterochrony arises because evolutionary trends are, like ontogenetic trajectories, unidirectional. For trends to develop, in addition to the intrinsic factor of heterochrony, extrinsic factors are also critical. Selection of either progressively more paedomorphic or more peramorphic traits must take place along an environmental gradient, such as in the aquatic environment from deep to shallow water, or from coarse to fine-grained sediments (McNamara 1982, 2006). An evolutionary trend from ancestors to descendants that show increasingly more paedomorphic characters is called a paedomorphocline. If the trend shows increasing peramorphic descendants, it is called a peramorphocline (McNamara 1982, 1990). Collectively these are called heterochronoclines. Many examples of heterochronoclines have been described in ammonoids and for various characters and in various directions in their shell morphospace (e.g., Gould 1977; Dommergues et al. 1986, 1989; Landman 1988, 1989; Meister 1988; Dommergues and Meister 1989; McNamara 1990; Dommergues 1990; Korn 1992, 1995a, 1995b; Landman and Geyssant 1993; Gerber 2011; Korn et al. 2013b; Fig. 5.4). Hence, not only developmental constraints play a significant role in ammonoid evolution, but also this role can be evaluated thanks to the accretionary mode of growth of mollusk shells, which provides an invaluable access to individual ontogenetic development in individual ammonoids. In this context, the recurrence of morphological evolutionary trends within ammonoids can be seen as the repetitive and preferential selection of the same heterochronic process because of similar environmental conditions/gradients and intrinsic constraints that canalize the evolution of ammonoid clades (Dommergues et al. 1989; McNamara 1990).

Heterochronoclines *ipso facto* induce a rough parallel trend between phylogeny and ontogeny that has been frequently described in ammonoid evolution. However, within the same lineages, the chronocline evolution of the different ammonoid shell characters is a mosaic pattern characterized by various trends and stases that are often at variance. For instance, in the case of the previously discussed Triassic acrochordiceratids, one important ontogenetic pattern is that several shell characters show significant and persistent shift during ontogeny (Monnet et al. 2012, Fig. 5.11). Members of this lineage became more involute, developed more compressed whorl sections, and reduced the number of ribs during development. Interestingly, while the ontogenetic trends in coiling and ribbing density mirror their long-term stratophenetic trend (this can be described as a size-based or allometric peramorphocline; McKinney 1988; Dommergues et al. 1989; McKinney and McNamara 1991), no ontogenetic trend in whorl shape compression could be found in the evolution of this group during the Anisian. Hence, evolutionary trends of the Anisian Acrochordiceratidae parallel their ontogenetic developments in part only. This partial concordance between the evolution of the group and its ontogenetic changes poses the question whether the direction of evolutionary change at the phenotypic level may be a product of the within-individual dynamics of development and/or of the within-population dynamics of natural selection. In other words, was the morphological evolutionary trend of increasing coiling of ammonoids driven by natural selection, by a developmental constraint, or by a combination of both (Arthur 2001, 2004)? Paleontologists and neontologists sometimes underestimate developmental constraints in the shaping of anagenetic morphological trends (McKinney 1990). Since the evolution of organisms is an equilibrium between various mutually interacting processes (Waddington 1941), what is the relative influence of the various constraints (selective, constructional, developmental, chance, etc.) on the evolution of the ammonoid shell? The exact contribution of each type of constraints remains to be investigated and also requires a better understanding of the morphogenesis of the ammonoid shell. Crucial information may come from the ongoing development of quantitative and theoretical modeling of the mollusk shell (e.g., Raup 1966; Ubukata et al. 2008; Monnet et al. 2009; Urdy et al. 2010a; Parent et al. 2010, 2012; Moulton et al. 2012, 2015; Chirat et al. 2013), as well as from the comparison with growth-monitored individuals in the wild or in aquaria (Urdy et al. 2010b).

5.5.5 Prospects on Long-Term Phenotypic Trends

Understanding the patterns of evolution requires identifying the processes that shape these patterns and in which context they apply. Currently, the knowledge and understanding of the fabrics and dynamics of long-term morphological evolutionary trends is complicated by two major sources of bias.

Natural selection as a driver of phenotypic evolution tends to be overrated, or, in the words of Graffin and Olson (2010), there is a "*false idol of natural selection*". Although adaptation has been historically overestimated, the existence of adaptation and selection as drivers of evolution with a much smaller role than originally thought appears reasonable. A fundamental epistemological problem of both is the near impossibility to prove the causal relationship between, e.g., an ecological factor and a morphological change. However, it is legitimate and stimulating to seek correlations between evolutionary change in ammonoid morphology and other factors such as ecological factors, paleogeography, predation patterns, and particular evolutionary patterns. At some degree of correlation between evolutionary patterns and ecological processes, randomness of evolutionary change becomes increasingly implausible, allowing near-hypothetical speculations on aspects of adaptation and selection influencing evolution.

A first example has been discussed in great detail above, namely the parallel evolution of two distantly related lineages of Devonian Auguritidae and Pinacitidae (Monnet et al. 2011). It appears unlikely that several morphological traits including highly unusual ones such as the umbilical lid evolve in parallel over millions of years without the slightest aspect of adaptation or selective mechanism as evolutionary driver. It is undoubted that covariation explains a significant part of the evolutionary change, but explaining the entire course of this case of parallel evolution would mean circular reasoning. At some point, adaptation or selection must have a played a role, even if only gently. Sexual selection is well-known to play an important role in extant organisms, but is hard to prove for extinct ones; it is well conceivable that sexual selection is also responsible for some evolutionary trends in ammonoid evolution (compare Knell et al. 2013).

A second example is a number of distinct evolutionary trends (although a left wall effect cannot be entirely ruled out in these cases) in early ammonoid evolution (Korn and Klug 2003; Klug and Korn 2004; De Baets et al. 2012, 2013b; Klug et al. 2015a), which are well documented for the embryonic shell (De Baets et al. 2012). These include a reduction in ammonitella size, increase in coiling of the ammonitella (Erben 1964, 1965, 1966; House 1996; De Baets et al. 2012, 2013b) but also of post-embryonic whorls (Klug and Korn 2004), the decrease of the size of the umbilical window until its closure (House 1996; De Baets et al. 2012) as well as an increase of the whorl expansion and soft-part volume (Korn and Klug 2003; Klug and Korn 2004). Several alternative explanation for these trends present themselves: (i) ammonitella-size decreased simultaneously with increasing soft-body size, suggesting increasing reproductive rates (and reduced survivorship of offspring) (discussion in De Baets et al. 2012); (ii) in the Early Devonian, an increase in coiling is documented from several clades (Ammonoidea, Dacryoconarida, Orthocerida) synchronous with a decrease in embryonic or larval shell size (Gastropoda, Ammonoidea)—a random coincidence appears less likely than selective pressure from profound macroecological pressures (Klug et al. 2010); (iii) with increasing coiling, the orientation of the aperture changed from vertically downward *via* oblique to horizontally upward (Korn and Klug 2003; Klug and Korn

2004)—a random evolutionary change appears, again, unreasonable, since it makes perfect sense from a hydrodynamic point of view (a more or less horizontal aperture enhances maneuverability and swimming; see discussion in Klug and Korn 2004); and (iv) increased coiling and improved swimming capabilities do make sense in the light that more or less synchronously the gnathostome fish underwent an explosive radiation, thus suggesting a selective pressure from evolving mobile predators, probably progressively occupying the same habitats as the ammonoids (compare Klug et al. 2010, 2015a).

Therefore, it appears easier and reasonable to keep hands off adaptive explanations for evolutionary change among ammonoids, but selection and adaptation must have played a role of unknown proportion in ammonoid evolution. Its denial is of no help in under-standing ammonoid evolution, but great care and openness towards criticism and discussion is essential.

A major second source of biases in the analysis of long-term trends is rooted in the data available and the approaches used to these analyses. Most studies are partly biased by one or a combination of the following aspects: absence of a rigorous phylogenetic framework, insufficient consideration of anagenetic and ontogenetic changes, insufficient taxonomic coverage, insufficient consideration of morphogenetic constraints, absence of comparison with simulated evolutionary patterns (especially to evaluate the impact of chance alone), among others. For instance, evolutionary changes in size were documented to apply to several ammonoid groups, but there are no quantitative data covering all ammonoid taxa (rather than specific-clades) of a distinct time interval, with a robust phylogenetic framework and with integration of covariation patterns of the diverse shell characters (compare Hallam 1975 and Dommergues et al. 2002). In this context, several questions on evolutionary patterns and processes remain to be investigated. What is the proportion between adaptive (selective constraints) and scaled (constructional constraints) morphological long-term evolutionary trends among ammonoids? Under which conditions did these trends occur? Are trends (be it adaptive and/or a secondary effect) restricted in time and space and clades? What is the influence of origination and extinction events on the fabrics of evolutionary trends (see Guex 2006)? All these questions among many others remain to be investigated and await adequate data collection and subsequent quantitative analyses.

Finally, the impact of chance on the frequency of ammonoid evolutionary trends remains also to be assessed. Theoretically, evolutionary trends in involution and suture indentation can be adaptive and/or scaling effects of size changes. Since apparent trends in evolutionary series can be produced randomly (Raup and Gould 1974; Raup and Crick 1981; Bookstein 1987, 1988; Raup 1997; Roopnarine et al. 1999; Hunt 2006), are these documented trends more frequent than what can be expected just by sheer random evolution? All morphological characters have lower and upper viable limits. Hence, the location of origination of a clade or taxon in its phenotype space directly influences the chance of having a trend among its descendants. Indeed, the chance of a taxon having a larger descendant (or with a more involute shell, or with a more indented suture, etc.) may be related to the distance from the limits of the considered character in the morphological space of the studied group.

Hence, it remains to be seen whether documented evolutionary trends of the ammonoid shell are caused (and in which proportion) by random evolution constrained by the constructional limits of the shell (left-wall effect).

Now, if we consider shell characters in the biological concept of adaptive landscapes (Wright 1932; McGhee 1999, 2007; Wilson 2013), shell form can be expected to exhibit repeated trends in some characters given the functional properties of the ammonoid shell (buoyancy device containing soft-tissues). In this case, is the distribution in time and space of trends concordant with adaptive hypotheses? Can we derive a morphological adaptive landscape of the ammonoid shell? Finally, in this context of evolutionary trends and morphological landscapes, several questions remain to be investigated. Are kinds of trends randomly distributed among shell characters (for instance, are cases of size trends restricted to particular morphologies)? Do trends originate at random locations in the morphospace of the studied group? New data delivering answers to these questions will provide insights on patterns and processes of long-term phenotypic trends of the ammonoid conch such as convergence, divergence, and parallel evolution.

5.6 Conclusions

Long-term morphological evolutionary trends of ammonoid cephalopods are numerous and suggest the existence of common processes acting regularly to mold their macroevolution. Although ammonoid cephalopods are extinct, their high evolutionary rates and the excellent fossil record of their shells make them superb study objects to reveal insights into patterns and processes of long-term phenotypic evolutionary trends. Unfortunately, quantitative studies are still rare and often lack a phylogenetic framework. As acknowledged by Jablonski (2000): "*only a few studies have met the necessary protocols for the analysis of evolutionary tempo and mode at the species level, and so the distribution of evolutionary patterns among clades, environments, and modes of life remains poorly understood*".

From the few existing studies, it appears that constructional (covariation) and adaptive constraints are not mutually exclusive. Both can contribute to the fabrics of evolutionary trends for ammonoid lineages. This underlines that evolutionary and developmental morphogenesis, and the controls upon them, can never be truly understood in separation from functional adaptation and constructional covariation. Distinction between covariation and adaptation in evaluating evolutionary trends is essential in order to avoid over-interpretation of the evolutionary patterns. For instance, the frequent increase in suture indentation is probably not a primary adaptation to water depth against implosion, but likely represents a secondary trend caused partly by an increase of adult shell size and shape due to covariation (constructional constraints). Hence, recurrence of particular combinations of morphology, which are commonly regarded as strong arguments for functional constraints, can also represent "fabricational noise" (Seilacher 1970, 1973). It is thus crucial for evolutionary analyses to understand the driving factors behind evolutionary morphological modifications.

Selective (adaptation) and constructional (covariation) constraints do occur in the evolution of the ammonoid shell. Taken separately, they do not explain every evolutionary trend, and their respective contribution to ammonoid evolution remains to be quantified. Understanding the underlying processes of directed evolution still require further research. Answers to such questions strongly needs adequate quantitative datasets framed with robust phylogenies, comparison against simulated random evolution (to evaluate the prevalence of constraints or chance in generating trends), a better knowledge of shell morphogenesis (to precisely quantify the expectable covariation between measured shell characters), and accounting for both anagenetic and cladogenetic changes.

We expect that further discoveries and the application of quantitative methods and better knowledge of mollusk shell morphogenesis will continue to reveal information on the evolutionary history of this major marine extinct group, the ammonoids, and contribute to the understanding of patterns and processes in macroevolution. If ammonitologists do so, they can become nomothetic scientists, which Stephen Jay Gould would probably have appreciated.

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Part II
Paleobiogeography of Ammonoids

Chapter 6
Biogeography of Paleozoic Ammonoids

Dieter Korn and Kenneth De Baets

6.1 Introduction

Ammonoids are rarely used for detailed paleogeographic studies because they are regarded as being too mobile for the separation of distinct biogeographic units. Due to their pelagic mode of life, their distribution could be influenced by various factors including mode of life, which can change through ontogeny (e.g., different reproductive strategies) as well as post-mortem dispersal (Kennedy and Cobban 1976; Cecca 2002; Ritterbush et al. 2014; Naglik et al. 2015). However, paleogeographic maps with ammonoid occurrences have been illustrated rather frequently for the Devonian (e.g., House 1964; Erben 1966; House 1973a, 1973b, 1981; Becker and Kullmann 1996; Becker 2000a, 2000b; De Baets et al. 2009, 2011, 2013a; Becker and Mapes 2010; Monnet et al. 2011; Bockwinkel et al. 2013), for the Carboniferous (Bogoslovskaya 1997; Korn 1997; Korn et al. 2005, 2012; Nikolaeva 2007; Korn and Titus 2011) and for the Permian (Ehiro 1997, 1998; Leonova 1999, 2011, 2013; Zakharov et al. 2008).

Usually, biogeographic patterns were narratively discussed, e.g. by Kullmann (1962), who already postulated the presence of two ammonoid provinces for the mid-Carboniferous. Quantitative analyses are rare (e.g., Korn 1997; Kutygin 2006; Korn et al. 2010b; Korn and Klug 2012; Korn et al. 2012).

The potential of Paleozoic ammonoids for biogeographic analyses is probably higher than generally assumed. An obstacle, however, is the uneven state of knowledge of the assemblages (lack of precise knowledge of ontogeny, intraspecific variation or biostratigraphy; taphonomic and collection biases), preventing precise

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D. Korn (✉)
Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung,
Invalidenstraße 43, 10115 Berlin, Germany
e-mail: dieter.korn@mfn-berlin.de

K. De Baets
GeoZentrum Nordbayern, Friedrich-Alexander-Universität Erlangen-Nürnberg, Loewenichstraße
28, 91054 Erlangen, Germany
e-mail: kenneth.debaets@fau.de

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analyses of time-equivalent faunas with respect to their taxonomic composition. Further refinement of stratigraphic units and an increase in the precision of morphological limits of species (compare Korn and Klug 2007, 2015; Monnet et al. 2011; De Baets et al. 2013a) will probably enhance the potential for using ammonoids for paleogeographic studies. In the following, four selected time intervals within the Paleozoic will be discussed in terms of ammonoid biogeography.

6.2 Emsian Ammonoid Biogeography

Well-studied species-rich Emsian ammonoid faunas are known from three principal regions (Fig. 6.1), the vicinity of Prague in the Czech Republic (Barrande 1865; Chlupáč and Turek 1983), the Harz and the Rhenish Mountains of Germany (De Baets et al. 2009, 2013b) and the Anti-Atlas of Morocco (Becker and House 1994;

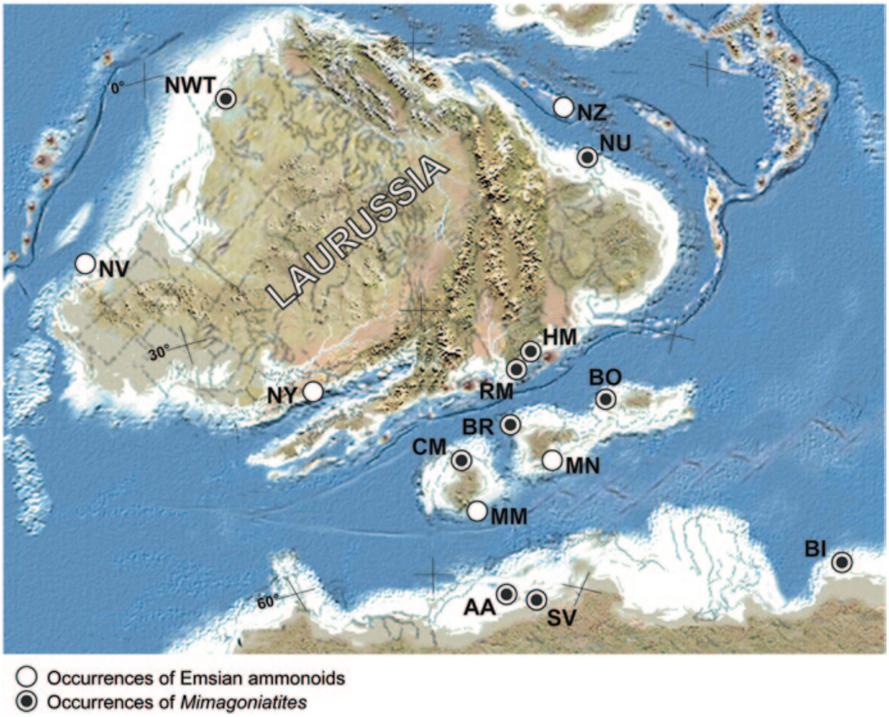

Fig. 6.1 Paleogeographic map for the North Atlantic region for the Emsian. (After Scotese 1997; modified after an image by Ron Blakey, http://jan.ucc.nau.edu/rcb7/) with the position of the most important ammonoid occurrences. *NWT* North West Territories, *NY* New York; *RM* Rhenish Mountains; *HM* Harz Mountains; *BR* Bretagne; *SU* South Urals; *CM* Cantabrian Mountains; *MM* Moroccan Meseta; *MN* Montagne Noire, *BO* Bohemia; *BI* Bithynia; *AA* Anti–Atlas; *SV* Saoura Valley; *NU* North Urals, *NZ* Novaya Zemlya

Klug 2001; De Baets et al. 2010; Ebbighausen et al. 2011). In these studies, distinctive paleogeographic patterns were not documented and many of the genera and species occur in two or even all three of these regions. For the following species, the occurrences in all three regions has been postulated: *Anarcestes lateseptatus* (Beyrich 1837), *A. plebeius* (Barrande 1865), *A. simulans* (Barrande, 1865), *Erbenoceras solitarium* (Barrande, 1865), *Gyroceratites levis* (Eichenberg 1931), *Mimagoniatites bohemicus* (Barrande, 1865), *M. fecundus* (Barrande, 1865), *Sellanarcestes crassior* Walliser, 1965 and *S. tenuior* Walliser, 1965. Several other species have occurrences in the Czech Republic and Morocco. This means that most of the dominant species have a rather wide distribution without any apparent geographic patterns (compare House 1973a, b). The genus *Mimagoniatites*, for instance is present in almost all of the occurrences of Emsian ammonoids (Fig. 6.1), *Erbenoceras* is also a widespread taxon (e.g., De Baets et al. 2013a, 2013b). Both taxa are also found in other species-rich Early Emsian ammonoid faunas like South China (Ruan 1996) and the Zeravshan-Gissar Range Uzbekistan (Becker et al. 2010).

It is unclear if the lack of any paleogeographic patterns is due to uniform faunas, which are spread across the ammonoid-bearing regions or if it is due to the fact that the oldest ammonoids only possess a small number of morphological characters. Variation within genera in these ammonoids is mainly seen in the conch shapes while ornaments and particularly suture lines are less variable (Chlupáč and Turek 1983). The picture is further complicated by a large intraspecific variation in conch shape demonstrated in some early ammonoids (De Baets et al. 2013a) and differences in preservation (De Baets et al. 2013b).

6.3 Late Famennian Biogeography

Ammonoids of late Famennian age are known from numerous localities; their distribution is probably the widest within the Devonian. The most diverse assemblages with the index genera *Gonioclymenia*, *Kalloclymenia* and *Wocklumeria* are known from the area between the Anti-Atlas of Morocco and South China (Fig. 6.2).

Initially, there are no distinct paleogeographic patterns to be seen. Some of the genera such as *Cymaclymenia* (occurring from Ohio to New South Wales), *Cyrtoclymenia* (Utah to South China), *Mimimitoceras* (Ohio to South China), *Sporadoceras* (Ohio to South China) and *Wocklumeria* (Oklahoma to South China) have a near global distribution in the tropical and subtropical zones (Fig. 6.2). Many of the other genera of this time interval are known from the Anti-Atlas to South China; their absence in other regions may be due to sampling effects.

The increasing number of morphological characters used for the descriptions of faunas led to a modified taxonomy with an increasing number of species with limited geographic distribution. New studies (e.g., Klein and Korn 2014; Korn et al. 2014) demonstrate that a species-based correlation of faunas from the Rhenish Mountains and the Anti-Atlas is not possible. Although the two regions share the same genera, their species composition differs based on conch shapes and shell ornamentation.

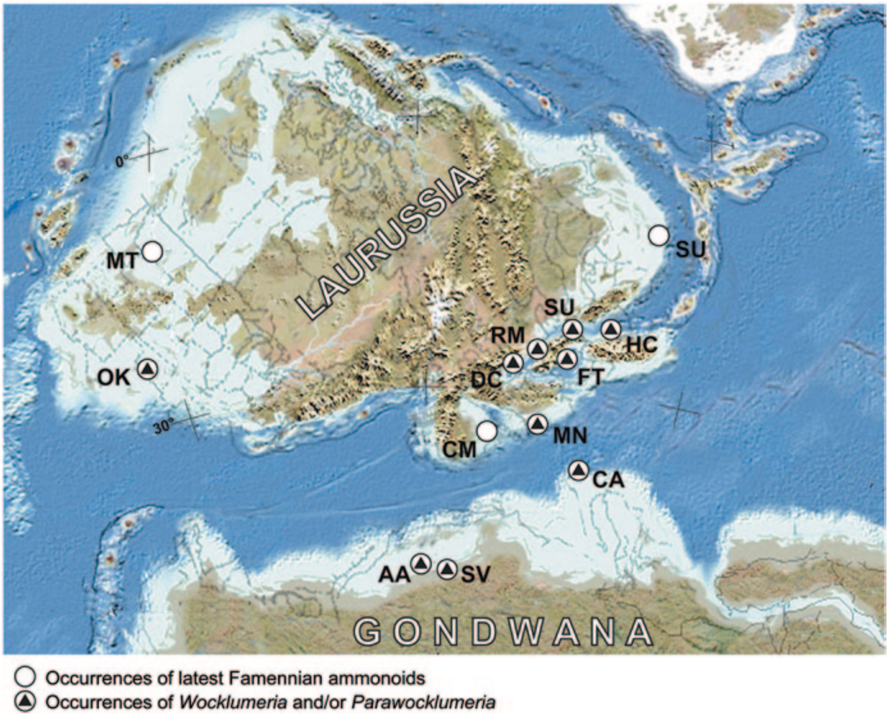

Fig. 6.2 Paleogeographic map for the North Atlantic region for the Famennian. (After Scotese 1997 and Korn et al. 2010b; modified after an image by Ron Blakey, http://jan.ucc.nau.edu/rcb7/) with the position of the most important ammonoid occurrences. *MT* Montana, *OK* Oklahoma; *DC* Devon and Cornwall; *RM* Rhenish Mountains; *SU* Sudetes; *FT* Franconia and Thuringia; *HC* Holy Cross Mountains; *SU* South Urals; *CM* Cantabrian Mountains; *MN* Montagne Noire; *CA* Carnic Alps; *AA* Anti–Atlas; *SV* Saoura Valley

Unfortunately, many of the late Famennian ammonoid species have either been described from insufficiently preserved material or without paying attention to ontogenetic characters or intraspecific variation (see Korn and Klug 2007 for a Frasnian example). Hence, a detailed paleobiogeographic analysis is currently not possible.

6.4 Late Viséan and Serpukhovian Biogeography

The paleobiogeographic distribution of Early Carboniferous ammonoids has been analysed by Korn et al. (2012); six time intervals spanning from the Early Tournaisian to the late Serpukhovian were analysed in that study using quantitative methods (cluster analysis and non-metric multidimensional scaling). The results of these analyses are (discussed in greater detail by Korn et al. 2012):

1. Tournaisian to early Late Viséan.—Ammonoid assemblages from the earliest Carboniferous (Early Tournaisian to early Late Viséan) show a similar wordwide

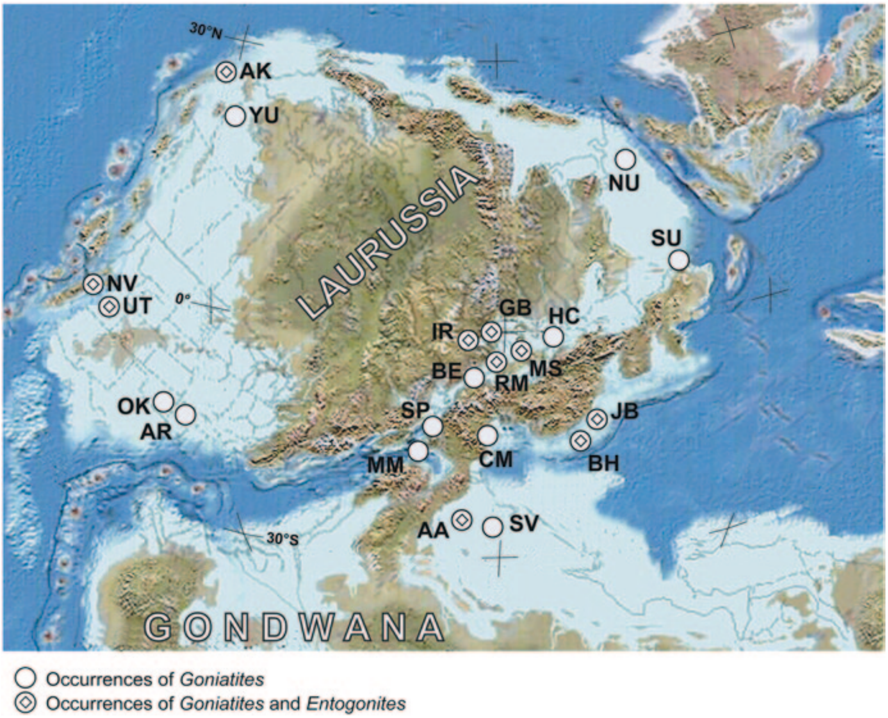

Fig. 6.3 Paleogeographic map for the North Atlantic region for the early Late Viséan. (After Scotese 1997 and Korn et al. 2012; modified after an image by Ron Blakey, http://jan.ucc.nau.edu/rcb7/), showing the distribution of the genera *Entogonites* and *Goniatites*. [*AK* Alaska; *YU* Yukon; *NV* Nevada; *UT* Utah; *OK* Oklahoma; *AR* Arkansas; *MM* Moroccan Meseta; *SP* South Portugal; *IR* Ireland; *BE* Belgium; *RM* Rhenish Mountains; *GB* England; *MS* Moravia and Silesia; *HC* Holy Cross Mountains; *SU* South Urals; *NU* North Urals; *CM* Cantabrian Mountains; *AA* Anti–Atlas; *SV* Saoura Valley; *BO* Bosnia and Herzegovina; *JB* Jadar Block of Serbia]

composition at the genus level. In a relatively short time span after the Devonian-Carboniferous boundary extinction event (Hangenberg Event), some of the most important ammonoid genera (*Acutimitoceras*, *Nicimitoceras*, *Gattendorfia* and *Eocanites*) became widely distributed in the equatorial zone. Distant regions (e.g. the Rhenish Mountains and Guizhou) have similar assemblages. This distribution pattern closely resembles that of the late Famennian. Faunal similarity was maintained up to the Tournaisian-Viséan transition, where several of the genera (e.g. *Dzhaprakoceras*, *Eurites*, *Merocanites*) had an almost global distribution. A similar situation is seen in the early Late Viséan ammonoid assemblages. The genus *Goniatites* is known from nearly all studied regions and *Entogonites, Bollandites* and *Bollandoceras* are widely distributed. The presence of the peculiar ammonoid genus *Entogonites* in very distant regions (Alaska, Nevada and Utah, Ireland, England, Rhenish Mountains, Anti-Atlas, Bosnia and Herzegovina, and Serbia) is of particular interest and may suggest connected shelf areas during the early Late Viséan (Fig. 6.3).

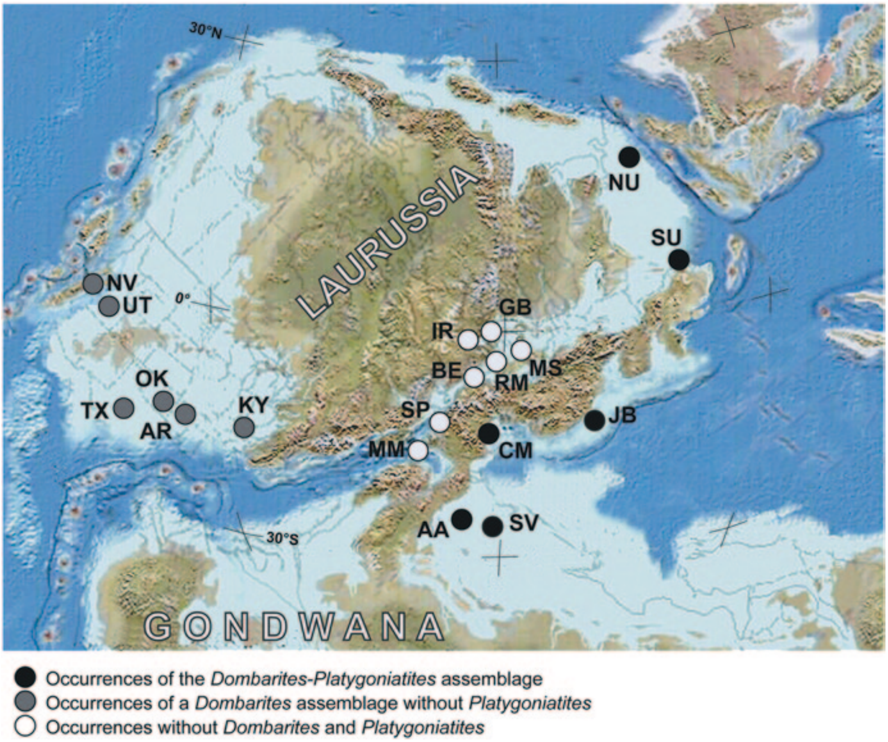

Fig. 6.4 Paleogeographic map for the North Atlantic region for the latest Viséan and early Serpukhovian. (After Scotese 1997 and Korn et al. 2012; modified after an image by Ron Blakey, http://jan.ucc.nau.edu/rcb7/). [*NV* Nevada; *UT* Utah; *TX* Texas; *OK* Oklahoma; *AR* Arkansas; *KY* Kentucky; *MM* Moroccan Meseta; *SP* South Portugal; *IR* Ireland; *BE* Belgium; *RM* Rhenish Mountains; *GB* England; *MS* Moravia and Silesia; *SU* South Urals; *NU* North Urals; *CM* Cantabrian Mountains; *AA* Anti-Atlas; *SV* Saoura Valley; *JB* Jadar Block of Serbia]

2. Middle late Viséan to late Serpukhovian. – During the middle late Viséan, the biogeographic relationships between ammonoid faunas changed drastically. None of the genera appears to be globally distributed and only a few (*Lusitanoceras*, *Sudeticeras*, *Neoglyphioceras*, *Lusitanites*) are known from more than seven of the nine analyzed regions. Two major biogeographic realms can be identified: a north-western realm consisting of the four North Variscan regions (Rhenish Mountains, North England, South Portugal and Moroccan Meseta, which together form a dense cluster in the scatter plot) as well as the American Midcontinent and the Antler Foreland Basin. The second realm includes the South Urals, which is the most diverse region (and thus has an isolated position), as well as the Cantabrian Mountains and the Anti-Atlas, of which the latter two closely resemble each other (Fig. 6.4).

During the early Serpukhovian, development of the biogeographic relationships between the assemblages followed the trend already visible in the Late Viséan. Differences in the ammonoid assemblages are principally caused by the absence of distinct taxa in some of the regions. The North American occurrences now show closer affinities with the Urals.

In the late Serpukhovian, the paleobiogeographic separation of the various regions was completed. The North American occurrences in the Antler Foreland Basin (California, Nevada, Utah) and the American Midcontinent (Texas, Oklahoma, Arkansas) form, together with the occurrences on Novaya Zemlya and the South Urals, a large paleogeographic realm, which also included the South Variscan (Cantabrian Mountains) and most probably the North Gondwanan (e.g. Béchar Basin, not included in this analysis) occurrences. The North Variscan realm (occurrences on the British Isles and Central Europe) became isolated and is mainly characterized by the absence of taxa typical for the other realm.

Assemblages in the North Variscan region are characterised by the genera *Anthracoceras*, *Cravenoceras*, *Cravenoceratoides*, *Eumorphoceras* (a cosmopolitan genus), and *Nuculoceras*. Representatives of the families Delepinoceratidae (*Delepinoceras*), Agathiceratidae (*Proshumardites*), Glaphyritidae (*Glaphyrites*, *Syngastrioceras*, *Eosyngastrioceras*), and Stenoglyphyritidae (*Euroceras*, *Rhadinites*, *Stenoglaphyrites*, *Zephyroceras*) characterise the large North American—Uralian realm.

The dissimilarity analysis of ammonoid assemblages in the selected Early Carboniferous time intervals demonstrates increasing provincialism. While the assemblages of the Tournaisian and early to middle Viséan do not show clear biogeographic patterns, the late Viséan and Serpukhovian faunas are strikingly different between the regions (Fig. 6.4). In detail, the investigations led to the following results (Korn et al. 2012):

1. The Antler Foreland Basin (Nevada, Utah) and the Marathon-Ouachita Foreland Basin (Texas, Oklahoma, Arkansas) form a fairly homogeneous biogeographic unit during the entire Viséan and Serpukhovian; the relationships between the North American and North Variscan ammonoid occurrences (e.g. Rhenish Mountains, North England) are close in the early and middle Late Viséan. Close to the end of the Viséan and in the Serpukhovian, the North American occurrences start to differ from the North Variscan. They show increasing similarity to the Uralian and North Gondwanan occurrences. The North Variscan and North Gondwanan (Anti-Atlas, Saoura Valley) ammonoid occurrences are similar until the early Late Viséan, but thereafter they become strikingly different.
2. The South Variscan (e.g. Cantabrian Mountains, Jadar Block) and North Gondwanan ammonoid occurrences are similar in all analysed time intervals; a wide Paleotethyan Ocean more than 1000 km across (Stampfli et al. 2001; Stampfli and Borel 2002) is thus very unlikely because ammonoid relationships between the South Variscan and North Gondwanan shelves suggest that at least the western end of the Paleotethys (north-western Africa) had to be much narrower to

allow faunal exchange between South Variscan and North Gondwanan shelves during the Late Viséan and Serpukhovian.

3. The Moroccan Meseta belongs, according to its Late Viséan ammonoid faunas, to the North Variscan realm (Korn and Ebbighausen 2008). There is disagreement about the position of the Moroccan Meseta; Stampfli and Borel (2002) place the Moroccan Meseta directly adjacent to the South Portuguese Zone, whereas Torsvik and Cocks (2004) as well as Cocks and Torsvik (2006) see it at the northernmost margin of Gondwana. The first interpretation was supported by Korn et al. (2012).
4. The Jadar Block of Serbia has a spectrum of ammonoid genera very similar to the South Urals and Cantabrian Mountains and belongs to the South Variscan province (Korn et al. 2010a). The ammonoid results confirm the paleogeographic reconstruction by Stampfli and Borel (2002) as well as Stampfli and Kozur (2006), who placed these terranes in a position adjacent to the southern margin of Laurussia.

Thus, at the Viséan-Serpukhovian boundary, two major biogeographic realms are recognisable (Korn et al. 2012): (1) A north-western realm consists of the four North Variscan regions (Rhenish Mountains, North England, South Portugal, and Moroccan Meseta) as well as the American Midcontinent and the Antler Foreland Basin. (2) The second realm includes the South Urals, which is the most diverse region and thus has an isolated position as well as the Jadar Block of Serbia, the Cantabrian Mountains of Spain, the Anti-Atlas of Morocco, and the Saoura Valley of Algeria.

6.5 Early Permian Biogeography

Early Permian biogeographic analyses were done by Leonova (2011) and Korn and Klug (2012), the latter researchers used cluster analysis, cladistic analysis and morphospace analysis. Of the four Early Permian (Cisuralian) stages, the Artinskian has produced the most diverse ammonoid faunas. Rather diverse assemblages are known from several places in the world belonging to various climatic zones and paleogeographic realms:

- Paleotethyan Realm (with Crimea, Central Asia, and South China);
- East Pacific Realm (with Texas and adjacent areas);
- Northern Boreal Realm (with occurrences in the Urals, East Asia, and Arctic Canada);
- Southern Hemisphere (with Western Australia).

The diverse faunas from the listed regions enable the application of several quantitative biogeographic methods, some of which have been used for an analysis outlined in the following.

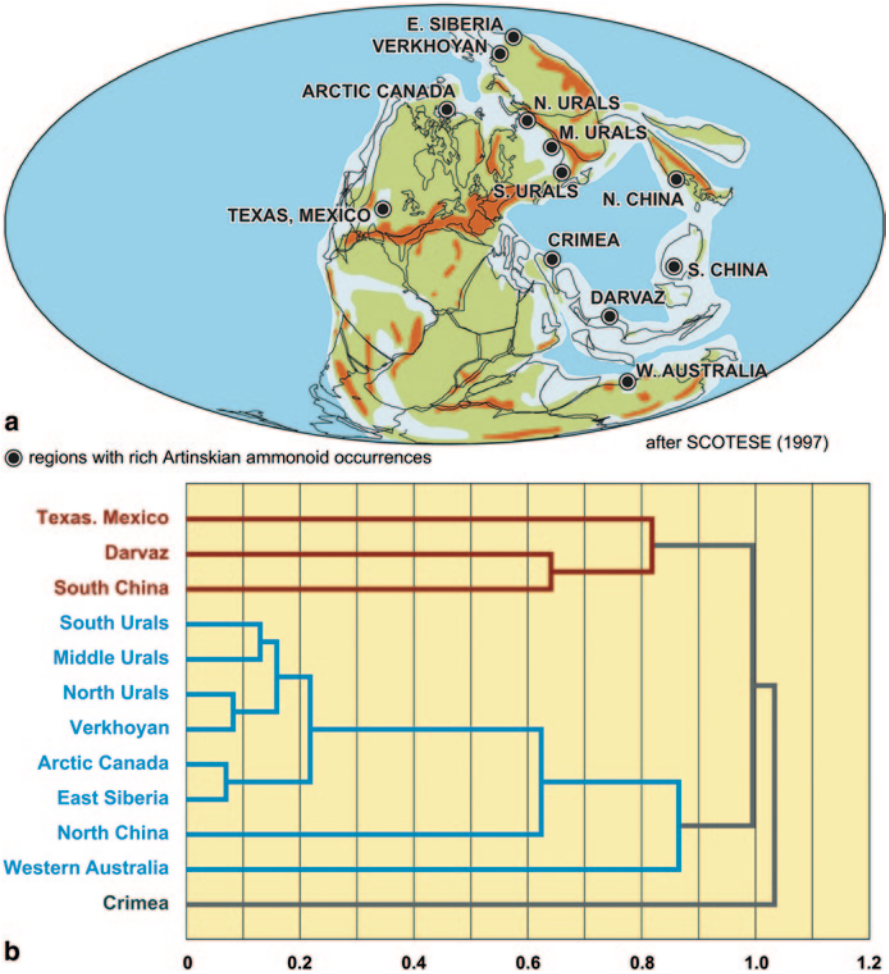

Fig. 6.5 Early Permian paleogeography (after Scotese 1997) and the most important regions with Artinskian ammonoids (**a**) and cluster analysis of the main regions with Artinskian ammonoids (**b**) based on the occurrence and species diversity of genera, calculated with 1-Pearson-r algorithm. *Brown* color refers to warm water faunas, *blue* color refers to temperate and cold waters (from Korn and Klug 2012)

6.5.1 Cluster Analysis

Investigation of the number of species per genus and region of the 12 most important regions (Fig. 6.5) by cluster analysis using the 1-Pearson r algorithm offers a clear view on paleogeographic relationships. The resulting diagram enables discrimination of two major clusters, which coincide with climatic zones:

1. The equatorial realm unifies the East Pacific and Paleotethyan occurrences, but with a rather wide distance between them separated by the Panthalassan Ocean.
2. The temperate and colder water occurrences form the second big cluster. Two subclusters are visible: Western Australia and northern China are separated from a dense subcluster, which contains occurrences in the Urals, eastern Asia and Arctic Canada.

Some of these paleobiogeographic patterns were expected and can be explained by geographic proximity, such as close clustering of the northern occurrences. However, other patterns raise questions, which currently cannot be answered: Why are the Eastern Pacific and Paleotethyan occurrences rather similar, and how can a co-occurrence of genera be explained? Why are occurrences in the northern realm rather similar to those in Western Australia, and how can co-occurrence of genera, missing in the equatorial region, be explained? Additional study of these and other occurrences may help resolve these questions.

6.5.2 Cladistic Analysis

Cladistic analyses have been applied only rarely in ammonoid research (Landman 1989; Korn 1997, 2001; Yacobucci 1999, 2012; McGowan and Smith 2007; Neige et al. 2007). A cladistic analysis with the paragastrioceratid ammonoids, which are particularly diverse in the Permian, allows integration of a sufficient number of characters. Twenty-one morphologically well-known genera were included with *Trochilioceras* representing the outgroup. Thirty-three characters were shown to be informative, resulting in three most parsimonious trees with 349 steps, of which the 50 % majority rule tree is shown here (Fig. 6.6).

The cladogram shows that two major monophyletic units can be separated, one consisting of the subfamily Paragastrioceratidae and the descendant family Spirolegoceratidae, the other consisting of the two subfamilies Pseudogastrioceratinae and Aulacogastrioceratinae. The paleogeobiographic distribution of these two clades is separated: the paragastrioceratids occur in the boreal province and the pseudogastrioceratids are characteristic of the equatorial belt. The results gained from the phylogenetic analysis of one of the major Permian ammonoid groups corroborate the results from the cluster analysis summarized above from Korn and Klug (2012).

6.5.3 Morphospace Analysis

In a third attempt, Korn and Klug (2012) analysed the conch morphology of all Permian ammonoids with respect to spatial and temporal patterns mainly based on the monographic descriptions by Miller and Furnish (1940), Ruzhencev (1956),

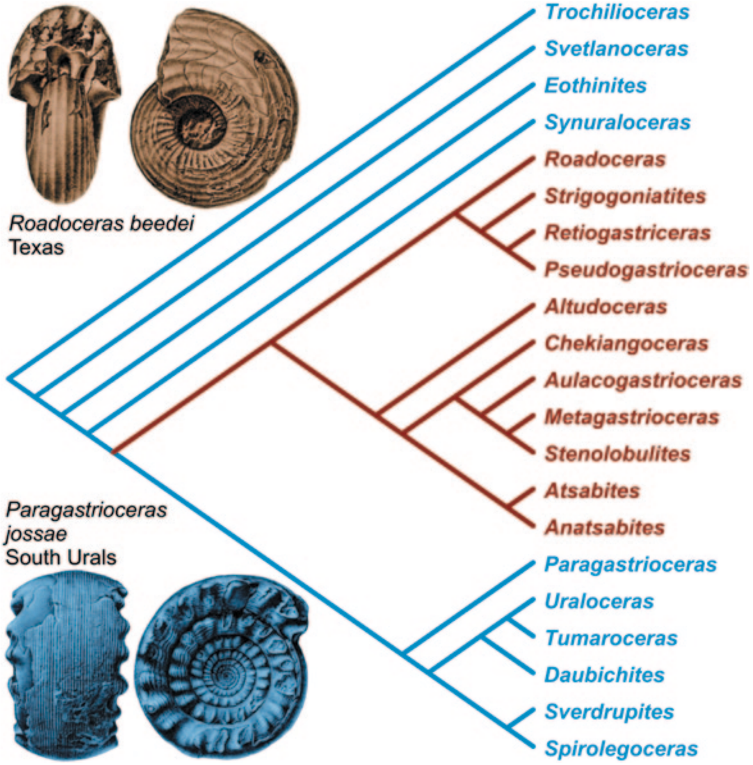

Fig. 6.6 Cladistic analysis of the Permian ammonoid family Paragastrioceratidae using PAUP 50% majority rule tree of three most parsimonious trees; 33 informative characters; tree length 349 steps; consistency index 0.39. *Brown* color refers to genera occurring in warm water faunas (with *Roadoceras* as a characteristic example), *blue* color refers to temperate and cold waters (with *Paragastrioceras* as a characteristic example) (from Korn and Klug 2012). Vote the monophyletic crown groups of cold water genera and warm water genera, respectively

Bogoslovskaya (1962), Andrianov (1985), Leven et al. (1992), etc. Of the cardinal conch parameters, the whorl expansion rate (WER) and the umbilical width index (uw/dm) produced, when plotted in bivariate morphospace diagrams, produced the most informative results (Fig. 6.7). All 180 investigated species display a distribution with three more densely occupied clusters, representing the three major ammonoid morphs of the Early Permian:

- *Paragastrioceras* Morph: Subevolute to evolute conchs (uw/dm = 0.30–0.65) with low aperture (WER = 1.35–1.90);
- *Almites* Morph: Involute to subinvolute conchs (uw/dm = 0.00–0.20) with low aperture (WER = 1.40–1.90);
- *Artinskia* Morph: Involute to subinvolute conchs (uw/dm = 0.00–0.20) with high aperture (WER = 2.20–3.30).

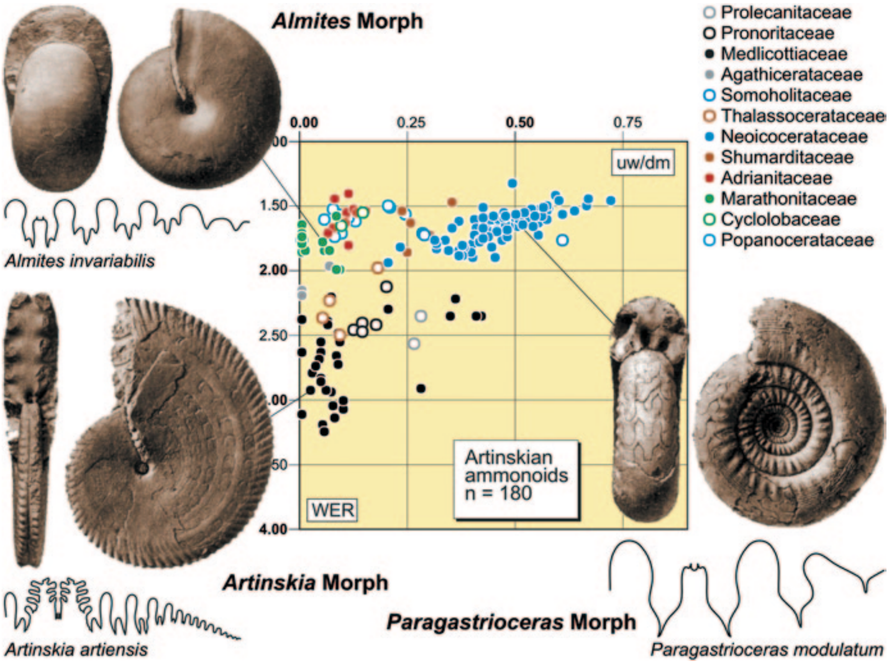

Fig. 6.7 Bivariate plots showing the WER and uw/dm values of Artinskian ammonoids with respect to their attribution to superfamilies (from Korn and Klug 2012)

Separation of the morphs by their conch shape is supported by patterns in the suture line and, to a lesser degree, by shell ornament (Fig. 6.7). The *Paragastrioceras* Morph has a simple goniatitic suture and often possesses a coarse radial or spiral ornament. The *Almites* Morph often shows increasing sutural complexity with addition of elements and serration of lobes; the shell is usually rather weakly ornamented. Finally, the *Artinskia* Morph also shows increase in suture elements and further subdivision, mainly in the ventral portion; the shell is weakly ornamented except for ventral nodes in a few species.

In the scatter plot of all 180 species using principal components analysis, the three morph clusters have a similar concentration (Fig. 6.8). When the various regions are plotted separately by using the umbilical width index and whorl expansion rate, striking differences between some of the regions are displayed. The most diverse assemblage is the one from the southern Urals. In this assemblage, the three morphs are separated, with the *Paragastrioceras* Morph being the most important followed by the *Almites* and *Artinskia* Morphs (Fig. 6.9). In occurrences farther north (Middle Urals, North Urals, East Asia and Arctic Canada), the two latter morphs decrease in their importance, whereas the *Paragastrioceras* Morph remains stable and strikingly dominant (Fig. 6.9c–6.9f). The equatorial occurrences differ from the boreal in the less important representation of the *Paragastrioceras* Morph;

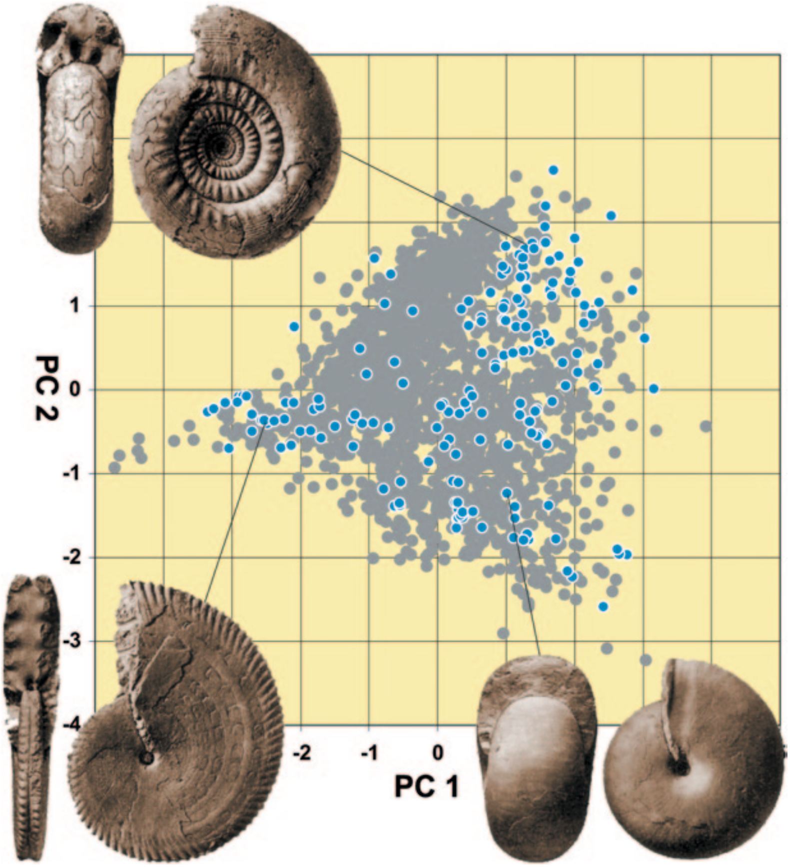

Fig. 6.8 Morphospace occupation using conch parameters: whorl expansion rate, umbilical width index, whorl width index, and imprint zone rate of the ammonoids from the latest Carboniferous to Early Triassic (from Villier and Korn 2004; Korn and Klug 2012)

here, the *Almites* and *Artinskia* Morphs are predominant (Fig. 6.9g). The results also confirm the results of cluster diversity analysis; the main ammonoid provinces are separated by the morphology pattern (Korn and Klug 2012).

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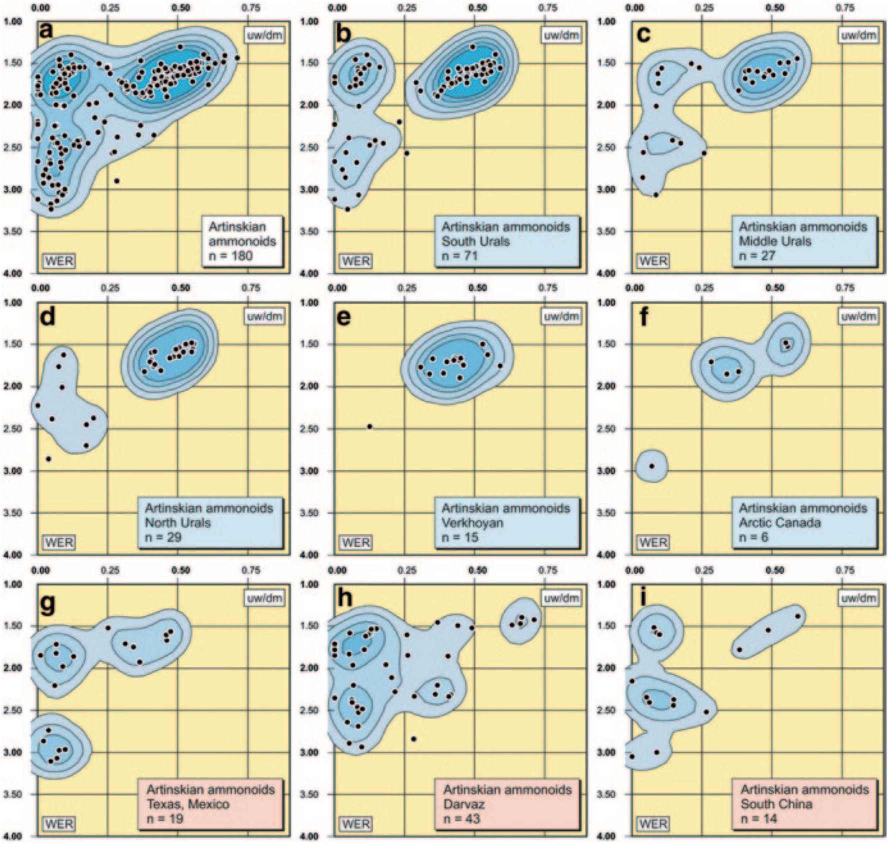

Fig. 6.9 Bivariate plots showing the WER and uw/dm values of Artinskian ammonoids in various regions (from Korn and Klug 2012)

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Chapter 7
Biogeography of Triassic Ammonoids

Arnaud Brayard, Gilles Escarguel, Claude Monnet,
James F. Jenks and Hugo Bucher

7.1 Introduction

Ammonoids nearly died out during the Permian-Triassic (PT) mass extinction (~252 Ma), but quickly and rather impressively recovered in less than ~1.5 myr during the Early Triassic (Tozer 1981a; Brayard et al. 2009a; Brayard and Bucher 2015; Fig. 7.1). Only one survivor group, a derivative of the Xenodiscaceae, is usually considered as the root-stock of all Triassic, and thus, all post-Triassic ammonoids (Kummel 1973a; Spinosa et al. 1975; Tozer 1981a, 1981b; Page 1996; Brayard et al. 2006), making post-PT ammonoids a "quasi-monophyletic" group (but see Kummel 1972; Glenister and Furnish 1981; Brayard et al. 2007a; McGowan and Smith 2007; Leonova 2011; Zakharov and Moussavi Abnavi 2013). The Triassic

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A. Brayard (✉)
UMR CNRS 6282 Biogéosciences, Université de Bourgogne, 21000 Dijon,
6 boulevard Gabriel, France
e-mail: arnaud.brayard@u-bourgogne.fr

G. Escarguel
UMR CNRS 5276, Laboratoire de Géologie de Lyon: Terre, Planètes, Environnement,
Université Claude Bernard Lyon 1, 27–43 Boulevard du 11 novembre 1918,
69622 Villeurbanne Cedex, France
e-mail: gilles.escarguel@univ-lyon1.fr

C. Monnet
UMR CNRS 8217 Géosystèmes, UFR des Sciences de la Terre—Bât. SN5,
Université de Lille 1, Avenue Paul Langevin, 59655 Villeneuve d'Ascq cedex, France
e-mail: claude.monnet@univ-lille1.fr

J. F. Jenks
1134 Johnson Ridge Lane, 84084 West Jordan, UT, USA
e-mail: jenksjimruby@gmail.com

H. Bucher
Paläontologisches Institut und Museum, Universität Zürich,
Karl-Schmid Strasse 4, 8006 Zürich, Switzerland
e-mail: hugo.fr.bucher@pim.uzh.ch

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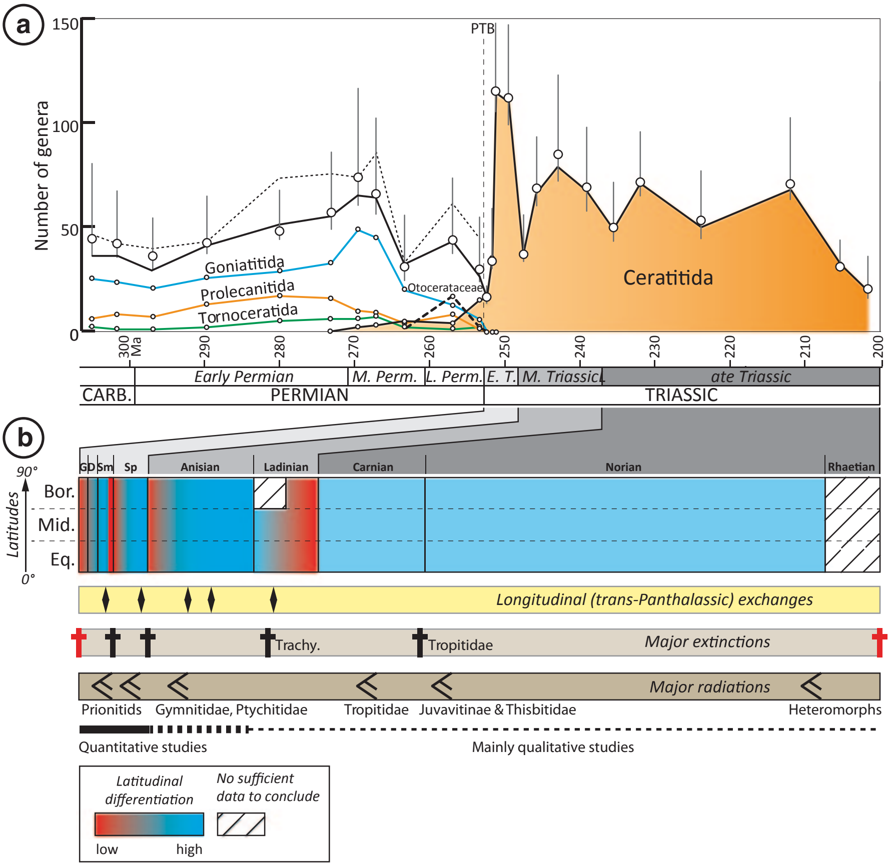

Fig. 7.1 **a** Total generic richness (*black bold line*: all ammonoids; *colored lines*: major ammonoid groups; *Permian bold line*: data from Goniat.org; *Permian dotted line*: alternate data from the AMMON database (Korn and Ilg 2007); *Triassic bold line* modified after Brayard et al. (2009a) based on an updated database) and mean Chao2 estimate of the overall generic richness with its 95 % Confidence Interval (*large circles* with vertical bars). *PTB* Permo-Triassic boundary. *E.T.* Early Triassic. Note that the end-Smithian ammonoid extinction event discussed in the text is not illustrated here due to its short time duration. **b** Present well-known biogeographical and evolutionary patterns. *Bor.* Boreal, *Mid.* Middle, *Eq.* Equatorial

remains one of the most interesting and intriguing periods for ammonoid evolution as it is marked by successive episodes of intense radiation and marked extinction associated with sudden biogeographic changes often closely related to major climatic and oceanographic changes (e.g. Tozer 1982; Dagys 1988; Dagys and Ermakova 1990; Brayard et al. 2006, 2007b, 2009a, c; Monnet and Bucher 2006a; Galfetti et al. 2007a; Konstantinov 2008; Zakharov et al. 2008; Balini et al. 2010; Monnet et al. 2013; Zakharov and Moussavi Abnavi 2013). The end of the Triassic is also marked by the enigmatic appearance of the first heteromorphs and a further near-annihilation at the Triassic/Jurassic boundary (~201 Ma).

Ammonoid diversity and disparity patterns are now well-known globally and certain restricted Triassic intervals have been intensively studied (e.g. for the Early

Triassic: McGowan 2004, 2005; Brayard et al. 2007b, 2009c; Brosse et al. 2013). However, until recently, the biogeographical trends of Middle and Late Triassic ammonoids for the most part were only superficially investigated, and the same is true for their potential underlying processes (Kummel 1973b; Tozer 1981a, 1981b, 1982; Dagys 1988; Page 1996; Fig. 7.1). Indeed, they most often were based only on qualitative comparisons between uneven geographic areas (e.g. from local outcrops to global realms, according to the author's subjectivity) or between distinct taxonomic groups. Previous biogeographic studies of Triassic ammonoids were not often focused on a specific time-interval and were rarely based on quantitative methods (but see Kummel and Steele 1962 for a noticeable exception).

Significant biogeographic progress has been made recently with regard to the use of quantitative methods on large datasets combined with computer modeling (Brayard et al. 2004, 2006, 2007b, 2009c). These large datasets benefited from the infusion of much new primary data generated by intensive fieldwork and carefully-revised taxonomy (e.g. Monnet and Bucher 2005; Jenks 2007; Brayard and Bucher 2008; Shigeta and Zakharov 2009; Guex et al. 2010; Jenks et al. 2010; Ware et al. 2011; Balini et al. 2012a, 2012b; Brühwiler et al. 2012a, 2012b, 2012c; Brayard et al. 2013; Zakharov and Moussavi Abnavi 2013) occasionally combined with recently-published radiometric ages (e.g. Galfetti et al. 2007a; Schaltegger et al. 2008). This chapter emphasizes these quantitative methods and inferred relationships between ammonoid biogeographical changes during the Triassic and potential controlling factors such as gradients of Sea Surface Temperature (SST) and oceanic circulation. The biostratigraphic framework used in the following discussion is detailed in the chapter "Triassic biostratigraphy" (Jenks et al. 2015).

7.2 What's New in Triassic Ammonoid Macroecological and Biogeographical Analyses?

7.2.1 Classical Analyses and Explored Patterns

The vast majority of studies of past and present-day global diversity have demonstrated the existence of pervasive geographic patterns such as a Pole-to-Equator gradient, both on land and sea (e.g. Stehli et al. 1969; Gaston 2000; Powell 2007). Others have shown for instance, different large-scale patterns in longitude (e.g. Connolly et al. 2003), altitude (e.g. McCain 2004), bathymetry (e.g. Pineda and Caswell 1998), endemism (e.g. Gaston 1994), range size (Gaston 2003), or size of organisms (e.g. Roy et al. 2001; Zhang and Payne 2012). However, the processes explaining the edification of such large-scale patterns, and especially the latitudinal diversity gradient, are still a matter of debates (e.g. Brayard et al. 2005; Colwell et al. 2005; Jablonski et al. 2006; Escarguel et al. 2008; Beaugrand et al. 2013). One of the core questions remains the very existence and overall importance of deterministic (functional) drivers over historical contingency in generating and controlling such macroecological patterns. Because evolutionary time is a dimension lacking in neontological studies, fossil-based deep-time analyses can greatly improve the knowledge and understanding of the edification of these large-scale patterns.

Ammonoids are generally well-suited for such analyses due to their widespread geographical distribution and high evolutionary rates. Most diversity and biogeographic studies are based on taxonomic count and geographic occurrences because these measures are (i) the simplest to acquire, (ii) expected to be the most robust to sampling biases, and (iii) less arbitrary in their definition and measurements. Temporal dynamics in richness and evolutionary rate changes in ammonoids are customarily represented as curves based on the succession of studied time bins. As these analyses often compare intervals with different duration, sampling intensity, paleoenvironments or geographic scales, their results may not be directly comparable, if not intrinsically biased. However, some of these biases can be controlled, if not at least partly ruled out, using for instance traditional sample-based rarefaction curves (Foote 1992; Dommergues et al. 2009) in order to compare the taxonomic diversity estimates at comparable levels of sampling effort. Other potential bias such as the unequal duration of time bins, from which diversity counts are obtained, can be circumvented by the use of Unitary Association Zones. These have been demonstrated to be largely immune to this problem (Escarguel and Bucher 2004).

Regarding ammonoid biogeographical structuring, quantitative large-scale analyses remain rather uncommon and are defined at different time-scales and taxonomic levels according to the available data (e.g. McGowan 2005; Brayard et al. 2006, 2007b, 2009c; Dommergues et al. 2009; Dera et al. 2011; Korn et al. 2012). Basic extraction of the biogeographical signal as the inter-locality compositional similarity is often (if not automatically) done by classical hierarchical cluster analysis (hCA) and nonmetric multidimensional scaling (NMDS), applied to different specific time slices (sub-zones to stages). Both hCA and NMDS analyses are based on the preliminary computation of a symmetrical matrix of dissimilarity using a coefficient chosen a priori by the author (e.g. for taxonomic occurrence data, the Dice [= Sørensen = Bray–Curtis for presence/absence data], Simpson, or Jaccard coefficients; Shi 1993; Legendre and Legendre 2012). On the one hand, hCA focuses on the nested taxonomic relationships between assemblages and is therefore not suited for the identification of a gradational signal. On the other hand, NMDS (usually preferred to more conventional ordination techniques such as Principal Component Analysis or Principal Coordinates Analysis due to the non-Euclidean, semi-metric nature of the taxonomical space defined by most of these [dis]similarity coefficients) is intended to extract inter-gradational information in a low-dimensional reduced space and is therefore not well suited to the identification of hierarchical structures. As these two approaches are based on distinct assumptions about the nature of the inter-assemblage similarities embedded in the analyzed dataset, a comparison and combination of their results reinforces the confidence in the identified biogeographical structures. Nevertheless, although intuitive and widespread in our community, both methods also have several disadvantages (Brayard et al. 2007b). For instance, NMDS may misrepresent a gradational similarity structure in a 2D or 3D reduced space whereas analyzed objects are distinct in higher (unseen) dimensions of the reduced space. hCA and NMDS analyses for the Middle and Late Triassic time intervals are herein presented and discussed for the first time (Figs. 7.2 and

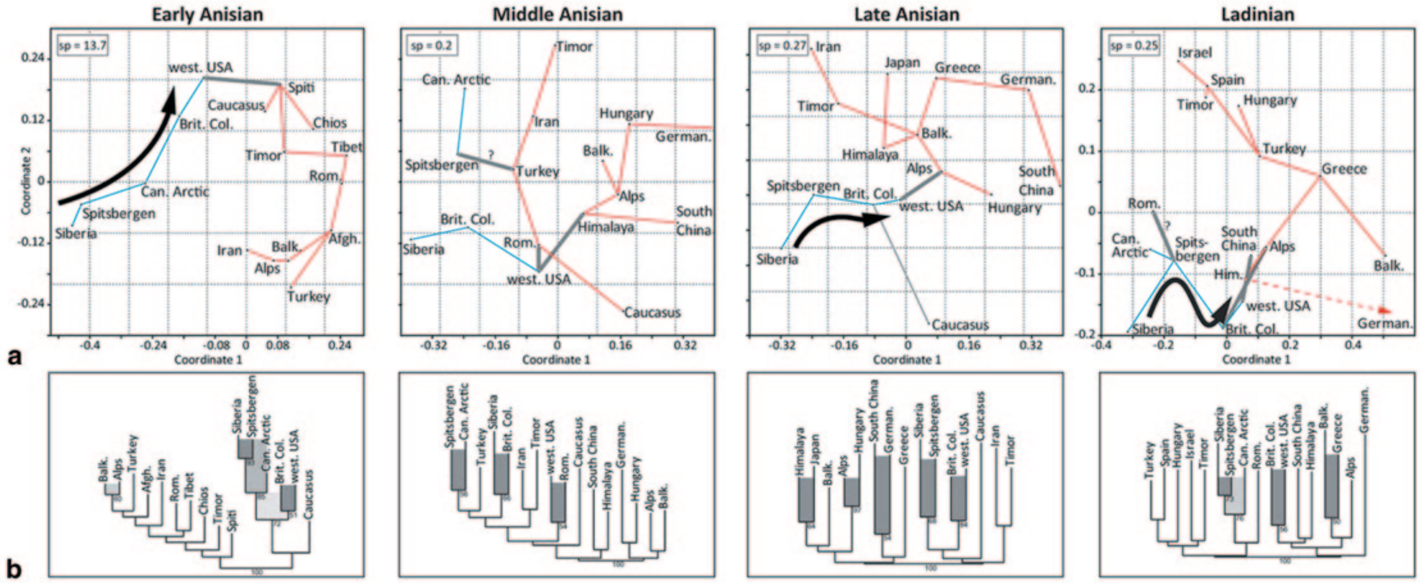

Fig. 7.2 Biogeographical structuring for each stages of the Middle Triassic based on Bray–Curtis dissimilarity matrices (see Brayard et al. 2007b, 2009c for the Early Triassic). **a** Nonmetric Multidimensional Scaling map and superimposed Minimum Spanning Tree (stress is indicated by the Shepard plot [sp] value). *Black arrows* indicate gradational biogeographic structures. *Can. Arctic* Canadian Arctic, *Brit. Col*. British Columbia, west. *USA* western USA, *Balk*. Balkans, *Rom*. Romania, *German*. Germanic. Basin, *Afgh*. Afghanistan. **b** Hierarchical Cluster analyses (bootstrap supports estimated with 1000 iterations;< 50 % when not indicated)

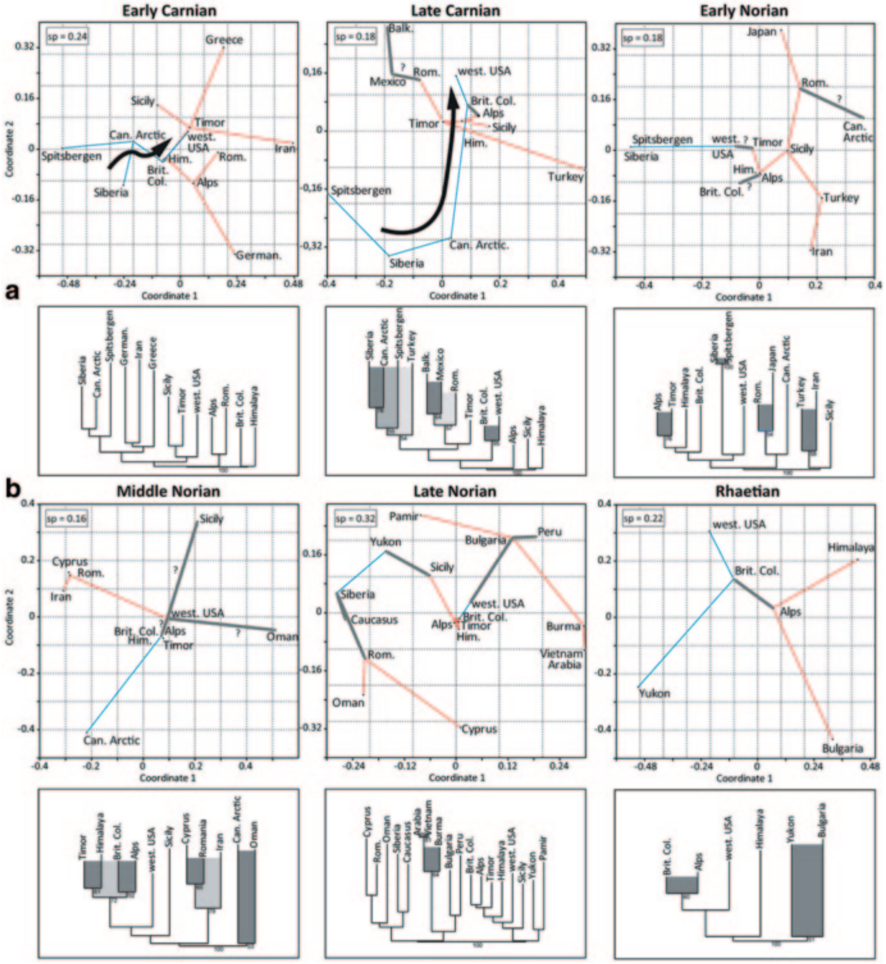

Fig. 7.3 Biogeographical structuring for each stages of the Late Triassic based on Bray–Curtis dissimilarity matrices. (See Fig. 7.2 for details)

7.3; for computational details about these analyses and Early Triassic results, see Brayard et al. 2007b, 2009c).

Remarkably, hCA analyses rarely identify strongly supported biogeographical hierarchies for Middle and Late Triassic ammonoids. Only the early and late Anisian show clusters with support values greater than 50 % and intuitive geographic associations. Complementary NMDS maps often better emphasize biogeographical differentiations especially between Tethyan and Panthalassic basins (early and late Anisian, Ladinian, Carnian, early Norian and Rhaetian), and a potential latitudinal structuring along the eastern Panthalassa (early and late Anisian, Ladinian, Carnian). Combining both methods, the middle Anisian, and the middle and late Norian do not show any well-defined biogeographical structuring.

7.2.2 Recent Analytical Advances

7.2.2.1 "Overall" Diversity Estimators

Based on the available (locality to basin-scale) occurrences of taxa among samples for each studied time bin, a bias-corrected incidence-based Chao's estimator (Chao2; Chao 1984, 1987) and second-order jackknife estimator (Jackniffe2; Smith and van Bell 1984) of "overall" (i.e. sampled + still unsampled) taxonomic richness can be computed. Both indices are well-known to ecologists (e.g. Walther and Moore 2005; Gotelli and Colwell 2011); they usually provide broadly similar results and are among the most reliable incidence-based nonparametric estimators of "overall" richness in ecological assemblages (Walther and Moore 2005). Nevertheless, in the context of paleobiogeographical studies, and according to the very nature of available data (often generic occurrences within basins), these quantities might not be viewed as statistical estimators of "overall" richness, but rather as indicators of (i) the sampling quality of the available fossil record and (ii) comparability of the inter-basinal structure of sampled incidence between the analyzed time bins (Brayard et al. 2009a; Escarguel ongoing work). Revised Chao2 estimates for the Early Triassic are given in Fig. 7.1, updating Brayard et al.'s (2009a) results.

7.2.2.2 Rarefaction and Extrapolation Curves

It is well known that the sampled taxonomic richness of a locality directly depends on the underlying sampling effort, and thus the available sample size. To circumvent this potential bias when comparing unevenly-sampled assemblages, ecologists and paleontologists traditionally use rarefaction methods as a means to "reduce" larger samples to the size of the smallest one, and then directly compare these rarefied richness estimates (Gotelli and Colwell 2001, 2011). However, this approach is not flawless. For instance, since the sample richness of a Tropical assemblage is usually far from its true richness due to the presence of many rare taxa, this can lead to a strongly underestimated rarefied richness when compared to the sample richness of a Boreal assemblage (Chao and Jost 2012). An alternate approach was recently offered by Chao and Jost (2012), who provided an elegant analytical solution for coverage-based rarefaction, "coverage" being a measure of sample completeness. Contrary to classical, sample size-based rarefaction, coverage-based rarefaction preserves the real degree of difference between the communities' richnesses, even for small sample size, and provides a sampling "stopping rule". Chao and Jost (2012) and Colwell et al. (2012) also provided an analytical solution for the extrapolation of sample richness to higher coverage instead of larger sample size, thus unifying coverage-based interpolation (rarefaction) and extrapolation into a single curve. Unified rarefaction and extrapolation curves for the 14 Triassic time intervals are given in Fig. 7.4.

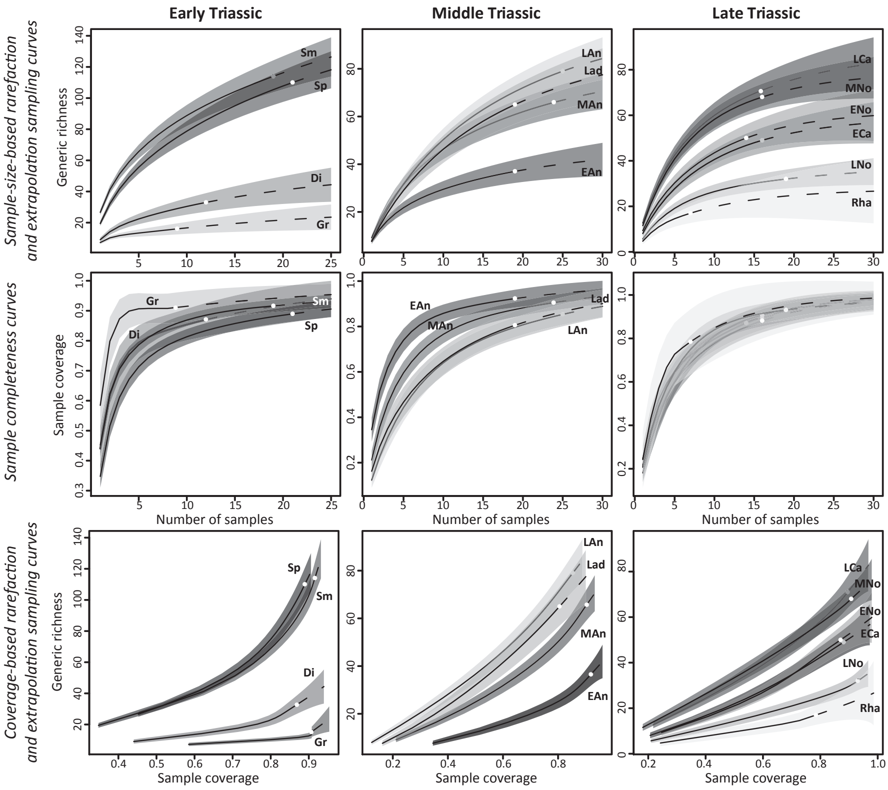

Fig. 7.4 Rarefaction and extrapolation curves for the Triassic. *Solid lines*: interpolation curves; *dashed lines*: extrapolation curves; *white circles*: sample coverages. *Gr* Griesbachien, *Di* Dienerian, *Sm* Smithian, *Sp* Spathian, *EAn* early Anisian, *MAn* middle Anisian, *LAn* late Anisian, *Lad* Ladinian, *ECa* early Carnian, *LCa* late Carnian, *ENo* early Norian, *MNo* middle Norian, *LNo* late Norian, *Rha* Rhaetian

Sample-size rarefaction and extrapolation curves for the Early Triassic indicate that the estimated richness for the Smithian and Spathian is much higher than for the Griesbachian and Dienerian. However, all time intervals have rather similar sample coverage values (between ~0.85 and ~0.92), indicating that: (i) data can be directly compared to each other and are not likely to result from major sampling artifacts, and (ii) extrapolation is thus not needed. Sample coverages for the Dienerian and the Spathian being slightly lower than the two others, also suggest that the sampling effort for these two sub-stages is currently lower than for the Smithian and possibly also for the Griesbachian. Lower values of sample coverages for the late Anisian and Ladinian also point to the same hypothesis. Extrapolation may be useful in these two cases, suggesting higher estimated richnesses than for the early and late Anisian. Concerning the Late Triassic, only the Rhaetian value of sample coverage is lower than for other time intervals, which therefore can be directly compared to each other. Extrapolation curves for the Middle and Late Triassic intervals do not significantly change interpretations based on rarefaction.

7.2.2.3 Endemicity

The degree of endemicity (or, conversely, cosmopolitanism), i.e. the relative number of sampling units within which a given taxon occurs (hereafter called its "occurrence ratio"), is a fundamental life history trait directly or indirectly related to several other ecological and evolutionary features, from demographic dynamics to extinction probability (Gaston 1994; Kunin and Gaston 1997). Brayard et al. (2006) proposed an original approach to test the "occurrence ratio profile" (ORP) of a set of taxa against the null hypothesis of a random distribution of those taxa within the sampled localities. An ORP is a 10-bin histogram summarizing the frequency distribution of the occurrence ratio estimated for each sampled taxon. Confidence intervals are estimated for each ORP-bin through nonparametric bootstrap (random re-sampling of taxa with replacement), whereas a null ORP-model is generated by random permutation of taxa within localities, corresponding to the null hypothesis that, contrary to taxonomical richness (which remains unchanged by this permutation procedure), the taxonomical composition of each assemblage is not controlled by its geographic location and/or its environmental properties (permutation model #3 in Legendre et al. 1997). The ORPs and associated null-models for the 10 Middle and Late Triassic time intervals are given in Fig. 7.5 (see Brayard et al. 2006 for the Early Triassic ORPs).

While the early Anisian, Ladinian and late Norian empirical ORPs clearly match their associated null-distribution model, thus suggesting lack of strong geographical and/or environmental constraints in the distribution of taxa among the sampled basins, all other ORPs depart from this null model by showing: (i) more than expected highly endemic (o.r. <0.1) and weakly to highly cosmopolitan (o.r. >0.5) taxa, (ii) less than expected moderately endemic taxa ($0.1<$ o.r. <0.2), but (iii) frequencies of weakly endemic taxa ($0.2<$ o.r. <0.5) close to expectation from the null model. Lastly, the Rhaetian ORP suggests a contrasted situation with abundant highly endemic and moderately to highly cosmopolitan taxa, but without any weakly endemic to cosmopolitan genera. Nevertheless, this ultimate ORP must be interpreted cautiously, as it is based on a very small dataset, thus precluding any firm conclusion.

7.2.2.4 Biogeographic Relationships: A Network-Based Approach

The combined analysis of inter-assemblage taxonomical similarities through hierarchical clustering and ordination techniques is not flawless with respect to taxonomical occurrence or abundance data (Legendre and Legendre 2012). Critically, these techniques implicitly assume that such datasets define continuous and homogeneous topological spaces, which is generally not the case. As several combinations of taxa are a priori impossible for historical (phylogenetic and/or biogeographic) as well as functional (ecological) reasons, taxonomical data indeed define pretopological spaces where the concepts of similarity and neighborhood are formally decoupled (Čech 1966). In order to account for this major methodological constraint, Brayard et al. (2007b) developed an original approach leading to the visualization of a simi-

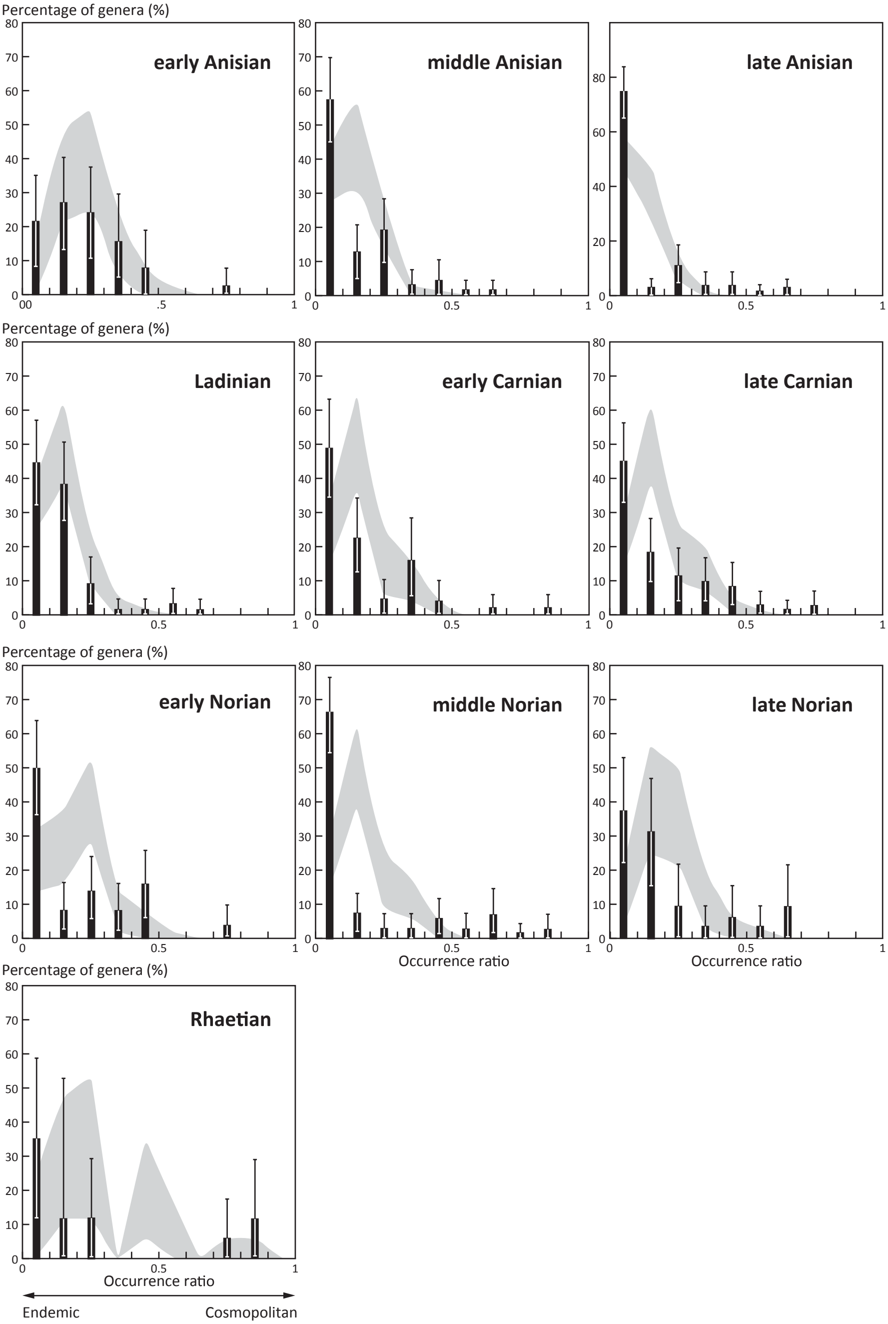

Fig. 7.5 Generic Occurrence Ratio Profiles for Middle and Late Triassic ammonoids (see Brayard et al. 2006 for the Early Triassic). Bootstrapped 95 % Confidence Intervals associated with the observed Occurrence Ratios (error bars on the histogram) estimated with 10,000 iterations; 95 % ORP null distribution (*shaded area*) estimated with 10,000 iterations under a lottery permutation model (see Brayard et al. 2006 for details)

larity structure as a connected network of neighborhoods called a "bootstrapped spanning network" (BSN). Departing from a combined set of undirected "minimum spanning networks" (Prim 1957; Excoffier and Smouse 1994) nonparametrically bootstrapped from the sampled data, a BSN is computed by iterative removal, from the weakest links (i.e. links with lowest bootstrap supports) up to the best-supported ones, until: (i) the resulting network is no longer connected, or (ii) the overall product of bootstrap supports of the remaining links no longer increases (see Brayard et al. 2007b for algorithmic details). As a consequence, a BSN is not a "minimal" structure (the length of a link is not considered in the removing procedure), but rather "the simplest connected network best supported by the available data" (Brayard et al. 2007b, p. 755). Here, we illustrate the spatialized BSN corresponding to the 10 Middle and Late Triassic time intervals (Figs. 7.6, 7.7 and 7.8; see Brayard et al. 2007b, 2009c for the Early Triassic BSNs).

As expected, the BSNs demonstrate the latitudinal structuring of ammonoids in eastern Panthalassa as previously suggested by NMDS for the early and late Anisian and Ladinian (Fig. 7.2), but they also identify such a connection for the middle Anisian (Fig. 7.6). They modulate the Ladinian (Fig. 7.6) and Carnian (Fig. 7.7) latitudinal structuring in eastern Panthalassa as suggested by NMDS (Figs. 7.2 and 7.3), thus highlighting that links between localities are sometimes weak (Ladinian) or reticulate (Carnian). Moreover, the BSN provides additional precision about the other remaining Tethyan localities. For instance, dense connections in the western Tethys for the early Anisian are evidenced as well as the relative (middle to late Anisian) to near complete (Ladinian) isolation of the Germanic basin. The BSN also shows intertropical trans-Panthalassic connections during the Middle Triassic (Fig. 7.6). These links increase in number and change in latitude during the late Carnian (Fig. 7.7) and middle and late Norian (Fig. 7.8), suggesting a more cosmopolitan distribution of ammonoids at that time.

Visual investigation of the BSNs coupled with the paleogeographic location of the compared assemblages usually allows the identification of groups of related basins (here, two or three, depending on the time interval) whose differences in taxonomical composition can be further tested for significance against the null hypothesis of among-group random compositional differences. This can be done readily through one-way analysis of similarity (ANOSIM; Clarke 1993) or nonparametric multivariate analysis of variance (NP-MANOVA; Anderson 2001), in both cases using the same coefficient of taxonomical similarity (in this work, using the Dice [= Sørensen = Bray–Curtis for presence/absence data] coefficient). Although the ANOSIM procedure always appears more conservative (larger *p*-values) than NP-MANOVA, both techniques identify the very same time intervals as having significant differences among groups of taxonomical assemblages (Table 7.1). Whereas all Smithian to Ladinian time intervals return significant results indicating marked compositional differences between the Panthalassic and Tethyan realms, all Late Triassic time intervals but the 2-group early Norian test return non-significant results, suggesting a more homogeneous distribution of ammonoid genera between the two realms at that time. The two first Early Triassic time intervals show marginally-significant (Griesbachian) to non-significant (Dienerian) differences at a 5 %-significance level, in both cases based on a small sample size, suggesting

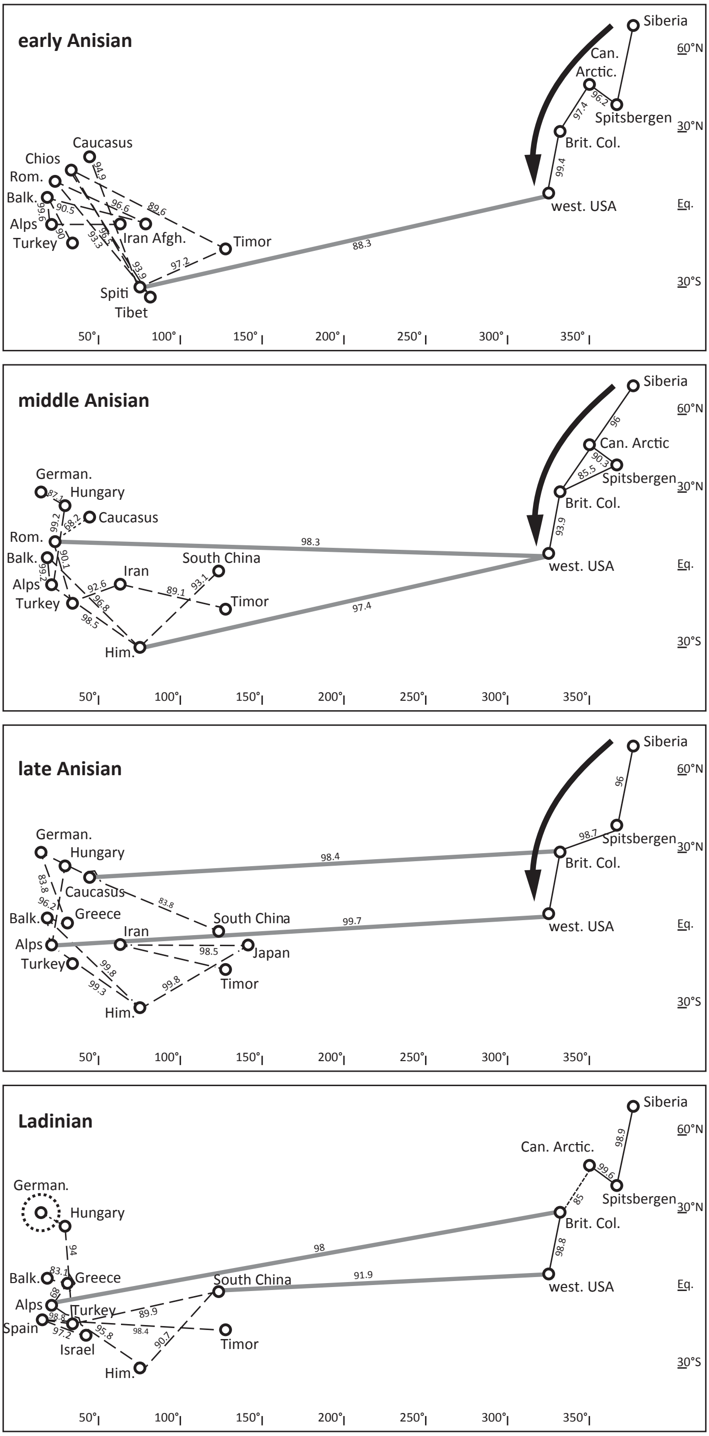

Fig. 7.6 Bootstrapped Spanning Networks for Middle Triassic ammonoids. Numbers indicate the bootstrap support values for each edge (100 % when not reported; see Brayard et al. 2007b, 2009c

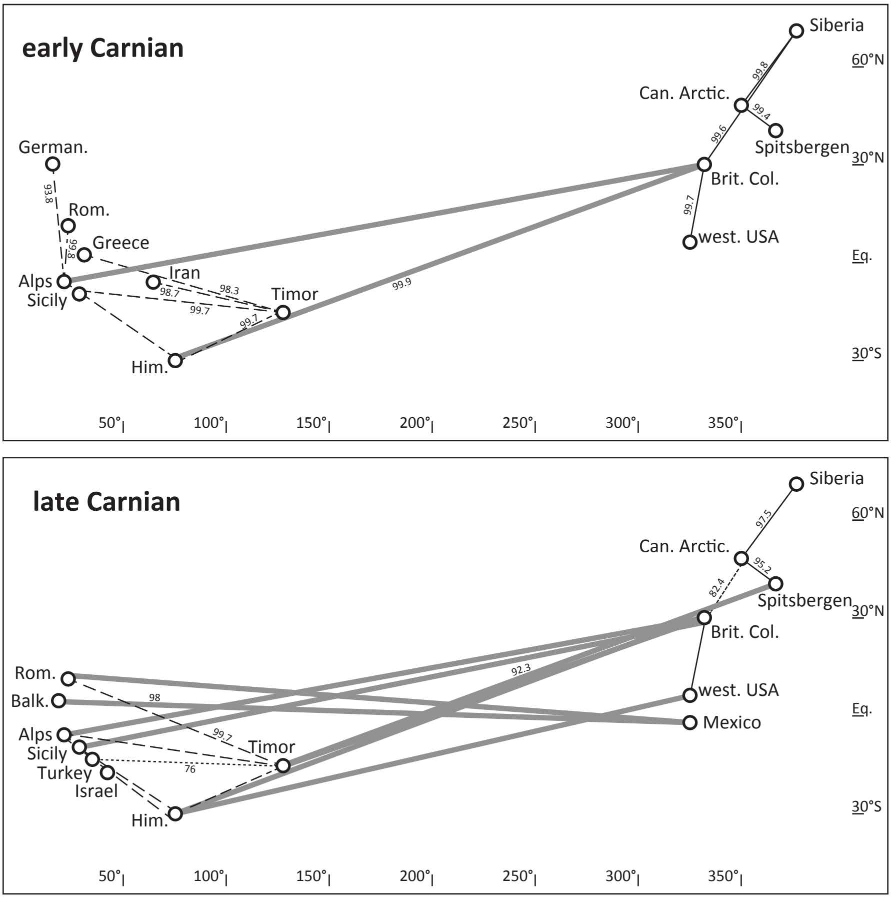

Fig. 7.7 Bootstrapped Spanning Networks for Carnian ammonoids. (See Fig. 7.6 for details)

the extremely low statistical power of such results, and thus lack of actual geographical structuring in these two cases. The early Anisian and Ladinian time intervals show a noteworthy configuration, as their respective ORPs do not depart from the null hypothesis of a random distribution of taxa within the sampled localities (see previous paragraph), whereas the present results demonstrate significant among-group compositional differences. These seemingly contradictory results point to taxonomically homogeneous groups of assemblages—hence a significant

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for details and Early Triassic BSN). Paleolatitudes are approximated from Early Triassic maps (see Brayard et al. 2006) and arbitrarily considered to not vary too much between the Middle and Late Triassic for graphic convenience. *Black arrows* indicate observed latitudinal gradational biogeographic structures. *Bold dotted line* around the Germanic basin during the Ladinian illustrates the isolation of this basin at that time.

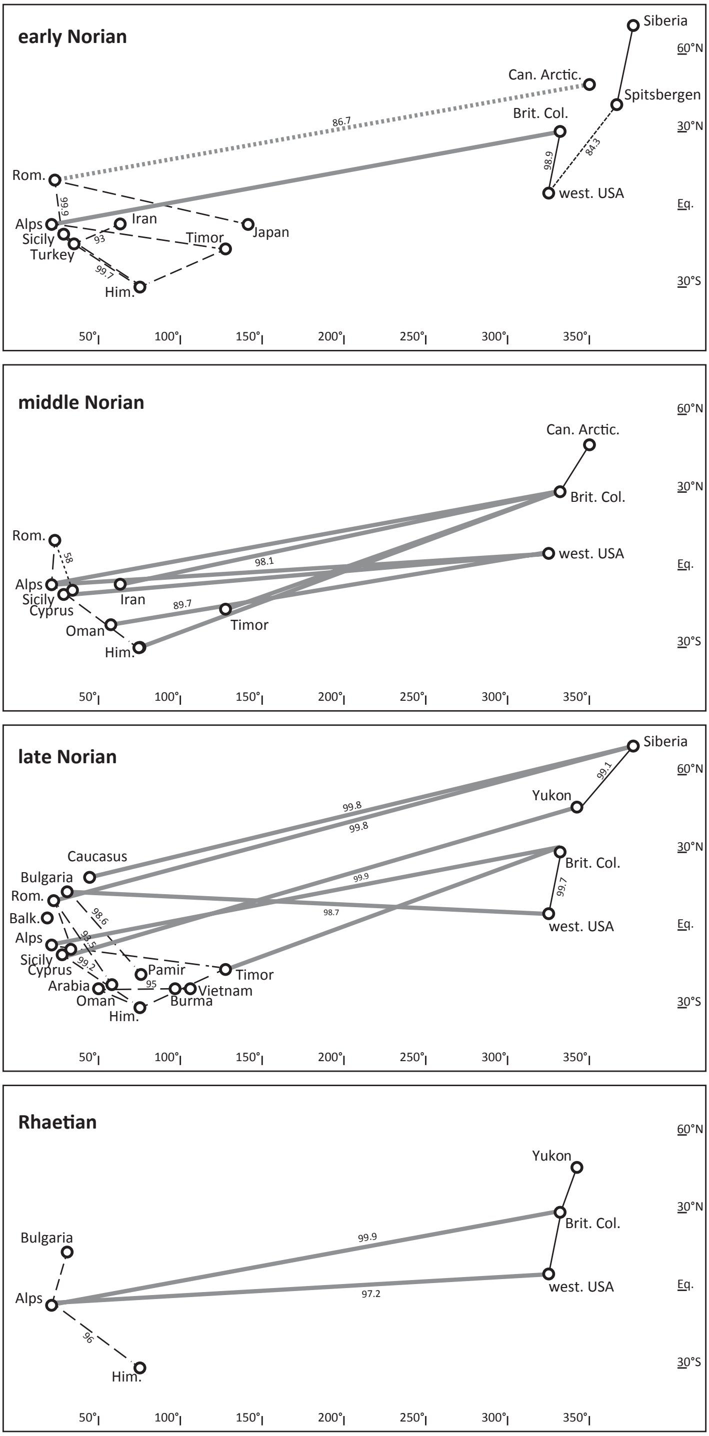

Fig. 7.8 Bootstrapped Spanning Networks for Norian and Rhaetian ammonoids. (See Fig. 7.6 for details)

Table 7.1 One-way ANOSIM and NP-MANOVA results, showing the Triassic time intervals with significantly different groups of taxonomical assemblages. Two-group partitioning: Eastern Panthalassa *vs*. Tethys; three-group partitioning: Eastern Panthalassa *vs*. Eastern Tethys *vs*. Western Tethys. Contrast analysis: ANOSIM- or NP-MANOVA-based pairwise comparisons, including a sequential Bonferroni correction for multiple testing

	ANOSIM		NP-MANOVA		Contrast analysis (pairwise comparisons, identifying groups of assemblages with significant differences)
	R	*P*	pseudo-F	*p*	
Griesbachian (2 gr.)	0.307	0.0285*	3.33	0.0285*	East. Panthalassa-Tethys
Dienerian (2 gr.)	0.207	0.054 NS	2.77	0.062 NS	None
Smithian (2 gr.)	0.246	0.006**	3.63	0.0032**	East. Panthalassa-Tethys
Spathian (3 gr.)	0.317	0.0025**	3.34	0.0008***	All (NP-MANOVA); all but West.-East. Tethys (ANOSIM)
Early Anisian (2 gr.)	0.841	0.0002***	11.09	0.0002***	East. Panthalassa-Tethys
Early Anisian (3 gr.)	0.553	0.00024***	6.33	0.00013***	East. Panthalassa-West. and East. Tethys
Middle Anisian (3 gr.)	0.295	0.01*	2.36	0.0056**	East. Panthalassa-West. Tethys
Late Anisian (3 gr.)	0.326	0.0023**	2.31	0.0002***	All (NP-MANOVA); all but West.-East. Tethys (ANOSIM)
Ladinian (3 gr.)	0.489	0.00006***	2.72	0.0001***	All
Early Carnian (3 gr.)	0.127	0.123 NS	1.445	0.075 NS	None
Late Carnian (3 gr.)	0.037	0.35 NS	1.21	0.24 NS	None
Early Norian (2 gr.)	0.375	0.01*	2.54	0.0045**	East. Panthalassa-Tethys
Early Norian (3 gr.)	0.096	0.21 NS	1.44	0.13 NS	None
Middle Norian (2 gr.)	−0.017	0.47 NS	0.813	0.61 NS	None
Middle Norian (3 gr.)	−0.028	0.58 NS	0.872	0.64 NS	None
Late Norian (3 gr.)	0.080	0.17 NS	1.352	0.165 NS	None
Rhaetian (2 gr.)	0.352	0.10 NS	1.69	0.20 NS	None

NS $p \geq 0.05$; *$p \geq 0.01$; **$p \geq 0.001$; ***$p < 0.001$

biogeographical structuring—where taxa tend to be relatively widespread within their group—hence a lack of highly-endemic genera.

Lastly, when a non-random compositional difference is detected by the ANOSIM and NP-MANOVA procedures, a SIMPER analysis (Clarke 1993) allows the identification of those taxa most contributing to the among-group "overall average dissimilarity" (OAD, using the same coefficient of taxonomic similarity as used

Table 7.2 SIMPER results for Triassic time intervals showing ANOSIM- and NP-MANOVA-based significant differences among groups of taxonomic assemblages (same group-partitioning as in Table 7.1). OAD: among-group overall average dissimilarity; $N_{50\%}$, $N_{80\%}$; number (percentage) of genera contributing to 50% and 80% of OAD, respectively; List of the $N_{50\%}$ genera: genera contributing to 50% of OAD, ranked in order of decreasing contribution to OAD

Time interval	OAD	$N_{50\%}$, $N_{80\%}$	List of the $N_{50\%}$ genera
Smithian (2 gr.)	55.6	19 (31 %), 34 (56 %)	*Melagathiceras*, *Clypeoceras*, *Prionolobus*, *Anaxenaspis*, *Arctoceras*, *Pseudoceltites*, *Euflemingites*, *Paranannites*, *Aspenites*, *Inyoites*, *Owenites*, *Flemingites*, *Wyomingites*, *Cordillerites*, *Prionites*, *Juvenites*, *Wasachites*, *Xenoceltites*, *Kashmirites*
Spathian (3 gr.)	70.8	24 (26 %), 49 (53 %)	*Procladiscites*, *Keyserlingtes*, *Sulioticeras*, *Prohungarites*, *Cordillerites*, *Columbites*, *Isculitoides*, *Stacheites*, *Metadagnoceras*, *Subcolumbites*, *Tirolites*, *Zenoites*, *Albanites*, *Procarnites*, *Ussurites*, *Proptychitoides*, *Leiophyllites*, *Paragoceras*, *Nordophiceras*, *Fengshanites*, *Dagnoceras*, *Dalmatites*, *Hemilecanites*, *Pseudodinarites*
Early Anisian (2 gr.)	80.3	10 (27 %), 21 (57 %)	*Lenotropites*, *Ussurites*, *Discogymnites*, *Grambergia*, *Stenopopanoceras*, *Gymnites*, *Psilosturia*, *Karangatites*, *Leiophyllites*, *Sturia*
Early Anisian (3 gr.)	69.9	10 (27 %), 20 (54 %)	*Psilosturia*, *Ussurites*, *Grambergia*, *Sturia*, *Lenotropites*, *Stenopopanoceras*, *Aegeiceras*, *Discogymnites*, *Paracrochordiceras*, *Gymnites*
Middle Anisian (3 gr.)	77.8	18 (27 %), 36 (55 %)	*Ussurites*, *Anagymnotoceras*, *Acrochordiceras*, *Balatonites*, *Gymnites*, *Intornites*, *Norites*, *Proarcestes*, *Megaphyllites*, *Stenopopanoceras*, *Ptychites*, *Bulogites*, *Ismidites*, *Proteusites*, *Nicomedites*, *Sageceras*, *Discoptychites*, *Beyrichites*
Late Anisian (3 gr.)	89.0	17 (21.5 %), 39 (49 %)	*Gymnites*, *Frechites*, *Nevadites*, *Intornites*, *Japonites*, *Proarcestes*, *Monophyllites*, *Kellnerites*, *Flexoptychites*, *Longobardites*, *Judicarites*,?*Megaphyllites*, *Paraceratites*, *Amphipopanoceras*, *Epigymnites*, *Reitziites*, *Parapopanoceras*
Ladinian (3 gr.)	84.7	15 (23 %), 33 (51 %)	*Istreites*, *Proarcestes*, *Indigirites*, *Asklepioceras*, *Protrachyceras*, *Argolites*, *Sphaerocladiscites*, *Daxatina*, *Frankites*, *Muensterites*, *Arpadites*, *Arctoptychites*, *Longobardites*, *Thanamites*, *Iberites*
Early Norian (2 gr.)	84.5	9 (18 %), 23 (47 %)	*Hypocladiscites*, *Paracladiscites*, *Pterosirenites*, *Cladiscites*, *Dimorphites*, *Juvavites*, *Arcestes*, *Griesbachites*, *Thisbites*

by the ANOSIM and NP-MANOVA), based on an additive decomposition of the contribution of each taxon to OAD (Table 7.2). In all cases studied here, ~25 % of the genera together generate half of the overall average compositional dissimilarity among groups of basins (~50 % controlling 80 % of OAD), highlighting the uneven contribution of each genus to the overall biogeographic signal. It is worth noting here that the lists of those genera driving the biogeographic differentiation bring together long- and short-ranging taxa, suggesting that ammonoid longevity is not strongly related to their endemicity level, a rather counterintuitive result that remains to be further investigated.

7.3 Exploring Revised Data: Refining Patterns and Underlying Processes

7.3.1 Early Triassic

Updated generic richness (GR) patterns for the Early Triassic are given in Fig. 7.1. Compared to Brayard et al. (2009a), the rapid rediversification of ammonoids is still obvious, with even higher estimated total GR for the Griesbachian, Dienerian and Smithian, which is a direct consequence of the numerous detailed monographs published recently from various areas (Shigeta and Zakharov 2009; Jenks et al. 2010; Ware et al. 2011; Brühwiler et al. 2012a, 2012b, 2012c; Zakharov and Moussavi Abnavi 2013). Unpublished Spathian data still lead to the underestimation of its GR, which is likely above the Smithian value. Evolution of the Early Triassic GR was already detailed in Brayard et al. (2009a).

The existence of a latitudinal gradient of generic richness (LGGR) was the first Early Triassic large-scale biogeographical pattern investigated based on a taxonomically homogeneous dataset (Brayard et al. 2006, 2007b). Based on a basin-level spatial resolution allowing realistic reconstruction of large-scale biogeographical patterns, this analysis departed from previously published macroecological studies on past diversity patterns. The results of this work mainly indicated that the global first-order trend in increasing ammonoid diversity was accompanied by a progressive change from cosmopolitan to latitudinally-restricted distribution during the Early Triassic (Brayard et al. 2006). This lead to the emergence of a clear latitudinal diversity gradient during most of the Smithian and Spathian sub-stages (Brayard et al. 2006, Fig. 11). Based on the likely assumption that ammonoids were temperature-sensitive organisms, this also strongly suggests the progressive appearance of a marked latitudinal temperature gradient during the Early Triassic, with maximum differentiation during the Smithian and Spathian (see also Kummel 1973b and Dagys 1988, 1997). However, this global trend was not a continuous process as it was interrupted at least once during a brief episode of ammonoid cosmopolitanism combined with a marked extinction event during the end-Smithian (e.g. Tozer 1981b, 1982; Dagys 1988, Brayard et al. 2006).

Brayard et al. (2006) also used quantitative analyses of endemicity based on the ORP to complete their study on the biogeographical structuring of faunas. They clearly indicated a rapid increase in the percentage of endemic genera concomitant with the edification of the LGGR, notwithstanding a sudden return to a cosmopolitan structuring during the end-Smithian (Brayard et al. 2006, Figs. 7–9).

The biogeographical structure of faunal assemblages was also explored by means of coupled hCA, NMDS and BSN analyses (Brayard et al. 2007b, 2009c). These three combined approaches provided further evidences for an increase in steepness of the latitudinal temperature gradient during the Early Triassic. In particular, identified inter-locality relationships confirmed that the very beginning of the Early Triassic (Griesbachian) corresponds to a very simple biogeographical setting with assemblages dominated by common cosmopolitan genera. This context shifts rapidly to a more heterogeneous configuration (as confirmed here by the NP-MANOVA and ANOSIM comparisons of Tethyan *vs*. Panthalassic assemblages; Tables 7.1 and 7.2), indicative of a more endemic and latitudinally-restricted distribution of ammonoids during the Smithian and Spathian. Nevertheless, BSN results also highlight the development of a marked intertropical faunal belt across the Tethys and Panthalassa at that time, due to the co-occurrence of certain ammonoid genera on opposite sides of the Panthalassa illustrating latitudinally-restricted faunal exchanges during the Smithian (Brayard et al. 2009b, 2013; Jenks et al. 2010), Spathian (Galfetti et al. 2007a; Guex et al. 2010) and end-Spathian (Monnet et al. 2013).

The formation of an ammonoid LGGR during the Early Triassic is likely concomitant with the emergence of a latitudinal temperature gradient in the world ocean. The end-Smithian event has been qualitatively recognized for over 30 years (Tozer 1982; Dagys 1988), but its potential causes remained elusive until recently. Indeed, the rapid collapse of the ammonoid LGGR, the common occurrence of low diversity and cosmopolitan faunas and the high taxonomic similarities among regional assemblages clearly point to a global oceanographic and climatic event such as a return to a weak latitudinal temperature gradient (Brayard et al. 2006, 2007b, 2009c). Additional evidence of a global end-Smithian event first came from various palynological, sedimentological and geochemical analyses (Galfetti et al. 2007a, 2007b, 2007c). Recent $\delta^{18}O$ isotopic analyses measured on conodont apatite, provide a good proxy for sea-surface temperatures and indicate that the Smithian-Spathian boundary was accompanied by a ~8 °C drop down in the Tethys (Romano et al. 2013).

Most if not all Early Triassic ammonoids are very likely derived from a single PT-survivor species. They thus represent an ideal case of a "quasi-monophyletic" clade evolving in a stable geologic framework, only depending on the oceanographic setting (SST, currents, etc.), Brayard et al. (2004) ran their "geophyletic model" (Brayard et al. 2004, 2005; Escarguel et al. 2008) using Early Triassic paleogeography to simulate the Early Triassic diversification and diversity distribution of ammonoids. The "geophyletic model" is a serial automaton simulation model of the "General Simulation Model" family (Gotelli et al. 2009); it has been shown to produce realistic large-scale diversity patterns under extant geographic and oceanographic settings (Brayard et al. 2005; Escarguel et al. 2008). The principal result of these simulations is that the formation of a LGGR basically depends on the shape and magnitude of the SST gradient, corroborating the working hypothesis of a direct causal link between changes in the SST gradient and the LGGR.

7.3.2 Middle Triassic

Ammonoid-based quantitative and global-scale analyses for Middle Triassic time intervals are much scarcer in the literature than for the Early Triassic, in that most of the known biogeographical patterns are only qualitatively characterized (Fig. 7.1). The Spathian/Anisian boundary is characterized by a marked faunal turnover associated with the radiation of mid-Triassic families such as Arcestidae (Dagys et al. 1979; Monnet and Bucher 2005; Konstantinov 2008; Balini et al. 2010). During the Anisian, latitudinal differentiation of assemblages seems to be maintained at levels comparable to the Smithian or Spathian (Galfetti et al. 2007c; Balini et al. 2010), which suggests a lingering tight link between the SST gradient and the LGGR. As shown here, the BSN approach underlines a clear latitudinalisation of the biogeographical structures with a northeastern Panthalassic gradient during the Middle Triassic (Fig. 7.6). Faunal heterogeneity also seems to have increased globally from the early Anisian to the late Anisian, as suggested by the increasing among-group overall average dissimilarity (OAD; Table 7.2), possibly due to climatic fluctuations (Zakharov et al. 2008) or tectono-eustatic events such as transgression on various epicontinental seas (Balini et al. 2010). For instance, beginning in the late Anisian, a significant number of endemic taxa repeatedly developed within the Germanic basins, where the endemism level fluctuated according to successive immigration events enabled by transgressions and corridors openings (Urlichs and Mundlos 1985; Klug et al. 2005). This is well illustrated by BSN analyses (Fig. 7.6) where the Germanic basin appears to be almost completely isolated from other localities during the late Anisian and Ladinian. This led to transient regional diversity hotspots that oftentimes complicated large-scale accurate correlation (e.g. Monnet and Bucher 2005, 2006b). The middle/late Anisian transition and the late Anisian are marked by an increase in taxa shared by both sides of the Panthalassa, but particularly more so along the western coast of Pangea (Dagys 1988; Monnet and Bucher 2005; Monnet et al. 2007, 2008). This biogeographic structuring is well confirmed by BSN results (Fig. 7.6). In contrast with the Anisian, Ladinian ammonoids are customarily assumed to be more cosmopolitan with extremely similar assemblages across latitudes, Tethys and the Panthalassa (Tozer 1981b; Dagys 1988). However, we provide evidence here with BSN analyses (Fig. 7.6) that a biogeographical latitudinal structure of faunal relationships persists during the Ladinian along the eastern Panthalassa, although possibly somewhat weaker than during the Anisian (see also Konstantinov 2008). A marked differentiation between the Tethys and Panthalassic basins is also confirmed by the NP-MANOVA and ANOSIM comparisons (Table 7.1), again indicative of rather heterogeneous distributions of ammonoids during the Ladinian. Nevertheless, the related ORP (Fig. 7.5) does not indicate an excess of moderately to highly endemic genera (o.r. < 0.2), showing that such structuring is driven by genera that are relatively well distributed within their respective biogeographical realms.

7.3.3 Late Triassic

Previous works on the biogeographical structuring of the Late Triassic have been mostly qualitative. Successive episodes of extinction and radiation (e.g. at the base of the late Carnian) are well known from the Carnian and Norian. However, the biogeographical differentiation of ammonoid faunas is more or less identical during both intervals, with an apparent marked LGGR that is probably due mainly to the paucity of the Boreal record (Dagys 1988; Balini et al. 2010). Boreal assemblages also appear rather endemic, but cosmopolitan genera persist, facilitating large-scale correlation (Balini et al. 2010). While both early and late Carnian BSNs clearly indicate an eastern Panthalassa latitudinal structuring (see also Konstantinov and Sobolev 2004), the intensity of biogeographical relationships between the Tethyan and Panthalassic realms markedly increases through time (Fig. 7.7). A weak but significant biogeographical distinction reappears during the early Norian (Fig. 7.8), as also evidenced by the NP-MANOVA and ANOSIM analyses (Table 7.1). However, this pattern does not hold true with a closer time resolution because the earliest early Norian ammonoid faunas from British Columbia clearly show boreal influences (Balini et al. 2012b), while those of the late Early Norian are more similar to those from the Tethys. Middle and late Norian BSNs do not show any clear pattern, illustrating the return to a globally homogeneous biogeographical configuration.

The base of the late Norian is characterized by the appearance of the first heteromorphic genus (*Rhabdoceras*) and the Rhaetian by the numerical increase in heteromorph taxa. These heteromorphs appear rather common, but known Rhaetian occurrences still remain scarce (e.g. Dagys et al. 1979; Tozer 1994), thus preventing any firm biogeographical interpretation, as also shown by the BSN based on the entire fauna (Fig. 7.8).

7.4 What's on the Horizon?

Until now, macroevolution, biogeography and macroecology have remained relatively independent research fields. However, bringing them together in a unified, descriptive and predictive approach offers new exciting perspectives in the understanding of modern and past biodiversity drivers and dynamics (Escarguel et al. 2011). This fertile cross-field emulation addresses new questions, such as how -and to what extent- biogeographical and macroecological properties of taxa are influenced by their evolutionary history? Because the fragmentary nature of the fossil record makes abundance information unreliable in most cases, we only considered here the taxonomic richness aspect of biodiversity. Yet, the biodiversity concept involves other dimensions also robust to the fossilization process, such as phylogenetic diversity (e.g. Emerson and Gillespie 2008), ecological (functional) diversity (e.g. Petchey and Gaston 2006), or morphological disparity (e.g. Foote 1997; Villier and Korn 2004; McGowan 2005). Based on previously acquired data and results, the objectives of future studies will be therefore to quantitatively assess and compare spatial and temporal dynamics of these complementary aspects of biodiversity, as well as their potential relationships with major biotic and abiotic parameters such as geographic rarity, taxon longevity, extinction probability, or climate.

From this point of view, the understanding of past biodiversity might be first investigated by exploring the intricate and multidimensional relationships among phylogenetic, geographic and morphological distances and their evolution through geological time since some of these properties are now available through large revised datasets (e.g., for Triassic ammonoids, Brayard et al. 2009a; Brayard and Escarguel 2013; Brosse et al. 2013). In the context of Triassic studies, such a multidimensional approach to biodiversity is expected to significantly improve our understanding of the Early Triassic biotic recovery (e.g. do latitudinal gradients in phylogenetic, functional or morphological diversity also emerge parallel to the LGGR?) as well as the Late Triassic long and rough road to the Triassic/Jurassic crisis (e.g. do the end Norian and Rhaetian extinction events show any structuring in phylogenetic, ecological or morphological loss?). In all cases, significant results and new questions are expected from integration of quantitative descriptions of diversity dynamics based on fossils already available as well as new fossils integrated in taxonomically-revised, geo-referenced datasets. When combined with more inductive, simulation-based approaches, this will allow the identification of the underlying evolutionary and functional processes, as well as the relative importance of potential parameters driving the observed patterns (see Brayard et al. 2004 for a preliminary example on Early Triassic ammonoid generic richness).

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Chapter 8
Macroevolution and Paleobiogeography of Jurassic-Cretaceous Ammonoids

Margaret M. Yacobucci

8.1 Introduction

Ammonoids of the Jurassic and Cretaceous Periods show remarkable patterns of evolution. While some clades, e.g., Phylloceratina, persist as stable evolutionary lineages throughout this time interval, others experienced incredibly rapid rates of speciation and extinction. The processes responsible for creating this evolutionary volatility have not been clear. While ammonoid extinction rates may reflect heightened sensitivity to environmental conditions, an explanation for their propensity to produce new species and higher taxa has remained elusive. The rich and well-sampled fossil record of ammonoids has enabled paleontologists to document the temporal and spatial context of ammonoid clades in great detail. Synthesizing phylogenetic, temporal, and geographic data may enable us to better understand the patterns and processes of evolution in this extraordinary group of cephalopods.

In this chapter, I briefly review the major clades of Jurassic and Cretaceous (hereafter, J-K) ammonoids, discussing their phylogenetic context and diversity dynamics. Next, I discuss key macroevolutionary processes relevant to understanding the evolutionary volatility of J-K ammonoids. These evolutionary processes are then linked to biogeographic patterns to produce an integrated model for how rapid diversification may occur within ammonoid clades. Throughout the chapter, I highlight topics of current interest that are in need of further study.

M. M. Yacobucci (✉)
Department of Geology, Bowling Green State University,
Bowling Green, OH 43403 USA
e-mail: mmyacob@bgsu.edu

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8.2 Phylogeny of Jurassic and Cretaceous Ammonoids

8.2.1 Major Ammonoid Clades

Six ammonoid suborders occurred in the Jurassic-Cretaceous interval: Phylloceratina, Lytoceratina, Ammonitina, Haploceratina, Perisphinctina, and Ancyloceratina. Note that here the traditional suborder "Ammonitina" is split into three suborders (Ammonitina, Haploceratina, Perisphinctina), following Bessenova and Mikhailova (1983, 1991); the term 'Ammonitina *sensu lato'* will be used for all three suborders together. Figure 8.1 shows the stratigraphic and phylogenetic context for the 18 superfamilies within these groups, as currently understood. The evolutionary relationships depicted in Fig. 8.1 are derived from a variety of literature sources, as listed in the figure caption. A comprehensive phylogenetic analysis including all these groups is sorely needed. Several large-scale evolutionary connections remain unclear, including:

a. the origin of Lytoceratina from either Phylloceratina (Arkell et al. 1957; Wiedmann 1969; House 1988) or Psiloceratoidea (Houša 1965; Page 1996, 2008; Guex 1995; Blau et al. 2008; Hoffmann 2010; Guex et al. 2012);
b. derivation of Eoderoceratoidea from either Psiloceratoidea (Schindewolf 1962; Page 1996) or Lytoceratoidea (Donovan et al. 1981; Howarth 2013); note that the latter interpretation makes Ammonitina polyphyletic unless Psiloceratoidea is excluded from it and elevated to suborder status, as suggested by Page (1996, 2008);
c. the origin of Ancycloceratina from Lytoceratina (Arkell et al. 1957; Wiedmann 1966), Spiroceratoidea (Wright et al. 1996), or Perisphinctina (Donovan et al. 1981; Bessenova and Mikhailova 1991; Page 1996; Mikhailova and Baraboshkin 2009);
d. the origin of Turrilitoidea from Lytoceratina (Doguzhaeva and Mikhailova 1981, Bessenova and Mikhailova 1991; Mikhailova and Baraboshkin 2009) or Ancyloceratoidea (House 1988; Wright et al. 1996);
e. derivation of Scaphitoidea from Ancyloceratoidea (Page 1996), Turrilitoidea (Wright 1981), or Perisphinctoidea (Engeser and Keupp 2002).

8.2.2 Biodiversity Through Time

Intensive collection of J-K ammonoids combined with their relatively high preservation potential (Foote and Sepkoski 1999) have allowed paleontologists to document their biodiversity trends through time. Ammonoids show higher evolutionary rates than other mollusks. For instance, Gilinsky (1994, 1998) found that family-level evolutionary volatility (i.e., average net change in diversity per million years) was twice as high for Phylloceratina and four times as high for Ammonitina *sensu lato* as for bivalve mollusks. Yacobucci (2005) calculated per capita origination

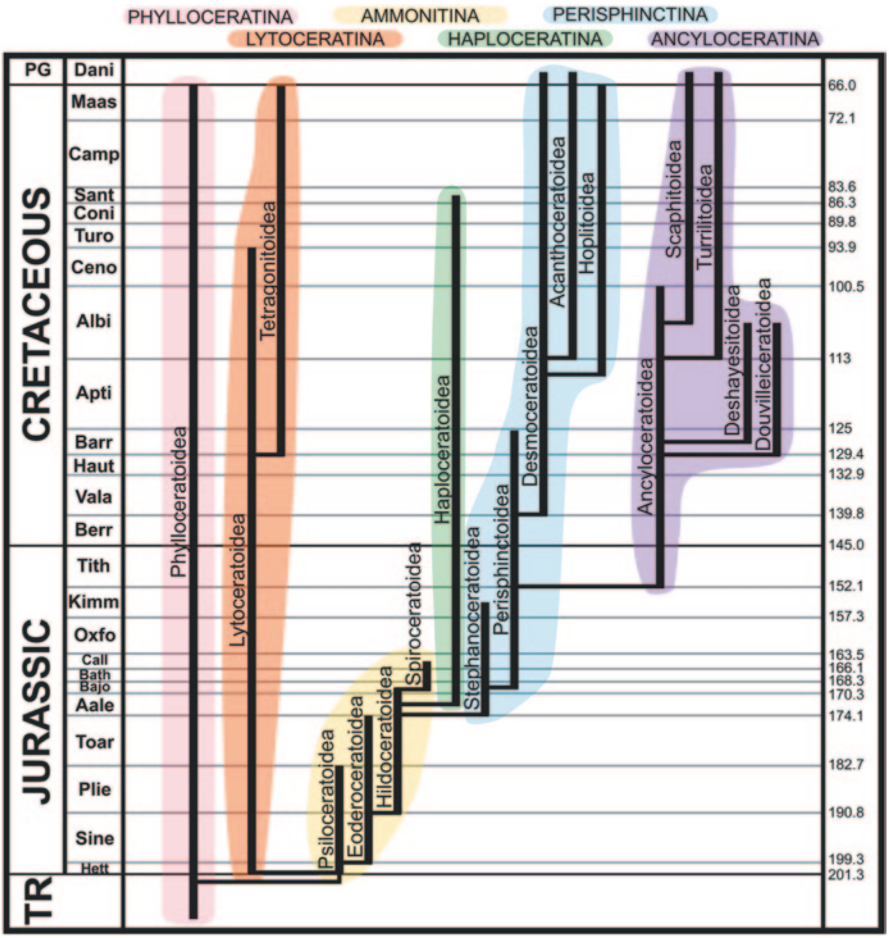
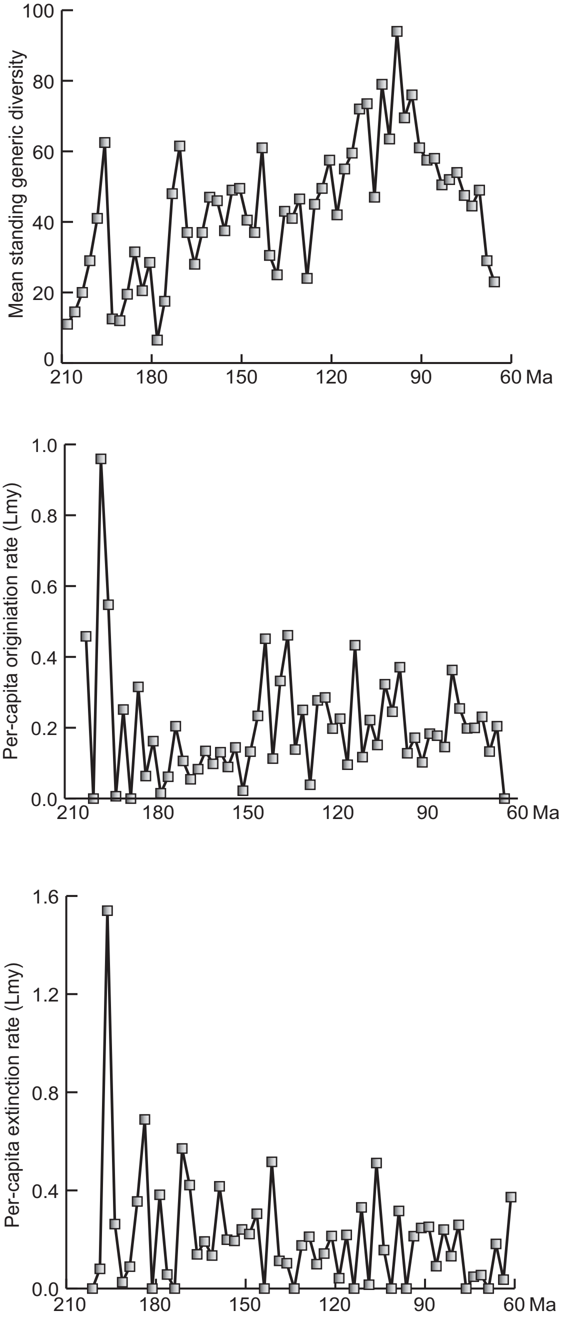


Fig. 8.1 Phylogenetic and stratigraphic context for Jurassic and Cretaceous ammonoid superfamilies. Suborders are indicated by shading, with corresponding suborder names arranged at *top* of figure. Stratigraphic ranges and phylogenetic relationships are synthesized from: Arkell et al. 1957; Schindewolf 1962; Houša 1965; Wiedmann 1969; Doguzhaeva and Mikhailova 1981; Donovan et al. 1981; Wright 1981; House 1988; Guex 1995; Page 1996; Wright et al. 1996; Engeser and Keupp 2002; Blau et al. 2008; Page 2008; Galácz 2012; Landman et al. 2012; Howarth 2013. Absolute time scale (right, in Ma) and stratigraphic stages (left) are derived from the 2013 Chronostratigraphic Chart of the International Commission on Stratigraphy (Cohen et al. 2013)

and extinction rates for J-K ammonoids averaging about 0.2 originations and extinctions per lineage-million years, though rates could be as high as 0.96 and 1.54 events per lineage-million years, respectively, for individual Early Jurassic substages (Fig. 8.2). By comparison, origination and extinction rates for marine metazoans as a group are typically less than 0.1 events per lineage-million years (Foote 2000).

Many have noted the relative evolutionary and morphological stability of the suborders Phylloceratina and Lytoceratina, relative to other ammonite suborders

Fig. 8.2 Diversity dynamics of Jurassic-Cretaceous ammonoids. **a** Mean standing generic diversity. **b** Per-capita origination rate in lineage-million years. **c** Per-capita extinction rate in lineage-million years. Generic diversity has been compiled at the substage level. Redrawn from Yacobucci (2005)



(Page 1996; but see Tanabe et al. 2003). The superfamily Desmoceratoidea (Perisphinctina) also shows a slower rate of evolution than other groups. Kennedy and Cobban (1976), for example, describe species longevities of 0.2–0.9 million years for Late Cretaceous ancyloceratines, while phylloceratine, lytoceratine, and desmoceratoid species show stratigraphic ranges from 8 to 25 million years. Possible explanations for this difference in evolutionary volatility among J-K ammonoid clades are discussed in Sect. 8.3.4.

The biodiversity history of J-K ammonoids is characterized by a distinctive "boom-and-bust" pattern of evolution and extinction, quite different from other mollusk classes (Vinarski et al. 2011). During the "boom" phase, a great variety of ammonoid taxa and morphotypes were produced in a very short interval. Higher taxa (families, superfamilies, and suborders) were established during these events. For instance, the initial Hettangian radiation of Early Jurassic ammonoids established Psiloceratoidea, Eoderoceratoidea, and Lytoceratoidea (Guex 1987), while Haploceratoidea, Stephanoceratoidea, and Perisphinctoidea appeared in the Middle Jurassic (Aalenian-Bajocian) diversification event (Donovan et al. 1981). Rapid radiations also occurred within superfamilies, notably in the Early Cretaceous for Desmoceratoidea (Hauterivian-Barremian) and Ancyloceratoidea (Aptian) and in the Late Cretaceous for Acanthoceratoidea and Hoplitoidea (Albian-Cenomanian) (Wright 1981). Biodiversity crashes were similarly frequent; these "bust" phases eliminated substantial proportions of the standing diversity of ammonoids. While virtually every stage and substage boundary of the Jurassic-Cretaceous interval is marked by at least regional ammonoid extinction events, more substantial extinctions also occurred, especially in association with ocean anoxic events (House 1985; Page 1996; Macchioni and Cecca 2002; Cecca and Macchioni 2004; Moyne et al. 2004; O'Dogherty et al. 2006; Moyne and Neige 2007; Dera et al. 2010, 2011; Hardy et al. 2012; but see Monnet et al. 2003, Monnet and Bucher 2007, and Monnet 2009 for a challenge to anoxia as the cause of the Cenomanian-Turonian turnover event). Hence, more or less distinctive ammonoid faunas characterize the Early Jurassic, Middle-Late Jurassic, Early-Mid Cretaceous, and Late Cretaceous. A few ammonoid species may have survived, if briefly, the end-Cretaceous extinction event (Machalski and Heinberg 2005; Landman et al. 2012).

8.2.3 Phylogenetic Analyses

The rapid evolution and extinction of ammonoids have made them valuable biostratigraphic index fossils. Their biostratigraphic utility, however, has hindered a more contemporary approach to their systematics. New ammonoid species are frequently described based on a stratophenetic view, in which species are initially distinguished by their stratigraphic occurrence, with anatomical features then identified as diagnostic for those groupings (Donovan 1994). Whether or not these groups are 'real' species in the biological sense may not be a concern for many biostratigraphers. However, to understand the macroevolution of ammonoids, a more rigorous, contemporary phylogenetic approach to document relationships among species must be employed (Rouget et al. 2004; Neige et al. 2007; Pardo et al. 2008; Yacobucci 2012; Bert and Bersac 2013).

Many cephalopod paleontologists have been reluctant to pursue a parsimony-based phylogenetic approach, in part because of the pervasive homeomorphy that characterizes many ammonoid groups (see Sect. 3.1 below). While homeomorphy is a concern in other mollusk classes as well (e.g., Schneider (2001) on bivalves; Schander and Sundberg (2001) and Wagner (2001) on gastropods), it is perceived as especially common in J-K ammonoids, which can make it difficult to separate convergent evolution from shared ancestry. Strategies do exist, however, to address homeomorphy, and rather than assuming it *a priori*, homeomorphy should be demonstrated by phylogenetic analysis. It may be that ammonoids are no more prone to homeomorphy than other groups, such as arthropods, bryozoans, and mammals, which are routinely subjected to phylogenetic analysis (Yacobucci 2012). It has also been shown that even homeomorphic characters still contain some phylogenetic signal (Poe and Wiens 2000).

The high levels of intraspecific variability shown by many J-K ammonoids represent another obstacle to phylogenetic analysis (see De Baets et al. 2015). A single ammonoid species may display morphological differences between specimens that might otherwise be used to diagnose separate genera (see Sect. 3.3 below). Such variability has been difficult to capture using standard phylogenetic techniques, although variable characters can now be coded as polymorphisms in most phylogenetic software programs. Perhaps a bigger challenge is determining which variable characters are phylogenetically meaningful and which represent non-phylogenetic processes such as ecophenotypic variation or taphonomic overprinting.

The majority of phylogenetic analyses of ammonoid clades have been conducted on Jurassic or Cretaceous groups, typically exploring relationships within a genus or family (Yacobucci 2012). A more comprehensive analysis to establish relationships among higher taxa has not been accomplished to date. Such an analysis, focusing not just on shell morphology but also on the timing of morphological development and life history traits, will be essential in order to rigorously test hypotheses about the tempo and mode of J-K ammonoid evolution.

8.3 Macroevolutionary Processes

8.3.1 Homeomorphy and Iterative Evolution

Homeomorphy here refers to the occurrence of similar shell forms in more or less distantly related groups. In ammonoids, the similarity is typically in shell shape and ornamentation, although suture patterns can also be similar in groups that are only distantly related (Schindewolf 1940; Haas 1942; Arkell et al. 1957; Kennedy and Cobban 1976; Saunders and Swan 1984; Dommergues et al. 1989; Dommergues

1994; Donovan 1994; Guex 2001; Monnet et al. 2011). Examples of homeomorphy have been particularly well-documented in ammonoids from the Jurassic (e.g., Dommergues et al. 1984; Dommergues and Mouterde 1987; Cariou et al. 1990; Meister 1993; El Hariri et al. 1996; Dommergues 2002; Cecca and Rouget 2006; Schlögl et al. 2006; Schweigert et al. 2012) and the Cretaceous (e.g., Reyment 1955; Obata 1975; Jeletzky and Stelck 1981; Delanoy and Poupon 1992; Maeda 1993; Kennedy and Wright 1994; Delanoy and Busnardo 2007; Bujtor 2010) Periods. Indeed, it is understood among J-K ammonoid workers that homeomorphy is to be expected when describing new species, and many taxonomic descriptions of ammonoid taxa therefore include sections on how to distinguish the new group from homeomorphs. Typically, the homeomorphic traits are restricted to adult forms, so homeomorphs can be distinguished by considering their entire ontogeny (Donovan et al. 1981). It should also be noted that modern coleoid cephalopods show extensive convergent evolution as well (Lindgren et al. 2012).

Iterative evolution involves similar-looking species repeatedly evolving through time. An early view among ammonoid workers was that many new J-K ammonoid groups were independently derived from Phylloceratina or Lytoceratina via iterative evolution, as deep water "root stocks" repeatedly gave rise to descendant forms inhabiting shallow shelves and epeiric seas. While this notion is no longer held by ammonoid paleontologists, at least for the origins of suborders and superfamilies (Wiedmann 1966; Donovan et al. 1981; Wright 1981), specific examples of homeomorphic evolution are frequently tied to sea level cycles. In particular, selection favoring certain morphs in certain habitats may be the most likely process driving the recurrent evolution of ammonoid homeomorphs. Seilacher and Gunji (1993) argued that certain shell shapes would be adapted to particular water depths, and therefore that parallel evolution of similar shell forms could be expected within shallow epeiric seas. Similar arguments relating homeomorphic shell forms to water depth and sea level cycles have been made by Bayer and McGhee (1984), Jacobs et al. (1994), Cecca and Pochettino (2000), Courville (2007), and Bujtor (2010). Courville (2007), for instance, proposed that Cenomanian-Turonian ammonites can be divided into (1) a cosmopolitan fauna adapted to life in open platform and shelf habitats and (2) groups of endemic ammonites that diversified within epeiric seaways (such as the Trans-Saharan Seaway of West Africa) during sea level highs. Each time sea level rose, a new group of seaway endemics evolved from open shelf ancestors. These endemics display homeomorphic adaptations to seaway habitats, with the same shell forms and ornaments recurring in each sea level cycle.

As an alternative to adaptation to particular water depths, Monnet et al. (2012) noted that repeated trends to larger shell size and increased shell coiling in Middle Triassic ammonoids might best be explained as a manifestation of Cope's Rule, the often-cited trend of increasing adult body size within a clade. De Baets et al. (2012) suggested that the opposite trend, towards smaller embryonic/hatchling size in at least three separate lineages of Devonian ammonoids, might represent adaptations for increased fecundity and higher mobility of hatchlings within the water column. These changes would have been favored during the Devonian 'Nektonic Revolution,' when free-swimming predators diversified. Such selection for larger or smaller adult sizes may also be applicable to J-K ammonoids, and is therefore in need of further exploration.

Finally, Guex (2000, 2001) has argued that environmental stress may be the root cause of homeomorphy in ammonoids. "[M]*ajor evolutionary jumps in ammonoids occur during severe extinction events, and are characterized by the sudden appearance of simple, primitive-looking forms which are atavistic with respect to their more complex immediate ancestors*" (Guex 2000, p. 115). For Guex, environmental stress preferentially causes more complex ammonoid forms to die out, while simpler forms that resemble distant ancestors evolve to take their place. In this view, homeomorphs are more likely to occur during or immediately after times of environmental perturbation and heightened turnover, and show atavistic or ancestral traits.

8.3.2 Heterochrony

The study of heterochrony in ammonoids extends back decades and is still an active area of inquiry (Dommergues et al. 1986; Landman 1988b; Marchand and Dommergues 1988; Korn 1992; Landman and Geyssant 1993; Gerber et al. 2007; Gerber 2011; Korn 2012). Both paedomorphosis (the retention of ancestral juvenile traits in the adult descendant) and peramorphosis ('overmaturation' of descendants past the ancestral adult form) have been described in ammonoids. Within the paedomorphic realm, progenesis (early sexual maturation) is most common, though examples of neoteny (slowed growth) have also been cited. Progenetic dwarfs have been described from the Jurassic (Cariou and Sequeiros 1987; Marchand and Dommergues 1988; Landman et al. 1991; Meister 1993; Mignot et al. 1993; Dommergues 1994; Linares and Sandoval 1996; Neige et al. 1997; Parent 1997, 1998), and Cretaceous (Kennedy 1977; Wright and Kennedy 1980; Kennedy 1988; Landman 1989; Kennedy and Cobban 1990a, b; Landman et al. 1991; Wright et al. 1996; Kennedy et al. 2001; Courville and Cronier 2003; Harada and Tanabe 2005) Periods. Peramorphosis is less common than paedomorphosis (Landman and Geyssant, 1993), and is often seen within taxa that also show paedomorphic changes, producing a mosaic form of heterochrony (Dommergues 1987; Linares and Sandoval 1996; Neige et al. 1997; Parent 1998; Courville and Cronier 2003).

Paleontologists have connected heterochronic patterns with other aspects of ammonoid paleobiology. For example, differences between sexual dimorphs (i.e., macroconchs and microconchs) have been related to heterochronic shifts. Tintant (1963), Guex (1981), and Parent (1997) all suggested microconchs were produced by progenesis or neoteny. Neige (1992) also identified progenesis as the source of some microconchs among Jurassic ammonites, but additionally recognized hypomorphosis as a contributing process in some taxa.

Paleobiologists have argued that certain heterochronic changes would be adaptively favored in particular environments. For instance, progenesis could be advantageous in unstable environments, as rapid maturation would allow individuals to exploit abundant juvenile resources. Neoteny (slowed growth), in contrast, would be favored in more stable environments (Gould 1977; Wiedmann 1988; McKinney and McNamara 1991). Many examples exist that document this relationship between heterochronic evolution and environmental stability. Mancini (1978) argued that the progenetic dwarfs of the Cretaceous Grayson Formation of Texas were better adapted than their larger ancestors to live on the unusually soft substrates present at that time. Alternatively, Enay and Gygi (2001) suggested that the Jurassic progenetic dwarfs they investigated would have been more tolerant of dysoxic bottom waters. In a similar vein, Mignot et al. (1993) argued that paedomorphosis within the Early Jurassic ammonoid *Hildoceras* was an adaptive response to sub-optimal environmental conditions, and Zatoń (2008) suggested that the range of mature body sizes seen in Jurassic tulitids was due to varying environmental conditions. Monnet et al. (2003) argued that paedomorphic changes resulting in smaller adult body sizes during the Late Cenomanian were driven by environmental perturbations such as sea level rise, temperature increase, and productivity changes. Stevens (1988) suggested that large adult body sizes (as are produced in certain heterochronic shifts such as neotenic or hypermorphic gigantism) might be expected in cold, deep-water environments. Landman and Geyssant (1993) reviewed 167 reported cases of heterochrony in ammonoids, relating the different heteromorphic processes to different modes of life (e.g., nektobenthic, oceanic, megaplanktonic). While paedomorphosis still predominated, neritic nektobenthic forms were more likely to show peramorphosis than other ecologies. Vertical migrators showed the highest rate of progenesis.

The prevalence of heterochrony among ammonoid clades has also been related to diversification rates and the production of species and higher taxa. As a Paleozoic example, Korn (1995) argued that the diversification of several Late Devonian goniatite and clymeniid clades was driven by sea level fluctuations that favored accelerated maturation and reproductive rates during times of relative sea level fall. Marchand and Dommergues (1988) suggested that the evolution of new ammonoid lineages in the Jurassic was associated with progenesis, while subsequent evolution within lineages was due to neoteny or acceleration. Geyssant (1988) also argued that progenesis produced new species, citing changes in homeotic genes controlling growth as the source for morphological novelty. Yacobucci (1999) linked the rapid endemic radiation of acanthoceratid ammonoids in the Late Cretaceous Western Interior Seaway of North America to their developmental flexibility, highlighting the prevalence of progenetic offshoots within this group. Landman (1989) noted that repeated instances of progenesis produced different ammonoid species that had nearly identical juvenile forms, but diverged at maturity. Landman et al. (1991) emphasized that the various Jurassic and Cretaceous progenetic species were not merely sexually mature juveniles, but also had unique mature traits that make them diagnosable taxa. They argued that this "novel combination of juvenile, adult, and unique features may endow progenetic species with the evolutionary potential to play a role in the origin of higher taxa." (Landman et al. 1991, p. 409).

Homeomorphic evolution has also been linked to heterochrony by several workers. Dommergues et al. (1989) argued that homeomorphy of shell forms in various Jurassic ammonoids was due to heterochronic processes that recurrently produced similar shell morphologies (e.g., disk-shaped oxycones, globular sphaerocones). Both Landman (1989) and Dommergues (1994) specifically cited iterative progenesis as the mechanism producing smaller-bodied species that resembled the juveniles of older or co-occurring ammonoid species. These progenetic trends repeated several times, producing similar-looking species –homeomorphs– in each iteration. Similarly, Meister (1993) suggested that paedomorphosis by neoteny was responsible for producing homeomorphic suboxyconic shell forms in multiple groups of Early Jurassic phylloceratine ammonoids.

8.3.3 Developmental Flexibility

In addition to heterochronic processes, various other forms of developmental flexibility have been documented in ammonoids and used for systematic purposes. This developmental flexibility may help explain the extreme intraspecific morphological variability that is seen in many J-K ammonoid groups (e.g., Reeside and Cobban 1960; Westermann 1966; Kennedy and Cobban 1976; Howarth 1978; Meléndez and Fontana 1993; Yacobucci 1999, 2003; 2004a, b; Morard and Guex 2003; Kakabadze 2004; Gangopadhyay and Bardhan 2007; Gerber et al. 2008; Reyment 2011; Knauss and Yacobucci 2014; De Baets et al. 2015). Certainly the sexual dimorphism that characterizes many J-K ammonoid species (Kennedy and Cobban 1976; Callomon 1981; Donovan et al. 1981; Davis et al. 1996) must relate to variations in the developmental growth program.

Perhaps not surprisingly, then, ammonoid paleontologists have been pioneers in the use of developmentally defined characters in systematics. The systematic description and differentiation of ammonoid species often includes reference to developmentally-based characters. One species of a genus might reach maturity at a smaller size than another. Features of ornamentation like ribs and tubercles may occur only on one portion of the shell, indicating a developmental shift in the shell's growth program. Traits like the density of ribs or the shape or pattern of spacing of tubercles may change during growth. The adult suture may remain relatively simple in one species while developing more complexity through ontogeny in a close relative. Characters like these are routinely used to diagnose and differentiate closely related ammonoid species. By contrast, systematists who study extant animals more rarely use juvenile traits and aspects of developmental timing in their work. Recently, modern biologists have argued that variations in developmental timing may be a driver of speciation, as they provide a source for new innovations, populational polyphenism, and pre-mating isolation mechanisms (Naisbit et al. 2003; West-Eberhard 2003, 2005; Minelli and Fusco 2012). Ammonoid paleontologists are well-situated to lead integrative research efforts on the role of developmental flexibility in speciation and the production of higher taxa.

8.3.4 Environment and Evolution

Ammonoid paleontologists have long argued that environmental factors, like sea level changes, water temperature, and oxygen content, had a primary impact on evolutionary dynamics, including incidents of homeomorphy and heterochrony, as noted above (Ziegler 1967; Kennedy and Cobban 1976; Futukami and Obata 1988; Marcinowski and Wiedmann 1988; Meléndez et al. 1988; Wiedmann 1988; Hallam 1989; House 1989, 1993; Hantzpergue 1991, 1995; Ross et al. 1992; Rawson 1993; Wiedmann and Kullmann 1996; Bengtson and Kakabadze 1999; Yacobucci 1999; Hirano et al. 2000; Sandoval et al. 2001, Navarro et al. 2005; Olóriz and Villaseñor 2006; Bardhan et al. 2007; Bourillot et al. 2008; Lehmann and Herbig 2009; Ifrim and Stinnesbeck 2010; Nagm and Wilmsen 2012; Ruban 2013). Biotic factors such as changes in plankton food sources were likely also important (Kruta et al. 2011; Ohkouchi et al. 2013). Ammonoids were subject to a variety of selective pressures, which likely varied both spatially and temporally. Key environmental variables may have occurred as spatial gradients (e.g., water depth, temperature, salinity, dissolved oxygen) or as more discrete patches (e.g., nutrients, substrate types), especially within epeiric seas. Ammonoid populations and species would necessarily respond to changes in these environmental parameters, whether by extinction, migration, or adaptive evolution.

The ammonoid suborders Phylloceratina and Lytoceratina and the superfamily Desmoceratoidea are characterized by relative evolutionary stability and morphological conservatism (Arkell et al. 1957; Page 1996; Neige et al. 2013; but see Bourillot et al. 2008). It has been argued that this stability stems from their more environmentally stable, open ocean habitats (House 1989; Tanabe et al. 2013). Ammonoids living in shallow shelves and epeiric seas, on the other hand, show higher taxonomic and morphological diversity and higher evolutionary turnover, presumably as a response to more unstable environmental conditions (Ziegler 1981).

This documented difference in evolutionary rates between deep open ocean and shallow restricted shelf/sea habitats has led paleontologists to tie ammonoid evolution to sea level cycles (Wiedmann 1973; Kennedy and Cobban 1976; Hirano 1988; Yacobucci 1999). Slowly evolving groups living offshore would provide the initial species that invaded newly created or accessible onshore habitats during transgressions. An adaptive radiation would ensue, producing many new ammonoid species during a short time interval. When sea level later fell, these shallow water species would rapidly become extinct. Then, when sea level rose again, a new suite of ammonoid species, derived from the stable offshore species, would radiate into shallow habitats once more.

Case studies of specific examples of this evolutionary pattern have revealed more complexity in the evolutionary processes involved. Hirano (1988), for instance, explored the evolution of the Cenomanian desmoceratids *Desmoceras* and *Tragodesmoceroides* and the tetragonitid *Gaudryceras* from Japan. He found species-level stasis over several million years in the open ocean *Desmoceras* (*P.*) *japonicum*, which then gave rise to *Tragodesmoceroides subcostatus* via relatively rapid allopatric speciation. *Gaudryceras*, on the other hand, showed episodes of increased polymorphism within a species, rather than the divergence of a new species. Macchioni and Cecca (2002) argued that both transgressions and regressions could change regional biodiversity and the degree of endemism in Early Jurassic ammonoid faunas. Lukeneder (2012) found that both abundance and diversity peaked during highstands in Early Cretaceous (Hauterivian-Barremian) ammonoids from the Italian Alps; the possibility that higher abundances influenced biodiversity counts is an open question.

Further complicating the link between sea level cycles and ammonoid diversity dynamics is the association of sea level highstands with episodes of ocean anoxia. Rising sea levels may be associated with global warming and a reduction in thermohaline ocean circulation. The rising seas may also bring the oxygen minimum zone up in the water column such that it impinges on the shallow seafloor. Such times of anoxia or dysoxia are known to be associated with ammonoid extinctions and turnover. Hirano et al. (2000), for example, documented the stratigraphic ranges of 902 Cretaceous ammonoid species from Japan. They found a diversity peak in the Late Albian, with lower diversities during mid-Cretaceous ocean anoxic events. Turnover among ammonoids during the Pliensbachian-Toarcian (Early Jurassic) has long been associated with ocean anoxia (Macchioni and Cecca 2002; Rulleau et al. 2003; Dommergues et al. 2009; Dera et al. 2011). Hence, ammonoid extinction may be elevated both at times of sea level rise and sea level fall, depending on the circumstances (Becker 1993; Korn 1995; Yacobucci 1999).

It may also be that sea level cycles and their associated environmental changes drive origination as well as extinction. Transgressions produce new habitat space, which may trigger adaptive radiations within a few invading higher taxa. Regressions may isolate previously connected regions and promote allopatric speciation (Yacobucci 1999, 2015).

8.3.5 Speciation Models

Few invertebrate paleontologists have explicitly connected the species they study with any particular species concept (such as the biological or phylogenetic species concepts; Allmon and Smith 2011). Dozens of different definitions of species exist in the scientific literature. The Biological Species Concept (BSC) is certainly the most widely cited (e.g., it is the species definition found in most introductory textbooks). The BSC states that species are groups of interbreeding natural populations that are reproductively isolated from other groups (Mayr 1942, 1963; 1995. While it is impossible to apply this definition directly to fossil species, it does express the core theoretical concept that species are distinct, isolated gene pools, each therefore with its own unique evolutionary history.

The ‘reality’ of species as distinct evolutionary units can be difficult to demonstrate, for living and extinct organisms alike. The paleontological morphospecies concept infers that morphological similarity should reflect evolutionary proximity

(Raup and Stanley 1978, p. 130). Given the prevalence of homeomorphy in J-K ammonoids, this inference may not always hold. The stratophenetic approach many workers have taken to J-K ammonoid classification means that nominal ammonoid species may or may not reflect "real" biological species. A tendency to oversplit highly variable ammonoid species further complicates our understanding of ammonoid diversity. In addition, Nardin et al. (2005) found that Jurassic ammonoid workers more readily named extreme forms than intermediate ones. Several workers (Kennedy and Wright 1985; Hallam 1990) have, indeed, suggested that ammonoid genera may be closer to "real" species than the nominal species are. Ideally, future workers will at least more explicitly describe the species concept they are using.

The speciation process has been intensively studied by modern biologists for decades. Proposed speciation mechanisms differ primarily in their geographic context and the degree of gene flow permitted between diverging populations. Allopatric speciation is widely accepted as the most common mode of speciation (Mayr 1942, 1963, 1995; Lieberman 2000; Coyne and Orr 2004; Marie Curie SPECIATION Network 2012; Nosil 2012). In the allopatric speciation model, lack of gene flow between populations is due to geographic separation. How much geographic separation is necessary to prevent gene flow is a function of the organisms' mobility and dispersal ability; allopatric speciation is known to occur across small geographic scales in shallow marine settings (Meyer et al. 2005; Krug 2011). Parapatric speciation involves populations occupying an ecological gradient that experience ecological divergence as each population adapts to its local environments; some gene flow can still occur between adjacent populations (Coyne and Orr 2004; Nosil 2008; Pinho and Hey 2010; Keller and Seehausen 2012). Sympatric speciation, in which populations show extensive geographic overlap and gene flow, has remained controversial, in part because the definition has shifted over time from a purely geographic one to one that focuses on the degree of gene flow between populations (Gavrilets 2003; Coyne and Orr 2004; Mallet 2008; Fitzpatrick et al. 2008, 2009; Mallet et al. 2009; Bird et al. 2012). One argument against sympatric speciation is that incipient species would occupy the same ecological niche and therefore one population would just out-compete the other, driving it to extinction before it can successfully diverge into a new species. Successful sympatric speciation, then, requires simultaneous reproductive isolation and ecological differentiation (Johannesson 2001; Coyne and Orr 2004), which could be produced by modifying certain traits that affect both the organisms' ecology and reproduction [coined "*magic traits*" by Gavrilets (2004)].

It has been suggested that these different speciation models may not be mutually exclusive; rather, speciation may involve an early allopatric stage when divergence begins and a later sympatric stage as the diverging population moves back into its parent population's range (Rundle and Schluter 2004; Rundle and Nosil 2005; Butlin et al. 2008; Aguilée et al. 2011; Marie Curie SPECIATION Network 2012). Parapatric speciation and mosaic sympatry (involving randomly distributed habitat patches within the overlapping ranges of diverging populations) may also be common (Mallet 2008; Mallet et al. 2009). Certainly, the speciation process typically takes place over tens of thousands of years, so populations are likely to experience a variety of geographic and environmental changes before becoming completely separate species (Norris and Hull 2012).

Rapid evolutionary radiations that involve frequent speciation, often within newly exploited habitats, provide a particularly interesting perspective on how speciation happens (Gavrilets and Losos 2009). The adaptive radiation of *Anolis* lizards in the Caribbean resulted in frequent parallel evolution of homeomorphic forms on different islands, suggesting that similar anatomical traits can evolve repeatedly within a clade that encounters similar environments (Mahler et al. 2013). Studies of Galápagos finches (Grant et al. 2006; Grant and Grant 2008) and cichlid fish (Albertson and Kocher 2006) have shown the importance of developmentally plastic traits as the source for anatomical variation involved in ecological divergence of rapidly speciating populations. The African cichlid fish radiations demonstrate the importance of both environmental factors and sexual selection on lineage-specific traits for fueling speciation (Wagner et al. 2012).

Ammonoid workers have primarily addressed the speciation process indirectly, by assessing the dispersal ability of ammonoids as juveniles. Mesozoic ammonoids had small eggs (0.5–2.6 mm) and hatchling sizes, and probably spent some time in the plankton during the early juvenile phase of their life cycle, before settling into a nektic or nektobenthic habit (Landman 1988a, Landman et al. 1996; Shigeta 1993; Tajika and Wani 2011). It should be noted, however, that ammonoid taxa associated with deep and cold water habitats (e.g., Phylloceratina, Lytoceratina) had larger eggs than taxa in shallow and warm water habitats (e.g., Ammonitina, Ancyloceratina; Laptikhovsky et al. 2013), so a planktonic juvenile phase may not have been universal among J-K ammonoids. Many examples exist of juvenile and adult ammonoids living in separate habitats (Kennedy and Cobban 1976; Morton 1988; Tsujita and Westermann 1998). Tajika and Wani (2011) studied hatchling size in species of *Gaudryceras* (Lytoceratina) and *Hypophylloceras* (Phylloceratina) from the Late Cretaceous of northern Japan, and estimated they were planktonic for at least five days. Ikeda and Wani (2012) and Yahada and Wani (2013) found that adult shell thickness ratios (width/diameter) change with depth within a wide range of ammonoid species while juvenile proportions do not; they interpreted this finding as evidence for planktic hatchlings and nektobenthic adults. Wani (2011) documented hatchling sizes in ammonoids and nautiloids throughout the Phanerozoic and compared them to those of modern cephalopods. He found that ammonoids showed consistently small hatchling sizes (<3 mm) through time, while nautiloid hatchling sizes increased in the Jurassic to their presently-observed size of 22–33 mm. Modern cephalopod hatchling size is related to planktonic (<3 mm) vs. nonplanktonic (>10 mm) habits. Hence, while J-K nautiloid hatchlings were likely nonplanktonic with limited dispersal and more restricted geographic ranges, J-K ammonoid hatchlings were likely planktonic with greater dispersal ability and larger geographic ranges. Wani (2011) concluded that sympatric speciation was more likely than allopatric speciation in ammonoids. However, while these studies support the possibility of sympatric speciation, we need more complete and detailed data on the geographic ranges of J-K ammonoid species, as well as careful mapping of possible microhabitats or mosaic habitats in shallow shelf and epeiric sea settings, to determine whether sympatric or allopatric speciation actually took place within a given ammonoid clade.

8.4 Role of Paleobiogeography in Macroevolution

8.4.1 The Mesozoic Earth System

The Mesozoic Earth System was marked by significant tectonic, oceanographic, and climatic changes. The supercontinent Pangea began rifting apart by the Early Jurassic, first with the opening of the North and Central Atlantic (Labails et al. 2010; Ruiz-Martínez et al. 2012) and later by the opening of the Hispanic Corridor, which produced an ocean passage connecting Western Tethys with the Eastern Pacific (Fig. 8.3a). No direct geological evidence exists for the Hispanic Corridor prior to the late Middle Jurassic, although a flooded rift zone that permitted ammonoid dispersal between Tethys and the Eastern Pacific could have been present earlier (Longridge et al. 2008). The Gondwanan continents separated later, in the Early to Mid-Cretaceous, with the South Atlantic opening from south to north beginning in the Hauterivian (Fig. 8.3b) (Owen and Mutterlose 2006; Rawson 2007; Torsvik et al. 2009; Geraldes et al. 2013).

High sea levels through the J-K interval (Haq et al. 1987, 1988) flooded large areas of the continents and offered marine connections between these opening ocean basins. The dispersal of Jurassic ammonoids through the Hispanic Corridor (Fig. 8.3a; Smith and Tipper 1986; Moyne et al. 2004; Arias 2008; Longridge et al. 2008; Fernández-López and Chong Díaz 2011; Galácz 2012; Stevens 2012; Sandoval et al. 2013) and Cretaceous ammonoids through the Trans-Saharan Seaway (Fig. 8.3b; Reyment 1980; Meister et al. 1992, 1994; Courville et al. 1998; Courville 2007; Lehmann and Herbig 2009; Nagm et al. 2010; Nagm and Wilmsen 2012) have been particularly well-documented. Rising sea level was driven both by increases in mid-ocean ridge volume and by global warming. Generally warm "greenhouse" conditions prevailed for most of the Jurassic and Cretaceous, although climate did vary through this interval. The Early and latest Cretaceous have been characterized as a "cool greenhouse" (with mountain glaciers and small volumes of at least seasonal polar ice) while ocean anoxic events (OAEs) during the Triassic-Jurassic transition, Toarcian, Aptian, and Cenomanian-Turonian intervals can be linked to extreme hothouse conditions, driven in part by the eruption of large igneous provinces (Kidder and Worsley 2010, 2012; Takashima et al. 2011; Hay and Floegel 2012). Hence, tectonics, climate, and sea level are strongly linked within the Earth System throughout the Jurassic and Cretaceous Periods.

The breakup of Pangea has long been thought to drive global biodiversity increases by increasing provinciality, with geographic isolation leading to higher origination rates for species and higher taxa (Valentine et al. 1978). However,

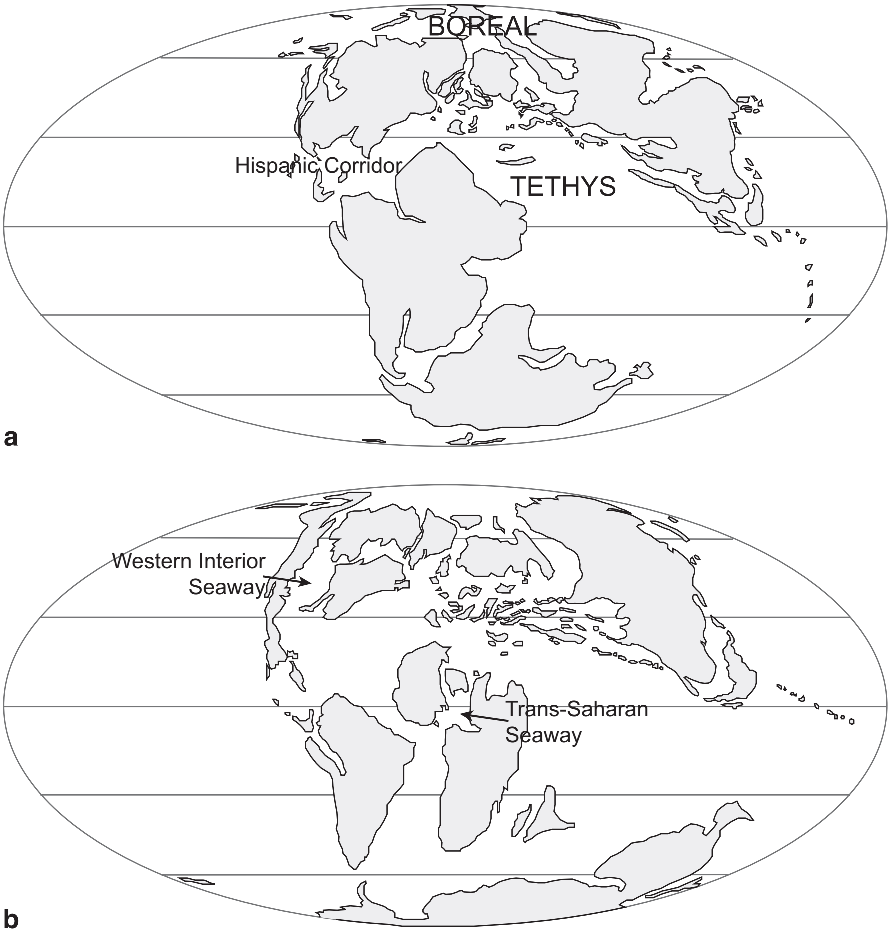


Fig. 8.3 Mesozoic paleogeography. **a** Late Jurassic (150 Ma). **b** Late Cretaceous (90 Ma). Mollweide projection. Maps redrawn from Blakey (2011a)

Miller et al. (2009) found, using a standardized dataset of brachiopod, bivalve, and gastropod occurrences derived from the Paleobiology Database, no increase in "*geo-disparity*" (i.e., faunal compositional differences as a function of geographic distance) through the Phanerozoic. On the other hand, they also found that the Mesozoic showed a unique pattern. Rather than the expected decreasing faunal similarity with geographic distance that was seen for the Paleozoic and Cenozoic Eras, the Mesozoic data showed an irregular relationship between these variables, implying greater cosmopolitanism among Mesozoic groups. Miller et al. (2009) suggested that Mesozoic settings were especially "*patchy,*" with epeiric seas, ocean-facing shallow shelves, and small land masses intermingled, most notably within Tethys. Given the longstanding belief that ammonoid diversity is linked to sea level and tectonics, a similar analysis focusing on the Mesozoic ammonoid occurrence record would make a useful comparison to that of Miller et al. (2009).

8.4.2 Ammonoid Paleobiogeography

Before discussing the paleobiogeography of ammonoids and its role in the macroevolution of this group, we must consider whether significant postmortem drift affected the geographic distribution of fossil remains, and therefore whether geographic patterns documented in the fossil record can be used to infer biological processes. Shells of modern *Nautilus* are known to drift substantial distances beyond their living range within the Indo-Pacific region (Reyment 1958, 1973; Toriyama et al. 1965; House 1987), a process supported by findings in experimental and observational taphonomy (Wani 2004, 2007; Mapes et al. 2010a, b). This propensity for postmortem dispersal has been inferred to apply to ammonoids as well (Reyment 1958, 2008; House 1987). Reyment (2008) reviewed the "*classical literature*" on the question of postmortem drift and concluded that "*nekroplanktonic dispersal is the rule rather than the exception*". However, Kennedy and Cobban (1976) and Cecca (1999), while acknowledging that post-mortem drift of dead ammonoid shells can happen, suggest it is possible to eliminate substantial drift in many specific cases. In particular, Kennedy and Cobban (1976) argued against postmortem drift by noting the large numbers of intact ammonoid specimens that are typically recovered from a fossil locality; they suggest postmortem drift is inadequate to explain these numbers. Maeda and Seilacher (1996) presented hydrostatic models that suggested a depth limit (which they left unspecified), below which dead ammonoid shells were likely to sink quickly and above which they were likely to float and drift in surface currents. This interpretation is supported by the occasional association of jaws with J-K ammonoid shells recovered from offshore settings (Tanabe et al. 2015). Hence, ammonoids living in shallow and/or surface waters might be more likely to experience post-mortem drift than deep water groups. Given the range of arguments on either side, the recommended best practice is to gather taphonomic evidence to support or refute postmortem drift for each particular case.

Ammonoid workers through the nineteenth and much of the twentieth centuries believed that J-K ammonoids were able to freely disperse across wide geographic distances, due to their nektonic mode of life. However, evidence has accumulated to support the view that many ammonoid species and genera were limited to relatively narrow geographic ranges, and show a significant degree of provincialism (Gordon 1976; Ziegler 1981; Thierry 1988; Marcinowski and Wiedmann 1988; Wiedmann 1988; Cecca 1999; Reboulet 2001; Macchioni and Cecca 2002; Cecca et al. 2005b; Dommergues et al. 2009; Dera et al. 2011; Yahada and Wani 2013). Kennedy and Cobban (1976) argued that many eurytopic ammonoid taxa had global distributions, due either to the dispersal by surface currents of planktonic hatchlings (see Sect. 3.5) or to active swimming of nektonic adults, while other ammonoids had limited temperature tolerances, restricting them to certain latitudes. They suggested that endemic ammonoid taxa are typically low-diversity, highly variable species that were prevented by geographic or environmental barriers from dispersing.

The geographic distributions of J-K ammonoids fluctuated through time. Sea level changes are widely thought to drive shifting geographic distributions, although local and regional barriers to dispersal are also important (Hancock and Kennedy 1981; Atrops and Meléndez 1988; Futakami and Obata 1988; Kotetichvili 1988; Meléndez et al. 1988; Hantzpergue 1991, 1995; Bengtson and Kakabadze 1999; Navarro et al. 2005; Olóriz and Villaseñor 2006; Moyne and Neige 2007; Sarih et al. 2007; Bourillot et al. 2008; Mitta 2008; Dommergues et al. 2009; Ifrim and Stinnesbeck 2010; Jagt-Yazykova 2011; Jagt-Yazykova and Zonova 2012). Early Jurassic ammonoids show a relatively cosmopolitan distribution, with the degree of provincialism increasing from the Middle Jurassic through the Middle Cretaceous (Gordon 1976; Westermann 2000). By the Middle Jurassic, two major biorealms—the Boreal and Tethyan Realms—are clearly established (Fig. 8.3a) (Kennedy and Cobban 1976; Rawson 1981; Westermann 2000). The Boreal Realm encompassed mid to high northern paleolatitudes while the Tethyan Realm spanned equatorial regions and the north and south margins of the Tethys Ocean. The Boreal Realm can be subdivided into Arctic and Boreal-Atlantic/Northwest Europe provinces while the much larger Tethyan Realm is varyingly divided into numerous provinces, including the Tethyan proper, West Tethyan, Mediterranean, Indo-Pacific, Indo-Madagascan, Andean, and Austral (southern high latitudes) provinces (Westermann 1981, 2000; Enay and Cariou 1997, 1999; Aguirre-Urreta et al. 2007; Bardhan et al. 2007; Obata and Matsukawa 2007). The East Pacific (i.e., localities in Western North and South America) is separated out as a third realm by some workers (Thierry 1976; Westermann 1981). Moyne et al. (2004) identified 16 ammonoid biogeographic provinces for the Middle Jurassic (Late Aalenian-Middle Bathonian; Fig. 8.4 top). They compiled global species diversity data for 23 ammonoid subfamilies, which produced a cluster diagram showing faunal similarities among regions (Fig. 8.4 bottom). Western Tethys and Circum-Pacific (including the Americas, Antarctic Peninsula, northeastern Pacific, Australia and New Zealand) groups were clearly defined. The Boreal Province was very distinct from all other regions, due to the dominance of the cardioceratid subfamily Arctocephalitinae, which was restricted to high latitudes.

Of particular interest to ammonoid paleontologists has been the European interface between the Boreal and Tethyan Realms. This interface shifted north and south throughout the Jurassic and Cretaceous, and varied from a relatively hard biogeographic boundary (with little mixing of faunas) to a much more porous boundary that permitted considerable mixing of Boreal and Tethyan ammonoid faunas, creating a distinctive European fauna (Callomon 1985, 2003; Thierry 1988, 2003; Cecca et al. 2005a; Alsen 2006; Wierzbowski and Rogov 2011). Provincialism within these larger realms also varied through time and could be strong (Cecca 1999).

A cooling interval in the Late Early Cretaceous (Late Aptian to Albian) redistributed ammonoids in the Pacific province (Iba and Sano 2007; Iba 2009; Matsukawa et al. 2012). As sea level peaked in the Mid-Cretaceous (Haq et al 1987, 1988), provincialism declined overall, although newly formed epeiric seaways such as the Western Interior Seaway of North America and the Trans-Saharan Seaway of Africa hosted radiations of endemic ammonoid clades (Kennedy and Cobban 1976; Marcinowski and Wiedmann 1988; Wiedmann 1988; Meister et al. 1992,

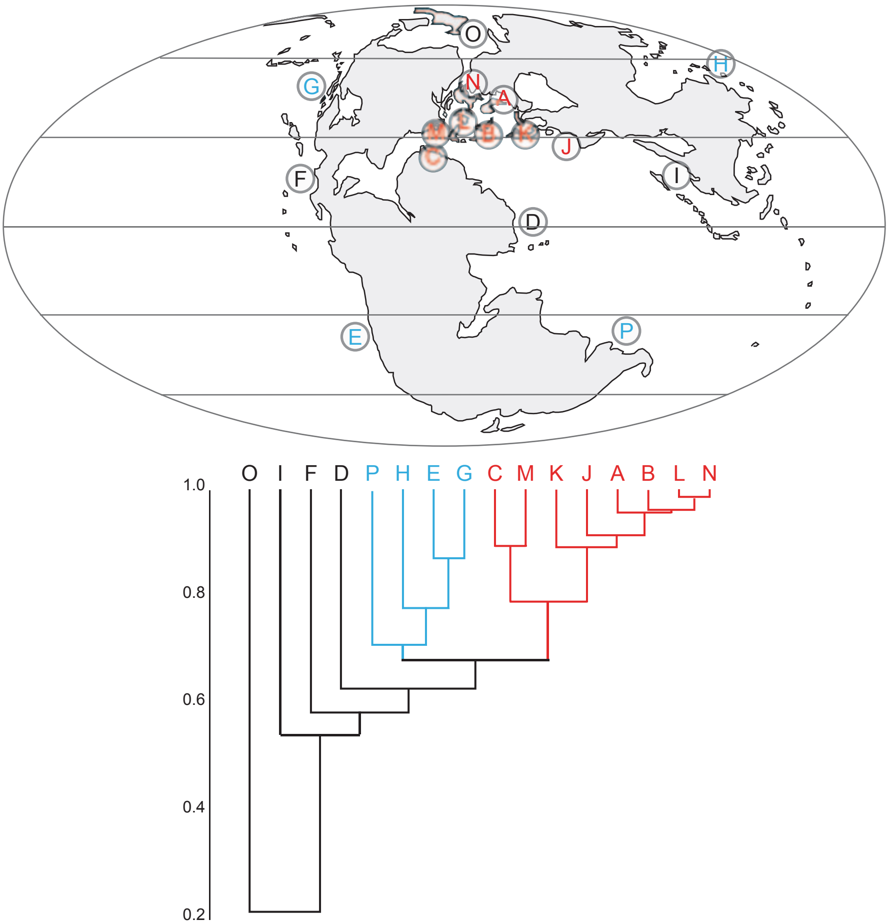


Fig. 8.4 Middle Jurassic ammonoid paleobiogeography. Sixteen biogeographic provinces were identified for the Middle Jurassic (late Aalenian-Middle Bathonian) by Moyne et al. (2004) (*top*), who produced a hierarchical ascendant classification from data on subfamily diversity in each province (*bottom*). They identified a Western Tethys group (in *red*) and a Circum-Pacific group (in *blue*). Note the pronounced difference between the Boreal province (*O*) and all other provinces, reflecting the dominance of the high-latitude cardioceratid subfamily Arctocephalitinae. Provinces: *A* North Mediterranean, *B* Middle Mediterranean, *C* Southwest Tethyan Margin, *D* South Tethyan Margin, *E* South America and Antarctic Peninsula, *F* Central America, *G* Western North America, *H* Japan and Eastern Russia, *I* Tibet and Southeast Asia, *J* Northeast Tethyan Margin, *K* North Tethyan Margin, *L* Southern Northwest European Platform, *M* Atlantic Basins, *N* Northern Northwest European Platform, *O* Boreal, *P* Austral. Province localities and cluster diagram redrawn from Moyne et al. (2004). Base map for Middle Jurassic (170 Ma) redrawn from Blakey (2011a)

1994; Courville et al. 1998; Yacobucci 1999, 2003; Monnet 2009; Nagm and Wilmsen 2012). By the latest Cretaceous, ammonoid faunas were becoming more geographically differentiated again, at least in shallow water settings (Gordon 1976; Rawson 1981; Kennedy et al. 1998; Olivero and Medina 2000). Zakharov et al. (2012), investigating Maastrichtian ammonoids and belemnites recovered from the

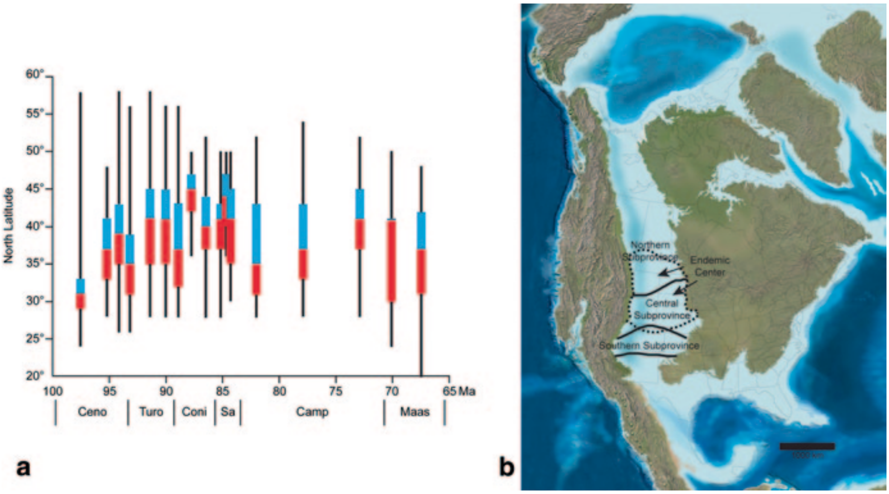


Fig. 8.5 Ammonoid paleobiogeography of the Late Cretaceous Western Interior Seaway of North America. **a** Diversity gradients per substage, based on counts of ammonoid genera present in 2° latitude bins. Box-and-whisker plots show minimum and maximum latitudes occupied (ends of *black lines*) and quartiles for generic diversity; median is marked by the boundary between the *blue* and *red boxes*. Note the northward shifts in diversity during the Cenomanian and Campanian global sea level rises. Stage abbreviations: Ceno-Cenomanian, Turo-Turonian, Coni-Coniacian, Sa-Santonian, Camp-Campanian, Maas-Maastrichtian. Absolute ages from Cobban et al. 2006. **b** Map of the North American Western Interior Seaway during the Late Cretaceous showing biogeographic provinces of Kauffman (1984). *Solid lines* are province boundaries; *dashed lines* show extent of endemic center. The endemic center, where the southern, central, and northern provinces overlapped, was home to a variety of endemic ammonoids. Map modified from 85 Ma North American reconstruction of Blakey (2011b)

mid-Pacific Magellan Seamounts, found evidence of mixing of ammonoids from middle and high northern latitudes into these deeper tropical waters. It may therefore be that open oceanic and/or deeper water ammonoids retained a cosmopolitan distribution through the Late Cretaceous.

Many studies of ammonoid paleobiogeography are essentially descriptive (what Dommergues and Marchand (1988) call an "*approche phénétique*"), documenting taxonomic occurrences in various regions and at various times. Such studies are critical for building comprehensive datasets of ammonoid occurrences through time, and have been used as input data for paleoceanographic models (e.g., Arias 2008). Interest is growing, however, in linking the spatial distributions of ammonoids to the underlying processes that control these distributions (Dommergues and Marchand's (1988) "*approche causale*"), and connecting geographic patterns to morphological evolution, diversification, and extinction. Dommergues et al. (2001) explored relationships among Early Jurassic ammonoid morphologies and their geographic distribution and found a complicated pattern, with no clear relationship between morphotype and dispersal ability or environment. Navarro et al. (2005), on the other hand, were able to link the biogeography of Middle Jurassic cardioceratid ammonoids with morphological evolution. They found that immigration of ammonoids into new areas (tied to sea level rise) led to increased morphological disparity within the group while the subsequent invasion of a different clade led to a reduction in the first group's disparity. Yacobucci (2004b) found a similar result for Middle Cretaceous ammonoids from northern North America: invasion by a second ammonoid group into an endemic genus' geographic range resulted in a shift in the endemic ammonoid's morphology, presumably to avoid direct competition with the newcomer.

Jurassic-Cretaceous ammonoids displayed the expected latitudinal diversity gradient, with highest taxonomic diversity at low latitudes, decreasing towards higher latitudes (Cecca et al. 2005b; Yacobucci and MacKenzie 2007b; Vinarski et al. 2011; Rogov 2012). Cecca et al. (2005b) found that at a single latitude, ammonoid diversity was lowest on epicontinental platforms and higher in both intracratonic basins and deeper oceanic settings. Rogov (2012) argued that the latitudinal diversity gradient was a function of both temperature and the coming and going of ocean connections between basins as sea level fluctuated. Yacobucci and MacKenzie (2007b) similarly found that sea level rises in the Cenomanian and Campanian shifted peak diversities northward within the North American Western Interior Seaway, with the latitudinal gradient shifting back south in the intervening intervals (Fig. 8.5a). Also notable is the presence of an endemic center at mid-latitude within the Western Interior Seaway, where northern and southern faunas overlapped (Fig. 8.5b; Kauffman 1984). A variety of endemic ammonoid species and genera arose within this small region of the seaway.

The relationship between geographic range and rates of evolution and extinction has been explored for many marine animal groups (Jablonski 1986, 2005, 2008; Jablonski and Roy 2003; Payne and Finnegan 2007; Lockwood 2008; Janevski and Baumiller 2009; Myers et al. 2013; Nürnberg and Aberhan 2013). Large geographic ranges may decrease speciation rates (as Jablonski and Roy (2003) found for Cretaceous gastropods) while also providing protection from extinction (Jablonski 2008). Interestingly, Jablonski (2008) found that larger geographic ranges reduced extinction probability for bivalves, gastropods, and nautiloid cephalopods during the Cretaceous-Paleogene extinction but were of no help to ammonoid cephalopods; he argued that this difference resulted from some trait specific to ammonoids that increased the group's extinction probability.

8.5 A Synthetic View of Macroevolution and Paleobiogeography

8.5.1 A Synthetic Model for Ammonoid Speciation

Summarizing the key points made in this chapter, Jurassic-Cretaceous ammonoids show remarkable rates of diversification. Ammonoid diversity appears to be controlled by both "internal" biological processes, such as developmental flexibility, and "external" environmental factors that control habitat space and geographic distributions, including sea level cycles, tectonic shifts, oceanographic conditions, and climate change. Contemporary biological studies have shown that microallopatric, parapatric, and sympatric speciation are all viable alternatives to the traditional allopatric model, and that speciation may be driven by divergent natural selection to occupy different ecological niches. These processes may occur repeatedly in similar habitats, producing a pattern of parallel evolution like that frequently seen in J-K ammonoids.

Integrating these concepts and observations produces the following speciation model for ammonoids:

1. The ancestral ammonoid species moves into a new habitat, such as a newly formed epeiric seaway created by a sea level rise.
2. Small random changes in the flexible developmental program of individuals produce variable adult sizes and shell forms.
3. These variable morphs sort into different ecological niches and/or occupy distinct microhabitats within the epeiric seaway.
4. Assortative mating and disruptive selection result in reproductive isolation and divergence. If these subpopulations persist, one or more new, endemic species may be produced.
5. Finally, if a related ammonoid species later moves into a similar new epeiric habitat, it will undergo the same sort of process. Developmental constraints on shell form will result in the production of anatomical variants similar to earlier endemic radiations (i.e., homeomorphs), which will then sort themselves into similar microhabitats.

Note that under this model, speciation is implied to be sympatric or microallopatric. Different anatomical variants are produced in situ, and then separate out into microhabitats. These microhabitats may be patchily distributed within the same general region (e.g., different benthic substrates), or may result in a fossil record that combines multiple microhabitats in a single location (e.g., ammonoids occupying different portions of the water column). The model predicts that ammonoid morphology should match specific ecological niches consistently, that is, a particular mode of life is reflected in shell anatomy and size. The model also requires that the ecological niches to which ammonoid morphs adapt are consistently available through space and time.

This model of speciation emphasizes the importance of both biological processes (developmental flexibility) and environmental factors (sea level change and a mosaic of microhabitats) in explaining high diversification rates among ammonoids. Neither by itself is sufficient to explain ammonoid evolution. The inherent developmental flexibility of ammonoids can produce a great diversity of forms, but these will persist and diverge only when environmental conditions allow it. Sea level rises that produce new shallow marine habitat area may represent a particularly important environmental change driving ammonoid diversification. However, Holland (2012) documented that not all sea level rises are equal. While sea level rises necessarily increase the total area of flooded continent, they need not increase shallow marine habitat area, depending on what depth range of habitat one considers (e.g., 0–25 m, 75–100 m). Hence, a clade's response to sea level change will be contingent on the specifics of the case: what the starting sea level was, the particular bathymetric profile of that region, and the larger paleogeographic context. These subtleties may help to explain conflicting specific ammonoid case studies that show diversification peaks during transgressions vs. regressions, and a variety of complex relationships between macroevolution and paleobiogeography.

Testing this model for ammonoid speciation will require detailed interdisciplinary data for each radiating clade. A robust phylogenetic hypothesis of evolutionary relationships within the clade is an essential first step, as putative ancestor and descendent species must be identified. The extent of developmental flexibility in the ancestral lineage must be documented through investigation of morphological and ontogenetic variation within the group. Paleoecological, sedimentological, and geochemical data can demonstrate the existence of different microhabitats within a seaway, and the recurrence of similar microhabitats in different seaways. It is also critical to establish linkages between ammonoid shell form and size and specific modes of life or microhabitats within the clade. High resolution stratigraphic and geographic occurrence data will show whether the ancestral lineage existed outside the seaway before it formed and then moved into the seaway. Such data are also essential to demonstrate sympatry between ancestor and descendent lineages within the seaway and endemism of newly arising species.

A comparative approach may be the most effective way of testing this speciation model. An ideal test case would involve two co-occurring ammonoid clades, one of which shows rapid speciation and one of which does not. The speciation model presented here would predict that the diversifying clade will show a higher degree of developmental flexibility, more heterochrony, a greater number of endemic species, and more sympatry among species within the clade. A correlation between the opening of new shallow marine habitat space and pulses of diversification is also expected. These predictions could be tested if suitable clades can be identified for comparison.

8.5.2 New Directions in Studying Ammonoid Macroevolution

Given their rich fossil record and long history of study, Jurassic and Cretaceous ammonoids can serve as a model system for many areas of macroevolutionary investigation. Of utmost importance will be developing and testing phylogenetic hypotheses of relationship for J-K ammonoid clades. With this sound phylogenetic context, integrative work can proceed to investigate the relationships among diversification, morphospace occupation, geographic distribution, extinction, and environmental change. Such studies will be valuable at a variety of taxonomic, spatial, and temporal scales; detailed studies of individual clades will be complemented by global studies of ammonoid macroevolution across the entire Jurassic and Cretaceous Periods.

Sorely needed are comprehensive databases of J-K ammonoid occurrences. While the Paleobiology Database (PBDB; http://paleobiodb.org) has been used to investigate Cretaceous ammonoid paleobiogeography (Hendy 2009), it currently contains a limited number of ammonoid occurrences and its taxonomic coverage is incomplete. Various workers have developed their own ammonoid occurrence databases for particular regions and time intervals (e.g., Late Cretaceous Western Interior Seaway of North America database; Yacobucci and MacKenzie 2007a, b, 2008; MacKenzie and Yacobucci 2008). A priority for the field should be to integrate existing data sources into a single, open-access database of J-K ammonoid occurrences that is suitable for a range of quantitative and qualitative analyses.

Fossil occurrence data must be analyzed in the context of potential sampling biases. The PBDB team and others have developed a range of sampling standardization techniques that take into account variations in sampling intensity through time (Alroy et al. 2001, 2008; Alroy 2008, 2010; Kiessling 2008). Such techniques have not yet been tested on J-K ammonoids. Another potential bias is the availability of rock for sampling through time. Temporal and spatial variations in the amount of accessible outcrop are known to affect biodiversity patterns (Raup 1976; Peters and Foote 2001; Smith 2007; McGowan and Smith 2008), although whether outcrop map area or rock exposure area is a better metric is debated (Dunhill 2012). Of particular interest to ammonoid workers is the apparent correlation of marine invertebrate diversity to sea level cyclicity and the expansion and contraction of sedimentary basins (Smith et al. 2001; Peters 2005; Smith and McGowan 2005; Peters and Heim 2010, 2011; Hannisdal and Peters 2011). Such a pattern may demonstrate a significant sampling bias (Smith et al. 2001; Smith 2007; Wall et al. 2009) or may result from real biological processes that are associated with sea level change (the "common-cause" hypothesis; Peters 2005; Peters and Heim 2010, 2011; Hannisdal and Peters 2011). These competing options can be evaluated by detailed studies of J-K ammonoid occurrences. More generally, the completeness of the ammonoid fossil record could be assessed by estimating preservation rates (Foote 2003) or evaluating stratigraphic gaps implied by phylogenetic hypotheses (Wagner 2000). And, of course, taxonomic revisions of major J-K ammonoid groups are sorely needed in order to produce taxonomically standardized datasets.

Quantitative approaches to the integrative study of ammonoid evolution and biogeography have become more common over the last decade (Brayard et al. 2007; Hendy 2009; Dera et al. 2011; Brayard and Escarguel 2013; Brosse et al. 2013). Brayard et al. (2007) used a combination of approaches, including hierarchical cluster analysis, nonmetric multidimensional scaling, and their own nonhierarchical Bootstrapped Spanning Network technique to document paleobiogeographic patterns in the radiation of Early Triassic ammonoids after the Permo-Triassic extinction. Dera et al. (2011) used a similar quantitative toolkit to study ammonoid evolution through the Pliensbachian-Toarcian (Early Jurassic) interval. Such approaches should be expanded to later time intervals with more complex paleogeographic contexts.

Modern biogeographers are turning to the use of geographic information systems (GIS) and spatial statistics to document, quantify, and model biogeographic patterns and processes. Fewer paleontologists have made use of these tools, although they are a powerful method for investigating an array of questions, including reconstruction of geographic ranges, assessment of habitat tracking, and documenting the environmental drivers of evolution and extinction (Lieberman 2000; Stigall 2011; Yacobucci and MacKenzie 2007a, b, 2008; MacKenzie and Yacobucci 2008; Myers et al. 2013). As a comprehensive database for J-K ammonoids is constructed, we must be mindful of building spatial data into it so that it is fully compatible with GIS-based analyses.

A synthetic and quantitative approach to ammonoid macroevolution and paleobiogeography is necessary for us to understand the evolutionary dynamics of this most remarkable group of animals. As our database expands and new computational techniques are brought to bear on wide-ranging questions, J-K ammonoids will become a model for how marine animals evolve in a Greenhouse World.

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Chapter 9
Paleobiogeography of Early Cretaceous Ammonoids

Jens Lehmann, Christina Ifrim, Luc Bulot and Camille Frau

9.1 Introduction

Ammonite dispersal is clearly related to paleogeographic patterns throughout the Mesozoic (Page 1996). Their distribution during life is thought to be controlled by physical barriers such as land masses and deep ocean basins, as well as by comprehensive environmental factors such as climate differences and oceanic circulation patterns (Kennedy and Cobban 1976; Cecca 2002; Cecca et al. 2005), while their biogeography is influenced by post-mortem transport along with other taphonomic and collection biases (Kennedy and Cobban 1976; De Baets et al. 2015; Naglik et al. 2015; Lukeneder 2015). Thus, a number of factors have an impact on their paleobiogeographic distribution.

The favored habitat of most ammonite families was the continental shelf (Westermann 1996), and these areas constantly changed as a result of fluctuating sea levels and plate tectonic movements on a large scale, particularly during the Early Cretaceous period (e.g. Föllmi 2012). Dynamic plate tectonic configurations that are strongly linked to sea-level changes trigger the migration of species

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J. Lehmann (✉)
Geowissenschaftliche Sammlung, Universität Bremen, Klagenfurter Straße,
28359 Bremen, Germany
e-mail: jens.lehmann@uni-bremen.de

C. Ifrim
Institut für Geowissenschaften, Ruprecht-Karls-Universität,
Im Neuenheimer Feld 234, 69120 Heidelberg, Germany
e-mail: christina.ifrim@geow.uni-heidelberg.de

L. Bulot
Aix-Marseille Université, UMR CNRS 7330 CEREGE, Centre Saint-Charles,
Case 67, 3 Place Victor Hugo, Cedex 03, 13331 Marseille, France
e-mail: bulot@cerege.fr

C. Frau
9bis Chemin des Poissonniers, 13600 La Ciotat, France
e-mail: camille_frau@hotmail.fr

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by opening new migration routes (e.g. Wiedmann 1988). A prominent Early Cretaceous example of this is the opening of the Atlantic Ocean. Ammonite faunas from Brazil suggest that the opening of the central Atlantic created new migration routes as early as the Aptian, and the deepening of the young ocean, accompanied by deep-water circulation, was not established until the late Albian (Bengtson et al. 2007). Besides the impact of these physical barriers, ammonite dispersal in the Early Cretaceous is also believed to be temperature-related (Scott 1940; Michael 1979; Mutterlose 1992; Reboulet 2001). In recent decades, it has been assumed that temperatures were cooler in the earliest Cretaceous and rather moderate and warm from the Albian onwards, with less pronounced climate belts (e.g. Frakes et al. 1992). However, in the Berriasian-Aptian, and even after the onset of a warmhouse world in the late Early Cretaceous, it is a matter of debate whether temperature differences were more pronounced than was believed near the end of last century (Mutterlose et al. 2009; Erbacher et al. 2011; Papp and Cociuba 2013; Zakharov et al. 2013). Ammonites apparently were able to cope with drastic sea-surface temperature changes. The magnitude and frequency of temperature change during the Cretaceous, however, are still poorly constrained (e.g. Schouten et al. 2003, Dumitrescu et al. 2006), and the challenging question arises whether restricted ammonite distribution patterns are caused by climatic conditions or other factors (e.g. Kemper and Schmitz 1981; Marcinowski and Wiedmann 1988; Owen 1988a). Besides the significance of overall temperature differences in their habitats, it is even more important to understand the ammonite lifestyle and reproduction strategies to correctly interpret paleobiogeographic affinities. The latter factor is very rarely addressed with regard to ammonites in general (Manger et al. 1999; Mapes and Nützel 2009; reviewed in De Baets et al. 2015), but there has been some progress made in reconstructing the ammonite lifestyle in recent years (Ritterbush et al. 2014; Lukeneder 2015; Moriya 2015). But there is still much to be learned. A few recent studies actually use an integrated approach to address paleoenvironmental change and ammonite occurrence in great detail for the Early Cretaceous (e.g. Reboulet et al. 2005). These could answer some crucial basic questions on the background of paleogeographic distributions of Early Cretaceous ammonites, but there are still many problems to solve as well.

Differing taxonomic concepts often obscure ammonite distributional patterns (Kennedy and Cobban 1976; compare De Baets et al. 2015) and here we address many of the currently debated problematic issues. We distinguish biogeographic areas based on the distribution of ammonite taxa, as was performed in the pioneer work byNeumayr (1883). However, paleobiogeographic terms are updated to comply with Westermann (2000) and Cecca (2002). In this nomenclature, superrealms are the largest biogeographic areas. In contrast to Page (1996), we recognize a number of realms: The Boreal Realm, the Tethyan Realm, and the Austral Realm (for late Barremian to Albian times only). Occassionally, the additional distinctions of an Arctic (= A Sr; Berriasian-Hauterivian and Albian), a Boreal-Atlantic- (= B-A Sr; Berriasian-Aptian) and a Boreal-Pacific (= B-P Sr;Valanginian-? early Barremian) Subrealm as parts of the Boreal Realm are found to be reasonable. Similarly, a Mediterran-Caucasian (= MC Sr; Berriasian-Aptian) and an Indo-Pacific (= I-P Sr, Berriasian—early Barremian) Subrealm are distinguished as part of the Tethyan Realm.

Despite abundant systematic descriptions, quantitative approaches to ammonite paleobiogeography are still lacking for the Early Cretaceous. The qualitative interpretations given here are therefore an interim state of the art and need quantification in the future.

9.2 Early Cretaceous Paleobiogeography

9.2.1 Berriasian

In the early Berriasian, no Tethyan immigrants are found in the Boreal Realm and, conversely, there are no boreal species recorded from the Tethyan Realm (Rawson 1995a; Bulot 1996). This is one of the reasons why the definition of the Jurassic/Cretaceous boundary has been highly debated for many years and correlations between the Boreal and Tethyan realms are still at a preliminary stage (Wimbledon et al. 2011). In recent years, integrated magneto- and biostratigraphy have allowed a better correlation between the two realms, and it is now generally accepted that the latest Volgian correlates with the earliest Berriasian (Zakharov and Rogov 2008; Wimbledon et al. 2011, 2013; Bragin et al. 2013; Rogov 2013). As a consequence, it is now clear that the Jurassic/Cretaceous boundary is not marked by a significant ammonite turnover above the suprageneric level, neither for the Boreal nor Tethyan realms (Tavera et al. 1986; Zakharov et al. 1996; Rogov 2013).

There is a clear difference between the Tethyan record and that of the Boreal Realm, underlining the distinction between these faunal realms (Fig. 9.1). In the Boreal Realm members of the family Polyptychitidae dominate the record, particularly *Craspedites, Praetollia* and *Chetaites* (Baraboshkin 2002; Zakharov and Rogov 2008).

In the earliest Berriasian, the Tethyan Realm ammonite faunas are more diverse than those of the Boreal Realm, and are dominated by ammonites of the family Neocomitidae. The distributions of *Berriasella, Pseudosubplanites, Malbosiceras, Delphinella, Dalmasiceras, Strambergella* and *Pseudoneocomites* are restricted to the Mediterran-Caucasian Subrealm (Le Hégarat 1973; Kotetishvili 1988; Wimbledon et al. 2013). Earliest Berriasian *Berriasella s. str.* are only known from southern and central Europe, North Africa, Ukraine, the Caucasus and northern Iran (unpublished data), in contrast to a much wider geographic distribution often attributed in recent decades (Fig. 9.1) due to a more casual definition of this genus.

A most interesting change in the ammonite distribution occurs during the (?) late early to early late Berriasian. The Boreal Realm is characterized by the decline of the Craspeditinae and Dorsoplanitinae and the diversification of the Tollinae (Baraboshkin 1999). The Arctic and Boreal-Atlantic subrealms both exhibit

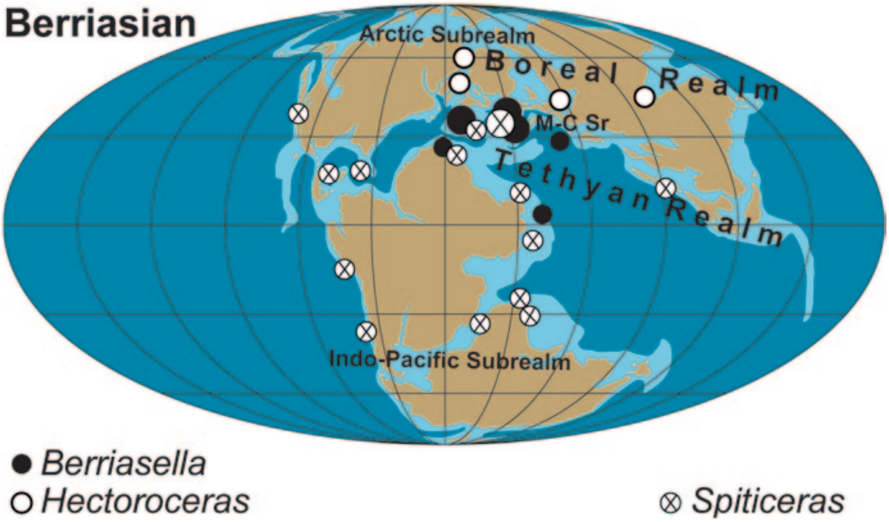

Fig. 9.1 Aspects of Berriasian ammonite paleobiogeography. Map based on 150 Ma reconstruction (paleomaps after Ronald Blakey, http://cpgeosystems.com/index.html, accessed 6th of June 2014). Larger dots indicate the home range and peak occurrence of a genus if it is more widely distributed. *M-C Sr* Mediterran-Caucasian Subrealm of the Tethyan Realm

the occurrence of *Hectoroceras* (Casey 1973; Birkelund et al. 1983; Baraboshkin 1999; Fig. 9.1). Among the Tolliinae, *Surites* is widely distributed in the late Berriasian of the Boreal Realm (Shul'gina 1985, 1989; Zakharov et al. 1996). According to Baraboshkin (1999), two areas of diversification of the Tolliinae can be distinguished that roughly correspond to the Arctic and Boreal-Atlantic subrealms. It should also be noted that the Eastern European part of the Boreal Atlantic Subprovince contains Tethyan genera that are also known from the eastern part of the Mediterran-Caucasian Subrealm, such as *Riasanites* and *Transcaspiites* (Mitta 2007, 2011).

Ongoing research (unpublished data) suggests that the affinities of the ammonites of Tethyan origin from the Polish Lowland and Russian Platform are even stronger with the fauna of Crimea, the Caucasus and Mangyshlak described by Luppov et al. (1988), Kvantaliani (1999) and Arkadiev et al. (2012). Assemblages of the eastern part of the Mediterran-Caucasian Subrealm (Caucasian and Transcaspian areas) are dominated by endemic Neocomitidae such as *Tauricoceras* and *Gechiceras*. Other important elements of the assemblage are *Euthymiceras* and *Hegaratia* (= *Balkites*), which are only known from a limited number of specimens in the western part of the Mediterran-Caucasian Subrealm (Le Hégarat 1973; Patrulius and Avram 1976). In contrast, the equivalent faunas from the western part of the Mediterran-Caucasian Subrealm are dominated by *Berriasella, Mazenoticeras, Tirnovella, Fauriella* and *Jabronella*.

Because of correlation problems (e.g. Zakharov et al. 1996), the limits of the Berriasian stage outside the areas discussed above are poorly understood. The marked endemism discussed above also affects the Indo-Pacific Subrealm. In Argentina and Chile, the faunas are dominated by *Andiceras*, *Argentiniceras*, *Frenguelliceras*, *Hemispiticeras*, *Cuyaniceras* and *Pseudoblanfordia* (Riccardi 1988; Aguirre-Urreta et al. 2007a; Parent et al. 2011; Vennari et al. 2012). Similarly, the endemic *Kossmatia*, *Durangites* and *Substeueroceras* assemblage of Mexico is now considered as Berriasian (Olóriz et al. 1999).

The conspecificity of the Berriasian ammonites described by Collignon (1962) from Madagascar with Mediterran-Caucasian taxa is still unsolved, at least regarding *Berriasella* (unpublished data). In our opinion *Subthurmannia* from Pakistan (Spath 1939; Fatmi 1977) are fully distinct from *Fauriella* of the Mediterran-Caucasian Subrealm (Bulot 1995).

Our ongoing research suggests that the endemism of the Neocomitidae at the genus level during the Berriasian is much higher than it has been previously assumed in the literature, and that homeomorphy (see Monnet et al. 2015) has led to erroneous taxonomic interpretations.

In our current stage of understanding, *Spiticeras*, and early Olcostephanidae originally described from the Himalayas are the only taxa spread throughout the Tethyan Realm. This links the Mediterran-Caucasian and Indo-Pacific subrealms, with populations reported from the Pacific Coast of America (Jeletzky 1965; Imlay and Jones 1970), Madagascar (Collignon 1962) and the shelf basins of South America and Antartica (Thomson 1979; Riccardi 1988; Aguirre-Urreta et al. 2007a; Parent et al. 2011).

9.2.2 Valanginian

As already outlined by Rawson (1981), Shul'gina et al. (1994), Baraboshkin (1999) and Alsen (2006), the paleobiogeographic patterns of the early Valanginian are almost identical to the late Berriasian. The faunas of the Boreal Realm are dominated by the Tolliinae and their derivatives the Polyptychitinae, while the Tethyan are still characterized by the abundance of the Neocomitidae (Kotetishvili 1983). The distribution of ammonites in the Boreal Realm is complex, partly due to the individual flooding history of former mainlands, and was discussed in great details by Jeletzky and Kemper (1988), Shul'gina et al. (1994), Baraboshkin (1999) and Alsen (2006).

A striking feature is the emergence and radiation of the Platylenticeratinae in the Boreal-Atlantic Subrealm. *Platylenticeras* characterizes the earliest marine beds resting on the continental Early Cretaceous (Wealden facies) in North Germany (Kemper 1961; Kemper et al. 1981; Elstner and Mutterlose 1996). Although there are conflicting opinions in the literature today (Bulot 1996), the idea that *Platylenticeras* is a neocomitid with a Tethyan origin is now favoured (see discussions in Alsen and Rawson 2005). At any rate, in Germany, *Platylenticeras* developed a high diversity (Kemper 1961, 1992; Hoedemaeker 2012 refers to drift occurrences, probably originating from Germany). This is in contrast to other European countries, from which only a limited number of species are known and where it is rare (Baumberger 1908, 1928; Thieuloy 1977; Vašíček 1979, 1997). In Greenland, and simultaneously on the Russian plate, *Delphinites* (*Pseudogarnieria*) faunas developed, ammonites belonging to the same subfamily Platylenticeratinae (Alsen and Rawson 2005). *Delphinites* (*Pseudogarnieria*) emphasize the very endemic character of early Valanginian ammonite faunas in the Boreal Realm, as in *Platylenticeras* there is a number of regionally occuring species only.

A transgression in the middle part of the early Valanginian wiped out these strong differences of the earliest Valanginian, and Polyptychitinae replaced the platylenticeratid faunas in the Boreal-Atlantic Subrealm (Jeletzky and Kemper 1988; Rawson 1981, 1993, 1994; Alsen 2006).

In contrast, the earliest Valanginian assemblages of the Tethyan Realm are dominated by neocomitids; the most prominently recorded genera are *Neocomites*, *Kilianella*, *Sarasinella* and *Thurmanniceras* (Rawson 1981; Kotetishvili 1983; Company 1987). Except for *Sarasinella*, these genera were originally defined based on species originating from the western part of the Mediterran-Caucasian Subrealm. There is no consensus on the definitions and the paleogeographic distributions of *Thurmanniceras*, *Sarasinella* and *Neocomites*. This problem has been addressed often in the literature (Company 1987; Bulot 1995; Aguirre-Urreta and Rawson 1999; Ettachfini 2004; Rawson 2007; Aguirre-Urreta et al. 2008). According to our current stage of knowledge, *Kilianella* is the only neocomitid that had a widespread distribution over the Mediterran-Caucasian and Indo-Pacific Subrealms of the Tethyan Realm.

Most interesting is the development of a very peculiar earliest Valanginian assemblage dominated by *Lissonia* and its potential macroconch *Raimondiceras* in South American basins of the Indo-Pacific Subrealm (Lisson 1907; Haas 1960; Leanza 1972; Etayo-Serna 1985; Mourgues 2004; Aguirre-Urreta et al. 2007a). As already pointed out by Aguirre-Urreta and Rawson (1999) and Aguirre-Urreta et al. (2008), these forms most likely evolved from the earliest Valanginian endemic Neocomitidae. Poorly constrained early Valanginian faunas were also reported from the Pacific coast of North America, where a mixture of endemic Neocomitidae (*Paskentites*, alleged '*Kilianella*' and '*Thurmanniceras*' as well as '*Sarasinella*' *sensu lato*) and Tolliinae (*Tollia*, *Neocraspedites*) were described by Imlay (1960) and Imlay and Jones (1970).

The continuous significant sea level rise that marks the Lower/Upper Valanginian boundary interval (see discussion in Föllmi 2012) led to an enhanced exchange of genera in the wider transitional zone between the Tethyan and the Boreal Realms in Europe (Kemper et al. 1981; Rawson 1993; Bulot 1993, 1996; Föllmi 2012). At this time a group of six Tethyan immigrant genera appeared, even in the fairly isolated epicontinental basins of North Germany, northeastern England and Poland (Kemper et al. 1981; Kutek et al. 1989; Kemper 1992; Kutek and Marcinowski 1996).

Some of these taxa, including *Olcostephanus* (Fig. 9.2), *Karakashiceras*, and *Neohoploceras,* originated in the central part of the Mediterran-Caucasian Subrealm, but were dispersed as a result of this event not only to the Boreal-Atlantic Subrealm, but also over most of the Indo-Pacific Subrealm. This assemblage is well documented in Pakistan, Madagascar and South Africa (Bulot, 1990), Central

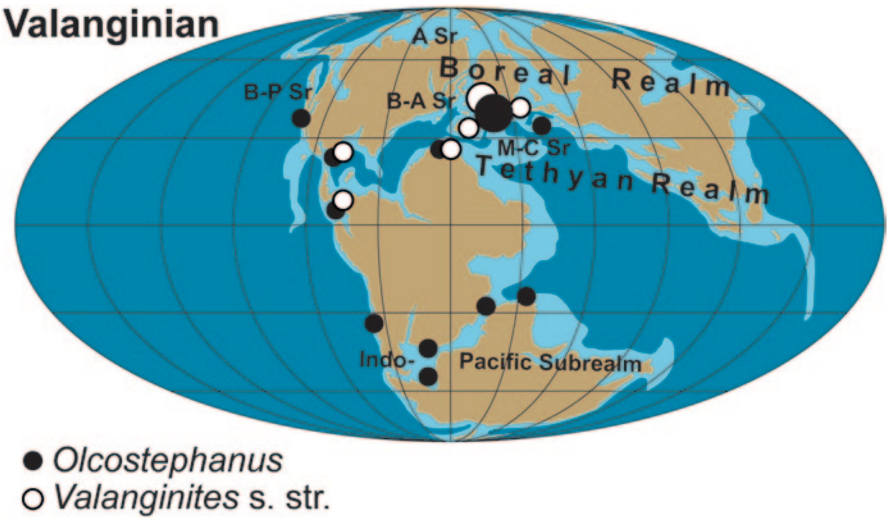

Fig. 9.2 Aspects of Valanginian ammonite paleobiogeography. Map based on 150 Ma reconstruction. *B-A Sr* Boreal-Atlantic Subrealm, *B-P Sr* Boreal-Pacific Subrealm, *A Sr* Arctic Subrealm, all of these are subrealms of the Boreal Realm. For further details see caption to Fig. 9.1

America (Etayo-Serna 1985; Young 1988; González-Arreola 2007) and the Andean Basins of South America (Rawson 2007; Aguirre-Urreta et al. 2007a, 2008). During that time *Olcostephanus* even reached the Pacific coast of North America (Imlay and Jones 1970) and Antartica (Howlett 1986).

In contrast, the worldwide distribution of the cadicone *Valanginites* appears doubtful. South American occurrences are clearly dated from the earliest Valanginian (see discussion in Aguirre-Urreta et al. 2008), whereas in the Mediterranean areas the stratigraphic distribution of *Valanginites* is well dated from the late early and early late Valanginian (Bulot et al. 1990). Aguirre-Urreta et al. (2008) claim that the South American *Valanginites* gave rise to the Mediterranean ones. In our opinion this view is open to discussion, and we favor the idea that *Valanginites* is paraphyletic and that two distinct lineages evolved from the *Olcostephanus* rootstocks at different times. We therefore indicate the distribution of *Valanginites* s. str. herein, contrasting a global distribution that is often attributed to this genus (Fig. 9.2). Dzik's (1990) interpretation of *Valanginites* as a macroconch of the small, spine-bearing *Saynoceras* refers to earliest Valanginian forms, but in addition to distinct shell features, the comparatively restricted paleobiogeographic distribution of *Saynoceras* compared to *Valanginites* argues against an interpretation as a dimorphic pair (see Ploch 2003, 2007 for an alternative interpretation).

In the Boreal Realm, the late early to early late Valanginian is marked by the rapid evolution of Polyptychitinae rising from the Polyptychitinae rootstock, and this radiation gave rise to new genera (*Hollwediceras*, *Prodichotomites*, *Dichotomites*, *Homolsomites*, *Ringnesiceras*, *Amundiptychites*) in the epicontinental basins of the Boreal-Atlantic, Boreal-Pacific and Arctic subrealms (Kemper 1978; Jeletzky and

Kemper 1988). The timing and phylogenetic relationships among those taxa remain largely unclear. Nevertheless, *Hollwediceras*, *Prodichotomites* and *Dichotomites* are known from scattered occurrences along the northern margin of the Mediterran-Caucasian Subrealm from Mangyshlak to southeastern France (Thieuloy 1977; Luppov et al. 1983; Thieuloy et al. 1990; Kuhn 1996; Reboulet 1996; Vašíček and Michalík 1999; Dziadzio et al. 2004; Lukeneder 2004).

Characterization of the latest Valanginian paleobiogeography in the Boreal Realm is difficult. It is generally accepted that *Homolsomites* and its junior subjective synonym *Wellsia,* dominate ammonite assemblages of the northern Boreal Realm, the Boreal-Pacific- and Arctic Subrealm of this time interval (Shul'gina et al. 1994; Wright et al. 1996; Baraboshkin 1999; Alsen 2006). Furthermore, successive pulses of Tethyan ammonite migrations from the Mediterran-Caucasian Subrealm characterize the latest Valanginian successions of the Boreal-Atlantic Subrealm, especially with regard to North Germany (Kemper et al. 1981; Kemper 1992; Rawson 1993). These progressive migrations peaked in the latest Valanginian with an ammonite assemblage almost entirely composed of Tethyan (*Olcostephanus*, '*Eleniceras*', *Teschenites*) or Tethyan derived (*Stoicoceras*) ammonites (Quensel 1988).

In the Tethyan Realm, the latest Valanginian is poorly documented outside the Mediterranean regions and Argentina. Recent investigations clearly show a strong endemism during this time interval in the Andean basins of the Indo-Pacific Subrealm with faunas dominated by endemic Neocomitidae (*Pseudofavrella*, *Chacantuceras*, *Decliveites*) (Aguirre Urreta and Rawson 2003, 2010). Outside Argentina, *Pseudofavrella* may be represented in Colombia (Etayo-Serna 1985), but the age of these Valanginian forms, which occur above the early Valanginian *Lissonia* fauna is very poorly constrained.

9.2.3 Hauterivian

The earliest Hauterivian is characterized by a radiation of the Neocomitidae (Ivanov and Aristov 1969; Baraboshkin 2002, with references; Baraboshkin et al. 2003; Alsen 2006). This excludes the Arctic Subrealm and the eastern part of the Boreal-Atlantic Subrealm, where impoverished polyptychitid faunas (*Homolsomites*, *Pavlovites*, *Subspeetoniceras* and *Gorodzovia*) occur. In the western part of the Boreal-Atlantic Subrealm, this faunal change is marked by the appearance of *Endemoceras*, a typical Tethyan-derived neocomitid (Kemper and Wiedenroth 1987; Rawson 1995a). The regularly coiled *Endemoceras*, a genus yielding important index species, progressed into the heteromorphic descendant *Distoloceras* (Kemper et al. 1981; Rawson 1993). *Distoloceras* is strictly restricted to the earliest Hauterivian of northern Europe, and the report of the genus from the late Valanginian is based on the misinterpretation of homeomorphic neocomitids that belong to *Rodighieroites* (Company 1987; Bulot 1995; Barragán and González-Arreola 2009). Interestingly, *Distoloceras* is a homeomorph (compare Monnet et al. 2015 for its definition) of crioceratids of Tethyan origin, with spines and a loosely coiled spiral (Kemper and Wiedenroth 1987).

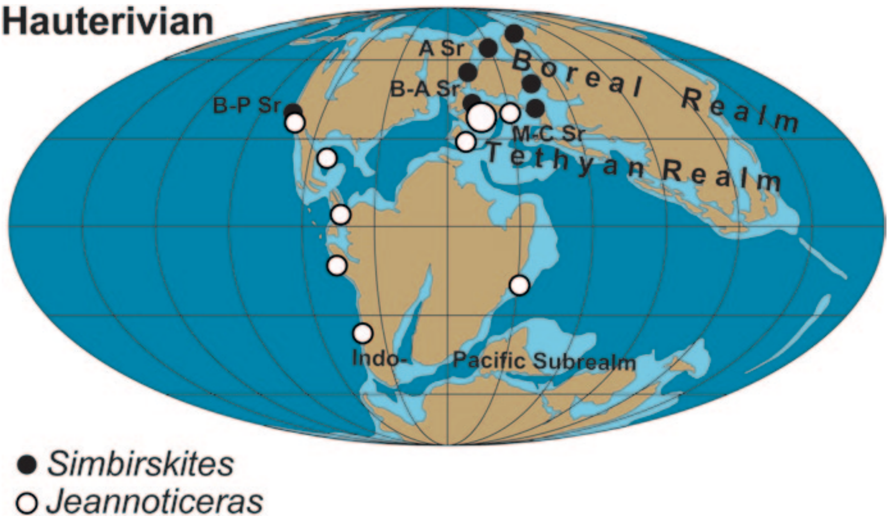

Fig. 9.3 Aspects of Hauterivian ammonite paleobiogeography. Map based on 120 Ma reconstruction. For further details see captions to Figs. 9.1 and 9.2

Acanthodiscus, *Leopoldia* and *Breistrofferella* are rare elements of the western Boreal-Atlantic ammonite faunas (Kemper 1992; Bulot 1995; Rawson 1995a). These genera provide a very useful link between the Boreal and Tethyan realms during the early Hauterivian. The paleogeographic distribution of *Acanthodiscus* and *Leopoldia* is facies-controlled and centered on the shelves of the northern margin of the Mediterran-Caucasian Subrealm (France, Switzerland, Ukraine), although a single occurrence is known from Morocco (Wippich 2001; Ettachfini 2004). As in the case of *Distoloceras*, reported occurrences of *Acanthodiscus* and *Leopoldia* in the late Valanginian are based on misidentified homeomorphic genera, including *Neohoploceras, Karakashiceras, Chacantuceras* and *Pseudofavrella* (Company 1987; Bulot 1995; Reboulet 1996; Aguirre-Urreta and Rawson 1999, 2010). Nevertheless, earliest Hauterivian faunas are poorly documented in the Indo-Pacific Subrealm except for the Neuquén Basin of Argentina, where the fauna is almost exclusively composed of *Holcoptychites*, an endemic member of the Spiticeratinae (Aguirre-Urreta and Rawson 2003; Aguirre-Urreta et al. 2008). The *Favrella* fauna of Patagonia and Antarctica is also an endemic development, but its early Hauterivian age needs final proof (Aguirre-Urreta et al. 2007a).

A major Hauterivian ammonite event is seen in the widespread distribution of the short-lived olcostephanid *Jeannoticeras* and associated *Olcostephanus* species that is well documented from the Boreal-Atlantic, Mediterran-Caucasian and Indo-Pacific subrealms (Bulot 1990; Bulot et al. 1993; Aguirre-Urreta and Rawson 2001) in the middle part of the early Hauterivian (Fig. 9.3). This appearance marks the onset of the mid-Hauterivian episode according to Rawson (1993, 1994). In the western part of the Mediterran-Caucasian Subrealm the neocomitids vanished progressively in the early Hauterivian and were replaced by *Crioceratites, Spitidiscus* and late

Olcostephanus (Rawson 1993). The paleobiogeographic development of neocomitids is made even more complex by the disappearance of *Endemoceras* in England, which is followed by a substantial re-appearance of *Lyticoceras* in France, with the latter probably evolved from the latest *Endemoceras* species (Kemper et al. 1981; Rawson 1993). Another highly significant ammonite faunal turnover for this stratigraphic interval is marked by the replacement of *Endemoceras* in the western limits of the Boreal-Atlantic Subrealm by *Simbirskites* that evolved in the Arctic Subrealm during the earliest Hauterivian (Rawson 1994; Baraboshkin 2002; Baraboshkin et al. 2003; Fig. 9.3). The mid-Hauterivian faunal change also strongly triggered the development of heteromorphic ammonites, which spread into the Boreal-Atlantic-, Boreal-Pacific- and Indo-Pacific Subrealm (Immel 1978, 1979a, b; Rawson 1993, 2007; Baraboshkin 2002; Aguirre-Urreta et al. 2008).

Generally, in the late Hauterivian, heteromorphs become increasingly important and dominate the ammonite assemblages of the Tethyan Realm while the Boreal Realm faunas are dominated by *Simbirskites* (Rawson 1994; Baraboshkin 2002). Whereas *Simbirskites* is absent from the western part of the Meditterran-Caucasian Subrealm, this genus represents a significant element in the Transcaspian area (Kakabadzé 1983; Kemper and Wiedenroth 1987; Baraboshkin 2002). Following the decline and extinction of the Olcostephanidae, Neocomitidae and Leopoldidae, new families appeared or flourished in the Mediterran-Caucasian Subrealm, such as the Abrytusitidae (*Spitidiscus*), Pulchellidae (*Subsaynella, Discoidellia*) and Barremitidae (*Plesiospitidiscus*), which reached the Andean basins of the Indo-Pacific Subrealm in the early late Hauterivian (Vermeulen 2002, 2005, 2007; Vermeulen and Bulot 2007; Rawson 2007; Aguirre-Urreta et al. 2008). In the latest Hauterivian, the recoiling of crioceratids brings rise to *Pseudothurmannia* (Wiedmann 1969) and allied genera/subgenera as important index species in the Western Tethys (Cecca et al. 1998; Company et al. 2003; Vermeulen et al. 2009; Hoedemaeker 2013).

Late Hauterivian successions of the Indo-Pacific Subrealm are as poorly known as those of the early Hauterivian. Re-examination of *Menuthiocrioceras* and *Malgasaynella* has showed us that these genera are of late Barremian age (see below) and thus Collignon's (1948, 1962) record of late Hauterivian in Madagascar and Indonesia is incorrect. In contrast, late Hauterivian strata are well developed in the Andean basins of Argentina and Chile (Aguirre-Urreta et al. 2007a). Although relationsships of the Andean basins to the Mediterran-Caucasian Subrealm have been known for quite a long time, a strong endemism was assumed by Leanza and Wiedmann (1980). This is relativized today because diversity in this area is higher than previously believed (Aguirre-Urreta et al. 2007a, b). The most striking feature of the faunas is the presence of local heteromorphs that evolved from Tethyan-derived *Crioceratites.* Identification of *Hemihoplites* from the Hauterivian of Patagonia (Riccardi and Aguirre-Urreta 1989; Aguirre-Urreta 2002) is questionable, since the evolution of *Hemihoplites* in the late Barremian of southeastern France has now been well established (Bert et al. 2006, 2008) and the Patagonian species show only superficial morphological similarities with the Mediterranean taxa. An *Aegocrioceras* species reported from Chile (Aguirre-Urreta et al. 2007b) is most likely a local offshoot of the Tethyan-derived *Crioceratites* of the *schlagintweiti* group rather than indicating paleobiogeographic affinities to the European Boreal Realm.

9.2.4 Barremian

The sea-level lowstand initiated in the late Hauterivian, and marking the early Barremian, is believed to be responsible for an increasing diversity in ammonite faunas, as individual basins became isolated (Rawson 1993). The Barremian was marked by the prevalence of continental conditions over most of the Arctic Subrealm (Jeletzky 1970; Rawson 1981; Baraboshkin 2002 with references) while carbonate platforms developed on both margins of the Mediterran-Causasian Subrealm (Philip 2003 with references). The key feature of the Barremian ammonite faunas is the development of rich faunas with heteromorphic ammonites.

Boreal Barremian ammonite faunas are known from the United Kingdom and Germany only, thus representing a comparatively small area of this realm. In the earliest Barremian of the Boreal Realm, the last occurrence of *Craspedodiscus* is remarkable, since it represents the last subgenus of the major Boreal ammonoid clade of the family Polyptychitidae (Rawson 1971, 1981). It is worth noting that the reported occurrence of *Simbirskites* (*Milanowskia*) sp. from the early Barremian of Japan (Matsukawa 1988) is highly doubtful and based on poorly preserved specimens that superficially match Hauterivian simbirskitids. As a consequence, the migration of Boreal ammonites in the Tethyan-dominated assemblages of the Far-East terranes of Asia is not substantiated.

Boreal-Atlantic shelf deposits are characterized solely by Tethyan and/or Tethyan-derived heteromorphs after the extinction of simbirskitids. The systematic treatment of these heteromorphs varies from one author to another. The most frequently cited genus is *Paracrioceras*. It is considered to be a senior subjective synonym of *Emericiceras* by Rawson (1975) and Wright et al. (1996), a view that is rejected by Vermeulen (2004, 2006) and Kakabadzé and Hoedemaeker (2010), albeit for different reasons. By contrast, Wiedmann (1962) and Immel (1978) regarded *Paracrioceras* as a synonym of *Crioceratites*. Thus *Crioceratites*, *Paracrioceras* and *Emericiceras* are defined inconsistently and reflect the poor state of early Barremian heteromorph taxonomy, which is confusing. The problem was also addressed by Klinger & Kennedy (1992) and Kakabadzé & Hoedemaeker (2004) when discussing the systematic assignment of South African and South American faunas. In our opinion, *Crioceratites*, *Emericiceras* and *Paracrioceras* are unsuitable to define paleobiogeographic groupings in the Barremian. As a consequence they are of little help to define the limits of paleobiogeographic units.

Therefore, the limits of distribution of normally coiled ammonites occuring in the Tethyan Realm, excluding heteromorphs, is extremely important in drawing the southern boundary of the Boreal Realm (Hoedemaeker 1990), particularly since they do not occur in the Boreal Realm (Rawson (1993, (1994). Among others, the earliest to early late Barremian Holcodiscidae (*Holcodiscus*, *Parasaynoceras*), Pulchelliidae (*Pulchellia*, *Nicklesia, Heinzia*) and Barremitidae are widely distributed from Japan to northern South America (Mexico, Colombia). Along the Pacific coast, spot occurrences of Pulchellidae extend as far north as California (Murphy 1975) and as far south as northern Chile (Aguirre-Urreta et al. 2007a) where they are associated with a fairly diverse assemblage of heteromorphs including the

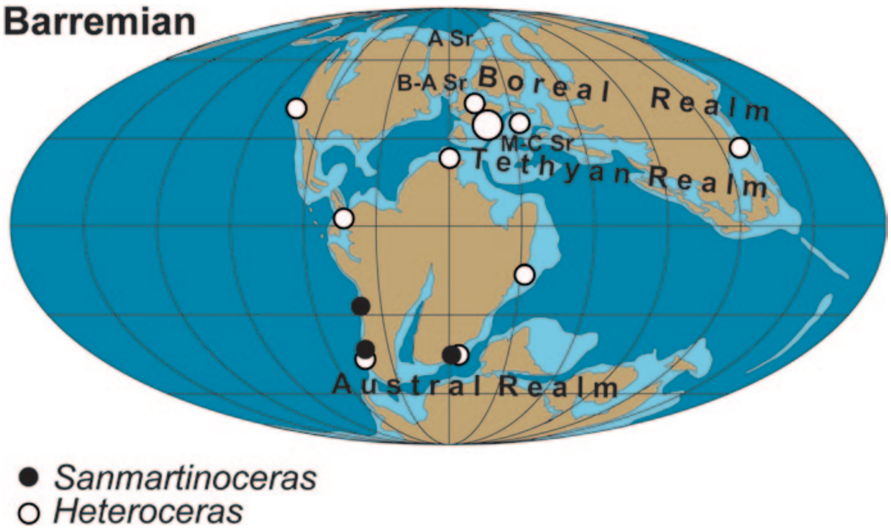

Fig. 9.4 Aspects of Barremian ammonite paleobiogeography. Map based on 120 Ma reconstruction. For further details see captions to Figs. 9.1 and 9.2

Circum-Pacific genus *Shasticrioceras*, which is also known from Arctic Canada (Jeletzky 1970) and Japan (Matsukawa and Obata 1993).

In the Mediterran-Caucasian Subrealm, the late Barremian is marked by a drastic change in the evolution of the ammonite faunas. Holcodiscidae and Pulchellidae have dissappeared and heteromorphs are highly diverse (Vermeulen 2005; Bert et al. 2008). Among heteromorphs the Hemihoplitidae and Heteroceratidae show the most striking morphological changes; the former are characterized by a recoiling of the shell, and the latter by the development of a helicoidally coiled inner whorls (the global distribution of *Heteroceras* is shown in Fig. 9.4). Both families provide faunal links with the Boreal-Atlantic Subrealm, since *Spinocrioceras* has been reported from Germany (Kemper 1973, 1995) and *Heteroceras* from the United Kingdom (Rawson 1995b).

Although imperfectly dated, the onset of the Austral Realm, centered on Patagonia, Australia, Africa and Madagascar, most likely took place in the late early to early late Barremian. Non-heteromorphic ammonites endemic to this area includes *Hatchericeras*, which stands among the candidates for the last representative of the Perisphinctoidea, even though its last occurrence is not accurately dated with respect to the Simbirskitinae (Riccardi 1988; Kennedy and Klinger 1990). Associated fauna include *Malgasaynella* and *Menuthiocrioceras* (a peculiar group of endemic heteromorphs to which *Cryptocrioceras* is herein considered to be a junior subjective synonym; Collignon 1948, 1962; Skwarko and Thieuloy 1989; Aguirre-Urreta 1990; Klinger and Kennedy 1992). Characteristic for the latest Barremian is the spreading of the Heteroceratidae from the Tethyan Realm toward the Austral Realm. Simultaneously, the Aconeceratidae, including the significant genus *Sanmartinoceras* (Fig. 9.4), most likely evolved as a separate offshoot of Desmoceratidae.

9.2.5 Aptian

In terms of ammonite paleobiogeography the Aptian is generally considered to be a cosmopolitan time due to a major transgression that begins in the early Aptian (Owen 1996). This global event was linked to the northward propagation of the Atlantic rift system, which led to the opening of numerous gateways and established new faunal connections (Rawson 1994; Hallam 1981; Bengtson & Kakabadzé 1999). The faunal dispersals are also linked to a shift toward warmer conditions that equalized climate belts and ultimately led to a global warmhouse (Föllmi 2012, with references). As outlined by Rawson (1994) and Baraboshkin (2002), this reorganization broke down the "*old Boreal/Tethyan dichotomy*" that had led to the widespread distribution of the ancyloceratid-deshayesitid assemblage during the early Aptian. As outlined by Wright et al. (1996) and Kakabadzé et al. (2004), the ancyloceratids are known by their widespread distribution in the Tethyan- (Mediterran-Caucasian Subrealm including the Caribbean area), Boreal- (Boreal-Atlantic and Boreal-Pacific subrealms) and Austral realms. However, due to homeomorphy of the body-chamber ornamentation, most ancyloceratid genera, such as *Ancyloceras*, are ill-defined taxa that are in need of revision. In our opinion, the species from the Mediterran-Caucasian and Boreal-Atlantic subrealms on which the Ancyloceratidae genera introduced by Spath (1930), Casey (1960), Vermeulen and Lazarin (2007) and Delanoy et al. (2008) are based, cannot be compared with the large tripartite heteromorphs that occur in California (Anderson 1938; Murphy 1975), Colombia (Kakabadzé and Hoedemaker 2004), South Africa (Klinger and Kennedy 1977), Japan (Shimizu 1931) and Australia (Day 1967). A similar view was expressed by Pictet et al. (2009) for *Lithancylus* taxa that are now restricted to Spain, France, England and the Russian Platform. As a consequence, endemism in Ancyloceratidae has certainly been overlooked and needs further investigation, although it is partly reflected by the introduction of such genera as *Shastoceras* from California (Anderson 1938), *Laqueoceras* from Colombia (Kakabadzé et al. 2004) and *Helicancyloceras* from South Africa (Klinger and Kennedy 1977).

Deshayesitidae are recoiled heteromorphs that evolved from heteromorphic representatives of the Heteroceratidae by a recoiling of the shell at the end of the late Barremian (Delanoy 1997; Bogdanova and Mikhailova 2004; Delanoy and Bert 2006). The family shows a wide distribution in the Tethyan and Boreal realms during the early Aptian (Bersac and Bert 2012, with references). According to the latter authors, there are no significant morphological differences between the genus *Deshayesites* and the regional genera, *Turkmeniceras*, *Prodeshayesites*, *Paradeshayesites* and *Obsoleticeras* that occur in the northern and eastern parts of the Mediterran-Caucasian Subrealm and/or on the Russian Platform and adjacent areas of the Boreal Realm. Although widely distributed, *Deshayesites* is rare or even missing in some hemipelagic and pelagic settings in the Tethys, probably due to a bathymetric and/or facies control (Landra et al. 2000; Lehmann et al. 2009). *Deshayesites* evolved anagenetically toward *Dufrenoyia*, which marks the maximum geographic extension of the Deshayesitidae in the latest early Aptian (Fig. 9.5). *Juandurhamiceras* and

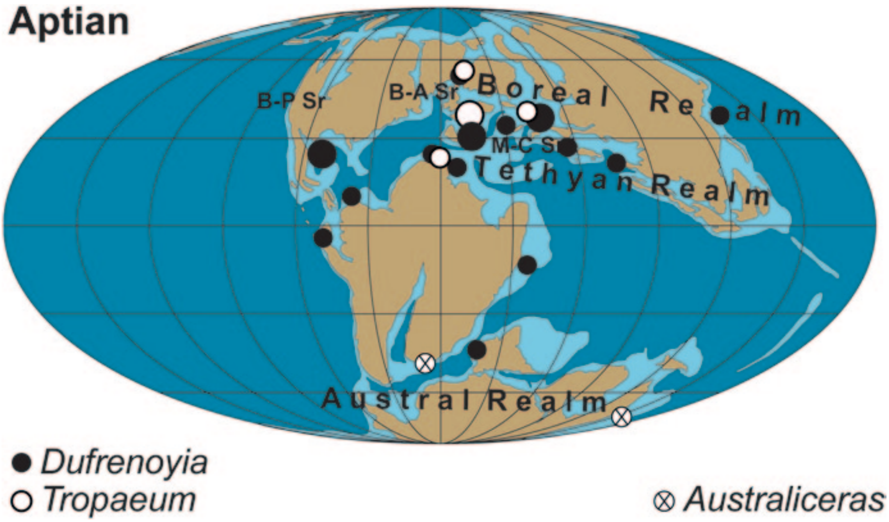

Fig. 9.5 Aspects of Aptian ammonite paleobiogeography. Map based on 120 Ma reconstruction. For further details see captions to Figs. 9.1 and 9.2

Burckhardtites (including *Burckhardites* reported from Turkmenistan (Bogdanova and Mikhailova 2004)) are Caribbean offshoots of *Dufrenoyia*. However, from our point of view the generic separation of these three genera also needs to be discussed carefully because of minor differences in shell shape only. The extinction of the family appears to be a sudden and almost synchronous event, marking the Lower/Upper Aptian boundary (Casey et al. 1998; Moreno-Bedmar et al. 2013).

During the continued Aptian trangression, faunas of isolated epicontinental basins show an increasing dispersal. Baraboshkin (2002), for example, recognized a Tethyan parahoplitid-douvilleiceratid and a Boreal ancyloceratid-aconeceratid assemblage around the Lower/Upper Aptian boundary on the Russian Platform. Simultaneously, large recoiled ancyloceratids occur almost worldwide, from the Austral to the Boreal Realm (Klinger and Kennedy 1977; Bengtson and Kakabadzé 1999). These forms have usually been referred to *Australiceras, Proaustraliceras* and *Tropaeum*, and are distinguished by the absence of a tuberculate stage on the inner whorls in the latter genus. Recently, McKenzie et al. (2014) argued that the two genera should be put in synonymy because the development of a tuberculate stage varies with intraspecific variability. Even if we agree that the Australian specimens attributed to *Tropaeum* in the literature (Whitehouse 1926; Day 1974) are macroconchs of *Australiceras*, comparison of the ornamental features of the early ontogeny of the European *Tropaeum* does not support the synonymy of the two genera. In our view, *Australiceras* is an endemic genus that characterizes the Austral Realm, since typical *Tropaeum* only occur on European shelves of the Mediterran-Caucasian Subrealm and the adjacent part of the Boreal Realm (Baraboshkin 2002; Fig. 9.5). *Proaustraliceras* shows a similar distribution, with no reliable records from the southern hemisphere (Kakabadzé et al. 2004). The relationships between these ancyloceratids are still obscure. Thus this group can not currently be used for defining paleobiogeographic boundaries. During the early Aptian, the Douvilleiceratidae are also a major component of the worldwide ammonite assemblage, although some genera possibly hint at a paraphyletic origin of this family. The *Procheloniceras*-*Cheloniceras*-*Epicheloniceras* lineage is characteristic of the Tethyan Realm and of the southern area of the Boreal Realm (Casey et al. 1998; Kakabadzé et al. 2004; Pictet 2012). In the late early Aptian, *Roloboceras* and *Megatyloceras,* closely-allied or possibly congeneric with *Cheloniceras*, are typically recorded during the early Aptian of the Mediterran-Caucasian Subrealm and southern area of the Boreal Realm (Casey 1961; Moreno-Bedmar et al. 2010; Ivanov and Idakieva 2013).

Dauphin (2002) documented a complex turnover in the earliest late Aptian that led to the appearance of the widespread family Parahoplitidae. This event was observed at the scale of the Tethyan Realm, from the Transcaspian to the Caribbean domains (Bogdanova and Tovbina 1995; Arnaud et al. 2002). The genus *Colombiceras* evolved from *Gargasiceras* in the late early Aptian and spread over the entire Tethyan Realm during late Aptian times, where it gave rise to the *Acanthohoplites*-*Hypacanthoplites* lineage (Bulot in Vincent et al. 2010, with references). *Colombiceras* may also be the rootstock of *Parahoplites* in the Mediterran-Caucasian Subrealm and adjacent Boreal areas, and of the closely allied genera *Sinzoviella* and *Kasanskiella* from the Caribbean. In the latest Aptian, the diversification of Acanthohoplitinae reached its peak. This is the case for *Diadochoceras* and the closely allied, if not synonymous, *Nodosohoplites,* which are considered to be an offshoot of *Acanthohoplites,* while *Neodeshayesites* is a New World derivative of *Hypacanthoplites s.l.* Other endemic genera of Acanthohoplitinae have been reported from North America (*Rhytidoplites* and *Immunitoceras*), eastern Mexico (*Penaceras*)*,* Colombia (*Riedelites*), northwestern Caucasus (*Chaschupseceras*), Japan (*Oshimaceras*) and Tunisia (*Melleguieiceras*). The phylogenetic relationships of all these genera also remain largely unclear (Bulot in Vincent et al. 2010; Latil 2011; Bulot et al. 2014).

9.2.6 Albian

Albian paleobiogeography is generally distinguished from that of the Aptian by a more pronounced provincialism, although this trend tends to diminish in the upper part of the stage (Owen 1996; Baraboshkin 2002, with references). The peak of endemism is reached in the earliest Albian, where three faunal provinces have been recognized in the Boreal Realm (Owen 1979, 1988a; Alabushev and Wiedmann 1994; Baraboshkin 2002; Jagt-Yazykova and Zonova 2012): the Boreal-Atlantic Subrealm, characterised by *Leymeriella*, *Sonneratia* and hoplitinid ammonites (the latter e.g. with *Euhoplites*, Fig. 9.6); the Arctic Subrealm, where *Arcthoplites*, *Freboldiceras* and Gastroplitininae flourished; and the Boreal-Pacific Subrealm, which was dominated by cleoniceratids (*Leconteites, Brewericeras, Grycia*). In the earliest Albian, arcthoplitid ammonites from the Arctic entered northwestern Europe and

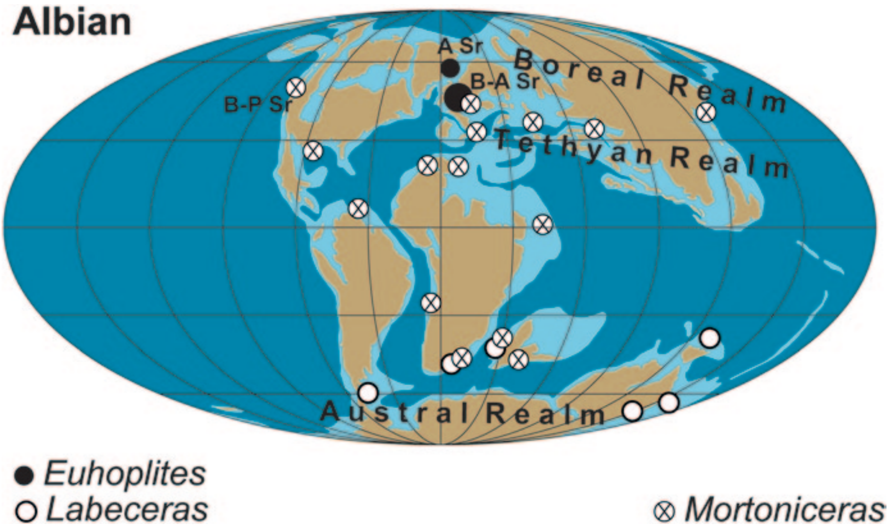

Fig. 9.6 Aspects of Albian ammonite paleobiogeography. Map based on 105 Ma reconstruction. For further details see captions to Figs. 9.1 and 9.2

Mangyshlak—thus these areas provide important information for the stratigraphic correlation on a global scale (Savel'ev 1973; Owen 11988a and b, 1996; Lehmann et al. 2013).

Compared to the limited area of the Boreal epicontinental shelf basins, the Tethyan Ocean had a vast expanse from northern South America and southern North America to Australia (Fluteau et al. 2007; Vrielynck 2010). In terms of ammonites, the assemblages of the Tethyan Realm mainly consist of brancoceratids (*Brancoceras*, *Prolyelliceras*, *Mirapelia*), lytoceratids (*Kossmatella*), desmoceratids (*Beudanticeras*), engonoceratids (*Parengonoceras*, *Knemiceras*, *Glotticeras*), and douvilleiceratids (*Douvilleiceras*) (Kennedy and Cobban 1976; Owen 1979, 1996; Marcinowski and Wiedmann 1990; Riccardi and Medina 2002; Robert and Bulot 2004; Bulot in Vincent et al. 2010; Latil 2011). In the earliest Albian new and distinguished families of heteromorphic ammonites (Anisoceratidae and Hamitidae) arose, spreading over most of the Tethyan Realm in the late early Albian (Monks 1999, 2002; Kennedy et al. 2000). During the early Albian the boundary between the Boreal and Tethyan realms was fairly sharp, despite scattered occurrences of *Leymeriella* on the Eurasian shelves of the northern margin of the Tethys (Kennedy et al. 2000, with references). Occasionally, in the late early and early middle Albian, *Douvilleiceras*, *Tegoceras, Lyelliceras* and *Oxytropidoceras* s.l. invaded the Boreal Realm of Europe and the northern Pacific coast of America (Owen 1971, 1988a; Amédro 1992; Amédro and Robaszynski 2005).

Different paleobiogeographic affinities between the early/middle and late Albian faunas are also recognized in the Austral Realm. However, in Australia itself these are influenced by a division into regional basins (Henderson and McKenzie 2002). In the middle Albian, fairly cosmopolitan anisoceratids and hamitids occur in the Great Artesian Basin in Australia (McNamara 1980; McKenzie 1999), but in the late Albian cosmopolitan genera occur only in the marginal areas of Australia, since, according to micro- and nannofossil data, the connection to the open ocean was restricted (Henderson and McKenzie 2002). Thus, a less diverse late Albian fauna evolved in the Great Artesian Basin, with dominant endemic heteromorph species of *Labeceras* and *Myloceras*, in contrast to the rich diversity of assemblages in Europe and elsewhere during this time interval, and only isolated records of Tethyan origin like *Goodhallites* (Henderson and Kennedy 2002). Although *Labeceras* (Fig. 9.6) and *Myloceras* characterize the ammonite province of the Austral Realm in the late Albian, endemic species developed also in the regional basins of Madagascar, southern Africa and South America (Förster 1975; Klinger 1976; Klinger and Kennedy 1989; Aguirre-Urreta and Riccardi 1988; Riccardi 1988).

During the late Albian a long-time trend toward more cosmopolitan faunas is established with the rapid rise and radiation of the Mortoniceratinae (e.g., *Mortoniceras*, Fig. 9.6) and Stolickaiellinae. However, the disappearance of the Early Cretaceous provincialism is a long-running process that did not end until the middle Cenomanian (Owen 1973; Wiedmann 1988; Ifrim et al. 2015).

Unusual insights to the paleobiogeographical affinities of Albian ammonite faunas in the Atlantic are given by a few drilling core sites of the DSDP/ODP programme (Wiedmann 1978; Wiedmann and Neugebauer 1978; Renz 1979a; Wiedmann 1988; Lehmann 2000; Owen and Mutterlose 2006). A fauna from the Biscay margin shows affinities to the Boreal realm for the early Albian, while middle to possibly late Albian ammonites indicate a Tethyan aspect (Renz 1979b). The other occurrences from the Atlantic are, as far as datable, late Albian faunas indicating strong Tethyan relations (with the Curacao debated, see Owen and Mutterlose 2006). Among these the relatively rich association from offshore Florida is remarkable, since it represents a hemipelagic or even pelagic assemblage with species with a preference for oceanic conditions and, despite the strong affinities to the Tethys, it generally reveals a cosmopolitan character (Lehmann 2000).

9.3 Conclusion and Future Perspectives

Many Early Cretaceous faunas are dominated by heteromorphic ammonites. While they play almost no role in the earliest Cretaceous, they dominate many faunal assemblages from the early late Hauterivian until the end of the Cretaceous period. However, reasons for this and most of the ecological constrains involved are still under debate, including trophic opportunities and sea-level changes (Wiedmann 1969; Nesis 1986; Cecca 1997; Keupp 2000). The global Cretaceous sea-level rise started in the Aptian, and despite an increased spreading of taxa, there is some strong provincialism in the Albian characterized by regularly coiled ammonites. This demonstrates that a complex pattern of sea-level changes and the opening and closure of seaways must be responsible for ammonite dispersal in the Early Cretaceous.

Ongoing research emphasizes that insufficient taxonomy is a factor masking paleobiogeographic affinities (Kennedy and Cobban 1976; Rawson 1993; Bengtson and Kakabadzé 1999), This is particularly true for the Berriasian, early Barremian and Aptian (present chapter). Furthermore, quantitative analyses of the spatial distribution of ammonoids—such as have been done for some other time intervals (Dera et al. 2011; Korn and Klug 2012; Korn and De Baets 2015)—are rare to absent for the Early Cretaceous Epoch. This hampers our ability to test the robustness of the paleogeographical affinities described in this chapter, and underlines the urgent need for quantitative studies earlier called for by Bengtson and Kakabadzé (1999). Therefore the interpretations presented here are thorough revisions and updates of earlier significant contributions in this field (Rawson 1981, 1993, 1994; Cecca 1998), but are likewise qualitative studies and thus still reflect a preliminary state.

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Chapter 10
Paleobiogeography of Late Cretaceous Ammonoids

Christina Ifrim, Jens Lehmann and Peter Ward

10.1 Introduction

Any attempt to synthesize the vast literature on Cretaceous ammonoids requires an acceptance of taxonomic identifications (and this comment is applicable to far more than our look here at Late Cretaceous ammonoid paleobiogeography). In the last century, there were paleontologists who mastered an understanding of ammonoid paleontology for entire Mesozoic periods, such as William J. Arkell and John H. Callomon for the Jurassic, and probably Leonard Frank Spath for the Cretaceous. In this young century, James W. Kennedy comes close to a global grasp of this enormous assemblage of regions and taxa. During the career of these and other researchers, the very diverse North Pacific Province and the Campanian and Maastrichtian of Antarctica were little known. Additionally, the exchange of literature and information was much more laborious than today.

Still, we faced challenges in the compilation of the data presented here: The information available for such a study is scattered, and many white areas remain on the maps. Another challenge in the compilation of the paleobiogeography of Late Cretaceous Ammonoidea is what can be called a "*monographic bias*", i.e. that diversity is often related to the number of scientists and research effort aimed at a

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C. Ifrim (✉)
Institut für Geowissenschaften, Ruprecht-Karls-Universität, Im Neuenheimer Feld 234,
69120 Heidelberg, Germany
e-mail: christina.ifrim@geow.uni-heidelberg.de

J. Lehmann
Geowissenschaftliche Sammlung, Universität Bremen, Klagenfurter Straße,
28359 Bremen, Germany
e-mail: jens.lehmann@uni-bremen.de

P. Ward
Sprigg Institute of Geobiology, University of Adelaide, North Terrace, Adelaide 5005, Australia
e-mail: peter.ward@adelaide.edu.au; ward.biology.uw@gmail.com

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given region. Our task is further challenged by the fact that much of the history of ammonoid research has been driven by questions of biostratigraphy: what is the highest biostratigraphic resolution of Cretaceous strata that can be obtained? This has caused biostratigraphers to search for taxonomic units with the highest use, and thus, intraspecific variability of Late Cretaceous ammonoids was hardly studied, reducing the comparability of assemblages between regions and stratigraphic units. The many, highly ornamented Cretaceous ammonoids have perhaps more than any other group of fossils been affected by this.

Ammonoids have variable morphologies (De Baets et al. 2015; Monnet et al. 2015). More and more studies show that, when large numbers of specimens of ammonoids with variable ribbing, nodes, and other surface ornament, and to some extent even coiling geometry are looked at anew, many seeming species are found to be only variants. Blame cannot be attached here: this is how ammonoid systematic paleontology was done for a long time, and passed on from advisor to student. Examples abound, including the differentiation of the many "*species*" of the early Campanian *Submortoniceras* in California by Anderson (1958). Perhaps the most notorious splitter of those defining Cretaceous ammonoids was Thomel (1972) who defined 56 species and subspecies of which most are not more than variants of previously known species (for synonymies see, e.g., Wright and Kennedy 1984–1996). Examples are everywhere in Late Cretaceous ammonoid literature, and the challenge of the young generation of ammonoid taxonomists will be in reducing the vast number of species-names more than discovering valid new species.

Equally egregious, is a phenomenon which we call here the "*geographic bias*". Quite often, ammonoids of the same species are given new names when found in different geographic regions. This phenomenon is quite pronounced among Cretaceous heteromorphic ammonoids. Because so many were unsuited for horizontal swimming of any efficiency (including turrilitids, most nostoceratids, ancyloceratids, diplomoceratids), when found in different countries, new names have routinely been given. This practice extended even to species of greatest biostratigraphic usefulness, with no case more egregious than in *Baculites*; Klinger and Kennedy (2001) listed more than 130 valid species names of *Baculites*. The work of William Cobban included the principle that the Late Cretaceous Western Interior was an endemic center, and among these were many species of *Baculites* unique to the Western Interior, or at most, ranging into the Gulf province of North America. Yet, new studies of *Baculites* from Antarctica show that North American *Baculites* species from there also occur in Antarctica, while some of our own work (still only published as abstracts: Ward et al. 2008, 2010; Ward 2009) has shown that, in fact, many of the Western Interior *Baculites* species are present on the West Coast of North America but with different names. Again, a challenge for the next generation of ammonoid specialists will be to reduce the nomenclature caused by this geographic bias, often compounded by preservation nature. The beautiful, aragonitic ammonoids from the Western Interior look quite different when they are found as molds in chalk facies of Denmark.

There has always been a wealth of data about Late Cretaceous ammonoid occurrences. This led to a series of interpretations of their paleobiogeography. A first detailed approach was made by Reyment (1956) who discussed the affinities of Ammonoidea from Nigeria and Cameroon with those of North Africa, but without maps. An early example of a paleogeographic map with identification of provinces was given by Freund and Raab (1969) for the early Turonian. Jeletzky (1971) defined North American Cretaceous biogeographic units from both the Arctic and North Pacific provinces. A larger approach was made in the classic work of Matsumoto (1973) who plotted the distribution of abundant genera on geographic maps and thus defined and discussed thirteen provinces throughout the late Cretaceous. All these authors used paleobiogeographic terms like "*realm*" and "*province*" in differing senses. Paleobiogeographic terms are used here in the sense of Westermann (2000a, b) and Cecca (2002). In this nomenclature, superrealms are the largest biochorema (i.e. biogeographic units), followed by realms and provinces. A biochore is a highly dynamic unit that not only expands and shrinks in range, but also changes in rank through time (Westermann 2000a): a realm can transform into a superrealm by increasing or into or a province by decreasing its dominance and extent with time. In contrast to Page (1996), we recognize several realms: The Tethyan Realm, the Boreal Realm, the Arctic Realm and the Austral Realm.

By the Late Cretaceous, continuing continental movement opened an equatorial, Tethyan-distributional pathway that created a low latitude, globe spanning distributional pathway for ammonoids due to the onset of circumequatorial oceanic surface circulation (Skelton 2003). One result of this is that former barriers to migration disappeared to ammonoids and many other organisms, and this Tethyan corridor gave rise to a superrealm. At the same time, ammonoid distribution patterns demonstrate the existence of two other biogeographic units defined by ammonoids: the Arctic and Austral Realms of the high latitude northern and southern globe, respectively. The Pacific Realm spans both hemispheres and is intermediate between the Arctic and the Austral Realms. During the Late Cretaceous, the Pacific Realm began to differentiate into different ammonoid provinces, leading to the varying definitions of an Indopacific biogeographic Province, which was further differentiated by Jeletzky (1971) and Matsumoto (1971) into a North Pacific and a more tropical Indopacific Province. Combined, these can be called a Pacific Realm, but as we shall show below, near the end of the Cretaceous, an important differentiation took place creating even more biogeographic differentiation.

The Boreal and the Euramerican Realms were limited southwards by the Tethyan Realm. India was part of either the Austral or the Tethyan Realm, depending on prevalence of taxa (Westermann 2000b).

At the beginning of the Late Cretaceous, latitude was the main factor controlling ammonoid occurrences. Provincialism increased during the Late Cretaceous, which was related to the breakup of Gondwana by several authors (Macellari 1987; Bardhan et al. 2002). Endemism was distinct in epicontinental seas such as the Western Interior Seaway. The endemic evolution of Western Interior Seaway *Baculites* and *Scaphites* has been outlined in detail by Cobban (1993) and even more detailed by Kennedy and Cobban (1976). The Trans-Saharan Seaway was less stable and only occasionally connected the southern Tethyan shelf to the South Atlantic during the Cenomanian-Turonian and the Campanian-Maastrichtian transition

(Zaborski 1982; Courville et al. 1998). The Tethyan Realm decreased in importance due to the opening of the Atlantic, which established as a new province during the Late Cretaceous. On the continental shelf, provincialism was increasingly reduced due to the opening of migrational pathways. The hallmark of Late Cretaceous faunas was the virtually pandemic distribution of their genera and species (Page 1996) such as, e.g., *Diplomoceras, Pseudophyllites*, *Phyllopachyceras*, or *Turrilites* (e.g. Kennedy and Cobban 1976).

10.2 Late Cretaceous Paleobiogeography

10.2.1 Cenomanian

At the beginning of the Cenomanian, ammonoid faunas are characterized by endemic assemblages, e.g., well documented for the Boreal Realm by the Schloenbachiidae (including hoplitids, Cooper and Owen 2011) and for the western Pacific (Bando et al. 1987; Shigeta et al. 2010). With time, these faunas were invaded by radiating clades such as the Kossmaticeratidae and the Acanthoceratidae (Jagt-Yazykova 2011, 2012). Acanthoceratids derived from the Albian subfamily Stoliczkaiellinae (Kennedy et al. 2005b) and became a group with cosmopolitan occurrence, but they were always associated with endemic elements of the Acanthoceratidae and of other ammonoid families. The Arctic Realm was dominated by belemnites, and closely connected to the Boreal Realm (Page 1996). The Boreal Realm included Europe and reached as far as the northeastern limit of the Arabian platform during the early and middle Cenomanian (see summary in Monnet 2009).

During the Cenomanian, the main control on the distribution of the Ammonoidea became latitude, i.e. the Tethyan became a Superrealm, with the continents showing only little endemism. In the same stage, the Western Interior Seaway of the USA and Canada spread out from the North. Initially, it contained an endemic ammonoid fauna of Gastroplitinae such as *Neogastroplites* (Kennedy and Cobban 1976; Kauffman 1977; Hancock et al. 1993). When it finally opened to the South, Tethyan taxa entered the Western Interior Seaway, and it became a transitional route between the Arctic Sea and the Gulf of Mexico-central Atlantic.

In the middle Cenomanian, *Turrilites* for a short phase, achieved an almost global distribution in the Tethyan Superrealm (Fig. 10.1). At the middle-late Cenomanian transition, the genus disappeared, and the Turrilitidae became rarer and less dominant (Wright and Kennedy 1984–1996). In contrast, the Acanthoceratidae remained dominant elements, although there was a strong turnover at the generic level (summarized, e.g., in Monnet et al. 2003). At the same time, an increased faunal interchange in lower and middle latitudes was noted by Monnet (2009). The Collignoniceratinae and Vascoceratinae evolved, the latter being widespread in the southern Atlantic and Africa (Wright 1996).

During the latest Cenomanian, the faunas were stepwise reduced severely by the upcoming Oceanic Anoxic Event 2 (OAE 2) (e.g., Elder 1991; Monnet and Bu-

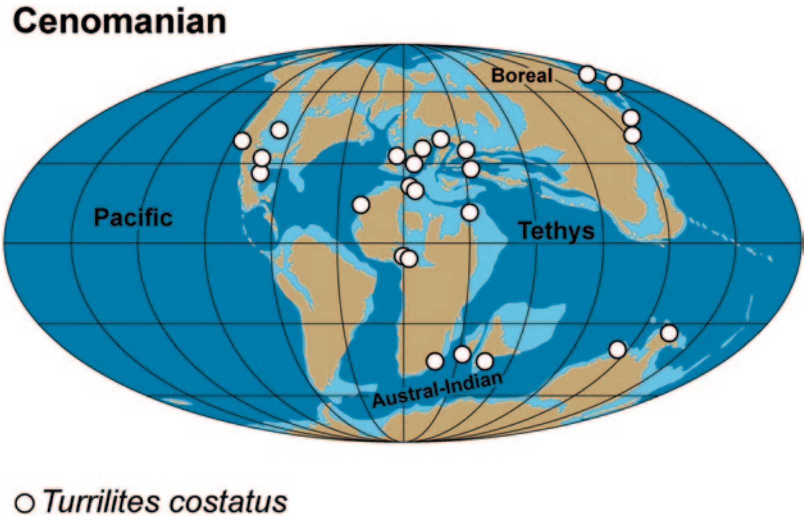

Fig. 10.1 The extension of the Tethyan Superrealm, exemplified by *Turrilites costatus* during the middle Cenomanian (Wright and Kennedy 1984–1996). Map based on 90 Ma reconstruction (Blakey 2002)

cher 2007), although several genera such as *Metoicoceras*, *Neocardioceras* or *Sciponoceras* still occupied the Tethyan Superrealm. Species longevity was shown to decrease during the Cenomanian (Monnet et al. 2003). Provincialism increasingly dominated the distribution of the remaining, more and more isolated species, e.g., in the Trans-Saharan Seaway (Courville et al. 1998; Courville 2007). In the same time, the last Turrilitidae occurred (Wright 1996). In latest Cenomanian sediments, ammonoids disappear from the fossil record, with very few exceptions preserved in sediments deposited in epicontinental seas such as the Western Interior Seaway and the Trans-Saharan Seaway (e.g., Cobban 1972; Kennedy and Cobban 1991; Courville et al. 1998).

10.2.2 Turonian

The distribution of the early Turonian ammonoids was dominated by the post-crisis radiation. By the beginning of the Turonian, provincialism was still not well defined: The realms were not well expressed, rather a subdivision into smaller provinces is noticeable (Freund and Raab 1969). The former realms re-established rapidly with the recovery from OAE 2 faunal crisis (Ifrim and Stinnesbeck 2007; 2008). Central Atlantic faunas differ from the rest of the Tethyan Realm (compare e.g., Kawabe 2003; Kennedy et al. 2005a; Ifrim and Stinnesbeck 2007; Nagm et al. 2010), but both are mixed in Brazil (Seeling and Bengtson 2002). This is the first clear expression of a new realm, the Atlantic Realm which is established more or less permanently from now on. In the western Pacific, faunas are composed of exclusively immigrating taxa (Jagt-Yazykova 2012). The Acanthoceratidae re-appeared and rapidly became dominant faunal elements, but with taxa from the subfamily Euomphaloceratinae. With the dispersion of *Mammites nodosoides*, a global index for the middle early Turonian, the Tethyan Superrealm established again, expressed, e.g., in the widespread occurrence of the Mammitinae and the Collignoniceratinae from then on. At the same time, the Trans-Saharan Seaway contained a high percentage of endemic taxa, but a small part represents Tethyan species which used the co-occurring maximum of the global sea-level for immigration (Courville 2007).

In the middle Turonian, the Trans-Saharan Seaway disappeared (Courville et al. 1998). The Nostoceratidae and Polyptychoceratidae appeared (Wright 1996). Faunas from the northeastern Pacific show affinities with Japanese faunas (Haggart et al. 2005), although there, the faunas tend to show a high degree of endemism (Matsumoto 1977).

During the late Turonian, a cooling episode caused the short-term extension of the Boreal Realm southwards, indicated by a short phase of immigration of cool-climate faunas into Europe (Wiese and Voigt 2002). Endemism increased as reflected in strong provincialism, with only few ammonoid species showing wider occurrence (discussed e.g. in Walaszczyk et al. 2004); only some of the Barroisiceratinae reached a global distribution in lower and middle latitudes. The affinities between California, Alaska and Japan still existed (Haggart et al. 2005).

10.2.3 Coniacian–Santonian

At the beginning of the Coniacian, cosmopolitan ammonoids are rare, and endemic taxa dominated the faunas (compare e.g. Kennedy et al. 1995; Walaszczyk et al. 2004; Stinnesbeck et al. 2005). Few taxa, however, spread out over the Tethyan Superrealm, e.g. from the Barroisiceratinae or the Texanitinae. Their distribution seems to be limited by latitude alone, and their distribution is similar to that of *Turrilites* (Fig. 10.1). From the late Coniacian on, a fast succession of endemic heteromorphic species provides a biozonation with a high resolution in the Western Interior Seaway (Cobban et al. 2006).

Ammonoids from the Austral Realm comprise cosmopolitan genera such as *Gaudryceras, Kossmaticeras*, *Menuites*, *Nostoceras*, *Pseudophyllites* and *Tetragonites*. Most of the species of these genera were endemic (Kennedy et al. 2007).

The paleobiogeographic composition of ammonoid faunas during the Santonian is similar to that of the Coniacian, although the faunas underwent a worldwide change (compare Kennedy et al. 1995; Remin 2010; Jagt-Yazykova 2012). In some provinces, ammonoids were rare and little diverse, e.g., in the Boreal Realm (Kennedy and Kaplan 2000). During the Santonian, the number of endemic forms was at its Late Cretaceous maximum, indicating a strong provincialism (Kennedy and Cobban 1976). At the same time, a rich diversity of species among both ornamented and heteromorphic forms evolved, among them *Eubostrychoceras*, *Glyptoxoceras*, *Polyptychoceras*, *Ainoceras, Neocrioceras*, *Hyphantoceras*, and others (Matsumoto 1977; Ward and Mallory 1977). This diversity is as high as or higher than in most other Late Cretaceous ammonoid faunas.

10.2.4 Campanian

During the early Campanian, endemism continued to be widespread among Ammonoidea (Fig. 10.2), expressed by their moderate potential for long-distance correlation. It may, however, be that both taxonomic and geographic biases (noted in the introduction to this paper) have influenced the emergent paleogeographic picture. Across the Atlantic and Tethys, faunas between the northern and southern hemisphere were separated, with even the exchange between the continents of the northern hemisphere to some extent limited (see discussion in Ifrim et al. 2013). By contrast, the diverse ammonoid fauna from Antarctica shows some species common with the Indopacific and even North Pacific regions. This is reflected in the shared occurrences of *Eubostrychoceras*, *Ainoceras*, *Metaplacenticeras* or *Hoplitoplacenticeras* (Crame et al. 1991; Olivero 2007), among others, and indicates that a certain degree of faunal exchange between these vastly separate geographic areas existed across the Pacific Realm. In a similar fashion, Ward et al. (2008) showed the presence of *Baculites* and other heteromorphic ammonoids of the Western Interior on the Pacific coast, but having previously been given other names. For example, the important (but curiously never formally given a species name) *Baculites* sp. 'smooth', and its successive, *Baculites* sp. 'weak flank ribs' are common globally,

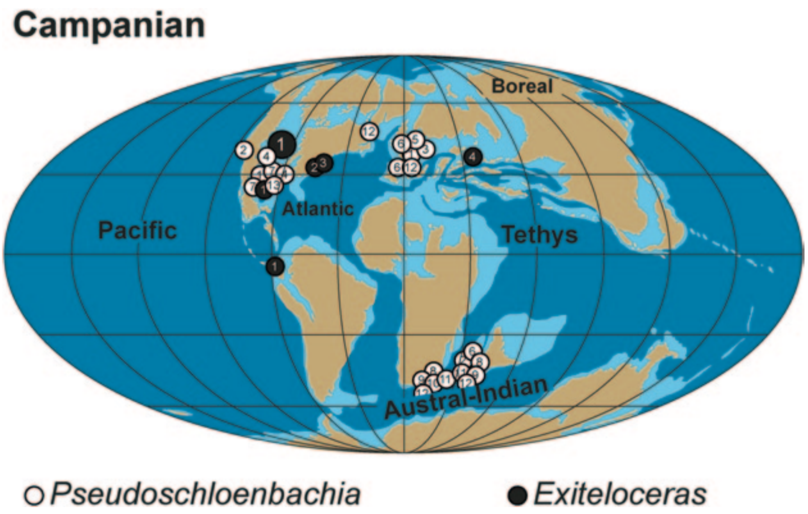

Fig. 10.2 Distribution of selected ammonoid genera during the Campanian: Distribution of *Pseudoschloenbachia*. 1 *P. bertrandi*, 2 *P. boulei*, 3 *P. casterasi*. 4 *P. chispaensis*. 5 *P. grossouvrei*. 6 *P. inconstans*, 7 *P. mexicana*, 8 *P. papillata*, 9 *P. spinosa*, 10 *P. subincisa*, 11 *P. trituberculata*, 12 *P. umbulazi*, 13 *P. wilsoni*. *Exiteloceras*: 1 *E. jenneyi*, 2 *E. oronense*, 3 *E. rude*, 4 *E. etequense*. Large dot: main distribution. The genera have a wide distribution, but at species level, provincialism is recognized. This pattern is applicable to many genera, although the biases described in the Introduction may play a role. Map based on 90 Ma reconstruction. (Blakey 2002)

with the name *B. inornatus* in the North Pacific. The same form is named *B. duharti* in South Africa, *B*. sp. in Europe, and is clearly global in its paleogeographic distribution (Ward et al. 2008, 2010; Ward 2009).

In the Western Interior Seaway, many new taxa did evolve (Myers et al. 2013), and it is currently accepted that few of these migrated into other realms; for example, *Scaphites hippocrepis* appeared in the Atlantic and Boreal realms. However, the extreme preservational differences between the Boreal chalk-preserved faunas and the Western Interior has perhaps importantly obscured some relations.

In the middle Campanian, cosmopolitan genera, like *Pseudophyllites* and *Diplomoceras,* and subgenera, like *Nostoceras* (*Nostoceras*) and *Nostoceras* (*Bostrychoceras*)*,* appeared and spread out over the world. These cosmopolitan taxa represent all orders of the Ammonoidea distinguished traditionally today (Wright 1996, although this subdivision was debated, e.g., by Engeser and Keupp 2002). This evolution and distribution of cosmopolitan taxa indicates an enhanced exchange between the hemispheres. Nevertheless, a considerable degree of provincialism was present to a certain degree everywhere.

In contrast, at the same time, there was a reduction, and finally complete removal of faunal exchange between Antarctica and the rest of the world. The Antarctic province showed the first and complete extinction of nostoceratids, scaphitids, baculitids, belemnites, and inoceramid bivalves, among others in the Late Campanian, millions of years before elsewhere in the world. A highly endemic fauna of largely kossmaticeratid ammonoids replaced this previous and largely cosmopolitan Antarctic ammonoid fauna (Olivero and Medina 2000; Olivero 2012). Some obstacle cut off the migration routes of ammonoids into, and out of Antarctica, and killed off two thirds of the fauna in the process.

10.2.5 Maastrichtian

Faunal provinces and realms were clearly expressed during the early Maastrichtian (Ifrim et al. 2004; Fig. 10.3); nevertheless, an exchange of taxa between the provinces was recognized and related to sea-level changes (Ifrim and Stinnesbeck 2010). By the end of the early Maastrichtian, a short cooling phase led to a mix of faunas from different latitudes and thus to a short appearance of Austral species in low latitudes (Ifrim et al. 2004).

During the early Maastrichtian, the northern connection of the Western Interior Seaway to the Arctic Sea was cut. Subsequently, this epicontinental sea disappeared at the beginning of the late Maastrichtian. At its final stage, it was inhabited entirely by specialized ammonoid taxa (Kennedy et al. 1998). At the same time, around the early-late Maastrichtian transition, nostoceratids became extinct (Goolaerts 2010).

The ammonoid diversity remained high during the late Maastrichtian, in some cases even higher than in the early Maastrichtian. This was first discovered for the sections in southwestern Europe and Antarctica (Ward 1990; Ward and Kennedy 1993) and later confirmed for eastern Russia (Jagt-Yazykova 2012), Tunisia

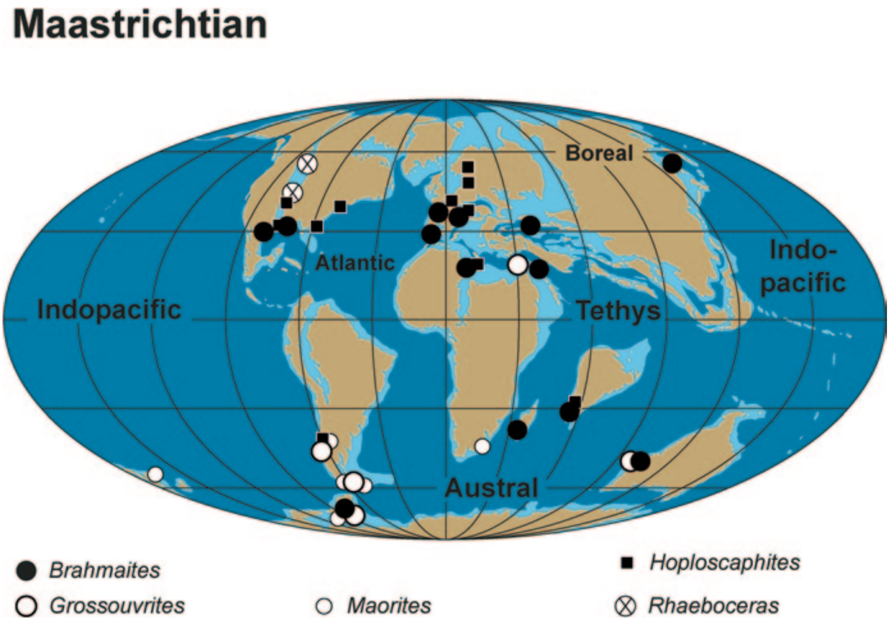

Fig. 10.3 Distribution of selected ammonoid genera during the Maastrichtian. The Atlantic Province was part of the Tethyan Realm. Whereas the Southern Pacific was part of the Austral Realm, shown by the distribution of *Maorites*, it forms an Indopacific subrealm in the lower-middle latitudes. (Map modified from 65 Ma reconstruction of Blakey 2002)

(Goolaerts et al. 2004; Goolaerts 2010), the North American Atlantic coast and Chile (Salazar et al. 2010). New species originated in many regions (Zinsmeister et al. 1989; Ward 1990; Ward and Kennedy 1993; Jagt 2002; Machalski 2005).

10.2.6 The Extinction of the Ammonoidea

The classic view in the literature is that ammonoids were already in decline several million years before the Cretaceous/Paleogene (K/Pg) mass extinction, with the whole group severely reduced in number and diversity (Kennedy and Cobban 1976). A large number of studies with high-resolution stratigraphy were carried out since then, and the density and stratigraphic resolution of the data has considerably increased, as discussed below.

One way of looking at the issue of whether there was a long term and progressive decrease in the ammonoids is simply to look at the number of species in any given region of outcrops. In the Bay of Biscay (Ward and Kennedy 1993) and the Tunisian sections (Goolaerts et al. 2004), 24 separate and valid species of ammonoids can be found in the same, highest Cretaceous strata, although they disappear in the last 2 m in the latter section. If one looks through literature asking for a mean number of ammonoids coexisting in a same, fossil accumulating basin from anytime during the long, Paleozoic through Mesozoic range of the Ammonoidea, in fact this number is rarely exceeded among studies where a thorough and modern definition of ammonoid species has been made, for instance, where the submission of single species of highly ornamented and ornamentally variable species has been taken into account.

The traditional interpretation of a long-term decline was proven only for Japan: there was a constant decrease in ammonoid diversity since the early Campanian (Toshimizu et al. 2003). In many other regions, highly diverse ammonoid assemblages are documented to few meters to centimeters below the boundary, e.g., southwestern Europe (Ward 2009; Ward and Kennedy 1993), central Europe (Jagt 2002; Machalski 2005), eastern Russia (Jagt-Yazykova 2012), Tunisia (Goolaerts et al. 2004; Goolaerts 2010), the North American Atlantic coast (Landman et al. 2004a, b, c), Chile (Salazar et al. 2010), and Antarctica (Zinsmeister et al. 1989). An overview over the distribution of randomly selected ammonoid genera within the last few meters below the K/Pg is given in Fig. 10.4 (which also exemplifies the "*monographic bias*"). These last survivors are again from all four suborders. Some of them are from the conservative taxa that evolved during the Campanian. In addition, ecologically very resistant species evolved like *Hoploscaphites constrictus* (Machalski 2005; Salazar et al. 2010; Machalski et al. 2012), *Discoscaphites iris* (Landman et al. 2010, 2012), or *Sphenodiscus pleurisepta* (Ifrim and Stinnesbeck 2010; Landman et al. 2010). None of the last North American Ammonoidea belongs to the conservative taxa, which are present virtually anywhere else. Figure 10.4

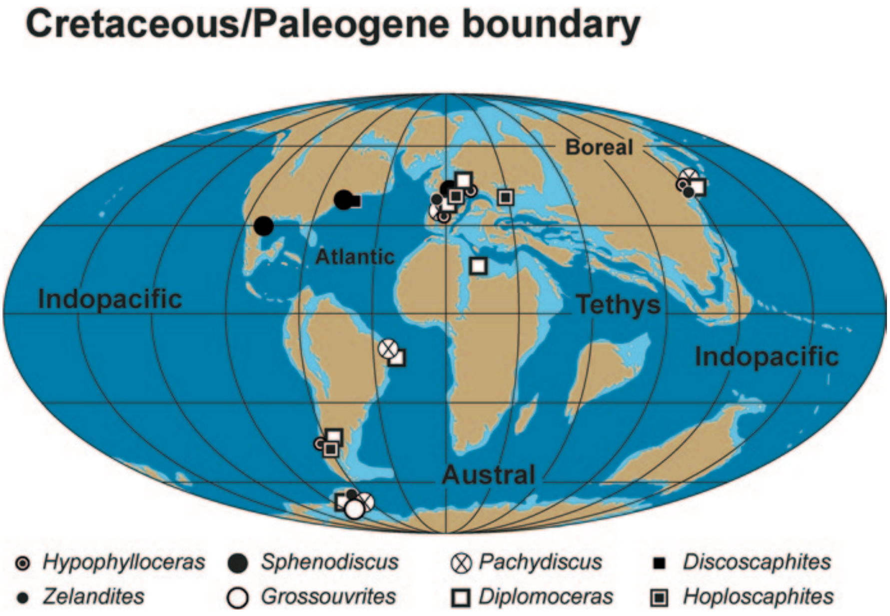

Fig. 10.4 Distribution of selected ammonoid genera at the Cretaceous–Paleogene boundary. The concentration of the taxa to defined biochorema is not recognizable anymore. (Map modified from 65 Ma reconstruction of Blakey 2002)

shows that the paleobiogeographic biochorema, which ruled Late Cretaceous biogeography until the late Maastrichtian, are not recognizable anymore at its end, with the exception of the long-term cut-off Austral Realm.

Occasionally, ammonoids are recorded from the earliest Paleogene, among them *Discoscaphites iris* and *Hoploscaphites constrictus* (Wiedmann 1988; Kennedy 1989, 1993; Birkelund 1993; Surlyk and Nielsen 1999; Machalski 2002, 2005; Machalski and Heinberg 2005; Landman et al. 2012), and most findings are clearly not reworked. These last representatives of the Ammonoidea occurred only in middle to high latitudes, but not in low latitudes (Stinnesbeck et al. 2012).

Conclusions

Despite (or because of?) the wealth of systematic descriptions, applications of quantitative approaches to ammonoid paleobiogeography are still lacking for the Late Cretaceous, but such are highly desirable. The qualitative interpretations given here are preliminary and need quantification using revised systematic and stratigraphic schemes.

The paleobiogeographic distribution of ammonoids was very dynamic throughout the Late Cretaceous. The strong endemism at the beginning of the Late Cretaceous was rapidly replaced by a Tethyan Superrealm. It broke down due to the crisis caused by the OAE 2 at the end of the Cenomanian but reestablished rapidly afterwards. During the Coniacian–Santonian, endemism increasingly ruled the distribution of ammonoids in the lower latitudes, with a peak in the early Campanian. In the late Campanian the interchange between the continents increased in the lower latitudes, whereas it was cut off in the Austral Realm. Genera and species which reach cosmopolitan distribution then appeared bit by bit. During the Maastrichtian, ammonoid diversity remained high, and realms and provinces were clearly expressed, although well connected. This provincialism broke down at the end of the Maastrichtian, when few ammonoids reached the K/Pg boundary and, in exceptional cases in middle and high latitudes, even crossed it.

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Part III
Ammonoids Through Time

Chapter 11
Ammonoids and Quantitative Biochronology—A Unitary Association Perspective

Claude Monnet, Arnaud Brayard and Hugo Bucher

11.1 Introduction

Biochronology is the branch of paleontology and stratigraphy, which assigns relative ages to rock strata by exploiting the time component embedded in the fossil record (biostratigraphy is a more commonly used term, but it applies to the study of the fossil content of the sedimentary rocks in general and not necessarily to its time component; Guex 1979, 1991; Gradstein 2012). Biochronology has profound implications not only for reconstructing past geological events but also for constraining phylogenetic hypotheses. It is one of the fundamental cornerstones of Geology and the Evolution of Life. Indeed, no matter what aspect of Geology one is working on, the most common question asked by geologists is "*what age is it*"? Biochronology and geochronology provide the framework for answering this question.

William Smith (1769–1839) and Alexandre Brongniart (1770–1847) were the first to formulate the principle of faunal successions based on the observation that sedimentary strata contain fossilized organisms, and that these fossils succeed each other vertically in a particular, reliable order that can be recognized over wide geographic distances. Leopold von Buch (1774–1853) coined the term "*index fossils*", and, in 1856, Albert Oppel first introduced the concept of biozone based on time intervals defined by the overlapping ranges of fossil species independently of the rock

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C. Monnet (✉)
UMR CNRS 8217 Géosystèmes, UFR des Sciences de la Terre (SN5), Université de Lille,
Avenue Paul Langevin, 59655 Villeneuve d'Ascq cedex, France
e-mail: claude.monnet@univ-lille1.fr

A. Brayard
UMR CNRS 6282 Biogéosciences, Université de Bourgogne, 6 boulevard Gabriel,
21000 Dijon, France
e-mail: arnaud.brayard@u-bourgogne.fr

H. Bucher
Paläontologisches Institut und Museum, Universität Zürich, Karl-Schmid Strasse 4,
8006 Zürich, Switzerland
e-mail: hugo.fr.bucher@pim.uzh.ch

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or facies, in which they are found. Oppel zones were a fundamental breakthrough in that they first made the distinction between lithological units (which can be diachronous) and biozones (which each represent a unique time interval). Biochronology is thus one of the founding fields within Geology and Biology and as illustrated by Oppel's own work, ammonoids played a leading role in this field since its inception. The crucial role of the tandem ammonoid/biochronology is exemplified by the cornerstone contribution of Alcide d'Orbigny (1802–1857), who defined most Mesozoic stages based mainly on ammonoids. He also was the first to precisely identify species characteristics with the purpose of using them to define stratigraphic stages. Because of their high evolutionary rates, broad paleogeographic distributions, and frequent preservation in marine deposits, ammonoids are one of the prime fossil groups for dating Paleozoic and Mesozoic marine strata (e.g., House 1985).

Most biostratigraphers have resisted, stubbornly the use of numerical methods and the construction of biochronological time scales has sometimes been perceived as an "*art*" by some scientists who were distant from the field (Brower 1982). Part of such a simplistic image may arise from various sources of noise. This is probably caused by the fact that many quantitative methods are rather complex and utilize methodologies that are basically foreign to biostratigraphers. The identification of species is obviously another major source of errors. As far as ammonoids are concerned, the initial typological approach has now been largely replaced by a dynamical approach, which integrates ontogenetic and inter-individual variation (see the precursory work of Silberling 1956 for such a "*biological*" approach). This purely taxonomic and systematic aspect is not the focus of this chapter and is addressed in other chapters of this volume (De Baets et al. 2015; Monnet et al. 2015). Another source of errors focuses directly on the intrinsic properties of the utilized biochronological approaches. These cover the whole spectrum from probabilistic to deterministic treatments depending on the various perceptions of the nature of the fossil record. A critical overview of these methods is the central topic of this chapter.

Some ammonoid biostratigraphers still use interval zones, whose bases are defined by the first appearance datum (FAD) of index species. However, the fossil record cannot be read at its face value. First, only a small fraction of organisms become fossilized. Second, sedimentary successions do not necessarily faithfully reflect the true relative order of evolutionary events (origination = First Appearance Datum/FAD; extinction = Last Appearance Datum/LAD) through time because of a whole array of primary and secondary causes that may blur their actual succession (e.g., ecological exclusions, selective preservation, sedimentary gap or reworking, taxonomic vagaries, sampling effort, amount of available exposures, etc.). For example, see studies on range offset and simulation of fossil occurrences among sections within a basin (Holland 2000, 2003; Holland and Patzkowsky 2002). Therefore, both first and last local occurrences of a taxon (FOs, LOs) in the rock record may result from a wealth of causes other than true evolutionary speciation or extinction (i.e. FADs, LADs). Finally, in most cases, the confusion or amalgamation between a local first occurrence (FO) and a FAD, or a local last appearance (LO) and a LAD, derives from the deeply entrenched practice of arbitrary segmentation of supposed anagenetic lineages assumed to have evolved gradually. Last but not

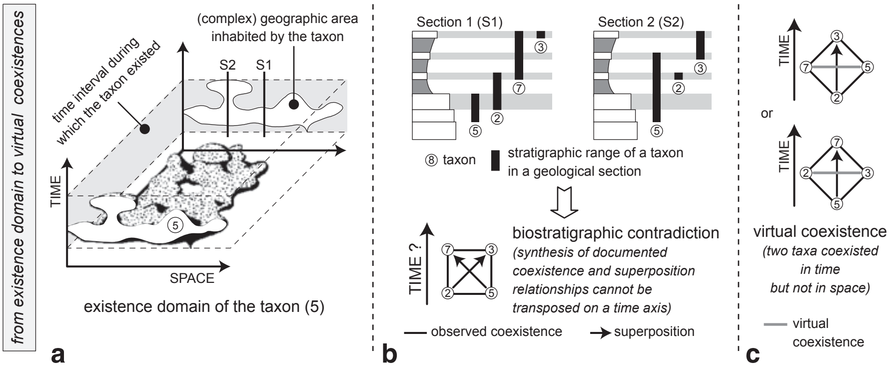


Fig. 11.1 Notions of existence domain (**a**), biostratigraphic contradiction (**b**), and virtual coexistence (**c**). See text for details

least, in the very exceptional situation where a FO or a LO may be demonstrated to match exactly a FAD or a LAD, respectively, speciation and extinction remain intrinsically restricted biological processes in space, thus complicating the use of evolutionary datum for constructing synchronous time lines across long distances. The theoretical applicability of any evolutionary datum is strictly restricted to the area where speciation or extinction took place. The practical applicability of evolutionary datum has thus limitations depending on the properties of the studied group (e.g., evolutionary rates, preservation states) and of the record (information degraded by the vagaries of the record and sampling efforts). Some will argue that the dispersion of a peculiar new species (e.g., planktonic foraminifers, conodonts, ammonoids) is geologically instantaneous, but unless this can be tested by means of an independent and truly isochronous time marker, such a statement will remain an *ad hoc* and circular statement. Interval zones, grade-datation and Global Boundary Stratotype Section and Point (GSSPs) are all based on the use of such FADs. The effects of all these parameters that generate conflicting stratigraphic positions between taxa across several sections are the so-called biostratigraphic contradictions (Fig. 11.1). Indeed, each taxon is characterized by a very irregular and complex paleogeographic distribution in space, which is in turn altered through time (Fig. 11.1a). Since biostratigraphic data are obtained from a necessarily finite number of sections, they represent only a small fraction of the true distribution in time and space of the studied taxa. Because of all these factors that degrade the true time and space distribution of species, real data usually contain contradictions, i.e. inconsistent superposition relationships between FOs and LOs, which make it impossible to obtain a unique order of species ranges along the time axis (Fig. 11.1b). Some of those biostratigraphic contradictions may result from virtual coexistences, i.e. species that actually coexisted in time but not in space (Fig. 11.1c).

With increasing size of biostratigraphic datasets including larger numbers of taxa and sections, the number of contradictions usually grows exponentially. In such cases, computerization has facilitated the development in biochronology of different quantitative methods welcomed by industrial requirements (Simmons and Lowe 1996). Over the last decades, quantitative biochronology has seen a consolidation of methods and a better understanding of their advantages and limitations has emerged. These methods are robust and allow resolving the numerous problems encountered in dating and correlating fossiliferous strata, be it at a global scale, across different basins, within a single basin, or within an oil field. This chapter aims to give an overview of some of these methods and their applications to ammonoids.

11.2 Quantitative Biochronological Methods

The construction of robust and highly resolved biozonations is a necessary prerequisite both in academic and in oil and mining studies using fossils for dating and correlating sections. In addition to these direct applications, such biozonations are also of primary importance for reconstructing changes of taxonomic diversity in time and space, especially in relation with mass extinctions and recoveries (e.g., Brayard et al. 2009b; Brühwiler et al. 2010). To achieve these goals of accuracy and precision, a number of quantitative biochronological methods have been developed during the last decades (Hay and Southam 1978; Guex 1979; Cubitt and Reyment 1982; Gradstein et al. 1985; Boulard 1993; Sadler 2004; Gradstein 2012). All these methods utilize strict and well-defined algorithms that allow not only the processing of large datasets but also to test the reliability of the underlying methods with sets of either real or simulated data of different quality. Some methods will always produce results whatever the quality of the data, some others will not as soon as a certain threshold in the decreasing quality (i.e. number of contradictions) of the dataset is reached. Computerized methods ensure a rigorous, exhaustive, and consistent treatment of the biostratigraphic data. They often produce better-resolved biozonations than empirical studies (Boulard 1993; Monnet and Bucher 2002; Sadler 2004). However, these quantitative methods often lead to partly different results (Baumgartner 1984; Agterberg 1985; Boulard 1993; Galster et al. 2010; Monnet et al. 2011). Such divergences are expected since these methods are based on different types of available biostratigraphic data (e.g., coexistence vs. apparition/extinction of taxa), on different theoretical assumptions and practical algorithms (e.g., probabilistic vs. deterministic approaches) in how to resolve the biostratigraphic contradictions, and on the expected types of results (e.g., continuous vs. discrete biozonations).

Among the existing quantitative biochronological methods the three most popular are Ranking and Scaling (RASC), Constrained Optimization (CONOP), and Unitary Associations (UAs). All these methods have computer softwares either separately or altogether (but often with less options) in the widely used free software of paleontological data analysis PAST (Hammer et al. 2001; http://folk.uio.no/ohammer/past/). These methods use different approaches and data (see below) and consequently their results often diverge (Galster et al. 2010; Monnet et al. 2011). Therefore, the biostratigrapher doing a quantitative biochronological analysis must make a choice based on his/her data and expectations in agreement with the advantages and constraints of each method (compare Gradstein 2012). The main properties of these three methods are briefly outlined below.

RASC (Agterberg and Nel 1982a, b; Agterberg and Gradstein 1999) is a probabilistic approach based on the distances among bioevents of taxa (i.e. their First Occurrence and Last Occurrence) along wells or sections to correlate. Basically, the method first ("*ranking*") produces a single, comprehensive ordering of bioevents, even if the data contains contradictions or longer cycles. This sequence of bioevents is constructed by following a "*majority rule*" (frequency), counting the number of times each event occurs above, below or together with all others. Then ("*scaling*"), it estimates the most probable stratigraphic distances between the consecutive bioevents by counting the number of observed superpositional relationships between each pair of consecutive events. This method resulted from a pragmatic approach to biostratigraphy in oil industry, which developed biozonation schemes that, rather than using classical bioevents, use local acme events and slight changes in assemblage characteristics to develop high resolution biozonations. These are essentially of local (i.e. field-wide) significance and are efficient in this context. This method has thus been commonly used in oil industry. It enables correlation of geographically closely related sections, and assigns the most probable age of studied stratigraphic levels. RASC has excellent graphic outputs, is optimal for large datasets with many fossil events, and handles noise (e.g., outliers and missing data) relatively well. One downside of the method may be that it may shorten the range of taxa and lead to dissociate actually coexisting taxa (Baumgartner 1984; Boulard 1993). Example applications can be found in Gradstein et al. (1999), among others.

CONOP (Kemple et al. 1989, 1995; Sadler and Cooper 2003; Sheets et al. 2012) is partly derived from the empirical Graphic Correlation method (Shaw 1964; Edwards 1989; Carney and Pierce 1995; Zhang and Plotnick 2006). It can be viewed as a multidimensional piecewise linear correlation of the position of bioevents along sections to correlate. Using the so-called Simulated Annealing method, CONOP searches for a global (composite) ordered sequence of events that implies a minimal total amount of range extension (penalty) in the individual sections. This method is efficient, robust, and good in handling and evaluating ranges of studied taxa. It can be used to directly correlate studied sections and evaluate changes in sedimentation rates. Its major constraints are long computation time with some parameters not easily tuned and it may also artificially lengthen the range of taxa, thus generating false coexistences as graphic correlations already did (Galster et al. 2010; Monnet et al. 2011). Example applications can be found in Cuartas et al. (2006) and Cody et al. (2008), among others.

UA (Guex 1977, 1991) is a deterministic approach based on the observed coexistences of studied taxa (and not their bioevents). It takes advantage of the fact that the intrinsic nature of biostratigraphic data (associations, superpositions, unknown relations) is identical with the kind of data processed by the mathematical graph theory founded by Euler (1741). This approach resolves the biostratigraphic contradictions by inferring virtual associations. A virtual association is defined as the coexistence of taxa in time, but not in space (Fig. 11.1). The biozonations constructed by means of the UAs are consequently composed by an ordered sequence of discrete units (the UAs), which are unique maximal sets of coexisting (really or virtually) taxa. This method has several advantages, which are discussed below. The major challenging requirement of the UAs is that it forces the biostratigrapher to think in four dimensions (space and time) instead of the usual one dimension of a section or a time axis. It is less intuitive for biostratigraphers used to work with continuous scales such as interval zones (as stimulated by stage boundaries defined on the FAD of index taxa).

A complete review of all available quantitative methods in biostratigraphy is beyond the scope of this study, and the reader is referred to previously cited references for further details and applications. Finally, note that the UAs method stands in sharp contrast to RASC and CONOP (for a recent review, see Gradstein 2012). UAs are based on the co-occurrences of taxa in successive levels, resolve biostratigraphic contradictions by focusing on coexistences and inferring virtual coexistences, and yield discrete biozonations. RASC and CONOP are based on the bioevents of studied taxa spotted on profiles, resolve biostratigraphic contradictions by focusing on the relative range of taxa and by modifying these ranges, and produce continuous biozonations made of interval zones based on the FOs and/or LOs of index taxa.

11.3 The Unitary Associations

Comparing the previously described quantitative methods in biostratigraphy, our preferred choice goes to the UAs. This selection is mainly driven by the theoretical and practical properties of the UAs (e.g., production of discrete bio-zones and preservation of all observed co-occurrences; for more details, see below), by its efficiency as shown by comparative studies (Baumgartner 1984; Boulard 1993; Galster et al. 2010; Monnet et al. 2011), and last but not least, by its panel of supplementary tools enabling critical assessment of the studied dataset (Monnet et al. 2011). Despite an ever increasing number of datasets and the need of higher resolved correlations, there are still a few studies applying these quantitative and robust biochronological methods to ammonoids. This is unfortunate since quantitative stratigraphic approaches produce results with a much higher resolution potential than empirical zonations (Boulard 1993; Monnet and Bucher 1999, 2002, 2007; Sadler 2004; Cody et al. 2008). Even if ammonoids have a long-standing reputation as excellent age biomarkers, ammonoid biozonations can be significantly improved by using these quantitative methods. Among these, it appears that UAs are most commonly used with ammonoids (e.g., Pálfy et al. 1997, 2003; Pálfy and Vörös 1998; Monnet and Bucher 1999, 2002, 2005a, b, 2007; Monnet et al. 2003, 2011; Galfetti et al. 2007a, b; Pálfy 2007; Brühwiler et al. 2010; Guex et al. 2012; Brayard et al. 2013).

11.3.1 History and Properties

The Unitary Associations method was developed by Guex (1977, 1991). It was initially based on the empirical rearrangement of matrices compiling the coexistences of taxa. It has been then largely expanded with the use of mathematical graph theory (Euler 1741), thus enabling a formal and logical treatment of the biochronological "*problem*". The development of personal computers led to the creation of a first software (Guex and Davaud 1984, 1986). Subsequently, the method was improved and associated with new computer software (Savary and Guex 1991, 1999). Finally, it is now replaced by a more robust implementation, which includes new options and improvements, available as a stand-alone software called UA-graph (http://folk.uio.no/ohammer/uagraph/) or within the paleontological software package PAST (Hammer et al. 2001). For typical applications with BioGraph, see Guex (1991), Angiolini and Bucher (1999) or Monnet and Bucher (1999), and with UA-graph, see Carter et al. (2010), Galster et al. (2010), Monnet et al. (2011), or Guex et al. (2012).

UAs have several attractive properties, some of which are listed below. It is a quantitative and deterministic method based on the co-occurrences of species in successive stratigraphic levels, which corresponds to the primary state of the fundamentally incomplete fossil record. Accordingly, it produces discrete (discontinuous) biozones in agreement with the nature of the fossil record. It preserves the integrity of the original dataset by preserving in the outputs all raw documented associations of taxa (coexistence in space). It is efficient to resolve complicated biochronological problems produced by taxonomic groups with very different completeness of their fossil record (from marine unicellular organisms like nannoplankton and radiolarians, over marine invertebrates like ammonoids and brachiopods to terrestrial mammals: Boulard 1993; Baumgartner et al. 1995; Angiolini and Bucher 1999; Guex and Martinez 1996; Monnet and Bucher 2002, 2007; Brühwiler et al. 2010; Carter et al. 2010). It usually leads to a significant improvement of biochronological resolution, even in the case of ammonites (Monnet and Bucher 2002, 2007). It allows also an *a posteriori* objective assessment of the diachronism of the studied taxa and the choice of actual characteristic taxa of each zone (compare Pálfy and Vörös 1998; Pálfy 2007). Finally, Escarguel and Bucher (2004) demonstrated that the unknown duration of the discrete UA-based biozones does not introduce a significant bias when using UA-zones as time bins for counts of species richness. Therefore, the UAs are a very powerful method to resolve biochronological problems, to rapidly produce robust zonations, and to assess critically the quality of the dataset. The quality of a dataset relates to the amount of discrepancy in the ranges of species. The longer the ranges of species, the more likely they will be discontinuous, thus generating larger amounts of contradictions. Unlike other methods, UAs will not yield "*good looking*"—but unreliable—solutions if the dataset is pervaded with contradictions. In such cases, UAs will yield low resolution—but robust—biozones. For instance, Mesozoic radiolarians have an intrinsically low quality record, because they are composed of mostly long ranging species with extremely discontinuous vertical occurrences (Baumgartner et al. 1995). Ammonoids, with their vast majority of short ranging species, provide an opposite example characterized by intrinsically good quality data. There is an unavoidable trade-off between the intrinsic quality of the data and the resolution of the constructed biozones. This obvious trade-off does not exist with other quantitative methods, which will always yield apparently highly resolved solution—but will either fail to recover all real documented associations or will generate false associations (i.e. neither real, nor virtual). Monnet et al. (2011) recently proposed directions of research for additional tools dedicated to evaluate in more details the results of the method (but see Guex 2011).

11.3.2 Major Principles and Steps of UAs

The method of UAs is logical and comprises a number of steps (Guex 1991; Savary and Guex 1991, 1999). The major principles and steps of the UAs are here illustrated with an imaginary and simple example, based on the occurrences of eight taxa within four sections (Fig. 11.2a). The first step is the construction of the biostratigraphic graph (Fig. 11.2b), which compiles and represents all observed biostratigraphic relationships. Its vertices represent the taxa, its edges represent their association (the range of corresponding taxa overlap), and its arcs represent the superposition between taxa.

The next step is the extraction of all unique maximal sets (a set is maximal if not contained in a larger set; see Guex 1988) of mutually coexisting species, called "*maximal cliques*" (Fig. 11.2c). The example proposed here contains 6 maximal cliques, among which one ("*mc4*", Fig. 11.2c) includes taxa 3, 5, and 7 that coexist altogether in time (but not necessarily in the same section). Then, the method resolves the superpositional relationships between these maximal cliques by the comparison of documented stratigraphic relationships of taxa in the biostratigraphic graph between each pair of cliques. Usually, conflicting stratigraphic relationships occur between some of the taxa ("*biostratigraphic contradictions*"). For instance, Fig. 11.2d reports one case (top), in which the superpositional relationships between the taxa are congruent (arcs in the same direction) and another one (bottom), in which the relationships are contradictory (arcs of opposed directions). The method solves such conflicting stratigraphic relationships by assuming that one of these contradictory arcs is wrong and is in fact generated by a virtual coexistence (i.e. inter-taxa coexistence that is real in time but not observed physically in the stratigraphic samples). The choice of the supposed badly oriented arc (or set of arcs) follows a "*majority rule*" (Guex 1991, p. 82; Galster et al. 2010, p. 244). This rule counts the number of arcs and their frequency in each direction separately, and then considers the most frequently observed direction as the correct stratigraphic order (Fig. 11.2d). Once all superpositional relationships between the maximal cliques have been resolved, one can construct a graph that exactly represents all these relationships (Fig. 11.2e).

Next, the method extracts the longest sequence (path) of superposed maximal cliques (Fig. 11.2f). Maximal cliques, which do not belong to the longest path, are merged (if possible) with contemporary maximal cliques of the path. Finally, one can transcribe the sequence of maximal cliques into the sequence of Unitary Associations (Fig. 11.2g). A unitary association is thus defined as a maximal set of mutually coexisting species, be it actually or virtually. The sequence of UAs is called

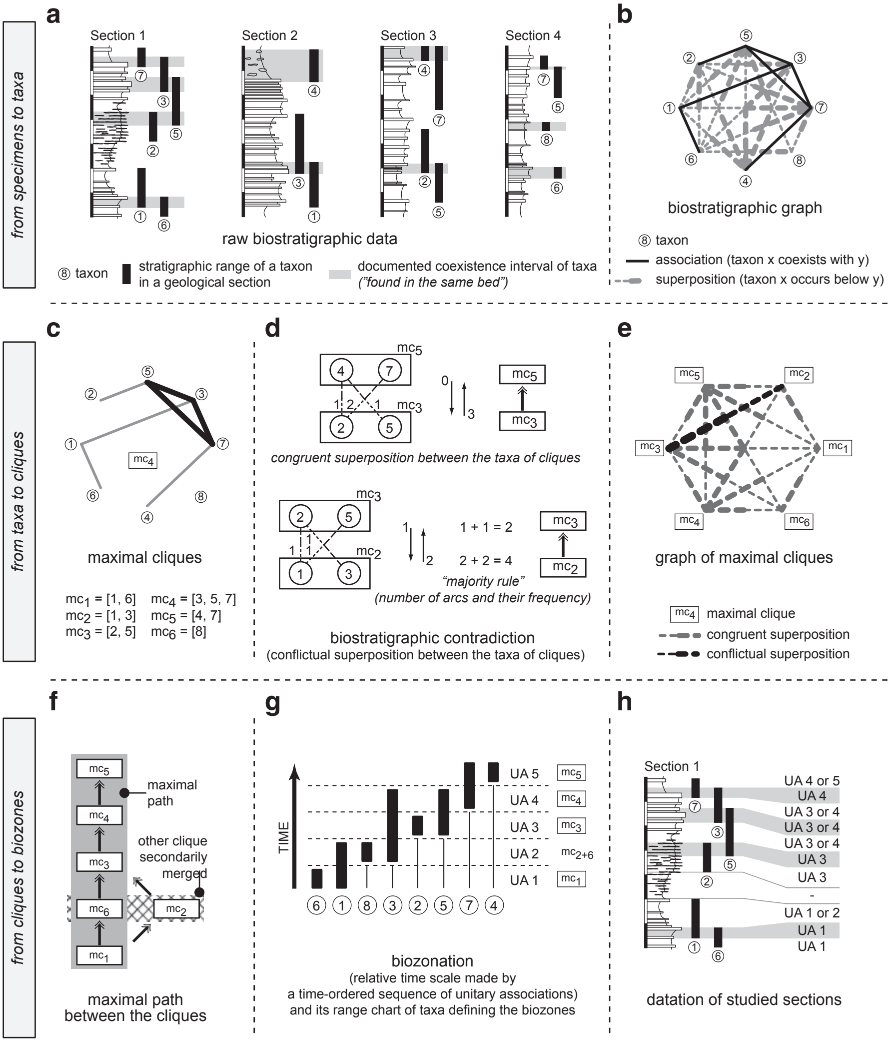
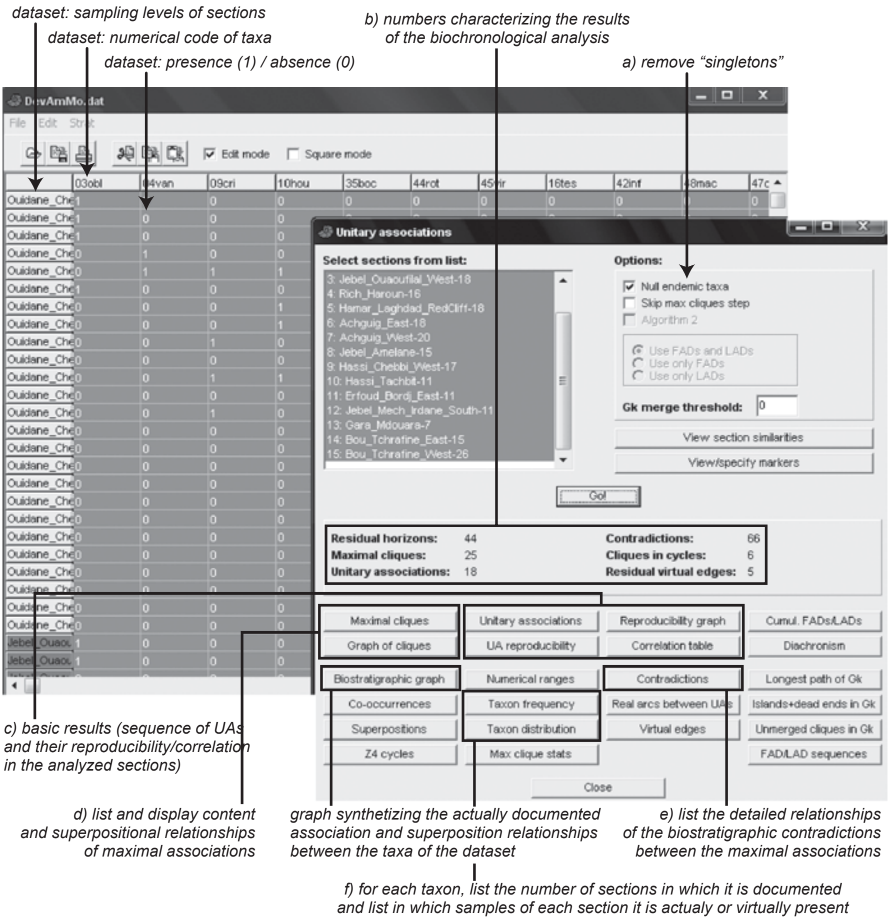


Fig. 11.2 Flow chart of the major analytical steps of the UA method (see text for explanation)

the "*protoreferential*" and along with the reproducibility matrix (a sections vs. UAs matrix), they constitute the zonation used to correlate the fossiliferous content of studied sections (Fig. 11.2h). Note that a strict association zone such as produced by the UAs is characterized either by the taxa occurring only within this zone or by the intersecting ranges of taxa observed within the zone: the FADs and LADs *per se* do not matter.



dataset: sampling levels of sections

dataset: numerical code of taxa

dataset: presence (1) / absence (0)

b) numbers characterizing the results of the biochronological analysis

a) remove "singletons"

c) basic results (sequence of UAs and their reproducibility/correlation in the analyzed sections)

d) list and display content and superpositional relationships of maximal associations

graph synthetizing the actually documented association and superposition relationships between the taxa of the dataset

e) list the detailed relationships of the biostratigraphic contradictions between the maximal associations

f) for each taxon, list the number of sections in which it is documented and list in which samples of each section it is actualy or virtually present

Select sections from list:
3: Jebel_Ouaoufilal_West-18
4: Rich_Haroun-16
5: Hamar_Laghdad_RedCliff-18
6: Achguig_East-18
7: Achguig_West-20
8: Jebel_Amelane-15
9: Hassi_Chebbi_West-17
10: Hassi_Tachbit-11
11: Erfoud_Bordj_East-11
12: Jebel_Mech_Irdane_South-11
13: Gara_Mdouara-7
14: Bou_Tchrafine_East-15
15: Bou_Tchrafine_West-26

Options:
☑ Null endemic taxa
☐ Skip max cliques step
☐ Algorithm 2
● Use FADs and LADs
○ Use only FADs
○ Use only LADs
Gk merge threshold: 0

Residual horizons: 44
Maximal cliques: 25
Unitary associations: 18
Contradictions: 66
Cliques in cycles: 6
Residual virtual edges: 5

Fig. 11.3 Graphic user interface of UA-graph and tools provided with it (see text for explanation; letters are referred to in the text; after Monnet et al. 2011)

11.3.3 UA Tools and Interface

To perform a quantitative biochronological analysis by means of the UAs, one must use the software UA-graph (http://folk.uio.no/ohammer/uagraph/). This software is accompanied by a graphic user interface to ease its use as well as supplementary tools to analyze the dataset and results. Figure 11.3 reports and illustrates the graphic user interface of the software (version 0.28). For a recent and exhaustive application of the method on ammonoids by means of this interface, see Monnet et al. (2011); only the major points are listed here.

The biochronological analysis can be pre-processed with the removal of taxa found in only one section (Fig. 11.3a, "*Null endemic taxa*"). Such singletons are known to significantly increase the amount of biostratigraphic contradictions while being of no help for correlation purposes (Boulard 1993; Savary and Guex 1999; Monnet and Bucher 1999). Once the analysis has been computed, the software directly reports some numbers (Fig. 11.3b), which characterize the results and the quality of the dataset (e.g., Boulard 1993; Monnet and Bucher 2002): e.g., the number of constructed UAs (here 18 biozones), the number of biostratigraphic contradictions (66) between the cliques (25), and the number of cliques involved in cycles (6). The major result of the biochronological analysis is a composite range chart representing the succession of the reconstructed discrete maximal sets of mutually coexisting species (UAs; Fig. 11.3c). This sequence synthesizes the association, superposition and exclusion relationships of the ammonoid taxa included in the analysis. This range chart, which thus defines the content of each UA, is complemented by its reproducibility matrix (Fig. 11.3c, "*UA reproducibility*"). It is a UA vs. section matrix, indicating, which UAs are identified in which sections. This enables assessment of the lateral (geographic) reproducibility of each UA, which is also a reflection of the variable completeness of each section and the degree of biogeographic differentiation (and/or the relative importance of facies control, depending on the geographic scale of the study). This set of information is important, because the goal of a biochronological analysis is to construct a zonation for correlations. Note that UA-graph automatically attributes (if possible) a UA or set of UAs to each sample of the dataset based on the resulting range chart produced by the method (Fig. 11.3c, "*Correlation table*").

One of the major strengths of UAs and of its software UA-graph is the specific accompanying tools for evaluating the quality of the dataset and tracing back the possible origin of the conflicting stratigraphic relationships. For instance, the UA-graph has tools for providing the list of maximal cliques and their taxonomic content (Fig. 11.3d, "*Maximal cliques*"), for showing the relationships between these cliques (Fig. 11.3d, "*Graph of cliques*"), and for providing a complete list of the conflicting inter-taxon relationships (Fig. 11.3e, "*Contradictions*"). These sets of information can help to identify the possible origin of cycles and conflicting biostratigraphic relationships; see Monnet et al. (2011) for a detailed example. Additional information is available such as the number of sections, in which a taxon is documented and where it is present (Fig. 11.3f, "*Taxon frequency*" and "*Taxon distribution*").

11.4 Example Applications

11.4.1 Early Triassic Ammonoids

About 252 Myr ago at the Permian/Triassic boundary, the Earth witnessed its major mass extinction of marine life of all time (Benton 2005; Shen et al. 2011). More than 90 % of marine species disappeared abruptly and the biosphere previously was considered to recover its previous state only after several millions years (Kirchner and

Weil 2000; Erwin 2001). In this context, ammonoids were among the first marine organisms to diversify, with a first diversity peak less than 2 Myr after the Permian/Triassic boundary (Brayard et al. 2009b). However, the Early Triassic biotic recovery was not continuous but experienced several extinction and diversification cycles often associated with other events recorded by the sedimentary, geochemical and palynological records (Galfetti et al. 2007a; Hermann et al. 2011, 2012). Major environmental (in e.g., carbon cycle, ocean acidification, anoxia, productivity, sea-level changes) and climatic changes occurred repeatedly during the Early Triassic. In this context, large-scale ammonoid biodiversity changes are now relatively well documented (Brayard et al. 2009b). Notably, generic richness reached a first peak during the Smithian before collapsing anew at the Smithian/Spathian boundary (Fig. 11.4a). These evolutionary events are interpreted to reflect global climate changes (Brayard et al. 2006; Galfetti et al. 2007b; Romano et al. 2013). However, the long-distance and fine temporal correlation of these various events was hampered by poorly resolved previous biozonations.

To overcome these various biases and evaluate the temporal matching, causes and processes of the events, as well as investigate mechanisms of biotic recovery, a new biochronological scale of ammonoids has been constructed by means of the Unitary Associations method. This new biozonation shows a high resolution previously unmatched for the Triassic and consequently enables large-scale correlation (compare Jenks et al. 2015). For instance, the biochronological revision of the Smithian substage integrates several biostratigraphic records with abundant ammonoid faunas from basins spread all over the world (Brayard et al. 2013). Among these regions, the North Indian Margin (NIM) revealed abundant new ammonoid faunas that enabled construction of a high resolution ammonoid biozonation by means of UAs (Brühwiler et al. 2010). Indeed, a sequence of units defined by maximal set of (actually or virtually) coexisting species was reconstructed for each basin of the NIM. These local associations were then analyzed altogether by the same approach to deduce a new set of maximal associations at the NIM scale (Fig. 11.4b). This process enabled obtaining a robust ammonoid biozonation, free of biostratigraphic contradiction and reproducible over the entire NIM and even globally (Brayard et al. 2013).

Finally, known abiotic and biotic events were calibrated against this new ammonoid biozonation (Fig. 11.4c; Galfetti et al. 2007a, b; Brühwiler et al. 2010). Briefly, the analysis of dynamics of ammonoid biodiversity shows several marked patterns that were previously unknown, especially a diversification during the early Smithian followed by a global and synchronous extinction at the end-Smithian. Furthermore, the turnover of ammonoid faunas was extremely high during the middle Smithian. Indeed, the new ammonoid biozonation was calibrated by recent radioisotopic ages (Fig. 11.4a; Ovtcharova et al. 2006; Galfetti et al. 2007a; Brayard et al. 2009a, b; Brühwiler et al. 2010), which suggest an average mean duration of 17.5 kyr per UA, the separation intervals between UAs being included. This implies that rates of origination and extinction were of about 100 species per Myr and that the end-Smithian event was abrupt and took place with 2 UAs only. Thanks to this new UA-based biozonation applicable at the low paleolatitudes, the carbon and oxygen

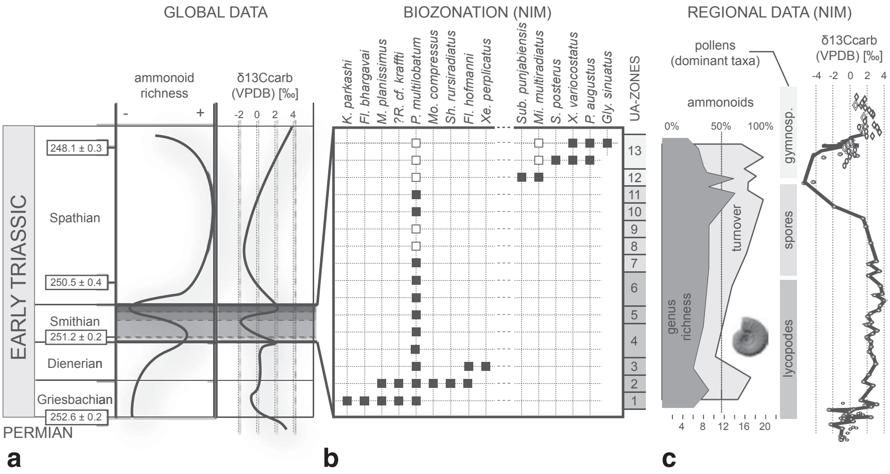


Fig. 11.4 Early Triassic ammonoid biochronology and calibrated biotic and environmental data. **a** Simplified global trends of ammonoid diversity and carbon isotope during the Early Triassic (after Brayard et al. 2009a). **b** Range chart of ammonoid species of the Smithian from the North Indian Margin (Salt Range, Spiti, and South Tibet) and biozones constructed by means of unitary associations (after Brühwiler et al. 2010). **c** Example of palynological and geochemical data calibrated towards this new UA-based biochronological scale

isotopic records and palynological records could be precisely dated and correlated in order to reconstruct a new extinction model linked with climate change (Romano et al. 2013).

11.4.2 Middle Triassic Ammonoids

Monnet and Bucher (2005a, b) synthesized and revised the ammonoid zonations of the Anisian (Middle Triassic) from North America. Their study focused on three basins, which were distributed along a latitudinal gradient (Fig. 11.5b): western Nevada (low paleolatitude, USA), British Columbia (mid- paleolatitude, Canada), and the Sverdrup Basin (high paleolatitude, Canada). They applied the UA method to reconstruct an ammonoid biozonation for each of the three basins, as well as the correlation between the three basins in a second, hierarchical step. This biochronological study benefited from recent and thorough taxonomic updates of Anisian ammonoids (Tozer 1994; Monnet and Bucher 2005a; Monnet et al. 2010, 2012, 2013).

Based on this quantitative analysis, the Anisian in the studied areas contains 13, 10, and 3 zones and a total of 174, 90, and 7 species, for western Nevada, British Columbia and the Sverdrup Basin, respectively (Fig. 11.5a). The use of such quantitative biochronological methods lead to new and more precise correlation. For instance, the *Buddhaites hagei* Zone (Canada) correlates only with the *Intornites* *mctaggarti* Subzone (Nevada) and not with the entire *Acrochordiceras hyatti* Zone (Nevada) as previously empirically assumed by other authors (compare Figs. 11.5a, c). The *Tetsaoceras hayesi* Zone (Canada) appears to correlate with the *Unionvillites hadleyi* Subzone (Nevada) of the *hyatti* Zone and not with the *Nevadisculites taylori* Zone. The *Hollandites minor* Zone (Canada) correlates with the *taylori* Zone (Nevada), not with the *Balatonites shoshonensis* Zone as is usually acknowledged (Tozer 1994).

The UA method also enabled quantifying the diachronism of studied taxa. It appears that about 67 % of the genera and 18 % of the species common to Nevada and British Columbia have diachronous FOs or LOs (Fig. 11.5d). Therefore, this diachronism is significant and its impact on correlation should not be overlooked.

Finally, these revised biochronological zonations enabled quantifying biodiversity of Anisian ammonoids from North America. This analysis reveals that the major diversity peak occurred during the early Middle Anisian exact correlatives *hadleyi* Subzone in Nevada and *hayesi* Subzone in British Columbia. A closer look at the taxonomic composition of these correlatives reveals short-lived faunal exchanges between the usually latitudinally restricted middle and late Anisian faunas. This event may reflect significant changes in climate or oceanic circulation at that time (for more details, see Monnet and Bucher 2005b).

11.4.3 Late Cretaceous Ammonoids

The marine Cenomanian–Turonian is one of the best-studied stratigraphic intervals of the Cretaceous. Such focus has been prompted by several, more or less interwoven, biotic and abiotic events, such as a moderate mass extinction, the highest sea-level of the Mesozoic and a global oceanic anoxic event coupled with a high positive excursion in the carbon isotope record (references in Monnet 2009). In order to decipher these global events and their consequences during the mid-Cretaceous, a wealth of biostratigraphic data for this critical time interval has been generated. Hence, the biostratigraphic distribution of major ammonite genera and species during the Cenomanian–Turonian is relatively well known. In addition, empirical ammonoid zonations have been established for this interval in such distant basins as north-west Europe, central Tunisia and the Western Interior (e.g., Robaszynski et al. 1994; Cobban 1984; Wright and Kennedy 1984; Kennedy and Cobban 1991; Kennedy et al. 2004; Fig. 11.6b).

The biochronology of Cenomanian-early Turonian ammonoids from three key stratotype areas (north-west Europe, central Tunisia and the Western Interior of North America) has been thoroughly analyzed and revised by means of the UA method (Monnet and Bucher 1999, 2002, 2007; Figs. 11.6a, c). This review was based on a taxonomic homogenization of ammonoid faunas from these key areas. The Cenomanian and early Turonian comprises 30 UA-zones in north-west Europe, 24 UA-zones in central Tunisia and 23 UA-zones in the middle Cenomanian–early Turonian of the Western Interior Basin (Fig. 11.6a). The UA method leads to a two-fold increase in resolution of these ammonoid zonations compared to the standard,

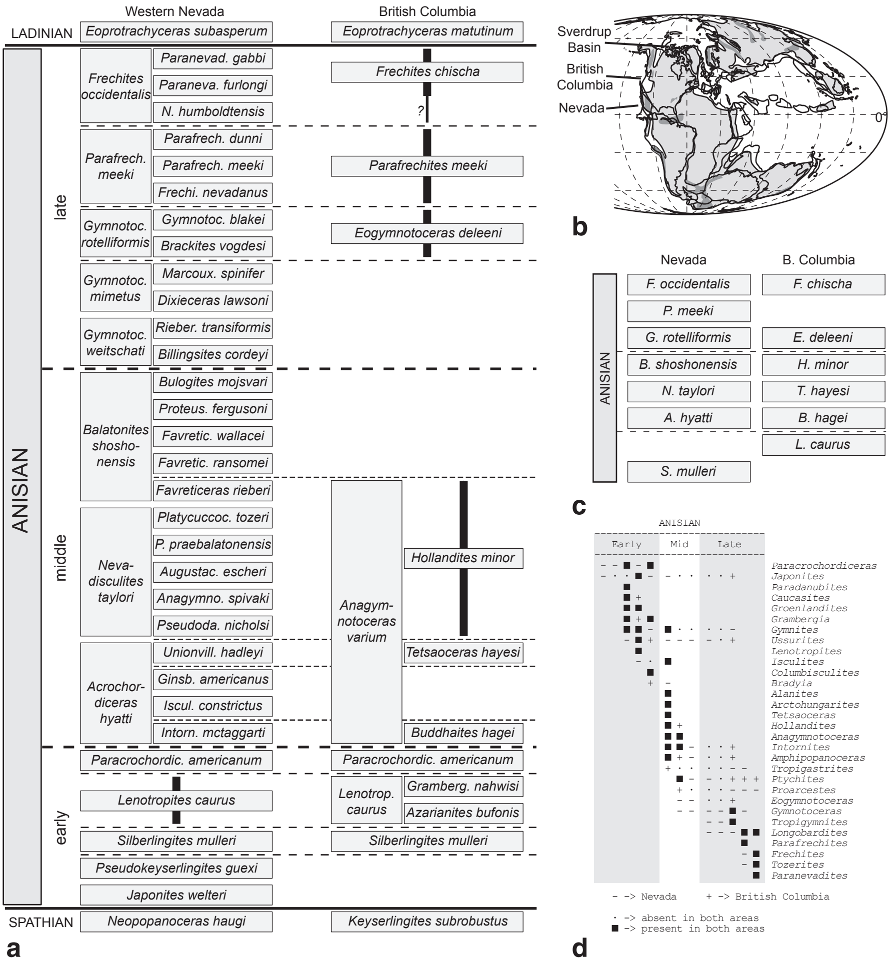


Fig. 11.5 Ammonoid biochronology of the Anisian (Middle Triassic). **a** Ammonoid zonations and correlation of western Nevada and British Columbia (after Monnet and Bucher 2005b). Compare with **b**. Thick vertical black bars indicate poorly constrained correlation with their length representing the maximal amount of uncertainty. **b** Paleogeographic location of western Nevada and British Columbia. **c** Correlation of Nevada and British Columbia ammonoid zones after Tozer (1994). **d** Biostratigraphic ranges and diachronism of Anisian ammonoid genera between Nevada and British Columbia at the zone level (after Monnet and Bucher 2005b)

empirical schemes. These correlations enable the designation of a new global marker for the middle/late Cenomanian boundary, which is characterized by the disappearance of the genera *Turrilites*, *Acanthoceras* and *Cunningtoniceras* and by the appearance of *Eucalycoceras*, *Pseudocalycoceras* and *Euomphaloceras*.

The correlation between the studied areas highlight the variable completeness and resolution of the faunal record through space and time, and reveal a significant number of diachronous taxa (Monnet and Bucher 2002, 2007; Fig. 11.6c). The only

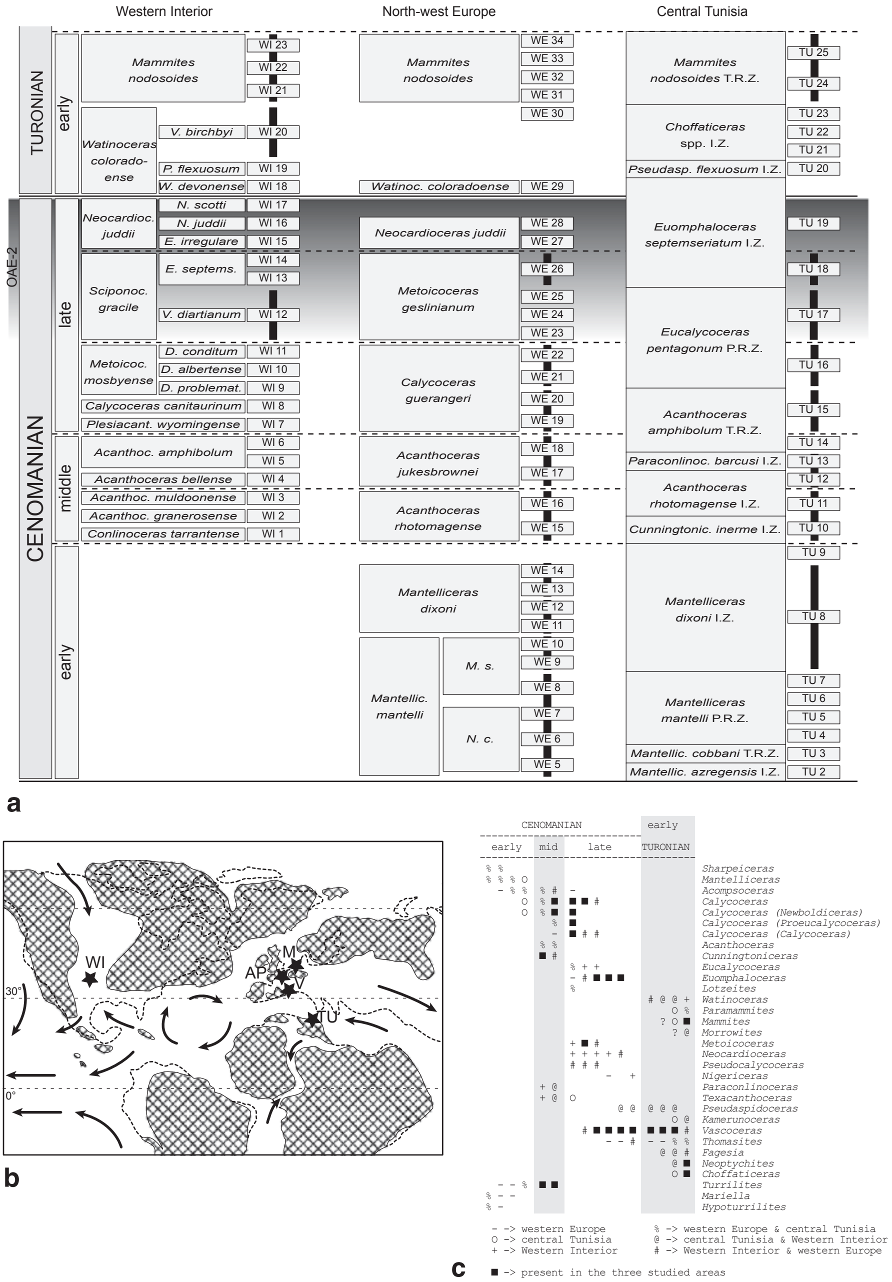


Fig. 11.6 Ammonoid biochronology of the Cenomanian–early Turonian (Late Cretaceous). **a** Ammonoid zonations and correlation after Monnet and Bucher (2002, 2007) between the three studied areas and between the previous empirical zonations and the reconstructed UAs. **b** Paleogeographic location of the three studied areas (Western Interior, Central Tunisia, and north-west Europe, which includes the Anglo-Paris, Vocontian, and Münster Basins). **c** Biostratigraphic ranges and diachronism of ammonoid genera between the three studied areas (after Monnet and Bucher 2007)

synchronous datum known to date is the last occurrence (LO) of *Turrilites acutus*, which may thus be potentially used as a marker for the middle/late Cenomanian boundary, provided that it does not turn out to be diachronous in the light of any new data (Monnet and Bucher 2007).

Finally, these revised quantitative ammonoid biozonations enabled precise investigation of biodiversity patterns of ammonoids during the Cenomanian–Early Turonian in these areas (Monnet et al. 2003; Monnet 2009) and to evaluate these in the face of known abiotic changes during this time interval. The biodiversity patterns of ammonoids (species richness, origination/extinction, turnover, poly-cohort survivorship, and taxonomic distinctness) highlight that the mass extinction of the Cenomanian/Turonian boundary is restricted to Europe, as far as ammonoids are concerned. Only Europe documents an actual decrease of species richness during the late Cenomanian, which results mainly from decreasing originations. In Tunisia, where the onset of anoxic waters is synchronous with Europe, species richness increases during the late Cenomanian and reaches its highest values in the early Turonian. The Western Interior records relatively high species richness during the late Cenomanian with only a single minor extinction event. Furthermore, major changes in biodiversity patterns of ammonoids occurred around the middle/upper Cenomanian boundary, i.e. about 0.75 Myr before the onset of the Oceanic Anoxic Event 2 (OAE2). Although there is extensive evidence for widespread anoxia during the Cenomanian/Turonian boundary interval in deep sea environments, the biodiversity patterns of ammonoids in Europe, Tunisia, and the Western Interior rule out global anoxia as a direct causal mechanism for changes in ammonoid diversity (Monnet and Bucher 2007). These biodiversity patterns question the global scale character of the so-called Cenomanian/Turonian mass extinction. Observed biodiversity patterns of ammonoids strongly support the global warming of the late Cenomanian as evidenced by the northward migration of taxa typical of the Tethyan Realm. Changes in ammonoid diversity are compatible with the exceptional high sea level occurring at that time and with concomitant regional climate changes (Monnet 2009).

11.5 Conclusions

As demonstrated by their application on ammonoids, quantitative biochronological methods are very efficient and robust to produce highly resolved biozonations. For all these methods, free computer software is available. Among these methods, the Unitary Associations approach is probably the best for academic purposes in our opinion: Comparisons of empirical zones based on the maximum association principle to UAs processed from the same dataset shows up to a threefold increase in resolution. UAs allow identifying and processing the (often complex) biostratigraphic contradictions generated by the highly discontinuous records resulting from selective preservation, facies control, ecology, and sampling effort. The reconstructed robust and high resolution UA-biozonations can thus be used to precisely date and correlate sections distributed across various geographic scales from a basinal to a global scope. Only UAs will not mask the limitations inherent to low quality datasets in term of resolution. The UA method offers additional powerful tools, which enable tracing back the origin of existing biostratigraphic contradictions to identify and evaluate the quality of the analyzed data. Last but not least, UA-biozones provide an ideal tool for the analysis of diachronism and biogeographic patterns. Rapidly evolving clades with a good quality record like ammonoids (or, e.g., conodonts) often lead the biostratigrapher to become somewhat overconfident in the *a priori* recognition of gradually evolving anagenetic lineages and the application thereof in dating. Among the phylogeny-free, quantitative biochronological methods, only UAs provide a logical and powerful tool for constructing reliable time frames without ignoring and masking the actual quality of the primary data.

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Chapter 12
Paleozoic Ammonoid Biostratigraphy

Dieter Korn and Christian Klug

12.1 Introduction

The research field of Paleozoic ammonoid biostratigraphy has undergone major changes in the last few decades. In early attempts at ammonoid biostratigraphy in the 1980s, research efforts mainly focused on the stratigraphical subdivision of the rock succession and the correlation of time equivalent assemblages with the aim of a uniform global scheme of stages and zones. After that, the next period lasting about 20 years, saw many researchers focused on the correlation of stratigraphical schemes developed for various fossil groups. The correlation of ammonoid zonation with emerging micropaleontological schemes, particularly for conodonts, was a major point of interest. Advances in morphological studies of Paleozoic ammonoids led to the third epoch in stratigraphical research, in which the detailed subdivision of sections in selected key regions plays the most important role.

The strict application of the Hedberg Code (Hedberg 1976; Salvador 1994) does not allow for the separation of biostratigraphical units apart from the biozone; however, so-called genus zones have frequently been used as a larger scale interval somewhere between a stage and a zone. Such stratigraphical units were used for instance by Becker and House (2000) in their review of Devonian ammonoid biostratigraphy. The use of genus zones bears the advantage of interregional correlation at least to some degree, when a more precise correlation based on species is impossible because of provincialism of the ammonoid faunas. However, in the case of an increasingly finer taxonomic scheme of Paleozoic ammonoids, even the genus level

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D. Korn (✉)
Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung,
Invalidenstraße 43, 10115 Berlin, Germany
e-mail: dieter.korn@mfn-berlin.de

C. Klug
Paläontologisches Institut und Museum, Karl Schmid-Strasse 4, 8006 Zürich, Switzerland
e-mail: chklug@pim.uzh.ch

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is sometimes not suitable for the definition of stratigraphical intervals above the biozone category (compare Korn and De Baets 2015).

In the following review, an overview of the numerous occurrences of Paleozoic ammonoids is given to provide a picture of the current state of stratigraphical research. The provided reference list does not claim completeness. Additional information can be found in the AMMON database (Korn and Ilg 2007).

12.2 Devonian Ammonoid Biostratigraphy

The ammonoid biostratigraphy of the Devonian has been developed in two principal regions, the Rhenish Mountains of Germany and the Anti-Atlas of Morocco (Becker et al. 2012). In the Rhenish Mountains Wedekind (1913, 1914, 1918) developed a stratigraphic scheme entirely based on ammonoid genera. The Late Devonian in particular was thereafter subdivided into zones and subzones by means of ammonoid species (Lange 1929; Schindewolf 1937; Korn 1981, 2002; Becker 1993b; Becker and House 2000).

In the Anti-Atlas, the excellent outcrop conditions led to a significant refining of the stratigraphic scheme, particularly for the Early and Middle Devonian successions. After the pioneering studies by (Petter 1959, 1960), in which the Central European scheme was largely applied, progress has been made during the past 25 years with the establishment of a zonal scheme which is finer than any other scheme in the world (Becker 1993b; Korn 1999; Becker et al. 2000a, 2002, 2012; Becker and House 2000; Klug 2002). A fine-scaled stratigraphical subdivision has been established based on the two aforementioned regions (Fig. 12.1).

The potential for a subdivision of the interval from the Emsian to the Famennian appears to be rather uniform within the stratigraphical succession. While the Emsian has been subdivided into eight zones (mean zone length is about 1.3 Ma), the Eifelian (eight zones; mean = 0.7 Ma), Givetian (nine zones; mean = 0.6 Ma), Frasnian (12 zones; mean = 0.9 Ma) and the Famennian (24 zones; mean = 0.6 Ma) have been divided to a finer resolution. However, recent studies (e.g. Korn et al. 2014) suggest that the stratigraphical resolution of certain intervals will be refined in the future.

12.2.1 Early and Middle Devonian

A continuous succession of Early and Middle Devonian ammonoids is known from only two regions, the Anti-Atlas of Morocco (Petter 1959; Bensaïd 1974; Becker and House 1994a, p. 200; Belka et al. 1999; Klug 2001, 2002; De Baets et al. 2010; Ebbighausen et al. 2011; Monnet et al. 2011) and the Saoura Valley of Algeria (Petter 1959; Göddertz 1987); the current ammonoid biostratigraphy (Fig. 12.2) for this time interval is thus mainly based on these successions.

Fig. 12.1 Composite Devonian ammonoid biostratigraphy, largely after Becker and House (2000), Klug (2002) and Korn (2002)

Diverse Emsian and Eifelian ammonoid faunas have been described from other regions such as Bohemia (Barrande 1865; Chlupac and Turek 1983) and the Rhenish Mountains, the Harz and the Eifel in Germany (Wedekind 1918; Erben 1953, 1960; De Baets et al. 2009, 2013), but these faunas are often isolated occurrences. Practically all occurrences worldwide can be attributed to the North African zonal scheme (Becker and House 2000), e.g. the occurrences in the Cantabrian Mountains (Kullmann 1960), Bithynia in Turkey (Kullmann 1973), the North Urals (Bogoslovsky 1969), the Zeravshan Mountains of Uzbekistan (Bogoslovsky 1980; Becker et al. 2010) and South China (Shen 1975; Ruan 1981b, 1996).

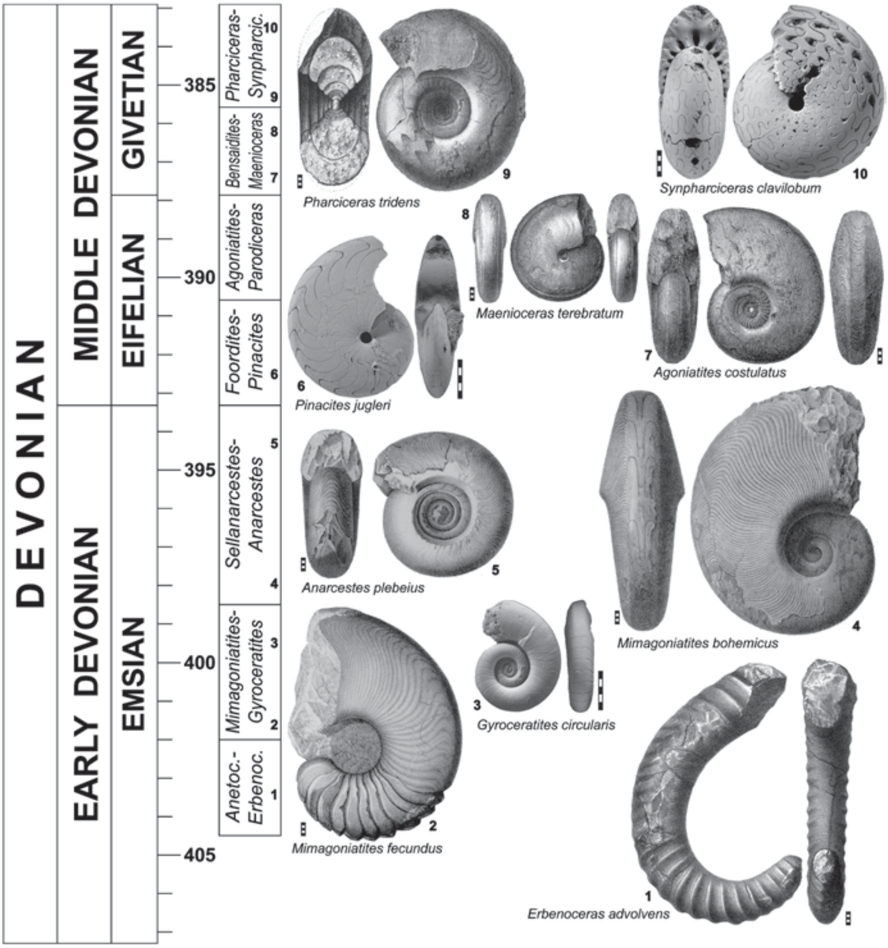
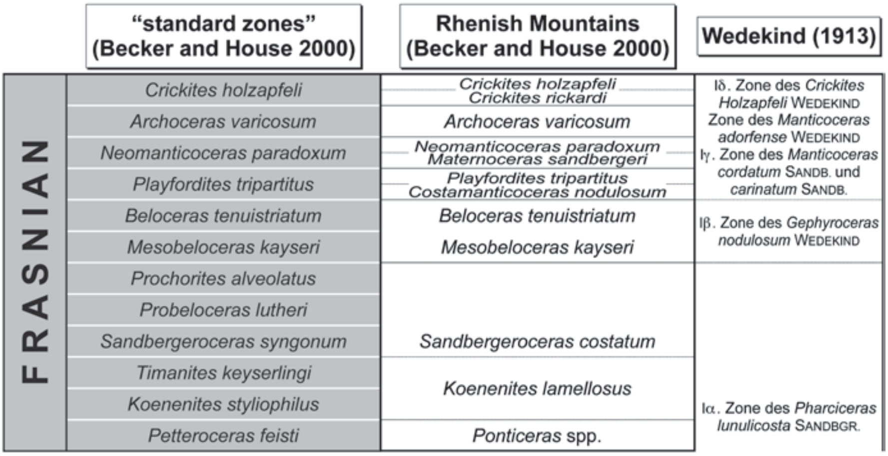


Fig. 12.2 Early and Middle Devonian stratigraphy and ammonoid genus zones with representative species. Images from Barrande (1865), Frech (1888), Holzapfel (1895), Klug (2002) and Korn and Klug (2002). Time scale from Becker et al. (2012)

Givetian ammonoid faunas are mainly known from two geographical regions, the Rhenish Mountains (Holzapfel 1895; Wedekind 1918; Matern 1931a; Bockwinkel et al. 2013b), and the Anti-Atlas of Morocco (Bensaïd 1974; Bockwinkel et al. 2009, 2013a).

12.2.2 Frasnian

Successions of Frasnian ammonoids are mainly known from four regions, (1) the state of New York (Clarke 1899; Miller 1938; House and Kirchgasser 2008), (2) the



	"standard zones" (Becker and House 2000)	Rhenish Mountains (Becker and House 2000)	Wedekind (1913)
FRASNIAN	*Crickites holzapfeli*	*Crickites holzapfeli* *Crickites rickardi*	Iδ. Zone des *Crickites Holzapfeli* WEDEKIND Zone des *Manticoceras adorfense* WEDEKIND Iγ. Zone des *Manticoceras cordatum* SANDB. und *carinatum* SANDB.
	Archoceras varicosum	*Archoceras varicosum*	
	Neomanticoceras paradoxum	*Neomanticoceras paradoxum* *Maternoceras sandbergeri*	
	Playfordites tripartitus	*Playfordites tripartitus* *Costamanticoceras nodulosum*	
	Beloceras tenuistriatum	*Beloceras tenuistriatum*	Iβ. Zone des *Gephyroceras nodulosum* WEDEKIND
	Mesobeloceras kayseri	*Mesobeloceras kayseri*	
	Prochorites alveolatus	*Sandbergeroceras costatum*	Iα. Zone des *Pharciceras lunulicosta* SANDBGR.
	Probeloceras lutheri		
	Sandbergeroceras syngonum		
	Timanites keyserlingi	*Koenenites lamellosus*	
	Koenenites styliophilus		
	Petteroceras feisti	*Ponticeras* spp.	

Fig. 12.3 Correlation of ammonoid zonations of the Frasnian; shown is the composite standard zonation after the succession of ammonoid assemblages in the Rhenish Mountains (both after Becker and House 2000) and the traditional subdivision by Wedekind (1913)

Rhenish Mountains (Holzapfel 1882; Wedekind 1913, 1918; Matern 1931a; House and Ziegler 1977), (3) Timan (Keyserling 1846; Bogoslovsky 1969; Becker et al. 2000b) and (4) the Canning Basin of Western Australia (Glenister 1958; Becker et al. 1993). These regions show deviating ammonoid successions, which can only be correlated at a coarse scale (Fig. 12.3) on the basis of genera. Other regions worth mentioning are the Anti-Atlas of Morocco and the Saoura Valley of Algeria (Petter 1959), Belgium (Matern 1931b), the Eifel Mountains (Clausen 1969; Korn et al. 2013), Thuringia (Müller 1956), the Holy Cross Mountains (Dzik 2002), the Montagne Noire (House et al. 1985), south-western England (House 1963) as well as the Altay (Bogoslovsky 1958).

Regarding the morphology of the ammonoids (Fig. 12.4), the Frasnian shows three intervals without sharp boundaries: (1) the early Frasnian with simple-sutured gephuroceratid ammonoids (e.g., *Ponticeras*), gephuroceratids with more complex suture lines (e.g., *Koenenites*, *Timanites*) and the enigmatic *Sandbergeroceras*, (2) the middle Frasnian with the dominance of *Manticoceras* and closely related genera as well as the diversification of the multilobate *Beloceras* (Korn et al. 2011) and (3) the late Frasnian with the rise of morphologically simplified genera (e.g. *Archoceras*) (e.g., Korn et al. 2013).

12.2.3 Famennian

Famennian ammonoid successions are known from a number of regions, of which the Rhenish Mountains, the Anti-Atlas, the Holy Cross Mountains and

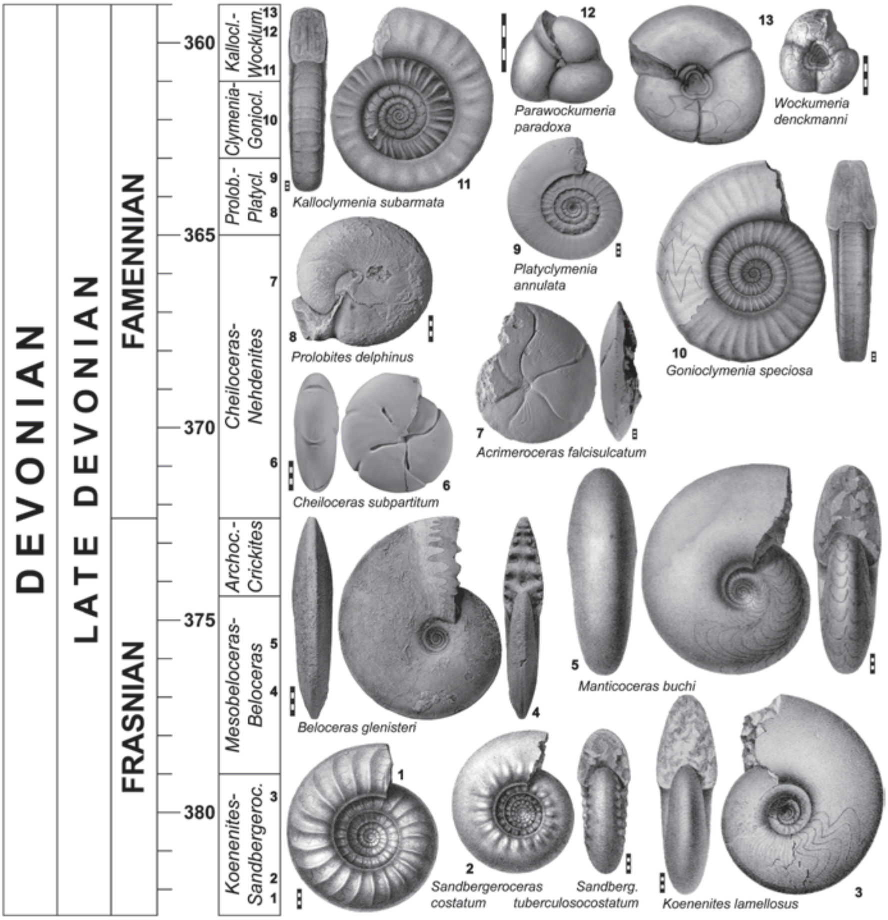


Fig. 12.4 Late Devonian stratigraphy and ammonoid genus zones with representative species. Images from Archiac and Verneuil (1842), Sandberger and Sandberger (1850), Gümbel (1863), Schindewolf (1937) and own material. Time scale from Becker et al. (2012)

the South Urals play the most important role. The ammonoid zonal scheme was introduced for the Rhenish Mountains (Wedekind 1914, 1918; Lange 1929; Schindewolf 1937; Korn 1981, 2002; Becker 1993b) but has also been used in other regions (Table 12.1).

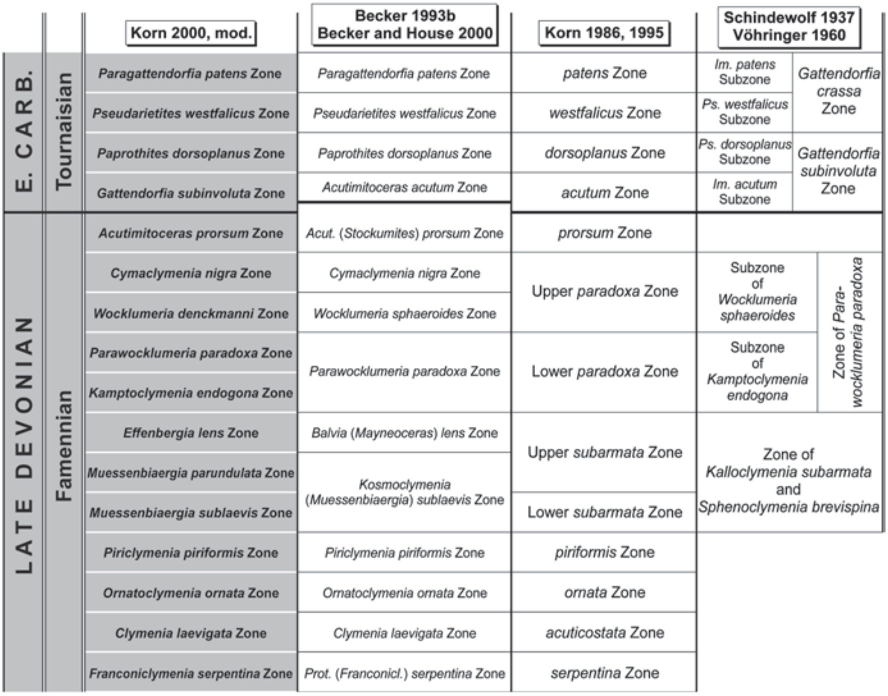
Traditionally, the Famennian stage was separated into four ammonoid ‘Stufen’ (stratigraphical units), i.e. *Cheiloceras*, *Prolobites-Platyclymenia*, *Clymenia* and *Wocklumeria* Stufen. Increasing progress in taxonomic research led to the result that these genera are only representative for some of the zones and that species of many other genera are required for the subdivision. Hence the former Stufen can

Table 12.1 Principal regions important for Devonian ammonoid biostratigraphy with selected articles and ammonoid monographs

New York region	Clarke 1899, Miller 1938, House 1962, Kirchgasser 1975, House 1978, House and Kirchgasser 2008
Cantabrian Mountains	Kullmann 1960, Montesinos Lopez 1990
Montagne Noire	Böhm 1935, Becker and House 1994b
Rhenish Mountains	Wedekind 1913, 1914, 1918, Lange 1929, Matern 1931a, Schindewolf 1937, Korn 1981, Becker 1993b, Korn 2002
Franconia, Thuringia	Schindewolf 1923, Müller 1956, Bartzsch and Weyer 1985, 2012
Bohemia	Barrande 1865, Chlupac and Turek 1983
Holy Cross Mountains	Dybczynski 1913, Sobolev 1914, Czarnocki 1989, Dzik 2002, 2006
North-western Africa	Petter 1959, 1960, Bensaïd 1974, Göddertz 1987, Becker 1993b, Belka et al. 1999, Korn 1999, Becker et al. 2000a, Becker and House 2000, Klug 2001, Becker et al. 2002, Klug 2002, De Baets et al. 2010, Monnet et al. 2011, Ebbighausen et al. 2011
South Urals	Perna 1914, Nalivkina 1936, 1953, Bogoslovsky 1969, 1971, 1981, Nikolaeva and Bogoslovsky 2005
South China	Sun and Shen 1965, Ruan 1981b, 1996
Western Australia	Glenister 1958, Petersen 1975, Becker et al. 1993

nowadays only work as a very coarse scheme. Indeed, the history of Famennian ammonoid evolution can be subdivided into three major epochs, which is reflected by the zonation scheme (Fig. 12.4): (1) The first interval corresponds to the former *Cheiloceras* Stufe and is characterized by the cheiloceratid goniatites including advanced lineages leading to the sporadoceratids. (2) The second interval marks the diversification of the tornoceratids; they gave rise to the rapidly diverging clymeniids and, more importantly, to all post-Devonian ammonoids. (3) The third interval (the former *Clymenia* and *Wocklumeria* Stufen) is characterized by the dominance of the clymeniids, which show an extensive radiation forming many different morphologies and were usually more diverse than the accompanying goniatites (Korn and Klug 2012) (Fig. 12.5).

The stratigraphical scheme was used in most of the numerous Famennian ammonoid occurrences, of which the most diverse are listed here with selected monographs: Montana (Raymond 1909; Korn and Titus 2006), south-western England (Selwood 1960), Thuringia (Müller 1956), Franconia (Münster 1832; Schindewolf 1923; Price 1982), Cantabrian Mountains (Kullmann 1960), Montagne Noire (Böhm 1935; Becker 1993b), Anti-Atlas of Morocco and the Saoura Valley of Algeria (Petter 1959; Becker 1993b; Korn 1999; Becker et al. 2002), Holy Cross Mountains (Czarnocki 1989; Dzik 2006), South Urals (Nalivkina 1936, 1953; Bogoslovsky 1969, 1971, 1981; Nikolaeva and Bogoslovsky 2005), South China (Sun and Shen 1965; Ruan 1981b) and Western Australia (Petersen 1975).



		Korn 2000, mod.	Becker 1993b Becker and House 2000	Korn 1986, 1995	Schindewolf 1937 Vöhringer 1960	
E. CARB.	Tournaisian	*Paragattendorfia patens* Zone	*Paragattendorfia patens* Zone	*patens* Zone	*Im. patens* Subzone	*Gattendorfia crassa* Zone
		Pseudarietites westfalicus Zone	*Pseudarietites westfalicus* Zone	*westfalicus* Zone	*Ps. westfalicus* Subzone	
		Paprothites dorsoplanus Zone	*Paprothites dorsoplanus* Zone	*dorsoplanus* Zone	*Ps. dorsoplanus* Subzone	*Gattendorfia subinvoluta* Zone
		Gattendorfia subinvoluta Zone	*Acutimitoceras acutum* Zone	*acutum* Zone	*Im. acutum* Subzone	
LATE DEVONIAN	Famennian	*Acutimitoceras prorsum* Zone	*Acut.* (*Stockumites*) *prorsum* Zone	*prorsum* Zone		
		Cymaclymenia nigra Zone	*Cymaclymenia nigra* Zone	Upper *paradoxa* Zone	Subzone of *Wocklumeria sphaeroides*	Zone of *Para-wocklumeria paradoxa*
		Wocklumeria denckmanni Zone	*Wocklumeria sphaeroides* Zone			
		Parawocklumeria paradoxa Zone	*Parawocklumeria paradoxa* Zone	Lower *paradoxa* Zone	Subzone of *Kamptoclymenia endogona*	
		Kamptoclymenia endogona Zone				
		Effenbergia lens Zone	*Balvia* (*Mayneoceras*) *lens* Zone	Upper *subarmata* Zone	Zone of *Kalloclymenia subarmata* and *Sphenoclymenia brevispina*	
		Muessenbiaergia parundulata Zone	*Kosmoclymenia* (*Muessenbiaergia*) *sublaevis* Zone			
		Muessenbiaergia sublaevis Zone		Lower *subarmata* Zone		
		Piriclymenia piriformis Zone	*Piriclymenia piriformis* Zone	*piriformis* Zone		
		Ornatoclymenia ornata Zone	*Ornatoclymenia ornata* Zone	*ornata* Zone		
		Clymenia laevigata Zone	*Clymenia laevigata* Zone	*acuticostata* Zone		
		Franconiclymenia serpentina Zone	*Prot.* (*Franconicl.*) *serpentina* Zone	*serpentina* Zone		

Fig. 12.5 Correlation of ammonoid zonations of the Famennian and Devonian-Carboniferous boundary, after (Schindewolf 1937, Vöhringer 1960, Becker 1993a, Korn 1995, Becker and House 2000, Korn 2000, 2002)

12.3 Carboniferous Ammonoid Biostratigraphy

The pioneers of Carboniferous ammonoid biostratigraphy were William S. Bisat and Hermann Schmidt, who in the 1920s developed two zonal schemes for the British and Central European sedimentary successions (Bisat 1924, Schmidt 1925). In the following years, nearly all of the subsequent authors working in the British Isles and continental Europe referred to these two schemes with the result that the two schemes, although developed in paleogeographically close regions, were manifested as parastratigraphies (Table 12.2).

Increasing provincialism during the Early Carboniferous is one of the main obstacles for the development of a widely accepted stratigraphical scheme based on ammonoids. The example of the two parallel zonations (British and continental Europe) within the same sedimentary basin can be used as an allegory for the general pattern. Within the last 80 years, for several of the regions with a succession of ammonoid faunas, independent zonations have been developed. These zonations

Table 12.2 Principal regions important for Carboniferous ammonoid biostratigraphy with selected articles and ammonoid monographs

Great Basin	Youngquist 1949, Miller et al. 1952, Titus 2000, Titus and Manger 2001, Korn and Titus 2011
American Midcontinent	Smith 1903, Girty 1909, 1911, 1915, Plummer and Scott 1937, Miller and Furnish 1940b, c, Miller and Youngquist 1948, Unklesbay 1962, McCaleb et al. 1964, Gordon 1965, McCaleb 1968, Saunders 1973, Saunders et al. 1977, Manger and Saunders 1980, Gordon 1986, Boardman et al. 1994
British Isles	Bisat 1924, Moore 1936, Hudson 1945, Bisat 1950, Yates 1962, Riley 1990, Korn and Tilsley 2006, Tilsley and Korn 2009
Belgium	Demanet 1938, Delépine 1940, Demanet 1941, 1943, Bouckaert 1961
Rhenish Mountains	Schmidt 1925, 1934, Ruprecht 1937, Patteisky 1959, Horn 1960, Kulick 1960, Patteisky 1965, Korn 1988, 1996, Korn and Horn 1997b, Korn 2010
SW Portugal	Korn 1997, Korn and Horn 1997a
Moroccan Meseta	Delépine 1941, Korn and Ebbighausen 2008
Cantabrian Mountains	Delépine 1943, Kullmann 1961, 1962, 1963, Wagner-Gentis 1963, 1980
Anti-Atlas	Delépine 1941, Korn et al. 1999, Klug et al. 2006, Korn et al. 2007
Western Algeria	Termier and Termier 1952, Pareyn 1961
Southern Algeria	Conrad 1984, Ebbighausen et al. 2004, Bockwinkel et al. 2010, Ebbighausen et al. 2010, Korn et al. 2010b
Donetz Basin	Popov 1979
North Urals, Novaya Zemlya	Librovitch 1938, Kusina 1974, 1980, Kusina and Yatskov 1999
South Urals	Ruzhencev 1950, 1966, Ruzhencev and Bogoslovskaya 1970, 1971a, b, 1975, 1978
Karaganda, Semipalatinsk	Librovitch 1940
Tien Shan (Kyrgyzstan)	Popov 1965, 1968
Tien Shan (Uzbekistan)	Librovitch 1927, Pitinova 1974, Ruzhencev and Bogoslovskaya 1978
Pamirs (Tajikistan)	Ruzhencev and Bogoslovskaya 1971a, 1978, Nikolaeva 1994, 1995
Xinjiang	Liang and Wang 1991
South China	Yang 1978, Ruan 1981b, a, Yang 1986, Ruan and Zhou 1987

are often based on species with a limited geographical distribution and hence a correlation between the regions is often difficult.

The subdivision of the Carboniferous by means of ammonoid genera leads to a number of genus zones, which at least in part can be correlated with the chronostratigraphical stages (Davydov et al. 2012). A global zonation based on species is not applicable because of the limited geographical distribution of many of the species.

The time resolution in terms of ammonoid zonation is highly variable for the duration of the Carboniferous. A zonation based on the succession of distinct species has been proposed for the early Tournaisian and for the interval from the Late Viséan to the end-Bashkirian; in the other intervals the species zones are largely equivalent to genus zones with longer durations. The Late Viséan successions of Central and North-Western Europe show an average zone duration of about 0.8 Ma (Korn and Kaufmann 2009) and are comparable to the Devonian zonations, while the average zone duration for the middle to late Tournaisian as well as the Moscovian to Gzhelian is probably more than 2 Ma. Probably the finest time resolution achieved using ammonoids occurs in the Serpukhovian and Bashkirian with more than 25 north-western European ammonoid zones within a time interval of about 13 Ma.

12.3.1 Tournaisian

The Tournaisian stage shows an indifferent picture with regard to the stratigraphical subdivision made possible by the use of ammonoids (Fig. 12.6). For the Early Tournaisian (representing the *Gattendorfia-Eocanites* Genus zone), a scheme similar to the latest Famennian zonation exists with four short-ranging zones established in the Rhenish Mountains (Vöhringer 1960). This scheme can be applied with some confidence to other regions such as the Thuringian Mountains (Bartzsch and Weyer 1982), the Sudetes (Weyer 1965; Dzik 1997), the Carnic Alps (Korn 1992) and South China (Sun and Shen 1965; Ruan 1981b). A global character of this zonation has not been proven. North-African occurrences (Ebbighausen et al. 2004; Bockwinkel and Ebbighausen 2006; Ebbighausen and Bockwinkel 2007) deviate in their faunal composition and may represent a slightly younger time interval.

The “Middle” and Late Tournaisian is a time interval with a low number of ammonoid occurrences. Considerably diverse “Middle” Tournaisian deposits (representing the *Goniocyclus-Protocanites* genus zone) are known only from three regions, the western United States (Gordon 1986), the American Midcontinent (Miller and Collinson 1951) and the Anti-Atlas (Korn et al. 2002). A subdivision appears to be impossible at the moment. The Late Tournaisian (representing the *Pericyclus-Progoniatites* genus Zone and the lower part of the *Fascipericyclus-Ammonellipsites* genus Zone) is currently coarsely subdivided; both genus zones may bear the potential for further subdivision.

Unfortunately, most of the richer ammonoid occurrences of the *Pericyclus-Progoniatites* genus Zone are more or less isolated assemblages, such as in the central and eastern United States (Miller and Garner 1955; Work and Mason 2003, 2004, 2005), Belgium (Delépine 1940), the Anti-Atlas of Morocco (Korn et al. 2003) and the Mouydir of Algeria (Korn et al. 2010a, b).

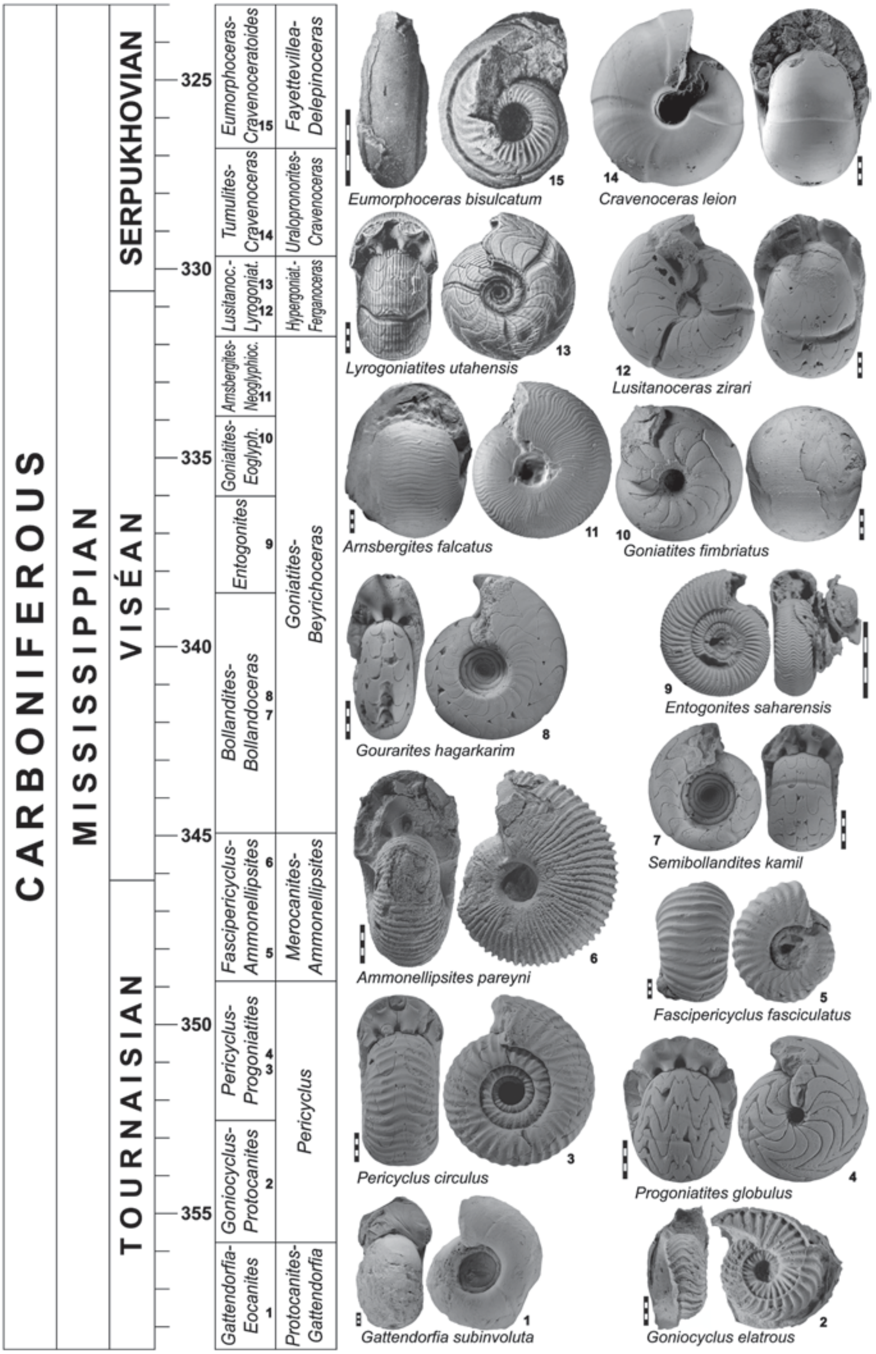


Fig. 12.6 Early Carboniferous stratigraphy and ammonoid genus zones with representative species. Images from (Miller et al. 1952), Gordon (1965), Korn et al. (2007, 2010a), Bockwinkel et al. (2010), Ebbighausen et al. (2010) and own material. Time scale from Davydov et al. (2012)

The *Fascipericyclus-Ammonellipsites* genus Zone, which probably ranges into the earliest Viséan, often appears as a uniform time interval with respect to ammonoid biostratigraphy. Diverse assemblages have been described from Belgium (Koninck 1878; Delépine 1940), the Rhenish Mountains (Holzapfel 1889; Schmidt 1925), Ireland (Crick 1899; Foord 1901, 1903), the Montagne Noire (Böhm 1935), the Anti-Atlas (Delépine 1941), the Harz Mountains (Schindewolf 1951), the Saoura Valley of Algeria (Pareyn 1961), the Tien Shan (Popov 1965, 1968), Northern England (Riley 1996; Tilsley and Korn 2009) and the Mouydir of Algeria (Ebbighausen et al. 2010). A succession of ammonoid faunas is known from the North Urals, where Kusina (1974, 1980) described assemblages of Late Tournaisian to earliest Viséan age.

12.3.2 Viséan

The beginning of the Viséan is, in terms of ammonoid biostratigraphy, a problematic time interval because there are only a few places which have yielded relatively diverse assemblages. A rather complete succession of ammonoids is so far only known from the North of England (Riley 1996); other regions show a much more patchy succession. Isolated ammonoid faunas from the Early and Middle Viséan are known from British Columbia (Work et al. 2000) and from South Algeria (Conrad 1984; Bockwinkel et al. 2010).

Late Viséan ammonoids are nearly globally distributed in the tropical and subtropical realms; their rapid evolution makes them excellent stratigraphical index fossils (Fig. 12.6). The subdivision of the Viséan into ammonoid zones was first achieved by Bisat (1924) who developed a detailed zonal scheme for the North of England.

Late Viséan ammonoid assemblages are characterized by increasing provincialism (Korn et al. 2012), which is a major obstacle for stratigraphical correlation across wide geographical distances (Fig. 12.7; compare Korn and De Baets 2015). This resulted in parallel stratigraphical schemes for the distinct regions. Interestingly, most assemblages of the early Late Viséan are dominated by the cosmopolitan genus *Goniatites*, such as those in Alaska (Gordon 1957), the Great Basin in the Western United States (Korn and Titus 2011), the American Midcontinent (Gordon 1965), the Cantabrian Mountains of Spain (Kullmann 1961), the British Isles (Bisat 1934; Korn and Tilsley 2006), Central and Eastern Europe (Nicolaus 1963; Korn 1988), South Portugal (Korn 1997), the Moroccan Meseta (Korn and Ebbighausen 2008), the Anti-Atlas of Morocco (Klug et al. 2006; Korn et al. 2007), the South Urals (Bogoslovskaya 1966) and Xinjiang (Liang and Wang 1991). Many of the regions, however, possess their own endemic species of *Goniatites*.

Increasing provincialism later in the Viséan makes a global correlation of ammonoid successions more difficult. Three major palaeogeographical realms with

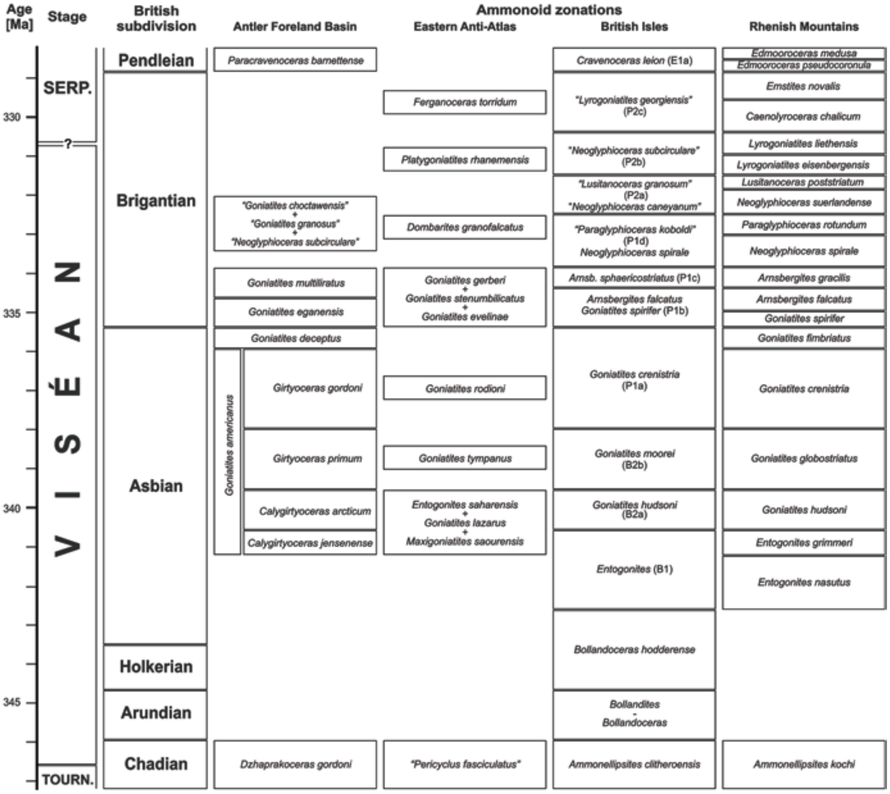


Fig. 12.7 Numerical time scale and integrated stratigraphy of the Viséan Stage of the Rhenish Mountains. Absolute ages after Davydov et al. (2012); ammonoid zonations after Korn and Titus (2011), Korn et al. (2007), Moore (1936) and Korn (1996). *TOURN.* Tournaisian; *SERP.* Serpukhovian

characteristic sets of genera can be separated, each of which possesses an independent ammonoid biostratigraphy. The North Variscan realm is dominated by the genera *Arnsbergites*, *Hibernicoceras*, *Paraglyphioceras*, *Neoglyphioceras* and *Lusitanoceras*, which occur in Ireland (Moore and Hodson 1958; Hodson and Moore 1959), northern England (Bisat 1924; Moore 1936), Germany (Korn 1988, 1996), South Portugal (Korn 1997) and the Moroccan Meseta (Korn and Ebbighausen 2008). A similar succession has been reported from Novaya Zemlya (Kusina and Yatskov 1999). The South Variscan, South Urals and the North American realms (including the American Midcontinent and the Great Basin) did not yield the first three of the listed genera; these may be replaced by advanced representatives of the family Goniatitidae and derived genera such as *Dombarites*, *Neogoniatites*, *Hypergoniatites* and *Platygoniatites* (Kullmann 1961; Pareyn 1961; Klug et al. 2006; Nikolaeva et al. 2009; Korn and Titus 2011). The South Urals show very diverse latest Viséan ammonoid assemblages, which at the generic and species level outnumber all of the other regions and thus possess a unique position (Ruzhencev and Bogoslovskaya 1971a).

12.3.3 *Serpukhovian, Bashkirian*

The paleogeographical separation of shelf areas in the Viséan was maintained during the Serpukhovian, thus discrete stratigraphical schemes had to be proposed for the various regions (compare Korn and De Baets 2015). The principal subdivision was developed by British researchers in the first half of the twentieth Century (Bisat 1924, 1950; Bisat and Hudson 1943; Hudson 1945) and adopted by workers on time-equivalent successions in other parts of Europe such as Ireland (Hodson 1957; Yates 1962), South Portugal (Korn 1997), the Netherlands (Dorsman 1945), Belgium (Dorlodot and Delépine 1930; Demanet 1938, 1941, 1943), northern France (Chalard 1960), the Rhenish Mountains (Schmidt 1934; Patteisky 1959; Horn 1960; Korn and Horn 1997b), North Moravia (Patteisky 1936), the Lublin Coal Basin of Poland (Bojkowski 1979), the Moroccan Meseta (Delépine 1941) and the Donetz Basin (Popov 1979). The stratigraphical subdivision of the sediments in these regions is mainly based on girtyoceratid, homoceratid, reticuloceratid and gastrioceratid ammonoids (Fig. 12.8).

In other areas, such as the NW Territories of Canada (Nassichuk 1975), the western United States (Youngquist 1949; Titus 2000; Titus and Manger 2001), the American Midcontinent (Gordon 1965; Saunders 1973; Saunders et al. 1977; Manger and Saunders 1980), the Cantabrian Mountains (Kullmann 1962), Novaya Zemlya (Kusina and Yatskov 1999), the South Urals (Ruzhencev and Bogoslovskaya 1971a, 1978; Nikolaeva et al. 2009), Karaganda (Ruzhencev and Bogoslovskaya 1971a), the Pamirs of Tajikistan (Nikolaeva 1994, 1995), Kyrgyzstan and Uzbekistan (Pitinova 1974; Ruzhencev and Bogoslovskaya 1978), Xinjiang (Liang and Wang 1991) and South China (Yang 1978; Ruan 1981a; Ruan and Zhou 1987), stratigraphical subdivisions operate also with advanced goniatitid and glaphyritid ammonoids.

12.3.4 *Moscovian to Ghzelian*

In contrast to the Bashkirian with numerous species-rich ammonoid occurrences, the Moscovian is a time with reduced numbers of regions in which ammonoids have been found. Occurrences in Europe are scarce and do not play an important role for ammonoid biostratigraphy. The important localities are situated in the NW Territories of Canada (Nassichuk 1975), the American Midcontinent (Miller and Moore

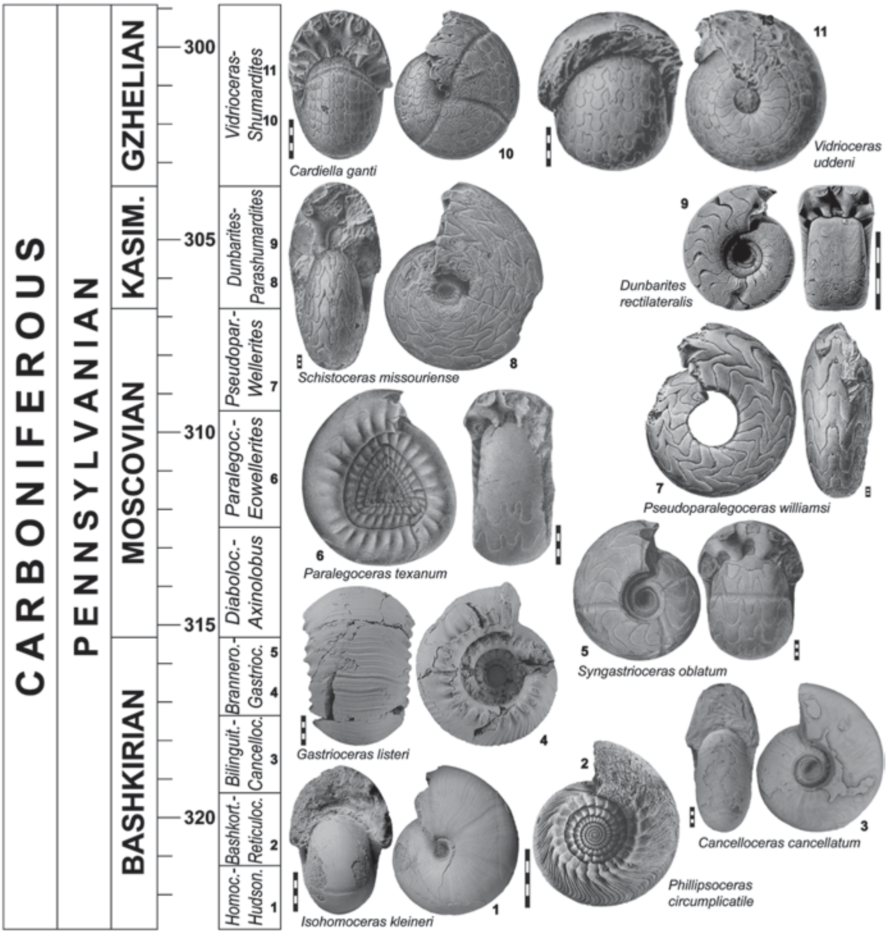


Fig. 12.8 Late Carboniferous stratigraphy and ammonoid genus zones with representative species. Images from Miller and Moore (1938), Miller and Furnish (1940a), Miller and Downs (1950), Hodson (1957), Work and Mapes (2009) and own material. Time scale from Davydov et al. (2012)

1938; Miller and Owen 1939; Unklesbay 1962; McCaleb 1963, 1968; Gordon 1965; Boardman et al. 1994; Mapes et al. 1997), the Moscow Basin (Shkolin 2001), Verkhoyan (Popov 1970), eastern Siberia (Ruzhencev 1975), Xinjiang (Liang and Wang 1991), South China (Yang 1978) and Akiyoshi in Japan (Nishida 1971). Despite the numerous fossil localities in some regions, a fine-scaled ammonoid biostratigraphy with a detailed subdivision of the Moscovian stage has not been developed (Fig. 12.8).

Kasimovian and Gzhelian ammonoid localities are even more restricted; the best occurrences are in the three major regions the American Midcontinent with a large number of single localities (Miller and Cline 1934; Plummer and Scott 1937; Miller and Moore 1938; Miller and Downs 1950; Unklesbay 1962; Boardman et al. 1994; Mapes et al. 1997), the South Urals (Ruzhencev 1950) and Fergana (Uzbekistan) (Popov 1992).

12.4 Permian Ammonoid Biostratigraphy

The historical development and current state of Permian ammonoid biostratigraphy has been outlined and discussed in great detail by Leonova (2011), and hence the following results are largely obtained from that article (Table 12.3). Permian ammonoid biostratigraphy is a comparatively young research project and the main subdivisions have been established since the 1950s (e.g. Ruzhencev 1955; Furnish 1966, 1973; Ruzhencev 1976; Jin et al. 1994, 1997; Chuvashov et al. 2002) (Fig. 12.9).

Permian ammonoid biostratigraphy is, in terms of resolution, much coarser than those of the Devonian and Carboniferous. Leonova (2011) summarized the situation as follows: "Ammonoids characterizing these rock units usually define to which stage or substage these units belong. In contrast to the Carboniferous stratigraphic scale, for which a detailed succession of ammonoid genozones and, for some intervals, of the species zones has been developed, zonal stratigraphy is neither substantiated nor accepted for the Permian."

Table 12.3 Principal regions important for Permian ammonoid biostratigraphy with selected articles and ammonoid monographs

Arctic Canada	Nassichuk et al. 1965, Nassichuk 1970, 1977
Texas and North Mexico	Plummer and Scott 1937, Miller and Furnish 1940a, King and Miller 1944, Spinosa et al. 1975
Sicily	Gemmellaro 1887, 1888
Crimea	Toumansky 1931
Urals	Ruzhencev 1951, 1952, 1956, Bogoslovskaya 1962
Verkhoyan	Andrianov 1966, 1985
Pamirs (Tajikistan)	Toumansky 1963, Ruzhencev 1978, Leonova and Dmitriev 1989, Leven et al. 1992
South China	Zhao and Zheng 1977, Zhao et al. 1978, Liang 1981, Zhou 1987b, a, Sheng 1988
Transcaucasus	Ruzhencev 1959, 1962, 1963, Shevyrev 1965, 1968, Teichert et al. 1973, Ghaderi et al. 2014
Central Iran	Bando 1979
Timor	Haniel 1915, Smith 1927, Gerth 1950
Western Australia	Glenister and Furnish 1961

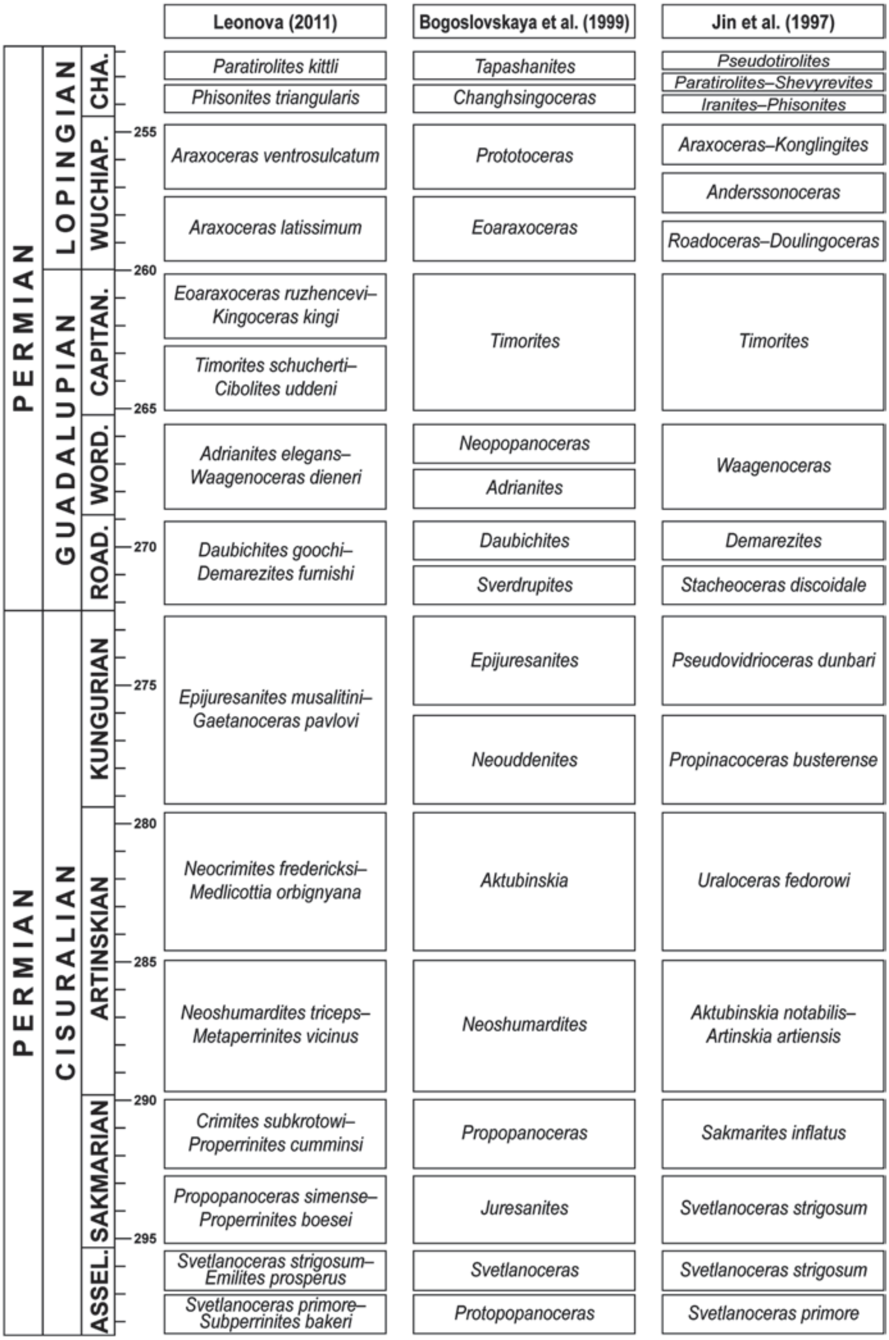


Fig. 12.9 Correlation of ammonoid zonations of the Permian, after Leonova (2011), Bogoslovskaya et al. (1999) and Jin et al. (1997)

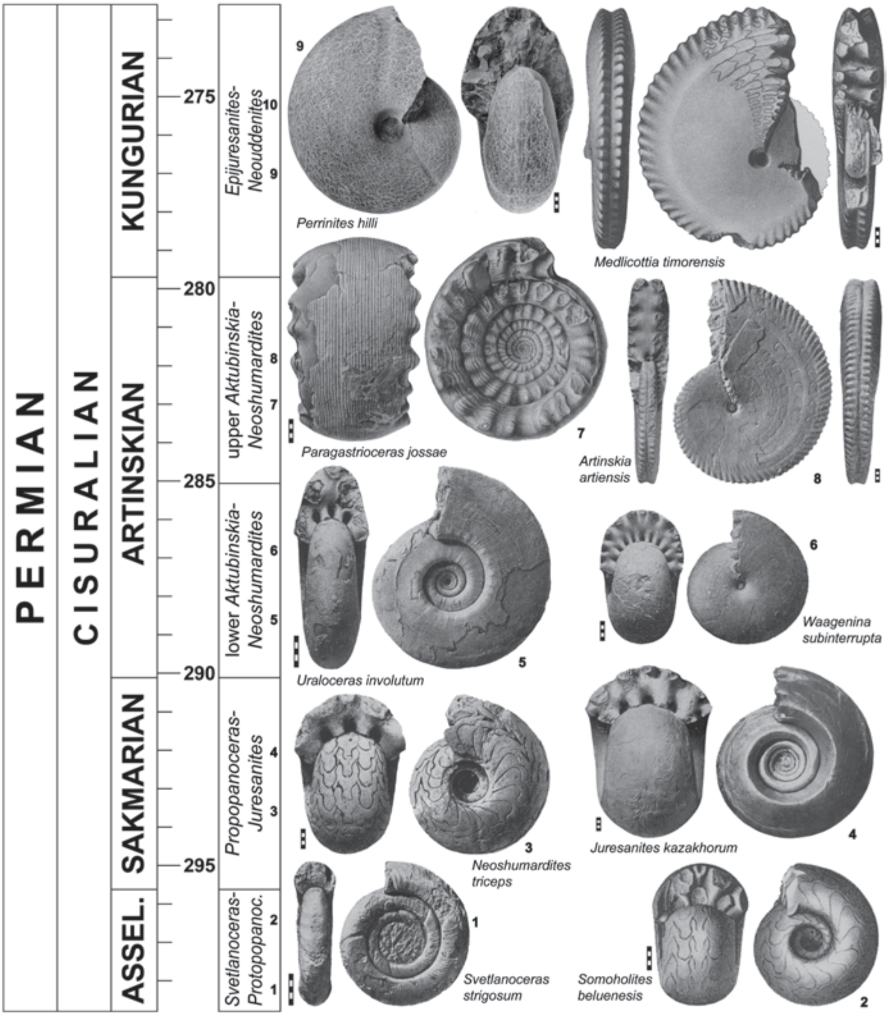


Fig. 12.10 Early Permian stratigraphy and ammonoid genus zones with representative species. Images from Haniel (1915), Miller and Furnish (1940a) and Ruzhencev (1952, 1956). Time scale from Henderson et al. (2012)

In total, only a maximum of about 20 units defined by ammonoids can be separated; a zonation for the Middle Permian (Guadalupian) stages has not been established (Figs. 12.10, 12.11). This means that the mean length of the Permian ammonoid units is about 2.5 Ma. The reason for this coarse stratigraphical resolution is not known.

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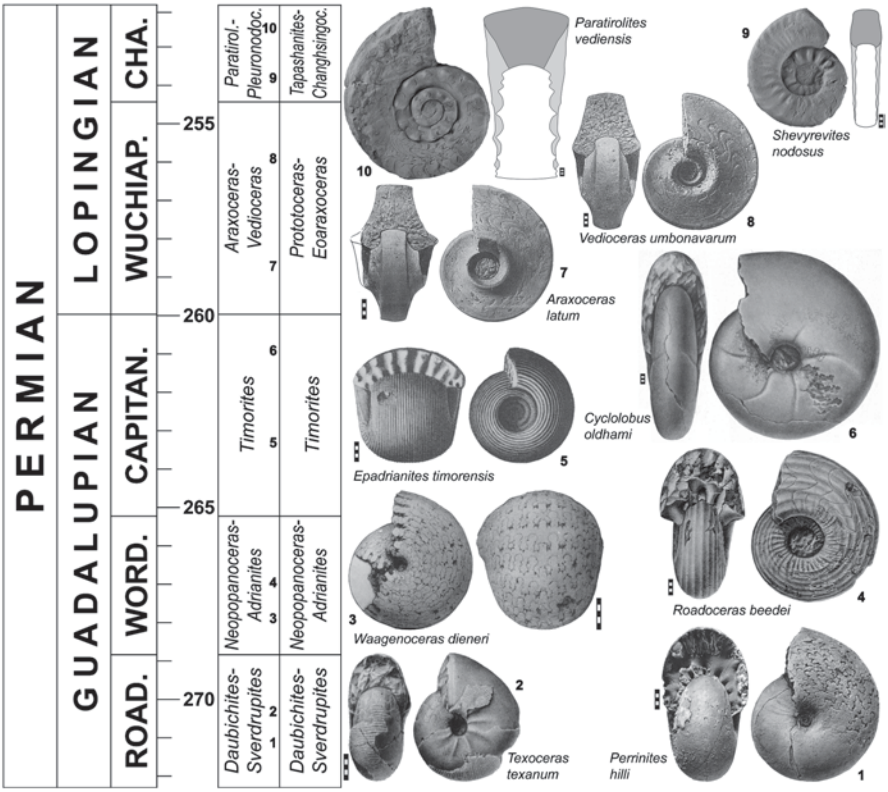

Fig. 12.11 Middle and Late Permian stratigraphy and ammonoid genus zones with representative species. Images from Waagen (1880), Haniel (1915), Miller and Furnish (1940a), Miller et al. (1957), Ruzhencev (1959, 1962) and Ghaderi et al. (2014). Time scale from Henderson et al. (2012)

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Chapter 13
Biostratigraphy of Triassic Ammonoids

James F. Jenks, Claude Monnet, Marco Balini, Arnaud Brayard and Maximiliano Meier

13.1 Introduction

During the Triassic (ca. 252.2–201.3 Ma; Gradstein et al. 2012; Cohen et al. 2013; Fig. 13.1), global biota diversified and modernized after the end-Permian mass extinction, which was the most severe biotic decimation of the Phanerozoic (Raup and Sepkoski 1982; Erwin 1993, 2006). Thus, it is a key time interval for both Earth and Life history (for a review of major biotic and abiotic events during the Triassic, see Ogg 2012). Hence, the time frame of geological and biotic events during the Triassic is critical to the interpretation of several unique and pivotal events in Earth and Life history. Ammonoids play a significant role by providing major insights in biotic evolution and recovery (Brayard et al. 2009) and correlating marine Triassic strata (Tozer 1984). The Triassic ammonoid timescale has been developed

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J. F. Jenks (✉)
1134 Johnson Ridge Lane, West Jordan, Utah 84084, USA
e-mail: Jenksjimruby@comcast.net

C. Monnet
UMR CNRS 8217 Géosystèmes, UFR des Sciences de la Terre (SN5), Université de Lille 1,
Avenue Paul Langevin, 59655 Villeneuve d'Ascq cedex, France
e-mail: claude.monnet@univ-lille1.fr

M. Balini
Dipartimento di Scienze della Terra "A. Desio", Via Mangiagalli 34, 20133 Milano, Italy
e-mail: marco.balini@unimi.it

A. Brayard
UMR CNRS 6282 Biogéosciences, Université de Bourgogne, 6 boulevard Gabriel,
21000 Dijon, France
e-mail: arnaud.brayard@u-bourgogne.fr

M. Meier
Paläontologisches Institut und Museum, Universität Zürich, Karl-Schmid Strasse 4,
8006 Zürich, Switzerland
e-mail: maximiliano.meier@uzh.ch

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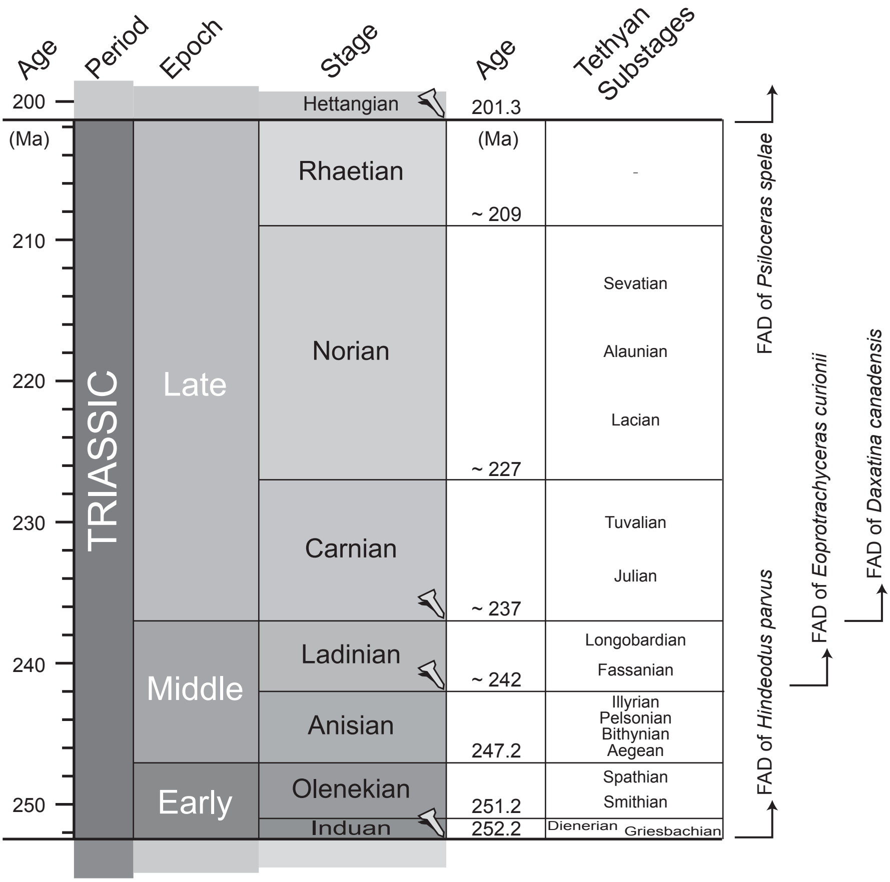

Fig. 13.1 The Triassic chronostratigraphic scale. Age calibration after Ogg (2012) with the long Rhaetian model and after Cohen et al. (2013). Stages with ratified GSSPs are indicated by the first-appearance datum (FAD) of the major correlation marker, which are ammonoids except for a conodont at the beginning of the Triassic

and refined for nearly two centuries. Knowledge regarding the Triassic has accelerated recently with numerous studies and much collaboration among geochemists, paleomagnetists, paleontologists and other stratigraphers, on both the revision of classical regions (Europe, North America) and the investigation of promising new areas (South China). This state of knowledge was reviewed recently in the book "The Triassic Timescale" (Lucas 2010a).

The Subcommission on Triassic Stratigraphy (STS; part of the IUGS International Commission on Stratigraphy) has endorsed the three long-standing series recognized by Alberti (1834) in southwestern Germany (Buntsandstein, Muschelkalk and Keuper) within the Triassic chronostratigraphic scale (Urlichs 1995). These continental and shallow-marine formations were difficult to correlate beyond Germany and therefore, most of the traditional stages (Middle to Late Triassic) were named after ammonoid-rich successions in the Northern Calcareous Alps in Austria. More than 50 different stage names have been proposed for subdivision of the Triassic (see compilation in Tozer 1984). The STS adopted seven standard stages (Visscher 1992; Fig. 13.1; Early: Induan and Olenekian; Middle: Anisian and Ladinian; and Late: Carnian, Norian and Rhaetian). These stages are sometimes subdivided into several substages of various scope; for instance, the Tethyan Realm has been subdivided into 15 substages, most of which were defined on ammonoid faunas (Fig. 13.1; Induan: Griesbachian and Dienerian; Olenekian: Smithian and Spathian; Anisian: Aegean, Bithynian, Pelsonian and Illyrian; Ladinian: Fassanian and Longobardian; Carnian: Julian and Tuvalian; Norian: Lacian, Alaunian and Sevatian). It is the responsibility of the STS to define the global stratotype section and point (GSSP) for the lower boundary of each of these stages. So far, widespread agreement among the subcommission's members has been elusive and only a few GSSP's have been chosen. The reasons for this are varied, but many issues of marine biostratigraphy are still unresolved and radio-isotopic ages are rarely well determined. Hence, much work remains to be done to refine the Triassic timescale. For instance, the major identified paths forward in development of the Triassic timescale are (STS missions as emphasized by Lucas 2010b): (i) finish formal definition of all Triassic stage and substage boundaries, (ii) improve integration of the various Triassic biostratigraphic schemes, and (iii) develop new radio-isotopic and magnetostratigraphic data, particularly for the Late Triassic. A thorough review of the state-of-the-art on the Triassic timescale has been recently published (Lucas 2010a) and the reader is referred to this book for additional details and discussion. Very recently, Lucas (2013) advocated a complete revision of Triassic subdivisions in series and stages, which are defined exclusively by ammonoid bioevents. Although promising, this scale has not been accounted for in the present study.

The distribution of fossils in marine Triassic strata represented the primary basis for construction of the Triassic timescale. In this regard, the most studied group has always been and continues to be the ammonoids, with supplementary contributions of conodonts, radiolarians, and bivalves. Indeed, as early as 1895, the Austrian geologist Edmund von Mojsisovics and his principal collaborators (Wilhelm Waagen and Carl Diener) published a detailed Triassic timescale based on ammonoids, which contained most of the stages and substages still recognized today (Mojsisovics et al. 1895). Moreover, most Triassic substages are currently recognized by ammonoid bioevents. The most important records for construction of Triassic ammonoid biozonation have been those in the Canadian Arctic Islands (especially Ellesmere and Axel Heiberg islands), British Columbia and the western American Basin (mainly Utah, Nevada, Idaho), the Germanic Basin, Western Tethys (the Alps from Italy to Turkey), Transcaucasia (Iran), Salt Range (Pakistan), Spiti (Himalayas), Tibet, South China (Guangxi and Guizhou provinces), and eastern Siberia (Fig. 13.2; for more details, see Balini et al. 2010b). Since Triassic ammonoids still play a central role in dating and correlating marine strata, this chapter reviews the Triassic biochronostratigraphic timescale based on ammonoids. It is in part an update and complement to the recent review of Balini et al. (2010b).

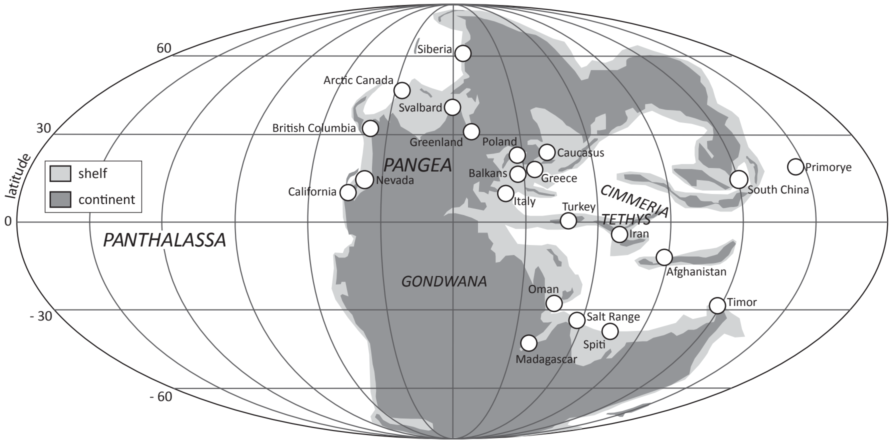

Fig. 13.2 Triassic paleogeography (modified after Blakey 2011) characterized by its unique supercontinent (Pangea), the vast Panthalassic Ocean, and the Tethys Ocean bracketed by terranes and an extension of Pangea

13.2 Historical Overview of Triassic Ammonoid Biostratigraphy

Beginning in the early nineteenth century when Alberti (1834) proposed the name Trias for a three formation succession in the Germanic basin and continuing to this day, ammonoids for the most part have provided the key component for the development of ever more precise Triassic biostratigraphic scales. Their usefulness for this purpose was first recognized in southwestern Germany as far back as the late 1700s (Lucas 2010b). Various authors have discussed the history of the development of these ammonoid-based biostratigraphic scales, beginning with Zittel (1901), Silberling and Tozer (1968) and Tozer (1984), who in particular provided a very detailed record of all contributors and their respective accomplishments. Then, Lucas (2010a) edited a comprehensive volume titled "The Triassic Timescale" that discusses all aspects of the timescale's development over the years including the contributions of ammonoids, conodonts, bivalves, radiolarians, conchostracans, tetrapods and palynology, as well as other geochronological disciplines. One section of Lucas' volume provides a historical review that emphasizes the development of the ammonoid-based biostratigraphic scale (Balini et al. 2010b). For the sake of brevity, the historical development of the Triassic biostratigraphic scheme can be summarized as occurring in three major phases as follows: (i) nineteenth century European beginning (especially Germany and Austria); (ii) development of the twentieth century North American biostratigraphic scale; and (iii) China, North Indian Margin (NIM), Russia and "modern" revision of European and North American scales. Part of the following historical overview is based on Tozer (1984), Lucas (2010b) and Balini et al. (2010b) to which the reader is referred for additional details and, thus, these works will not be subsequently repeated. This historical overview has primarily focused only on those workers whose efforts have resulted in major improvements to biostratigraphy. It is recognized that many other specialists (e.g., taxonomists, paleobiologists) have influenced biostratigraphy to varying degrees, but because of space constraints, their contributions cannot be individually acknowledged.

13.2.1 The Nineteenth Century European Biostratigraphic Scales

During the first 60 years of the nineteenth century, numerous Triassic ammonoids were documented from the Alpine regions of western Europe, namely Austria, Italy and Germany. Then, Friedrich A. von Alberti (1795–1878) proposed the term Trias for a sequence of three well-studied formations in southwestern Germany consisting of, in ascending order, the Buntsandstein, Muschelkalk and Keuper (Alberti 1834). Of these, only the Muschelkalk is of marine origin and its Middle Triassic ceratite ammonoid record is well known. In fact, it is this particular record that greatly facilitated the extension of Alberti's Trias from its type section southward into marine strata of the Austrian and Italian Alps, resulting in recognition of the "Alpine Muschelkalk" (Rassmus 1915; Hagdorn et al. 1998). During the latter half of the nineteenth century, Triassic aged rocks came to be recognized in other European countries as well as many worldwide areas, including the United States, Russia, India and Japan.

Perhaps one of the most important contributions to the development of the Triassic ammonoid biostratigraphic scale is that of Edmund von Mojsisovics (1839–1907), an Austrian paleontologist employed at the Geological Survey of Austria. During his 40 year career in the latter half of the nineteenth century, he came to be recognized as the world authority for Triassic ammonoids. He not only studied new collections sent to him from various worldwide locations, but he also made extensive collections of his own from various locations throughout the Alps. His work over the years included many landmark publications (Mojsisovics 1869, 1873, 1874, 1882a, 1886, 1888a, b, 1893, 1896, 1902), but one of the best known is his "Die Cephalopoden der Mediterranen Triasprovinz" (1882b). Although the beautifully hand-drawn ammonoid illustrations in this work are most impressive, his most important contribution is his careful documentation of various ammonoid zones based on faunas recognized from several facies and localities. Two of his colleagues, Carl Diener (1862–1928) and Wilhelm H. Waagen (1841–1900), are equally famous for their taxonomic and biostratigraphic work with ammonoids from the Early and Middle Triassic of the Himalayas (India) and the Early Triassic of the Salt Range (Pakistan), respectively (Diener 1895, 1897, 1907; Waagen 1895). Diener is also well known for his work with Alpine Middle and Late Triassic ammonoids (Diener 1906, 1907, 1908a, b, 1912, 1913, 1915, 1920a, b, c, 1921, 1923, 1926). Mojsisovics' collaboration with Diener and Waagen (Mojsisovics et al. 1895) resulted in an integrated succession of ammonoid zones for these three areas upon which a system of substages, stages and series was based. This work represented the first chronostratigraphic scale for the Triassic System and it had broad influence over the development of Triassic stratigraphy for much of the twentieth century. Even though a few of the ammonoid zones were later shown to be in the wrong order because of condensed facies, the overall contribution of their work to ammonoid biostratigraphy was far beyond its time. Indeed, many of its stage and substage names are still commonly used today. The nineteenth century is also marked by Philippi (1901) and Riedel (1916), who established the endemic ceratite chronocline-based biozonation of the Muschelkalk (Middle Triassic), which shows an excellent resolution. Finally, another central figure of this period was Franz Ritter von Hauer (1822–1899), who was very active in research on the Alpine Triassic. He described many of the ammonoids that would eventually become the index fossils of Triassic zones (Hauer 1865, 1887, 1892, 1896). In particular, he correlated the Hallstatt Limestone of the Northern Alps with the Cassian Formation of the Dolomite Mountains, thus providing firm grounds for correlation within the Alpine belt (Hauer 1850). He is also credited with being the first worker to recognize the large facies differences in the Triassic.

With regard to ammonoid biostratigraphy and taxonomy, the first half of the twentieth century is marked by Leonard F. Spath (1888–1957), a British Museum paleontologist. He is known for his subdivision of the Triassic System into a succession of ages of substage rank, each of which is named after an ammonoid whose chronological range represents that particular age (Spath 1934). At first glance, it does not appear that Spath emphasizes stratigraphy in his biochronological scale, but a closer examination of his work reveals that he did assign ammonoid zones to each of his ages and included specific ammonoid-containing beds from other localities that he considered to be “age equivalent”. Even though Spath never worked in the field, his biochronological scale based on museum collections continued to exert a wide influence on many workers for about 35 years (Tozer 1984).

13.2.2 The Twentieth Century North American Biostratigraphic Scales

In contrast with the European record, Triassic strata of marine origin were not discovered in North America until the late nineteenth century when Charles A. White (1826–1910) described new ammonoids collected in southeastern Idaho (USA) by one of the Territorial Surveys and recognized their age as Early Triassic (White 1879; Jenks et al. 2013). The following 50-year period saw numerous other discoveries of marine Triassic rocks in western USA (Idaho, Utah, Nevada and California) as well as Canada (British Columbia). Ammonoids from these discoveries, which included material from the Early, Middle and Late Triassic, were first monographed by Alpheus Hyatt (1838–1902) and James Perrin Smith (1864–1931) in a now classic work titled “The Triassic cephalopod genera of America” (Hyatt and Smith 1905). Smith then followed this work with ammonoid monographs for each of the three Triassic series (Smith 1914, 1927, 1932). Hyatt and Smith (op. cit.), and Smith (op. cit.) in particular, grouped their various ammonoid faunas into zones and attempted to correlate them with those reported by Mojsisovics et al. (1895) with varying degrees of success, thus illustrating Mojsisovics' influence on their work.

Over the next 30 year period, two geologists, one an American, Stanford University professor Siemon W. Muller (1900–1970) working in Nevada and the other, a Canadian, Frank H. McLearn (1885–1964) working in British Columbia, made significant contributions to Triassic ammonoid biostratigraphy. Muller worked out most of the enormously complex Mesozoic geology of western Nevada and unraveled much of the ammonoid succession for the Early, Middle and Late Triassic (Muller and Ferguson 1936, 1939, 1951), while McLearn accomplished much the same thing for the equally complex Triassic geology of the American Cordillera in northeastern British Columbia and its ammonoid succession (McLearn 1945, 1947a, b, 1960, 1969).

Then, in the mid-1950s, Edward T. Tozer (1928–2010), a geologist with the Canadian Geological Survey began exploring and mapping the geology of the Queen Elizabeth Islands in the Canadian Arctic. This work continued for many years and he eventually began dividing his time between the Arctic islands and northeastern British Columbia (Frisch 2011). During these years, he developed an ever increasing intense interest in Triassic ammonoids and their biostratigraphy as evidenced by a lengthy list of publications (Tozer 1961a, b; 1963a, b; 1965a, b) dealing with ammonoids of Early Triassic age from the Arctic islands and Middle and Late Triassic age from British Columbia. Then, Tozer (1967) published a detailed biochronological ammonoid-based timescale for the Arctic islands and British Columbia containing 31 ammonoid zones, each represented by a particular type area. This timescale was unique in that he abandoned the use of the Scythian Stage that formerly represented the entire Early Triassic and replaced it with four stages, each of which was (i) named for a former renowned Triassic ammonoid worker and (ii) represented by a particular type area in the Canadian Arctic.

More or less concurrent with Tozer's career in Canada is that of Norman J. Silberling (1928–2011), an American geologist affiliated first with Stanford University and then the United States Geological Survey. Silberling spent much of his career working on the Triassic geology and ammonoids of the American west (Silberling 1956, 1959, 1961, 1962; Silberling and Wallace 1969; Nichols and Silberling 1977; Silberling and Nichols 1982). Indeed, his meticulous bed by bed sampling approach and modern taxonomic treatment of ammonoid faunas accomplished for the marine Triassic of this region much of what Tozer did for the Canadian Triassic. Silberling and Tozer collaborated for much of the mid to late 1960s and this cooperation culminated in the now classic 1968 work titled "Biostratigraphic classification of the Marine Triassic in North America", a timescale whose stage boundaries are based entirely on North American ammonoid localities (Silberling and Tozer 1968). Both Silberling and Tozer acknowledged the pioneering contributions to this timescale made by S.W. Muller and F.H. McLearn some 35 years earlier.

13.2.3 The Twenty first Century and Modern Revision of Biostratigraphic Scales

The relatively recent approach that tends toward global correlation and integrated biostratigraphy is well exemplified by the designation of GSSPs. Indeed, the designation of a GSSP emphasizes the reproducible correlation of events (e.g., various fossil groups, magnetostratigraphy, or isotope analysis) by cross-comparison with various candidate sections (GSSP's thus far chosen: Permian/Triassic boundary, Yin et al. 2001; Anisian/Ladinian boundary, Brack et al. 2005; Ladinian/Carnian boundary, Mietto et al. 2012; Triassic/Jurassic boundary, Hillebrandt et al. 2013). In this context, the role of ammonoid biostratigraphy for the definition of Triassic stages and substages has thus been confirmed and even enhanced. A comparison of ammonoid biostratigraphy with conodont, radiolarian, bivalve, and palynomorph biostratigraphies demonstrates without doubt that ammonoids are the taxonomic group with the highest power of temporal resolution within Triassic marine environments.

13.2.3.1 South China and the North Indian Margin

The South China and North Indian Margin (NIM: Spiti, Tibet, Salt Range) areas are characterized by the pioneering work of Diener (1897) and Waagen (1895), in particular on Early Triassic stratigraphy and ammonoid faunas in the Himalayas and Salt Range of present-day Pakistan, respectively. These studies were highly significant for their day and are still widely quoted, nearly 120 years later, for example Waagen's lithostratigraphic subdivisions in the Salt Range (e.g., Brühwiler et al. 2011, 2012c). Following the work of Waagen and Diener, the next 100 + year period saw comparatively few contributions of biostratigraphic significance in the South China—NIM area. Perhaps not as well-known but still significant are the works of Hsu (1937, 1940, 1943) and Chao (1950, 1959) on the Early Triassic ammonoid faunas of South China, Wang and He (1976) on the Triassic of southern Tibet, and Wang (1983) on the Ladinian–Carnian of Guizhou. Hsu was the first to discover Early Triassic ammonoids from Guizhou, but Chao was the first to document abundant ammonoid faunas from Guangxi and directly integrate his work with a robust biostratigraphic scheme, i.e. the subdivisions of Spath (1934). The significance of Hsu and Chao's work becomes all the more remarkable when one considers that horses were their only mode of transportation in the field. Wang and He (1976) described a large collection of Early to Late Triassic ammonoids collected during the 1960s Chinese expedition to the Mt Jolmo Lungma (Mt Everest) area. This was the first comprehensive report of Triassic ammonoids from the Himalayas, since the time of Diener's monographs, more than 50 years earlier. Then, a few years later Wang (1983) described some peculiar Ladinian to Early Carnian faunas that were quite different from those of the Tethyan Realm. In addition, Guex (1978) published a well-documented description of a relatively small Dienerian, Smithian and Spathian ammonoid fauna from the Salt Range and proposed an alternative three stage subdivision of the Early Triassic.

Then, beginning in 2003 an extensive research project was initiated by H. Bucher to intensively sample marine Lower Triassic successions in South China and several NIM localities and to subject their respective ammonoid faunas to a modern taxonomic treatment with the ultimate goal of achieving much broader biochronological correlation. In South China, sampling of the Luolou Formation (northwestern Guangxi) in addition to new sampling in the Daye (southern Guizhou) Formation has resulted in the recognition of a significant regional Griesbachian and Dienerian ammonoid succession (Brühwiler et al. 2008). This sequence contains certain widely occurring taxa that facilitate correlation with other areas (British Columbia, Arctic Canada, Himalayas and South Primorye). Extensive sampling field work in the Luolou Formation at several localities in northwestern Guangxi resulted in the recognition of several new Smithian-aged ammonoid faunas and the erection of a new Smithian biostratigraphic zonation for the paleoequatorial region (Brayard and Bucher 2008). These new faunas significantly expanded the scope of the Smithian and the new zonal scheme facilitates correlation with other mid and high paleolatitudinal successions. Also in South China, several Anisian ammonoid faunas have been described (Stiller and Bucher 2008) that can be correlated with those of the Southern Alps.

In the Salt Range, a very thorough sampling of Waagen's lithographic subdivisions at several localities produced abundant, well-preserved ammonoid faunas that were utilized to create an even higher resolution biostratigraphic zonation for the entire Smithian that can be readily correlated with many other Tethyan localities (Brühwiler et al. 2012c). In the Spiti area (northern India), the work of Brühwiler et al. (2010c, 2012b) in the "*Parahedenstroemia*" beds at several localities in the Mikin Formation has resulted in the documentation of an additional high resolution biostratigraphic scheme spanning the middle to late Smithian. Additional sampling in the Spiti area has documented the existence of new ammonoid faunas in the Dienerian/Smithian boundary beds at Mud, the Induan/Olenekian GSSP candidate site (Brühwiler et al. 2010c). These faunas provide an enhanced biostratigraphic resolution in the beds below the proposed GSSP level. Finally, intensive sampling of the Lower Triassic Tulong Formation in South Tibet by Brühwiler et al. (2010b) has revealed the existence of yet another correlative biostratigraphic sequence of ammonoid faunas spanning the middle and late Smithian.

13.2.3.2 Russia

Very little was known of Russian Triassic ammonoid faunas until the latter half of the twentieth century other than for a few obscure reports by European workers regarding collections sent to them for study (e.g., description of a fauna from the lower reaches of the Olenek River; Mojsisovics 1888b). Then, pioneer Russian Triassic ammonoid workers L.D. Kiparisova (1905–1978) and Y.N. Popov (1894–1979) introduced the now-familiar two-stage subdivision (Induan and Olenekian) for the Early Triassic, which eventually was formally accepted by the STS in 1991

(Kiparisova and Popov 1956; Visscher 1992). Since that time numerous workers have made notable contributions to the taxonomy and biostratigraphy of Russian Triassic ammonoids (e.g., Popov 1961a, 1961b; Kiparisova 1961, 1972; Kiparisova et al. 1966; Shevyrev 1968, 1986, 1995; Zakharov 1968, 1978; Ermakova 1981, 1988, 2002a, b; Konstantinov 1995, 1999, 2000; Dagys and Konstantinov 1997; Konstantinov and Sobolev 2000a, b; Zakharov et al. 2004a, b), but the career of A.S. Dagys (1932–2000) stands out above all others. Dagys focused on Triassic brachiopods early in his career and quickly became an acknowledged world authority (Dagys 1963, 1965, 1974). Then, his interests shifted to the Early and Middle Triassic ammonoids of northeastern Siberia, and his work on these faunas (Dagys et al. 1979; Dagys and Ermakova 1981, 1988, 1990, 1996; Dagys 1998, 2001) again earned him worldwide recognition. His collaboration over the years with W. Weitschat and E.T. Tozer culminated in highly precise Boreal realm correlation charts for Siberia, Arctic Canada and Svalbard (Dagys and Tozer 1989; Weitschat and Dagys 1989; Dagys and Weitschat 1993).

The past ten years are characterized by Shigeta and Zakharov's work in South Primorye and by Konstantinov's efforts in northern Siberia. Shigeta et al. (2009) reported the existence of diverse, well-preserved Griesbachian, Dienerian and Smithian ammonoid faunas from the Abrek Bay area, South Primorye. Many taxa are endemic, but a few widely occurring taxa present in the sequence enable an approximate correlation with other Tethyan localities. Work by Konstantinov and colleagues on the Triassic in northern Siberia has significantly refined the zonation of Ladinian to Early Norian ammonoid faunas and improved their correlation with those of North America (Konstantinov et al. 2003; Konstantinov and Sobolev 2004; Konstantinov 2006, 2008b; Konstantinov and Klets 2009).

13.2.3.3 Modern Revision of North American Timescales

Over the years, Tozer continued to update his 1967 Canadian biostratigraphic scale; this work culminated in his monographic treatment of all Canadian Triassic ammonoid taxa and included a refined timescale based on 37 ammonoid zones (Tozer 1994). Triassic ammonoid biostratigraphy in the American west has been refined more or less continuously over the past 25 years. Much of this work has focused on the Middle Triassic, but significant improvements have been made in the Early and Late Triassic as well.

With regard to the Early Triassic, Ware et al. (2011b) recently described a long known but never illustrated ammonoid fauna of Early Dienerian age from the old Candelaria mining district in Nevada. Extensive work by Brayard in west-central, southern and southeastern Utah over the past 5 years has revealed for the first time in the American west, the existence of a much expanded Smithian ammonoid succession that includes early Smithian forms (Brayard et al. 2013). This new biostratigraphic succession results in a sequence with much higher resolution that can be correlated not only with other Utah sites, but with other major worldwide localities as well. Many years of sampling various Spathian ammonoid sites in Idaho, Utah, Nevada and California have enabled Guex et al. (2005a, b, 2010) to document a new, very precise Spathian biochronological ammonoid zonation for the American west consisting of 23 ammonoid horizons. This work provides a zonation with much higher resolution than known anywhere else in the world for the Spathian (Guex et al. 2010; Jenks et al. 2013).

As for the Middle Triassic, Bucher (1988, 1989, 1992a, b) thoroughly reviewed the ammonoid faunas of the Anisian at several localities in northwestern Nevada. This work produced a new, high resolution biostratigraphic scale for the early and middle Anisian with the revision of previous biozones and the erection of several new ones, most of which have significant potential for correlation with other basins. A noteworthy contribution to the Anisian ammonoid biostratigraphy of Nevada is the monographic description of new ammonoid faunas bracketing the middle/late Anisian boundary (Monnet and Bucher 2005a). This work expands the uppermost range of the middle Anisian *shoshonensis* Zone and it adds two new zones to the base of the late Anisian. These new faunas are of importance for low paleolatitudinal correlation from the eastern Panthalassa to the western Tethys (Monnet and Bucher 2005a, b; Monnet et al. 2008).

With regard to the Late Triassic, extensive sampling efforts at South Canyon (New Pass Range, central Nevada) resulted in the description and revision of ammonoid taxonomy and biostratigraphy bracketing the Ladinian/Carnian boundary (Balini and Jenks 2007; Balini et al. 2007; Balini 2008; Balini et al. 2012a). Briefly, this work has revealed that the trachyceratid-like ammonoids in the lowermost beds (formerly assigned to *T. desatoyense*) actually belong to the genus *Daxatina*, whereas true *Trachyceras* s.s. occurs only in the upper beds, thus modifying previous biostratigraphic schemes (Balini et al. 2012a). In addition, an integrated bed by bed study of the latest Carnian/earliest Norian transition within the Luning Formation is currently underway in Nevada's Berlin Ichthyosaur State Park (Balini et al. 2014). Although the rich ammonoid faunas within this interval were described by Silberling (1959), recent studies have also documented never before reported rich conodont faunas as well as numerous occurrences of *Halobia* in these transition beds. These occurrences, together with the rich ammonoid record, permit correlation of the succession with those of British Columbia and hopefully, will contribute to the definition of the GSSP for the Norian stage.

13.2.3.4 Modern Revision of European Timescales

The revision of European Triassic ammonoid biostratigraphic scales has more or less kept pace with that in North America and numerous workers have made significant contributions. In addition to the well-known work of Riccardo Assereto (1937–1976) on classical Italian Anisian localities, he is perhaps best remembered for his deciphering of Anisian biostratigraphy on the Kokaeli Peninsula, Turkey and his work on the Greek island of Chios (Assereto 1969, 1971, 1974; Assereto et al. 1980), both of which eventually lead him to propose a four-fold subdivision of the Anisian (Aegean, Bithynian, Pelsonian, and Illyrian). Hans Rieber is best known for his extensive work in the Anisian–Ladinian interval in the Southern Alps that culminated in a very accurate, high resolution ammonoid biostratigraphic scale with wide correlation potential (Brack and Rieber 1986, 1993). Rieber's work also proved instrumental for the eventual selection of the FAD of *Eoprotrachyceras curionii* as the key marker for the GSSP of the Ladinian Stage (Brack et al. 2005). Extensive fieldwork by Marco Balini in the Southern Alps not only has resulted in the description of numerous new Anisian to early Carnian ammonoid taxa (Balini 1993, 1994, 1998; Balini et al. 2006), but most importantly, his careful analysis of the ammonoid faunas in the Prezzo Limestone has led to a significantly refined ammonoid taxonomy for the various taxa within the *Paraceratites trinodosus* Zone (Balini 1992a, b). Paolo Mietto is primarily known for his extensive work on Anisian, Ladinian and Carnian ammonoid biostratigraphy of the Southern Alps and his efforts proved influential in the selection of *Daxatina canadensis* as the key marker for the GSSP of the Carnian Stage at the Prati di Stuores/ Stuores Wiesen section in northeastern Italy (Mietto and Manfrin 1995a, b; Mietto et al. 2008, 2012). Attila Vörös' work on ammonoids of the Anisian–Ladinian interval in the Balaton Highland, Hungary (Vörös 1987, 1998, 2002, 2003, 2010; Vörös and Pálfy 1989) also resulted in a well-defined regional biostratigraphic scale. Work by Claude Monnet et al. (Monnet et al. 2008) in eastern Lombardy–Guidicarie (Italy) has clarified the middle/late Anisian boundary and demonstrated the worldwide correlation potential of this region. The meticulous work of Leopold Krystyn on the condensed facies in the Northern Alps (Sommeraukogel and Feuerkogel sections) has contributed significantly towards resolving the complex Carnian–Norian ammonoid biostratigraphic problems associated with these former sections of Mojsisovics (Krystyn and Schlager 1971; Krystyn et al. 1971; Krystyn 1973, 1978, 1980). Krystyn's data from the Northern Alps have recently been integrated with new bed by bed collected data from the Carnian/Norian succession at Pizzo Mondello (western Sicily), resulting in taxonomic descriptions for key taxa and refined biostratigraphy across the Carnian/Norian boundary (Balini et al. 2012b). Finally, the biostratigraphy of the endemic ceratite-based Upper Muschelkalk (Middle Triassic) in Germany has also been refined with the establishment of 14 biozones (Urlichs 1993; Hagdorn 2004).

13.3 Early Triassic Ammonoid Zonation

Several stage and substage names have been successively applied to the Early Triassic. For instance, the Lower Triassic series is coeval with the Scythian stage, which today is not included in the official timescales, but can be found in older literature and sporadically in some modern works, even if not widely accepted (Kozur 1993). In 1991, the STS adopted the two-fold standard subdivision with a lower Induan stage and an upper Olenekian stage (Visscher 1992). The Induan and Olenekian stages of Kiparisova and Popov (1956, 1964) were named after exposures in the

Indus river basin in the Hindustan region of Asia, and in the lower reaches of the Olenek river basin of northeast Siberia, respectively.

Most noteworthy, a suite of four substages, namely the Griesbachian, Dienerian, Smithian and Spathian, which were originally defined by ammonoid zones, is also widely used. These were established for exposures on Ellesmere and Axel Heiberg islands in the Canadian Arctic, which in turn were named (Tozer 1965a, 1967) after the Triassic paleontologists Carl L. Griesbach (1847–1907), Carl Diener (1862–1928), James P. Smith (1864–1931) and Leon Spath (1888–1957).

Recent radio-isotopic ages from South China (Ovtcharova et al. 2006; Galfetti et al. 2007a) indicate that these substages are of very uneven duration. Indeed, the Spathian (ca. 2.4 ± 0.7 Myr) accounts for about half of the duration of the Early Triassic, whereas intervals for the Griesbachian–Dienerian and Smithian have been estimated at 1.4 ± 0.4 Myr and 0.7 ± 0.6 Myr, respectively. These ages imply an average ammonoid biochronozone of about 0.17 Myr at most for each zone level shown in Figs. 13.5, 13.9, and 13.10 (0.20 Myr for the Induan, 0.06 Myr for the Smithian, and 0.30 Myr for the Spathian).

13.3.1 Induan

Substage divisions of the Early Triassic (Griesbachian, Dienerian, Smithian, and Spathian) have long been based on a succession of ammonoid bioevents. The base of the Griesbachian is marked by the FAD (First Appearance Datum) of *Otoceras*, an ammonoid genus found in both Tethyan and Boreal ammonoid assemblages (Tozer 1965a; Kummel 1972; Zakharov 2002). This FAD of *Otoceras* has traditionally been considered to be the base of the Triassic (Griesbach 1880; Mojsisovics et al. 1895; Tozer 1986, 2003; Dagys and Ermakova 1996). However, more recently, the base of the Induan has been formally defined by the IUGS as the FAD of the conodont *Hindeodus parvus* at the Meishan section in southern China (Yin et al. 2001), which is a section having only scarce and poorly preserved ammonoids (Yin et al. 1996). This definition places the FAD of *Otoceras* in the latest Permian (Kozur 1993; Orchard and Tozer 1997a, b; Yin et al. 2001), a choice not widely accepted by Triassic workers (e.g., Tozer 2003; Shevyrev 2006) since it violates a very long held consensus. Hence, the base of the Triassic is now placed within the classical Griesbachian, close to the FAD of *Ophiceras*, which marks a significant ammonoid event at the base of the late Griesbachian (appearance of abundant ophiceratids). Therefore, the Induan is now equivalent to the late Griesbachian and Dienerian, while the early Griesbachian is roughly of Permian age (Baud 2001; Baud and Beauchamp 2001). The base of the Dienerian substage is marked by the appearance of abundant meekoceratids, gyronitids and proptychitids, a globally recognizable event (e.g., Tozer 1974; Shevyrev 2001; Brühwiler et al. 2008; Ware et al. 2011b).

The Induan is characterized by the diversification and recovery of ammonoids after the Permian/Triassic boundary mass extinction. The group nearly went extinct at this boundary with only very few genera that survived this extinction. Episageceratidae, the youngest representatives of Prolecanitida, is among the few Permian clades that crossed the Permian/Triassic boundary (Glenister and Furnish 1980; Tozer 1980; Zakharov and Moussavi Abnavi 2013). Xenodiscaceae and Otocerataceae, both Ceratitida, also crossed the boundary. It is commonly agreed that Xenodiscidae represent the rootstock of all Triassic Ceratitida (e.g., Kummel 1973a, b; Spinosa et al. 1975; Tozer 1980), with the exclusion of Otoceratidae and possibly of Sagecerataceae. The lineage of Otocerataceae also survived this extinction event (e.g., *Proharpoceras*), but it dwindled away for some 2 Myr before going extinct (Brayard et al. 2007a). Recent biodiversity studies (Brayard et al. 2009) demonstrated that ammonoids recovered rapidly in the Early Triassic and even reached higher levels of taxonomic richness compared to the Permian only 1 to 2 Myr after the Permian/Triassic boundary (see Brayard and Bucher 2015). Some characteristic ammonoids of the Griesbachian and of the Dienerian are illustrated in Figs. 13.3 and 13.4.

Induan ammonoid zonal schemes (Fig. 13.5) are relatively rare, thus reflecting the scarcity of the ammonoid record at that time. Indeed, despite the extensive history of research on the Permian/Triassic boundary, relatively little is known about Griesbachian and especially Dienerian ammonoids. Well-preserved Induan material has only been reported from a few areas, namely Canada (Tozer 1965a, 1967, 1994), the Salt Range in Pakistan (Waagen 1895; Ware et al. 2011a, ongoing work) and Spiti in the Himalayas (Diener 1897; Krafft and Diener 1909; Krystyn et al. 2004, 2007a; Brühwiler et al. 2010c), and more recently South China (Tong et al. 2004; Brühwiler et al. 2008; Mu et al. 2007). Schemes have also been proposed for South Primorye (Zakharov 1997; Shigeta et al. 2009), Nepal (Kummel 1970; Waterhouse 1996), and Siberia (Dagys 1994; Dagys and Ermakova 1996), as well as East Greenland (Trümpy 1969; Bjerager et al. 2006). Isolated faunas have also been described from Japan (Bando 1970) and Nevada (Ware et al. 2011b). Correlation of these biostratigraphic schemes is sometimes hampered by poor ammonoid preservation and conflicting taxonomic interpretations. Induan ammonoid faunas and their respective correlation remain poorly understood, but current ongoing work will probably result in a much more refined ammonoid record for this stage. Finally, correlation and definition of ammonoid zones at the Permian/Triassic boundary remain under debate and must be revised by means of new data (see Shevyrev 2006).

13.3.2 Olenekian

There is a broad agreement that the Olenekian is equivalent to the Smithian and Spathian, which are ammonoid-based substages, but the base of the Olenekian stage has not yet been formally designated. Interest in the Dienerian/Smithian (Induan/Olenekian) boundary is relatively recent, and several sections from China, the Himalayas and South Primorye have been proposed as GSSP candidates (Zakharov et al. 2002; Tong et al. 2003, 2004; Krystyn et al. 2007a; Brühwiler et al. 2010c). Agreement on this GSSP remains elusive and is still the subject of a lengthy debate (Zakharov 1994; Dagys and Sobolev 1995; Shevyrev 2002, 2006; Chinese Triassic Working Group 2007; Krystyn et al. 2007b), but it most likely will eventually be resolved by the

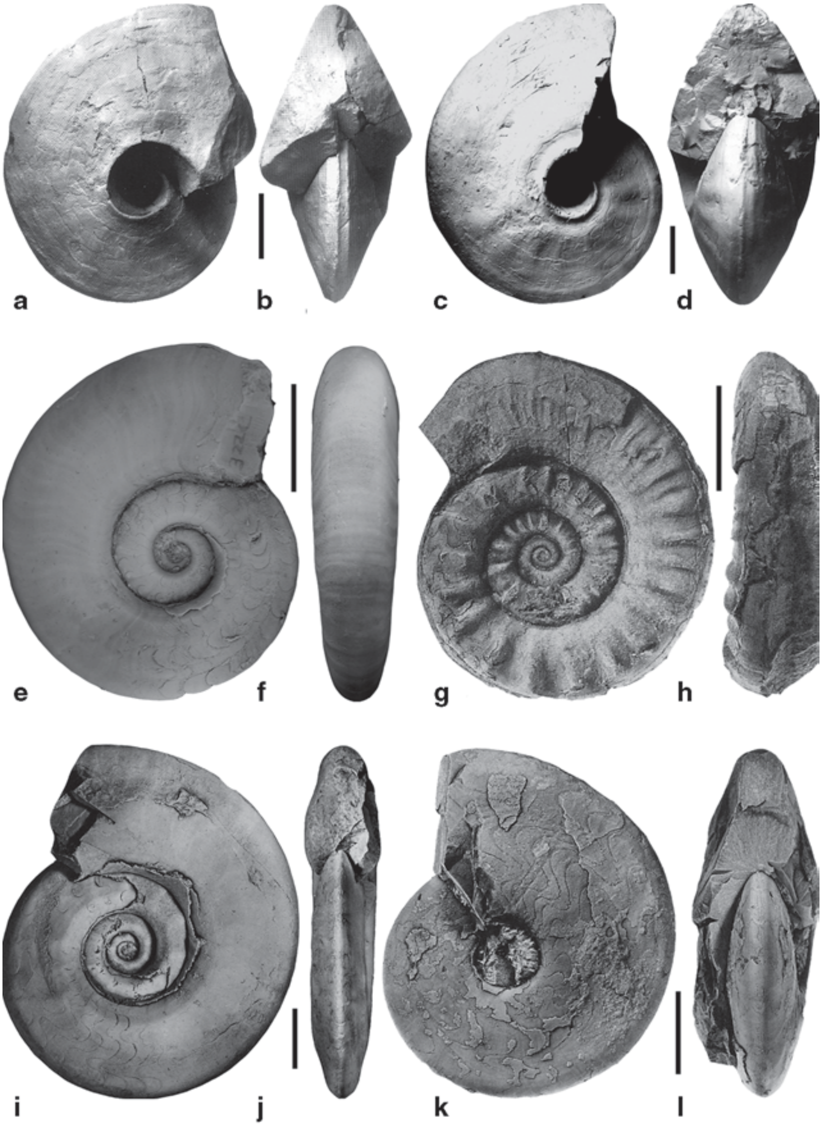

Fig. 13.3 Some characteristic ammonoids of the Griesbachian (Early Triassic). **a**, **b**, *Otoceras concavum* Tozer 1967, YIG 921/165 (after Dagys and Ermakova 1996, pl. 2, Figs. 4a, b). **c**, **d**, *Otoceras boreale* Spath, 1935, YIG 921/171 (after Dagys and Ermakova 1996, pl. 5, Figs. 1a, b). **e**, **f**, *Ophiceras commune* Spath 1930, JJ322C (coll. JF Jenks). **g**, **h**, *Tompophiceras extremum* (Spath 1935), GSC 28040, hypotype (after Tozer 1994, pl. 3, Figs. 4a, b). **i**, **j**, *Wordieoceras wordiei* (Spath 1930), GSC 28060, hypotype (after Tozer 1994, pl. 5, Figs. 3a, b). **k**, **l**, *Bukkenites strigatus* (Tozer 1961a), GSC 28079, hypotype (after Tozer 1994, pl. 8, Figs. 2a, b). Scale bars = 2 cm. **a–d** from Arctic Siberia, **e–f** from northeastern Greenland, **g–l** from Arctic Canada

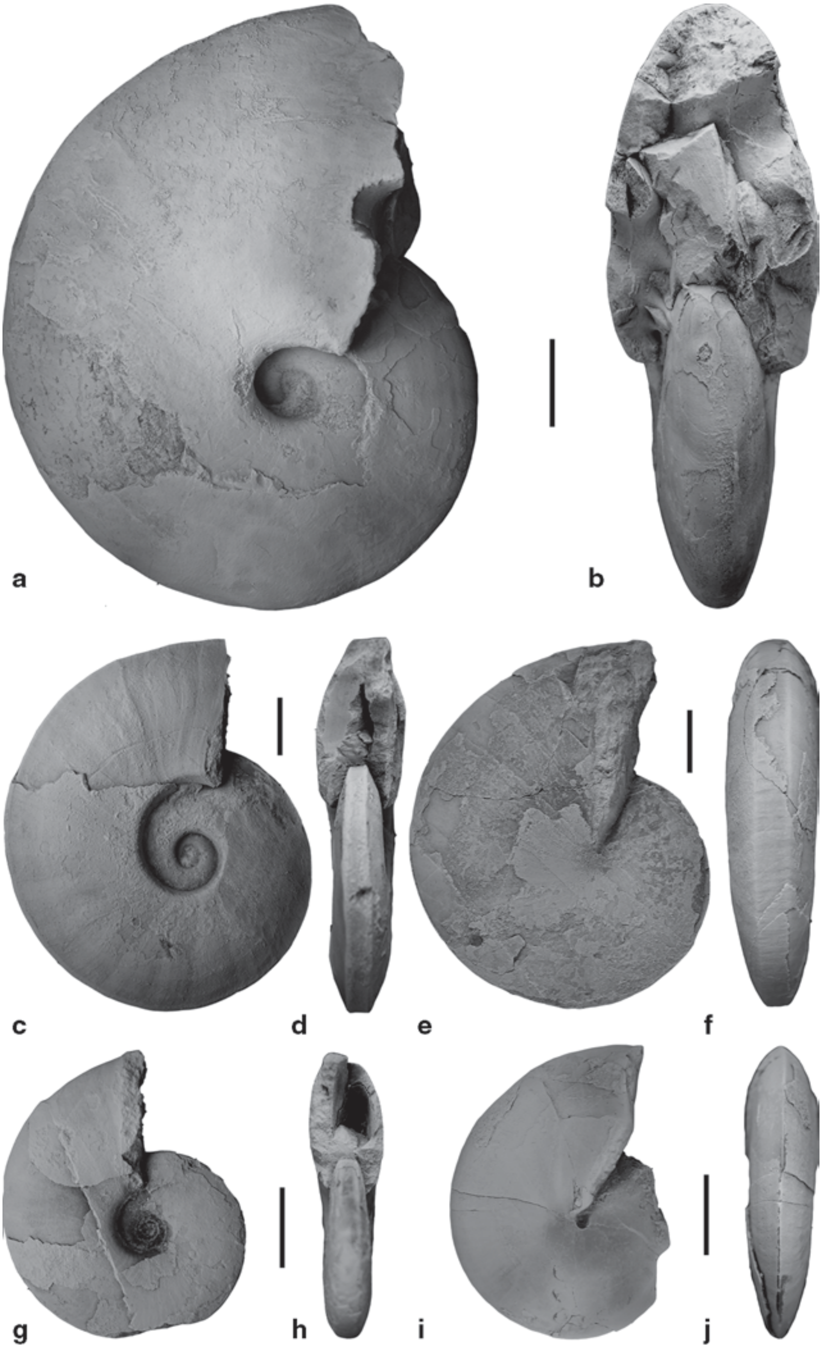

Fig. 13.4 Some characteristic ammonoids of the Dienerian (Early Triassic). **a**, **b**, *Proptychites haydeni* (Krafft and Diener 1909), USNM542461 (after Ware et al. 2011b, Fig. 15:1a–c). **c**, **d**, *Ambites lilangensis* (Krafft and Diener 1909), USNM542474 (after Ware et al. 2011b, Fig. 4:2a–c). **e**, **f**, *Mullericeras spitiense* (Krafft and Diener 1909), JJ2223C (coll. JF Jenks). **g**, **h**, "*Koninckites*" aff. *kraffti* Spath 1934, JJ2031C (coll. JF Jenks). **i**, **j**, *Parahedenstroemia kiparisovae* Shigeta and Zakharov 2009, JJ2164C (coll. JF Jenks). Scale bars = 1 cm. All from Candelaria Hills, Nevada

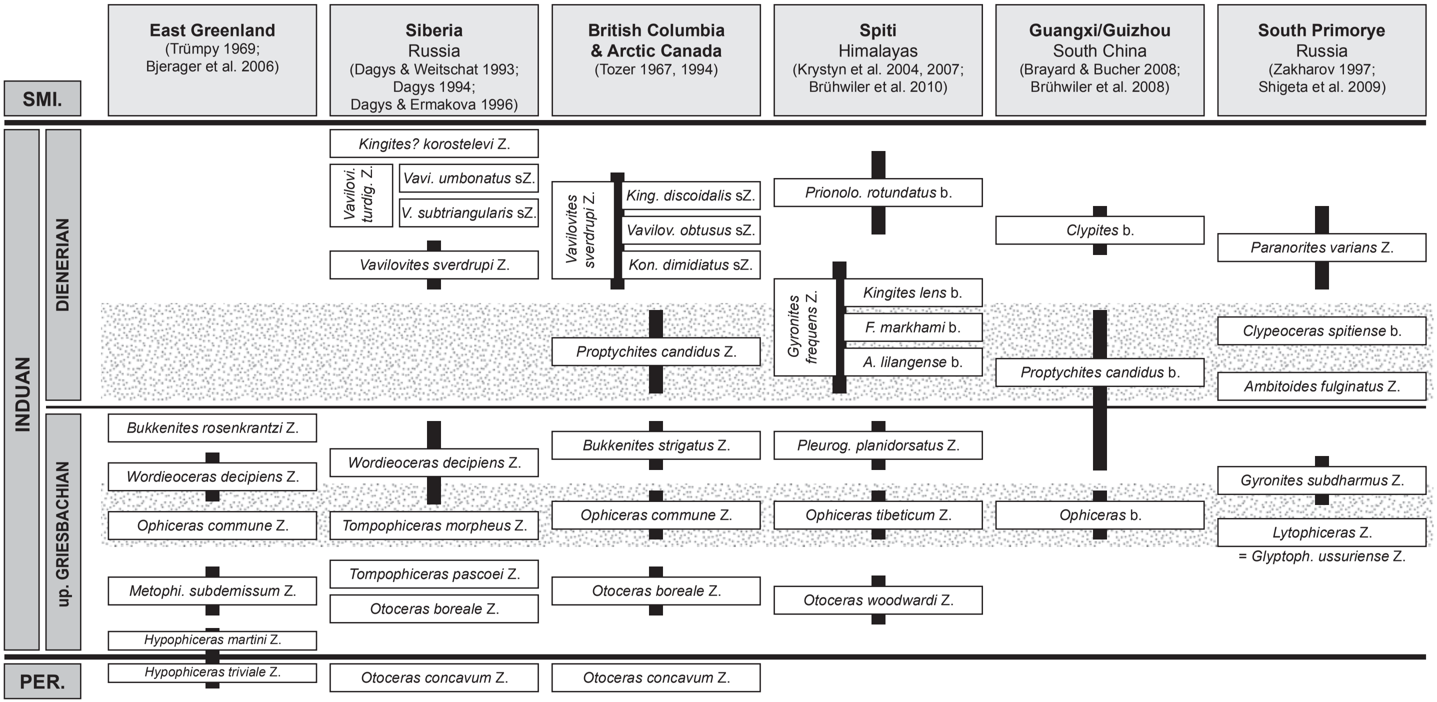

Fig. 13.5 Induan (late Griesbachian and Dienerian; Early Triassic) ammonoid zones and correlation (*vertical bars* indicate poorly constrained correlation; *Z* zone, *sZ* subzone, *b* beds)

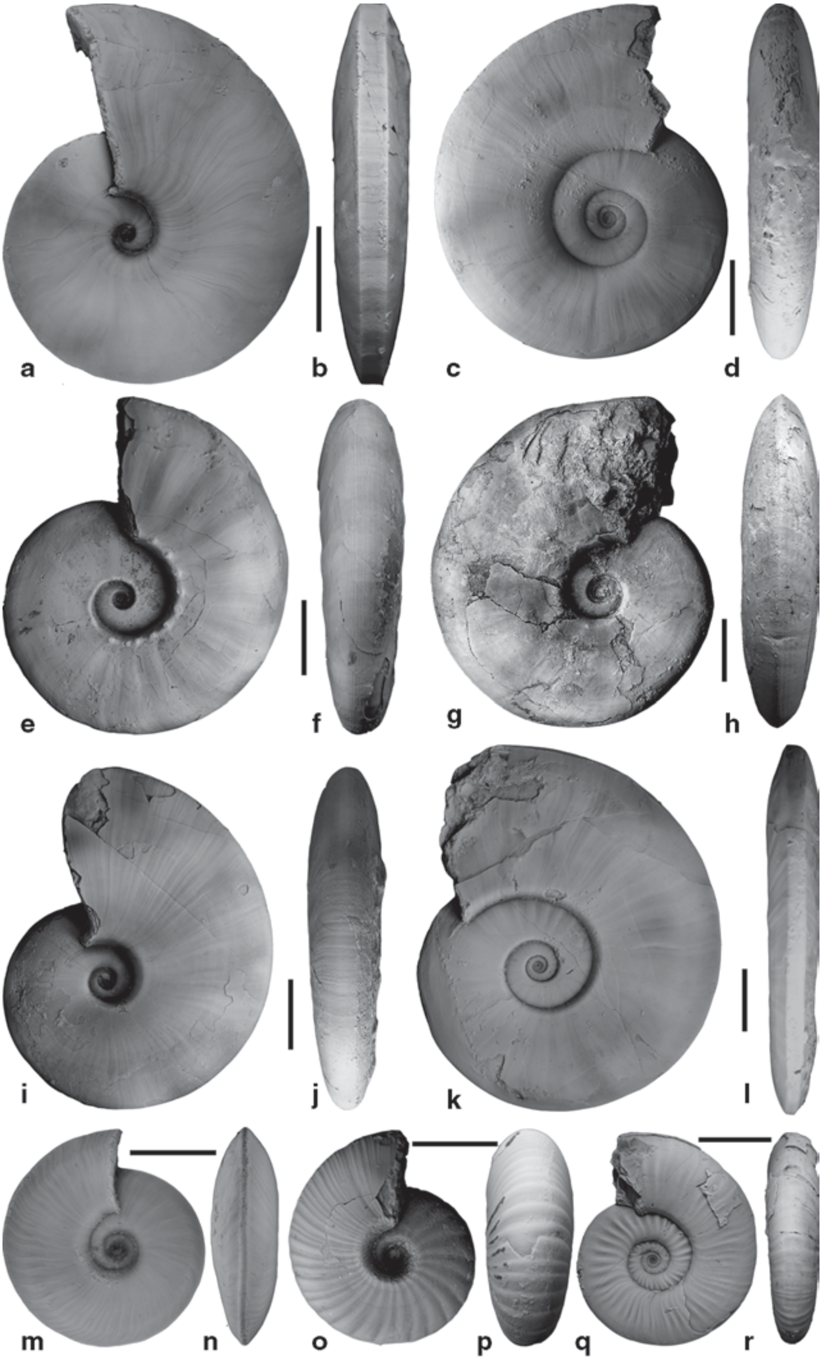

Fig. 13.6 Some characteristic ammonoids of the middle Smithian (Early Triassic). **a**, **b**, *Meekoceras gracilitatis* White 1879, JJ594C. **c**, **d**, *Anaflemingites silberlingi* Kummel and Steel 1962, JJ144C. **e**, **f**, *Arctoceras tuberculatum* (Smith 1932), JJ686C. **g**, **h**, *Churkites noblei* Jenks 2007, KB2D03. **i**, **j**, *Pseudaspidites silberlingi* Jenks et al. 2010, JJ693C. **k**, **l**, *Galfettites lucasi* Jenks et al. 2010, JJ90C. **m**, **n**, *Owenites koeneni* Hyatt and Smith 1905, JJ20C. **o**, **p**, *Paranannites*

selection of the FAD of the conodont *Neospathodus waageni*, with the likely GSSP located in the Mud section in India (Krystyn et al. 2007a, c; Brühwiler et al. 2010c).

The base of the Smithian is characterized by a major diversification event that not only included the appearance of many new ammonoid families, such as Flemingitidae, Kashmiritidae and Hedenstroemiidae (with the appearance of the following genera: *Hedenstroemia*, *Meekoceras*, *Juvenites*, *Arctoceras*, *Flemingites*, and *Euflemingites*), but it was also accompanied by the formation of a pronounced latitudinal diversity gradient (Brayard et al. 2006, 2007b, 2015). A major ammonoid extinction event occurred at the end-Smithian, which was then followed by a rather rapid major evolutionary radiation during the Spathian with the notable appearance of dinaritids, tirolitids and columbitids (Tozer 1980; Dagys 1988; Galfetti et al. 2007b; Brayard et al. 2009). This event corresponds to major perturbations known in the sedimentological, geochemical (major positive peak of carbon isotope), palynological and climatic records (Brayard et al. 2006; Galfetti et al. 2007b; Romano et al. 2013). It also marks "the biggest crisis in Triassic conodont history" (Orchard 2007b). The Spathian is characterized by the ammonoid genera *Tirolites*, *Columbites*, *Subcolumbites*, *Prohungarites* and *Keyserlingites*, among others. Some characteristic ammonoids of the Smithian and of the Spathian are illustrated in Figs. 13.6, 13.7 and 13.8.

Smithian ammonoid zonal schemes (Fig. 13.9) have undergone a thorough update and revision over the past two decades thanks to the description of abundant ammonoid faunas from classical and newly discovered localities. These schemes include: South Primorye (Shigeta et al. 2009), Siberia and Spitsbergen (Weitschat and Lehmann 1978; Weitschat and Dagys 1989; Dagys 1994; Ermakova 2002a, b), British Columbia and Arctic Canada (Tozer 1994; Bucher 2002), South China (Brayard and Bucher 2008), Southern Tethys with Oman (Brühwiler et al. 2012a), Spiti (Brühwiler et al. 2010a, 2012b), South Tibet (Brühwiler et al. 2010b), and Salt Range (Brühwiler et al. 2011, 2012c), as well as North America with Nevada (Silberling and Tozer 1968; Jenks 2007; Jenks et al. 2010) and Utah (Brayard et al. 2013). These relatively recent works as well as ongoing studies describe ammonoid successions that are much more comprehensive and easier to correlate. A complete illustration of these areas and their correlation can be found in Brayard et al. (2013). With an estimated duration of 0.7 ± 0.6 Myr (Ovtcharova et al. 2006; Galfetti et al. 2007a) and including up to 14 ammonoid zones (Brühwiler et al. 2010a, 2011), the biostratigraphy of the Smithian has a very high resolution (average subzone duration of only 50 only, inclusive of the separation intervals).

Spathian ammonoid zonal schemes (Fig. 13.10) for the most part remain poorly resolved and their correlation is not good. This supposition may reflect a high level of endemism at that time, but more accurate correlation must await the results of numerous ongoing works on Spathian ammonoids (e.g., from South China). Thus far, the most detailed sequence is that for western USA, which was recently revised after intensive field sampling by Guex et al. (2005a, b, 2010) and Jenks et al. (2013).

aspenensis Hyatt and Smith 1905, JJ274C. **q**, **r**, *Preflorianites toulai* Smith 1932, JJ244C. Scale bars = 2 cm. All specimens from Crittenden Springs, Nevada (JF Jenks coll.) except **g**–**h** (Confusion Range, Utah, courtesy Kevin Bylund)

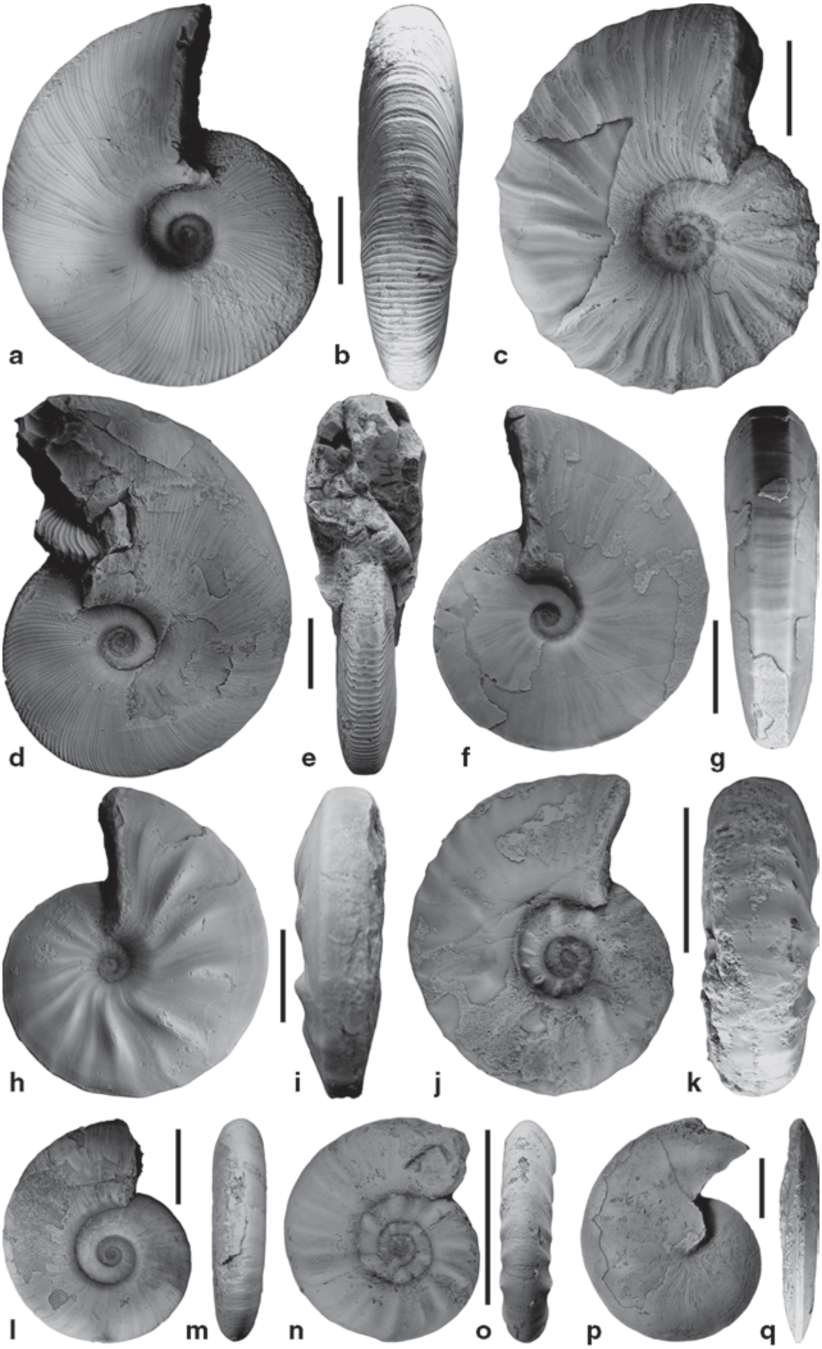

Fig. 13.7 Some characteristic ammonoids of the late Smithian (Early Triassic). **a**, **b**, *Anasibirites multiformis* Welter 1922, JJ232C. **c**, *Anasibirites kingianus* (Waagen 1895), JJ34C. **d**, **e**, *Anasibirites multiformis* Welter 1922, JJ146C. **f**, **g**, *Hemiprionites* cf. butleri (Mathews 1929), JJ108C. **h**, **i**, *Arctoprionites resseri* (Mathews 1929), JJ656C. **j**, **k**, *Wasatchites perrini* Mathews 1929, JJ767C. **l**, **m**, "*Xenoceltites*" *youngi* Kummel and Steele 1962, JJ275C. **n**, **o**, *Glyptophiceras* sp., JJ250C. **p**, **q**, *Pseudosageceras augustum* (Brayard and Bucher 2008), JJ649C. Scale bars = 2 cm. All specimens from JF Jenks coll. (**a**, **b**, **d**–**g**, **j**, **k**) from Georgetown, Idaho, other from Crittenden Springs, Nevada

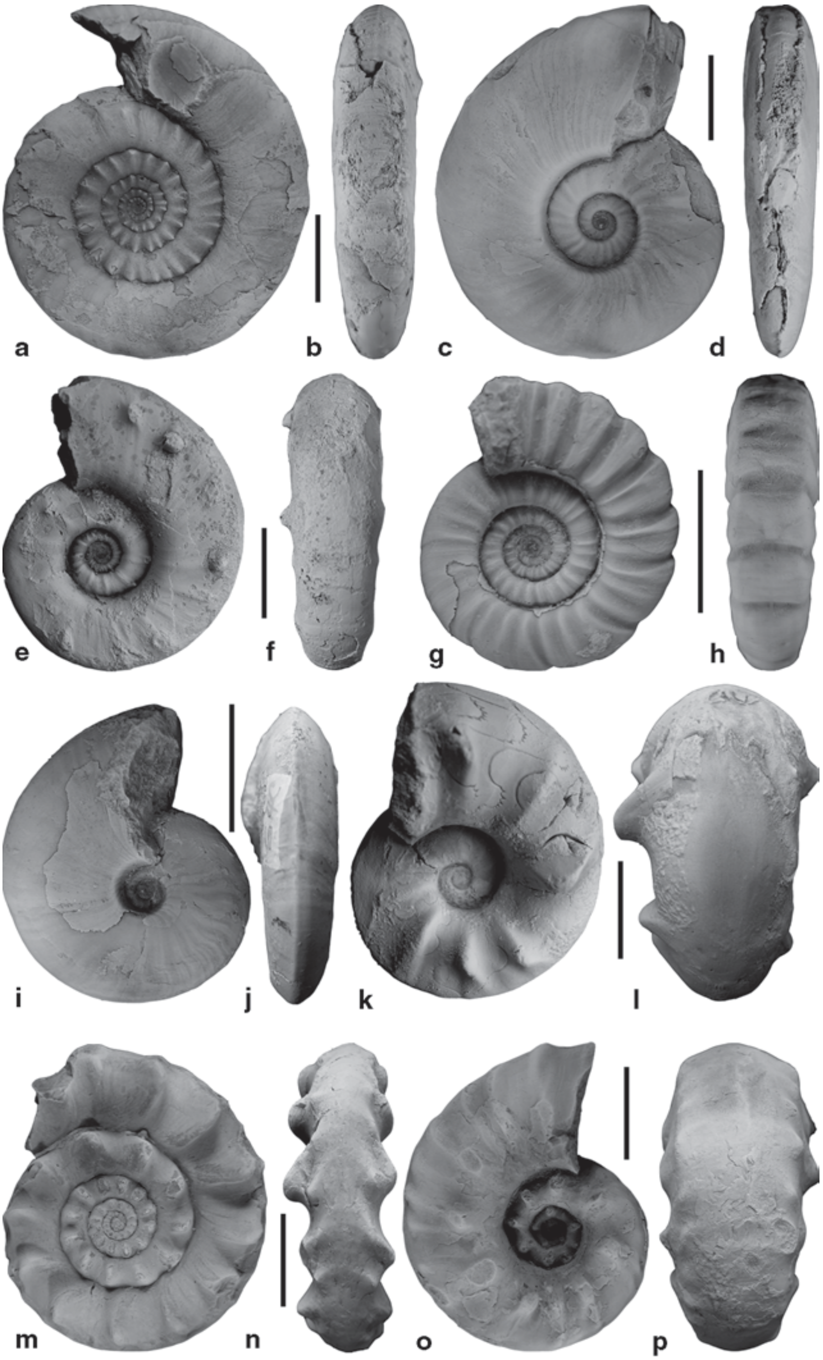

Fig. 13.8 Some characteristic ammonoids of the Spathian (Early Triassic). **a**, **b**, *Columbites parisianus* Hyatt and Smith 1905, JJ497C. **c**, **d**, *Bajarunia pilata* (Hyatt and Smith 1905), JJ86C. **e**, **f**, *Tirolites smithi* Kummel 1969, JJ159C. **g**, **h**, *Procolumbites karataucicus* Astahova 1960, JJ2260C. **i**, **j**, *Prohungarites mckelvei* Kummel 1969, JJ64C. **k**, **l**, *Silberlingeria bearlakensis* (Kummel 1969), JJ91C. **m**, **n**, *Parasibirites kolymensis* Bychkov 1976, JJ812C. **o**, **p**, *Keyserlingites subrobustus* (Mojsisovics 1886), JJ832C. Scale bars = 2 cm. All specimens from JF Jenks coll. (**a**–**l**) from Bear Lake Valley, Idaho and (**m**–**p**) from Olenek River, Siberia

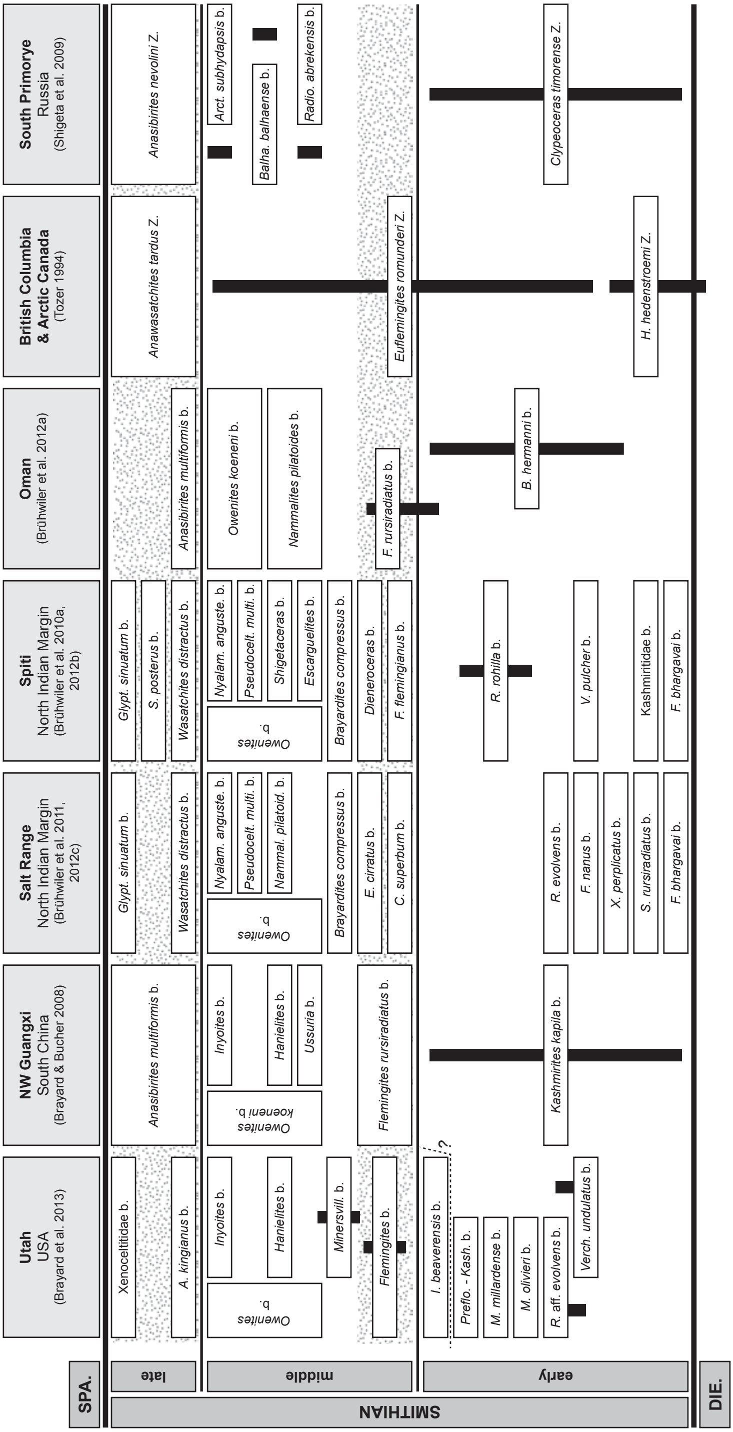

Fig. 13.9 Smithian (Early Triassic) ammonoid zones and correlation (*vertical bars* indicate poorly constrained correlation; *Z* zone, *sZ* subzone, *b* beds). (After Brayard et al. 2013)

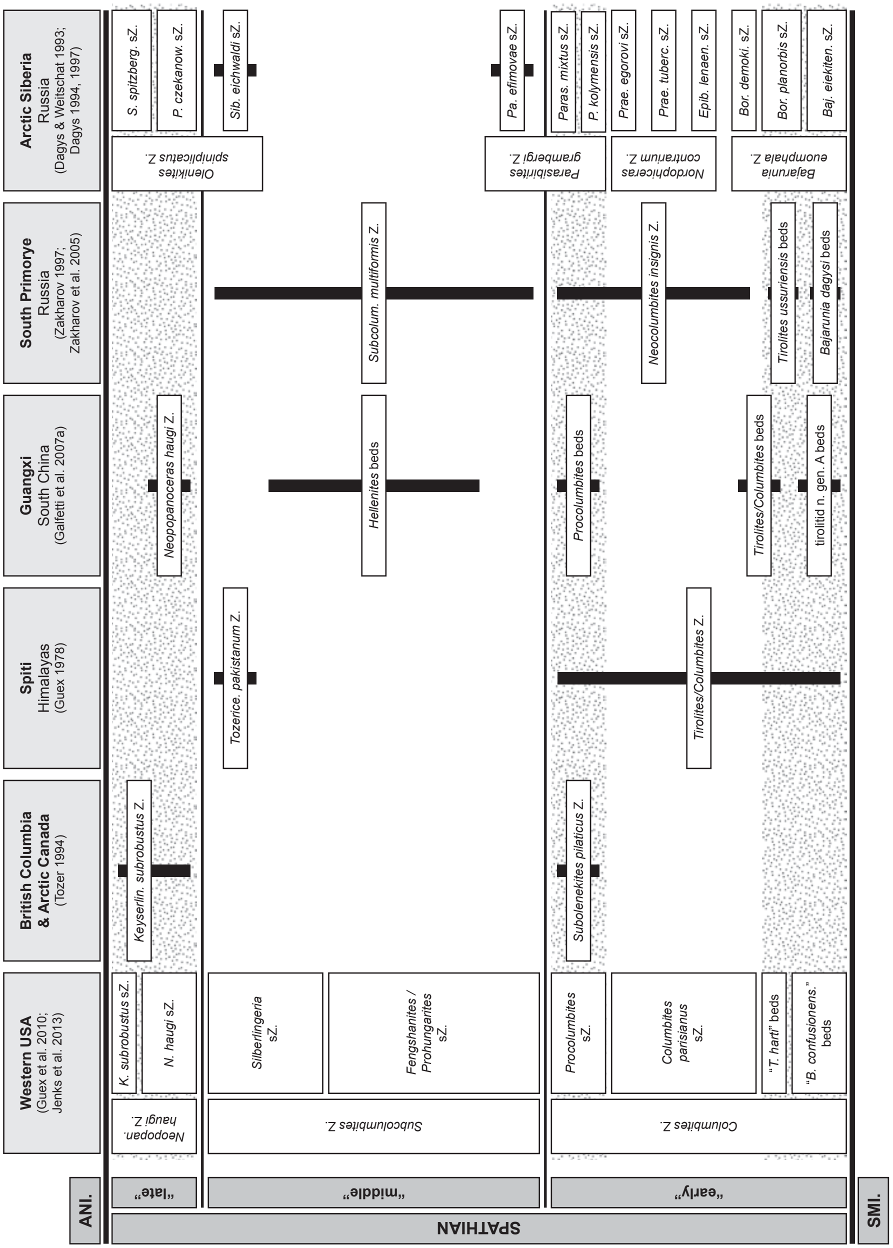

Fig. 13.10 Spathian (Early Triassic) ammonoid zones and correlation (*vertical bars* indicate poorly constrained correlation; *Z* zone, *sZ* subzone, *b* beds)

These authors subdivided the Spathian of western USA into 8 zones and 24 biohorizons, but their lateral reproducibility awaits similar high resolution ammonoid records from other paleogeographic settings. Arctic Siberia also records abundant Spathian ammonoid faunas, which have been subdivided into 12 subzones (Dagys 1994, 1995, 1997, 1999; Dagys and Sobolev 1995). Other major paleogeographic areas for which ammonoid biozonation schemes have been discussed include British Columbia (Tozer 1994), the Salt Range of Pakistan (Kummel 1966; Guex 1978), South China (Galfetti et al. 2007a), and South Primorye (Zakharov 1997; Zakharov et al. 2005). A few faunas that are either poorly preserved and/or of low diversity have also been described from various localities (e.g., Iran: Balini et al. 2009; Vaziri 2011; Mongolia: Ehiro et al. 2006; Croatia: Golubić 2000; Vietnam: Shigeta et al. 2014). Correlation of these various schemes is mainly based on Shevyrev (2002), Dagys (1994, 1997), and Dagys and Sobolev (1995), but further progress awaits a formal revision and discussion based on recent data.

13.4 Middle Triassic Ammonoid Zonation

The Middle Triassic is defined by the long recognized two-stage subdivision consisting of the basal Anisian stage and overlying Ladinian stage. Waagen and Diener (in Mojsisovics et al. 1895) named the Anisian stage for limestone formations near "Anisus" (the Latin name of the river Enns) at Groβreifling in Austria, whereas the Ladinian stage was named after the Ladini inhabitants of the Dolomites region of northern Italy, where Ladinian strata include the Buchenstein and Wengen beds (Bittner 1893).

Both the Anisian and Ladinian have been further subdivided into informal substages, in ascending order, the Aegean, Bithynian, Pelsonian and Illyrian, and the Fassanian and Longobardian, respectively. However, these subdivisions are not widely accepted and they are probably only of limited regional value (Europe). Assereto (1974) proposed a stratotype for his newly named early Anisian Aegean substage in beds containing the ammonoid genus *Paracrochordiceras* at Mount Marathovouno on Chios Island (Aegean Sea, Greece). The middle Anisian has been subdivided into two substages: the basal Bithynian after the Kokaeli Peninsula (Bithynia) of Turkey (Assereto 1974), and the overlying Pelsonian, from the Latin name for the region around Lake Balaton in Hungary (Pia 1930) that spans the *Balatonites balatonicus* ammonoid zone (Assereto 1974). The late Anisian is named Illyrian after the Latin term for Bosnia (Pia 1930). Mojsisovics et al. (1895) divided the Ladinian into two substages: the Fassanian (named after Val di Fassa in northern Italy, where it was equated with the Buchenstein Beds and Marmolada Limestone) and the Longobardian (named after the Langobard people of northern Italy), which spans the Wengen Beds. This substage boundary is located approximately at the base of the *Protrachyceras longobardicum* ammonoid zone of the Alpine zonation or the base of *Meginoceras meginae* ammonoid zone of the Canadian zonation.

Radio-isotopic data for the Middle Triassic are scarce, often contradictory and poorly correlated between marine biozones and dated rocks (see Brack et al. 2005; Lehrmann et al. 2006; Ovtcharova et al. 2006, 2010; Brühwiler et al. 2007; Mundil et al. 2010; Ogg 2012; Cohen et al. 2013). Interpolated ages of the Global Time Scale 2012 (Gradstein et al. 2012) indicate durations for the Anisian and Ladinian of ca. 5.6 ± 1 Myr and 4.5 ± 1 Myr, respectively. These ages imply an average ammonoid biochronozone of about 0.51 Myr at most for each zone level shown in Figs. 13.13 and 13.14 (0.43 Myr for the Anisian, and 0.64 Myr for the Ladinian) (and up to 0.18 Myr for each subzone level for the Anisian).

13.4.1 Anisian

The base of the Anisian stage has not yet been formally established and designated. Gradinaru et al. (2007) proposed a candidate section at Desli Caira Hill in north Dobrogea (Romania) and Lehrmann et al. (2006) discussed an alternative section at Guandao in the Nanpanjiang Basin (Guizhou Province, South China) with a good conodont record and volcanic ashes that produce radio-isotopic dates. However, neither of these candidates is fully satisfactory: for instance, the Romanian section occurs within a condensed Hallstatt limestone facies that may be missing some ammonoid zones, whereas the Chinese section is based on the FAD of the conodont *Chiosella timorensis*, which may be significantly diachronous (Goudemand et al. 2012). Unfortunately, Waagen and Diener's original Anisian stratotype (in Mojsisovics et al. 1895) lacks ammonoids in its lower part thus complicating the original interpretation of the Spathian/Anisian boundary. Nevertheless, Assereto (1974) demonstrated in the Mediterranean region that the early Anisian is characterized by the appearance of several ammonoid genera, such as *Aegeiceras*, *Japonites*, *Paracrochordiceras* and *Paradanubites* (see also Bucher 1989; Gradinaru 2000; Gradinaru and Sobolev 2006; Monnet et al. 2012, 2013). Several other markers have been proposed to define the base of the Anisian stage, but they are presently somewhat contradictory. These include the FAD of the conodont *Chiosella timorensis*, which may be diachronous and difficult to recognize taxonomically (Orchard 2010; Goudemand et al. 2012), a positive peak in carbon isotope values (Tanner 2010a) and a change from reversed-polarity- to normal-polarity-dominated magnetostratigraphy (base of normal-magnetozone MT1n of Hounslow et al. 2007; Hounslow and Muttoni 2010).

The Anisian stage was a time of major ammonoid diversification, distinguished by the appearance of several important long-ranging "leiostracan" ammonoid families such as Gymnitidae, Isculitidae, Ptychitidae and Arcestidae, which may also extend up into the earliest Ladinian. It was also characterized by the significant radiation of members of the Ceratitaceae, as well as by the peculiar evolutionary trends of certain families (Tozer 1980; Brayard et al. 2009) such as Acrochordiceratidae (Monnet et al. 2012, 2013) and Arctohungaritidae (Dagys 2001) among others. The Aegean substage is marked by the ammonoid genera *Paracrochordiceras*, *Japonites* and *Aegeiceras* (Bucher 1989; Gradinaru and Sobolev 2006), while the Bithynian substage is characterized by the radiation of Beyrichitinae (*Nicomedites*, *Hollandites*, *Anagymnotoceras*), Ptychitidae, and Acrochordiceratidae (Bucher 1988, 1992a; Monnet et al. 2013). The Pelsonian substage is marked by the diversification of Balatonitidae; its most typical representative *Balatonites* is a remarkable guide fossil, which occurs in the Muschelkalk, Tethys, Sephardic and Pacific paleobioprovinces. In spite of the worldwide occurrence of *Balatonites*, the definition of the base of the Pelsonian is still a matter of debate. Finally, the Illyrian substage is characterized by the radiation of Paraceratitinae and the disappearance of Acrochordiceratidae and Balatonitidae. Some characteristic ammonoids of the Anisian are illustrated in Figs. 13.11 and 13.12.

Anisian ammonoid zonal schemes are diverse (Figs. 13.13, 13.14), especially for the Western Tethys, several of which were probably triggered by past competition for defining the Anisian/Ladinian boundary. Current ammonoid biozonation of the Anisian stage also well illustrates the historical development of the Triassic chronostratigraphic scale with its early foundation in Europe (western Tethys), followed by a significant complement from North America, and then during the last decades a revision of ammonoid faunas and scales in both paleogeographic areas. Hence, the most developed and recent schemes are for Western Tethys (Brack and Rieber 1986, 1993; Vörös 1987, 2003; De Zanche and Gianolla 1995; Mietto and Manfrin 1995a; Vörös and Palfy 2002; Vörös et al. 2003; Brack et al. 2005; Monnet et al. 2008), North America (Silberling and Nichols 1982; Bucher 1988, 1989, 1992a, b, 2002; Tozer 1994; Monnet and Bucher 2005a, b), and Siberia (Dagys and Weitschat 1993; Dagys 1998, 2001). Other areas such as South Primorye (Zakharov 1997; Zakharov et al. 2004b, 2005), South China (Wang 1978; Wang and He 1980; Stiller and Bucher 2008) and Nepal (Waterhouse 1999, 2002a, b) have received attention, but on a less frequent basis. Faunas have also been described intermittently from other scattered areas (e.g., Germanic Basin: Kaim and Niedźwiedzki 1999; Spiti: Balini and Krystyn 1997; Iran: Krystyn and Tatzreiter 1991; Balini et al. 2009; Vaziri 2011; Mexico: Estep et al. 1997; Greece: Jacobshagen et al. 1993; Malaysia: Ahmad and Mohd 2010; Vietnam: Shigeta et al. 2010). Correlation of these various faunas and biostratigraphic schemes has been discussed to a certain extent by several authors (Bucher 1989; Dagys and Weitschat 1989, 1993; Mietto and Manfrin 1995a; Zakharov et al. 1997; Monnet and Bucher 2005b; Waterhouse 2002b).

13.4.2 Ladinian

The base of the Ladinian stage was formally established at the Bagolino section (Southern Alps, Italy), which is characterized by multiple stratigraphic records including the bracketing of the boundary interval by dated volcanic ashes (Brack et al. 2005; Brack 2010). This GSSP is defined by the FAD of the ammonoid *Eoprotrachyceras curionii*, a decision that finally ended a determined decade-long debate

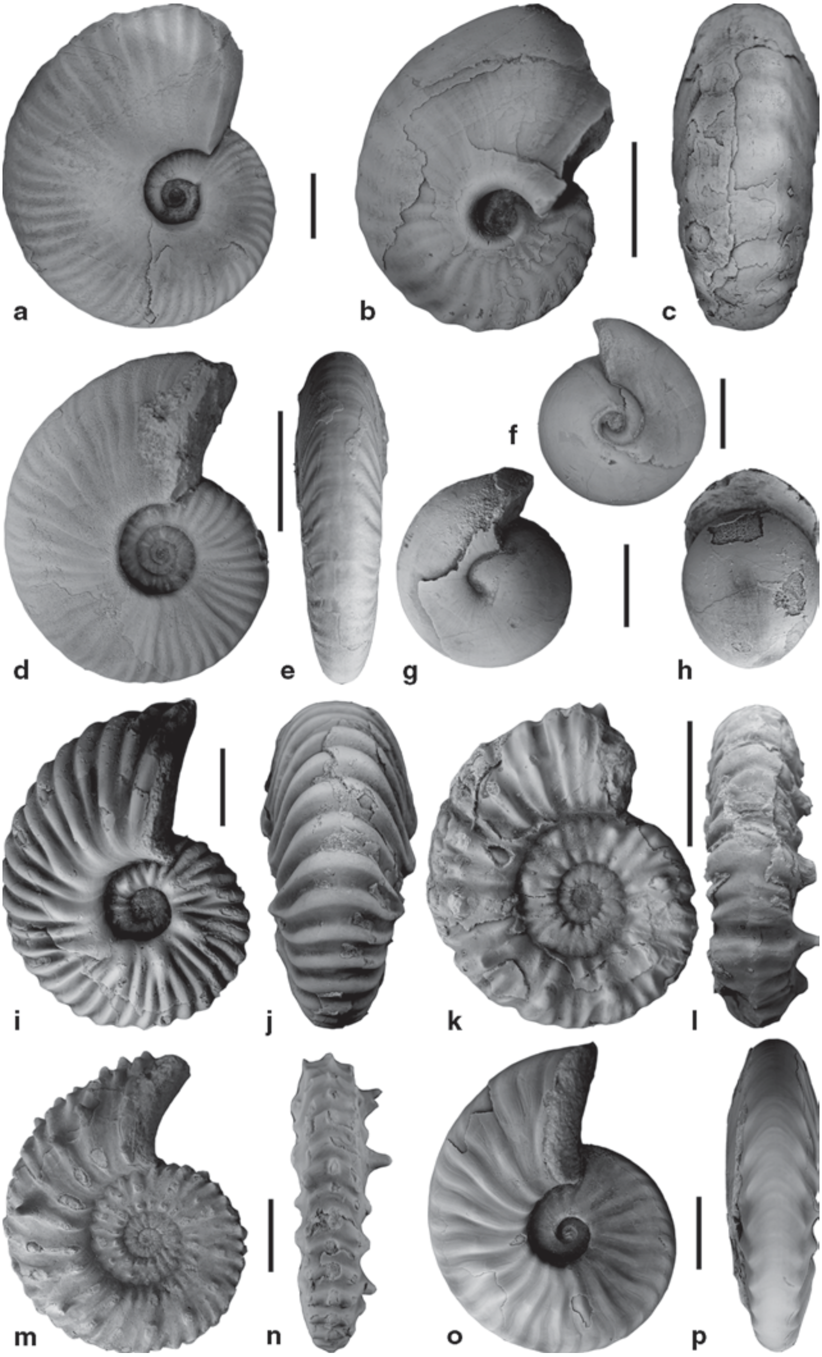

Fig. 13.11 Some characteristic ammonoids of the middle Anisian (Middle Triassic). **a**, *Acrochordiceras hyatti* Meek 1877, JJ1082C. **b**, **c**, *Alanites costatus* Bucher 1992a, JJ1115C. **d**, **e**, *Hollandites silberlingi* Bucher 1992b, JJ1863C. **f**, *Isculites tozeri* Silberling and Nichols 1982, JJ1536C. **g**, **h**, *Nevadisculites taylori* Bucher 1988, JJ1512C. **i**, **j**, *Acrochordiceras carolinae* (Mojsisovics 1882b), JJ1521C. **k**, **l**, *Augustaceras escheri* Bucher 1988, JJ1708C. **m**, **n**, *Balatonites whitneyi* Bucher 1992b, JJ1154C. **o**, **p**, *Favreticeras wallacei* Bucher 1992b, JJ1780C. Scale bars = 2 cm. All specimens from JF Jenks coll. All from northwestern Nevada

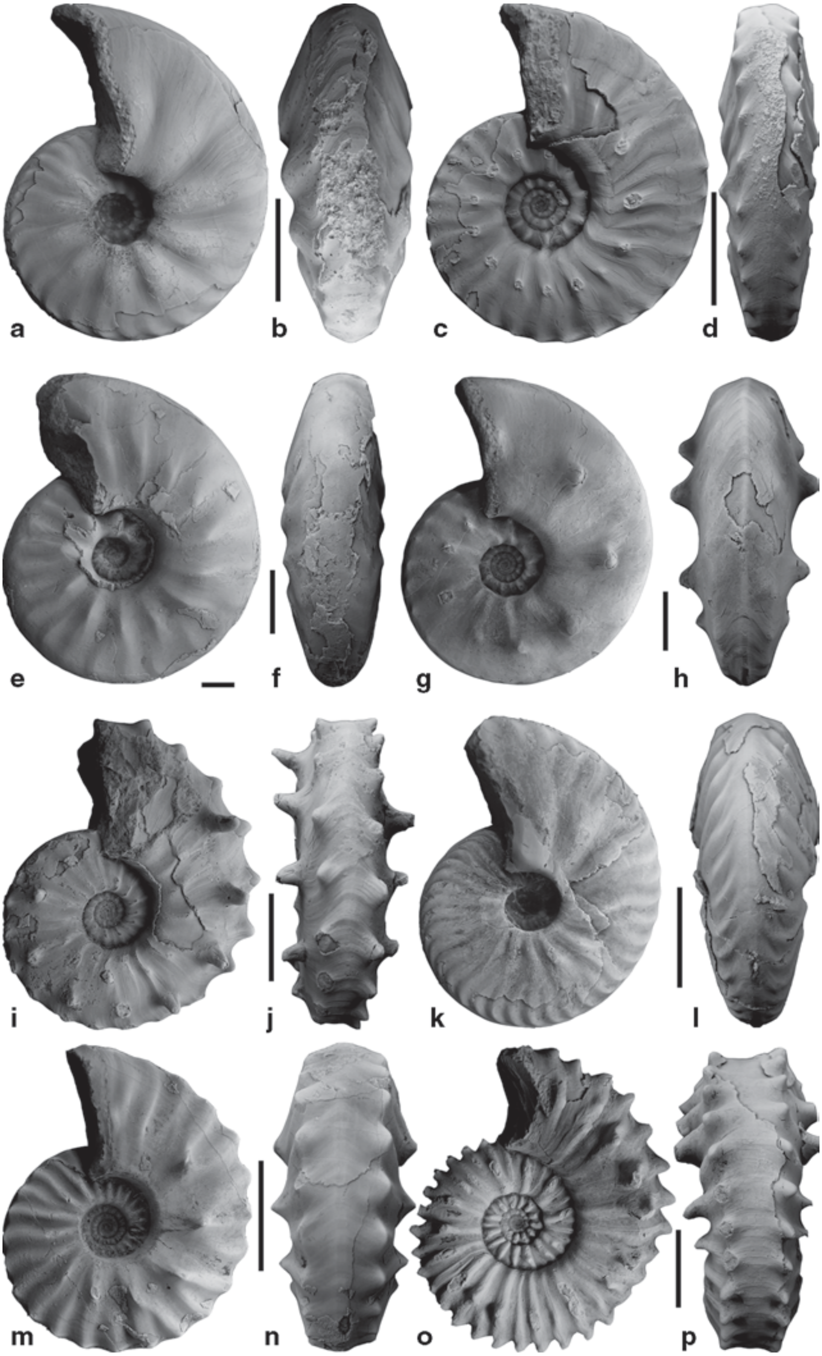

Fig. 13.12 Some characteristic ammonoids of the late Anisian (Middle Triassic). **a**, **b**, *Dixieceras lawsoni* Monnet and Bucher 2005a, JJ1025C. **c**, **d**, *Rieppelites shevyrevi* Monnet and Bucher 2005a, JJ1537C. **e**, **f**, *Gymnotoceras blakei* (Gabb 1864), JJ1454C. **g**, **h**, *Silberlingitoides cricki* (Smith 1914), JJ1455C. **i**, **j**, *Brackites vogdesi* (Smith 1904), JJ941C. **k**, **l**, *Parafrechites meeki* (Mojsisovics 1888a), JJ1462C. **m**, **n**, *Frechites nevadanus* (Mojsisovics 1888), JJ1787C. **o**, **p**, *Nevadites hyatti* (Smith 1904), JJ1538C. Scale bars = 2 cm. All specimens from JF Jenks coll. All from northwestern Nevada

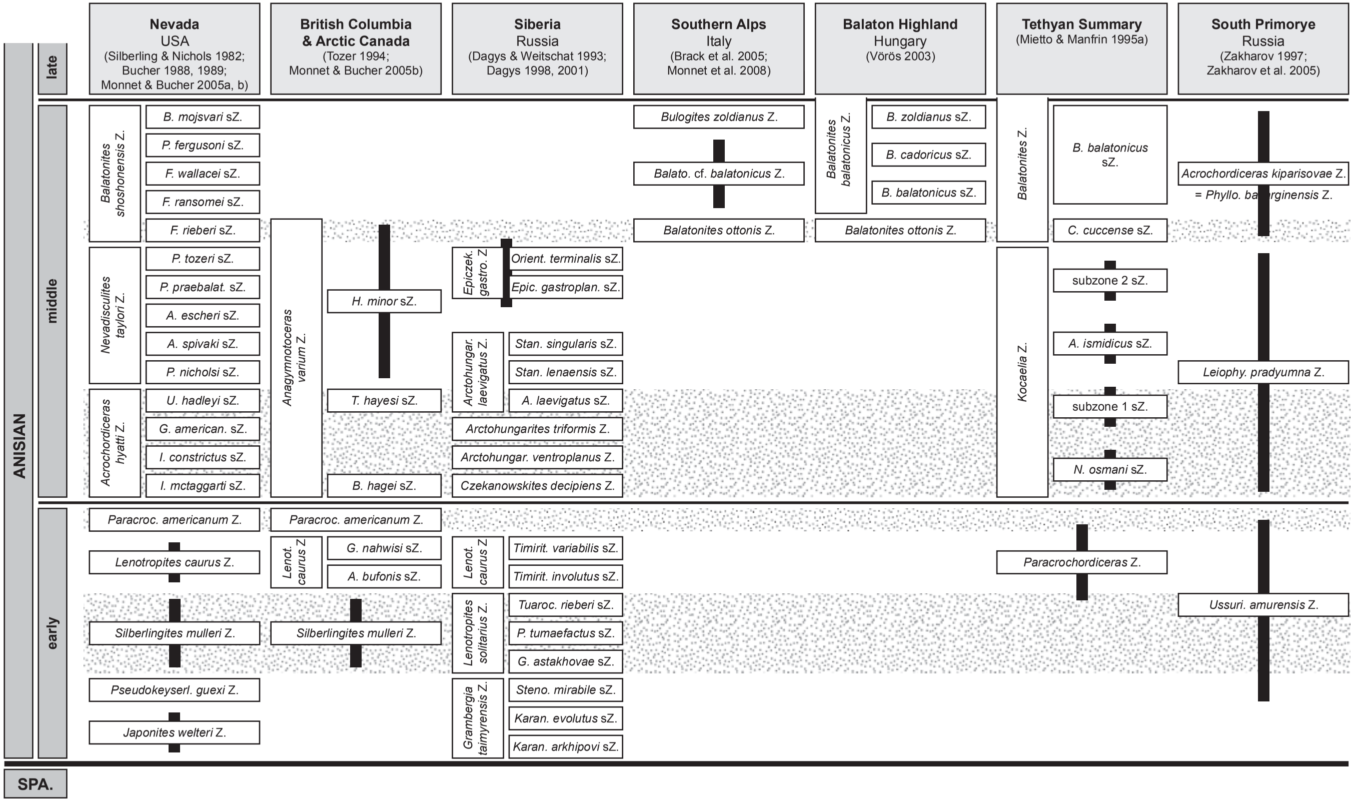

Fig. 13.13 Early and middle Anisian (Middle Triassic) ammonoid zones and correlation (*vertical bars* indicate poorly constrained correlation; *Z* zone, *sZ* subzone, *b* beds)

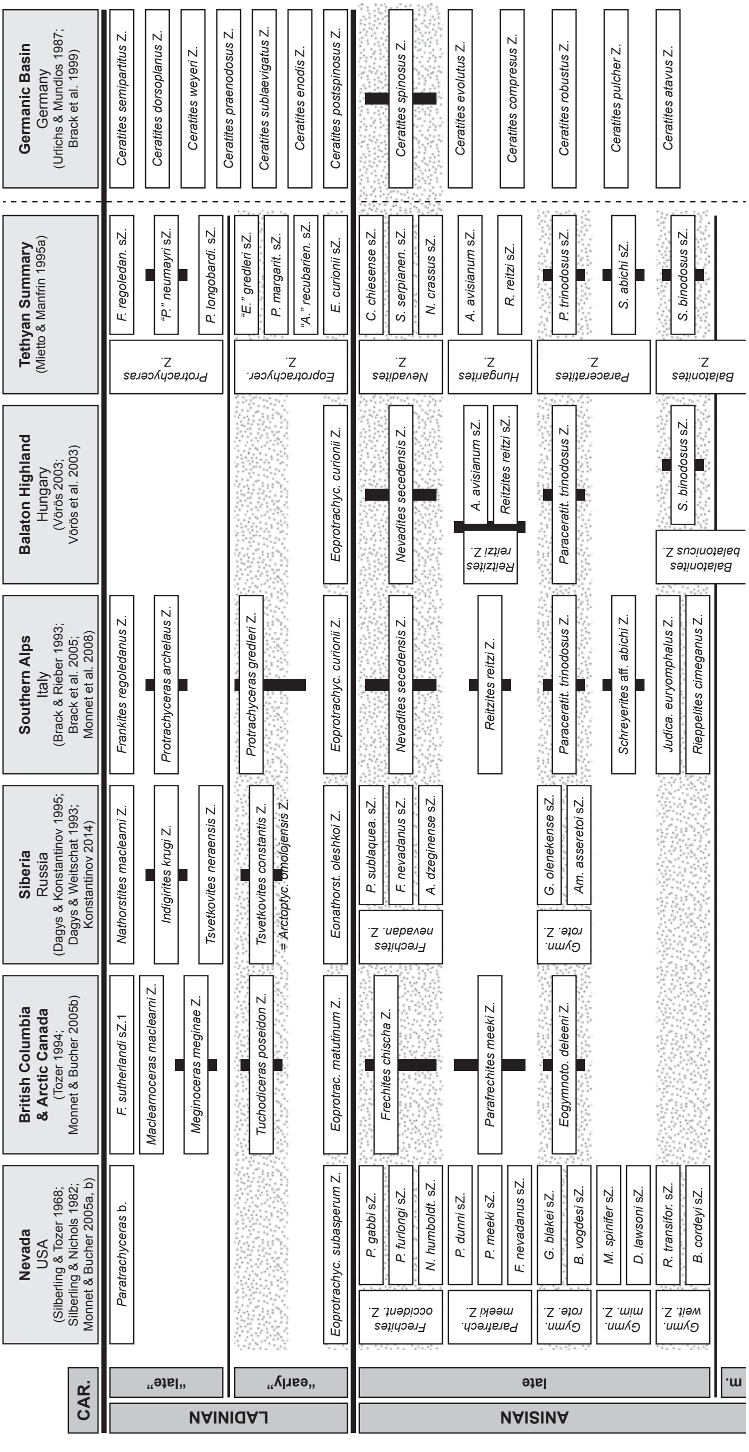

Fig. 13.14 Late Anisian and Ladinian (Middle Triassic) ammonoid zones and correlation (*vertical bars* indicate poorly constrained correlation; *Z* zone, *sZ* subzone, *b* beds)

between supporters of various candidate sections in Western Tethys (e.g., Gaetani 1993; Brack and Rieber 1993, 1994, 1996; Brack et al. 1995, 2003; Vörös et al. 1996, 2003; Orchard and Tozer 1997b; Balini 2003; Kozur 2003; Mietto et al. 2003; Shevyrev 2006).

Ammonoid diversity notably decreased at the beginning of the Fassanian due to the extinction of several short-ranging Anisian groups of Ceratitaceae, such as Balatonitidae and Paraceratitinae, and the severe decline and subsequent extinction of Beyrichitinae. The most important short-ranging ammonoid group of the Ladinian and Early Carnian is the family Trachyceratidae, which provides most of the index taxa for the Tethyan and North American scales. Ceratitaceae were still present in the Ladinian with Ceratitinae, Hungaritidae and Israelitinae, but were restricted to particular environments such as shallow water isolated basins (Germanic and Sephardic basins) and carbonate platforms (Fantini Sestini 1994, 1996). Some characteristic ammonoids of the Ladinian are illustrated in Fig. 13.15.

The base of the Longobardian has not yet been formally defined and thus far, three alternative options should be discussed. The first is the FAD of *Protrachyceras*, within the *Eoprotrachyceras–Protrachyceras* lineage. This option is somewhat problematic because the suture line of some species around the Fassanian/Longobardian boundary is unknown, and their generic assignment to *Eoprotrachyceras* (ceratitic suture) or to *Protrachyceras* (ammonitic suture) is uncertain. The second option is to draw the boundary at the top of the uppermost ammonoid fauna of the Buchenstein Formation of the Southern Alps, in agreement with the original definition by Bittner (1893). The third is to mark the base of the substage with the increasing diversity of Arpaditidae (FADs of *Meginoceras* and *Silenticeras*).

Ladinian ammonoid zonal schemes are relatively few in number, but they document all Triassic paleobioprovinces. Calibration is obviously influenced by endemism (Fig. 13.14), especially when considered with regard to the estimated duration of the stage. Future studies are urgently needed that will focus not only on stage boundaries, but on the entire stage as well. Ladinian zonal schemes with the highest resolution include the Western Tethys (Mietto and Manfrin 1995a, b; Mietto et al. 2008), Canada (Tozer 1994), and Siberia (Dagys and Konstantinov 1986, 1995; Dagys et al. 1993). Correlation of the very meticulous zonation of the Germanic Muschelkalk, which was historically crucial for the birth of the Triassic timescale, is complex because of the occurrence of endemic Ceratitinae (e.g., Urlichs 1993, 2006; Klug et al. 2005). At present only the *spinosus* Zone can be directly correlated to the Tethyan *secedensis* Zone and this is based on the occurrence of a single specimen of *Nevadites* (Brack et al. 1999). Other scales that are difficult to correlate with Western Tethys and North America include those from South China (Wang 1983) and Israel (Parnes et al. 1985). Additional isolated ammonoid faunas have also been described from other areas (e.g., Spain: Pérez Valera 2005).

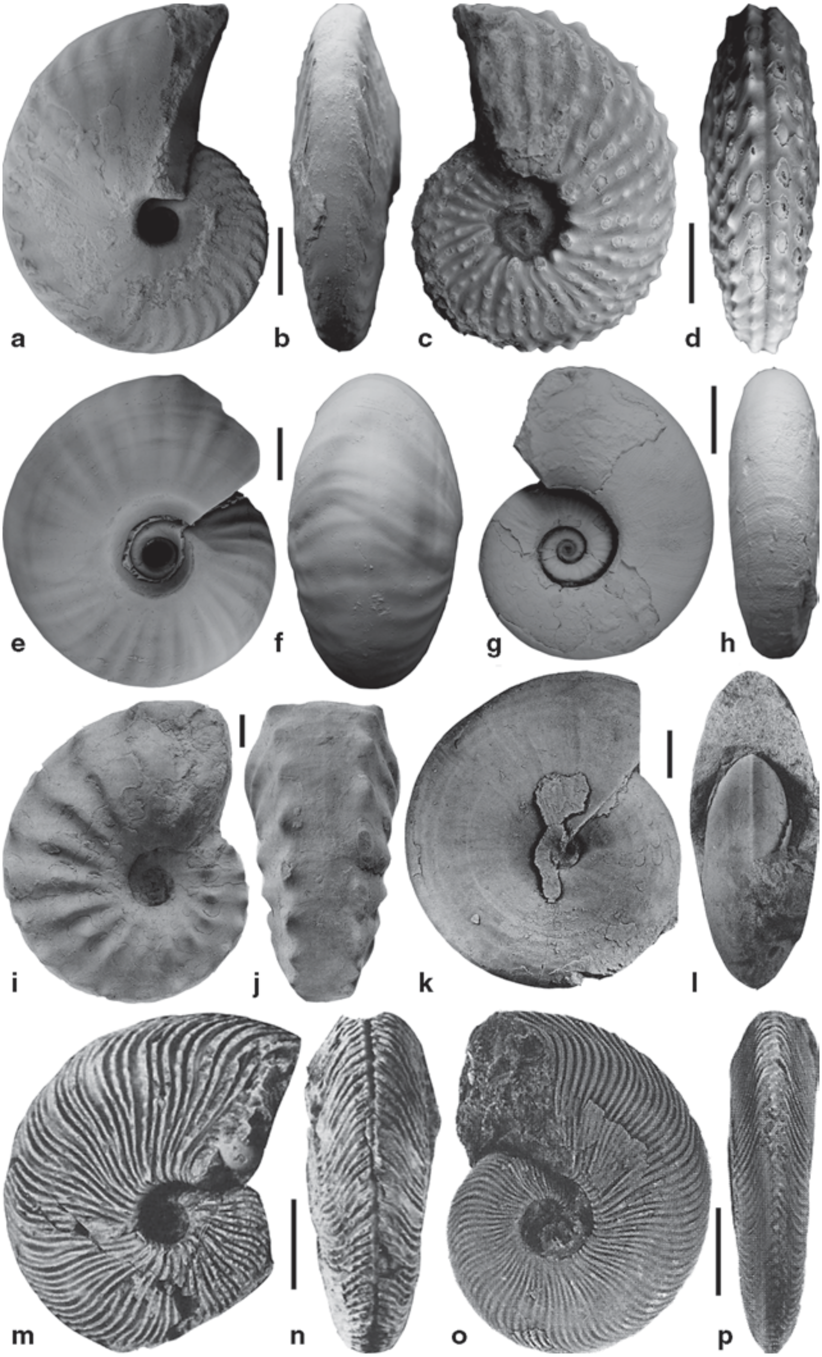

Fig. 13.15 Some characteristic ammonoids of the Ladinian (Middle Triassic). **a**, **b**, *Frechites johnstoni* Silberling and Nichols 1982, JJ1734C. **c**, **d**, *Protrachyceras subasperum* (Meek 1877), JJ1732C. **e**, **f**, *Ptychites euglyphus* (Mojsisovics 1886), JJ785C. **g**, **h**, *Indigirophyllites spetzber-*

13.5 Late Triassic Ammonoid Zonation

The Late Triassic includes three stages (Carnian, Norian, and Rhaetian; Fig. 13.1) that were originally defined by ammonoids (Mojsisovics 1869). Initially, these stages were recognized from different locations in the Northern Alps of Austria with uncertain stratigraphic relationships. Obviously, this led to eventual age controversies, which have been thoroughly reviewed by Tozer (1984). The Carnian stage, of uncertain origin and named after either the Kärnten (Carinthia) region of Austria or the nearby Carnian Alps, was originally applied to Hallsatt Limestone beds containing ammonoids belonging to the genera *Trachyceras* and *Tropites* (Mojsisovics 1869). The Norian stage was named for the Roman province of Noricum, south of the Danube, which includes the area of Hallstatt, Austria (Mojsisovics 1869). The Rhaetian stage was named after the Kössener Schichten from the uppermost Triassic rocks in the Northern Calcareous Alps of southern Germany (Gümbel 1861), which belonged to the Roman province of Rhaetia.

In the Tethyan realm (Europe), the Carnian stage is subdivided into two substages (Julian and Tuvalian; and initially a third Cordevolian substage subsequently united with the Julian), while the Norian stage is divided into three substages (Lacian, Alaunian and Sevatian), all of which were initially based on characteristic ammonoids. These substages were named for the following European Alpine localities: Julian (*Trachyceras aonoides* Zone of Mojsisovics et al. 1895)—Raibl Formation of the Julian Alps in southern Austria; Tuvalian (*Tropites subbullatus* Zone of Mojsisovics et al. 1895)—Tuval Mountains, the Roman term for the region between Berchtesgaden and Hallein near Salzburg, Austria; Lacian—the Roman name for the Salzkammergut region of the northern Austrian Alps; Alaunian—the Alauns, who lived in the Hallein region of Austria during Roman times; and Sevatian—the Celtic tribe who lived between the Inn and Enns rivers of Austria (Mojsisovics et al. 1895).

Relatively little radio-isotopic data for the Late Triassic are available, which has led to poorly constrained durations for the stages and even to several competitive and alternative models for the length of the Norian and the Rhaetian (for further details, see review by Ogg 2012). In the International Commission on Stratigraphy, the estimated numerical ages are (Cohen et al. 2013) for the Carnian, Norian and Rhaetian ca. 8.7 ± 1 Myr, 18.9 ± 2 Myr, and 8.2 ± 1 Myr, respectively. These ages imply an average ammonoid biochronozone of about 1.63 Myr at most for each zone level shown in Figs. 13.17 and 13.20 (0.87 Myr for the Carnian, 2.70 Myr for the Norian, and 1.64 Myr for the Rhaetian).

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gensis (Oeberg 1877), JJ789C. **i**, **j**, *Ceratites nodosus* (Schlotheim 1820), SMF: XI 43161 (after Urlichs and Mundlos 1987, Fig. 2). **k**, **l**, *Nathorstites maclearni* Tozer 1994, GSC 28606, holotype (after Tozer 1994, pl. 81, Figs. 6a, b). **m**, **n**, *Daxatina canadensis* (Whiteaves 1889), GSC 18812, hypotype (after Tozer 1994, pl. 85, Figs. 6a, b). **o**, **p**, *Frankites sutherlandi* (McLearn 1947b), GSC 28802, hypotype (after Tozer 1994, pl. 83, Figs. 10a-c). Scale bars = 1 cm. All specimens from JF Jenks coll. unless otherwise noted. (**a**–**d**) from northwestern Nevada, (**e**–**h**) from Spitzbergen, (**i**–**j**) from Germany, (**k**–**p**) from British Columbia

13.5.1 Carnian

The base of the Carnian stage, recently ratified (Gaetani 2009; Mietto et al. 2012) at the Prati di Stuores/Stuores Wiesen section in northern Italy (Broglio Loriga et al. 1998; Mietto et al. 2007a, b, 2012), is defined by the FAD of the ammonoid *Daxatina canadensis*. Secondary markers include the FAD of the conodont *"Paragondolella" polygnathiformis* and the palynomorphs *Vallasporites ignacii* and *Patinasporites densus* (Mietto et al. op. cit.). In addition, the evolutionary transition of the well-known Triassic bivalves *Daonella* and *Halobia* probably occurred near this level (McRoberts 2010).

In terms of ammonoids, the Julian is dominated by Trachyceratinae (in particular *Trachyceras* and *Austrotrachyceras*) and Sirenitinae. The base of the Tuvalian is marked by one of the major Triassic ammonoid evolutionary changes, namely the crisis of Trachyceratinae, whose only survivor in the late Carnian is *Trachysagenites*, as well as the radiation of Tropitidae (*Tropites* and closely allied forms) and Juvavitidae, and to a lesser extent Arpaditinae. The ammonoid turnover at the early/late Carnian boundary is thus more important than at the bases of the Carnian and of the Norian (Tozer 1984). This event also left its mark on other faunal groups (e.g., conodonts, Mazza et al. 2010; radiolarians, Kozur and Bachman 2010; crinoids, Hagdorn 2011) and also coincides with the end of a peculiar climatic and oceanographic event (Breda et al. 2009; Kozur and Bachman 2010; Dal Corso et al. 2012). Some characteristic ammonoids of the Carnian are illustrated in Fig. 13.16.

Carnian ammonoid zonal schemes (Fig. 13.17) are relatively rare. Those for Canada (Tozer 1994), Western Tethys (Mietto and Manfrin 1995a), and Siberia (Dagys et al. 1993; Konstantinov 2014) have the highest resolution, but even these have potential for further refinements. Such potential has been demonstrated by research aimed at the definition of the GSSP of the Carnian stage carried out in recent years in North America and Tethys. Detailed investigations in the Dolomites (Italy) resulted in the discovery of a faunal succession (Broglio Loriga et al. 1998; Mietto et al. 2007a, b) very similar to that of British Columbia (Tozer 1994). Also, a very similar faunal succession was reported from Spiti (Balini et al. 1998, 2001; Krystyn et al. 2004), but the best results were achieved in Nevada. Extensive sampling efforts at South Canyon (New Pass Range, central Nevada) have resulted in the description and revision of ammonoid taxonomy and biostratigraphy at the Ladinian/Carnian boundary (Balini and Jenks 2007; Balini et al. 2007; Balini 2008; Balini et al. 2012a). Briefly, this work has revealed that the trachyceratid-like ammonoids in the lowermost beds (formerly assigned to *T. desatoyense*) actually belong to the genus *Daxatina*, whereas true *Trachyceras* s.s. occurs only in the upper beds. The *desatoyense* Zone will be replaced by a lower informal biozone termed the *Daxatina* beds and an overlying formal range biozone named for the newly described taxon *Trachyceras silberlingi*. Such ongoing works are urgently needed and will no doubt improve correlation of Carnian ammonoid biostratigraphic schemes.

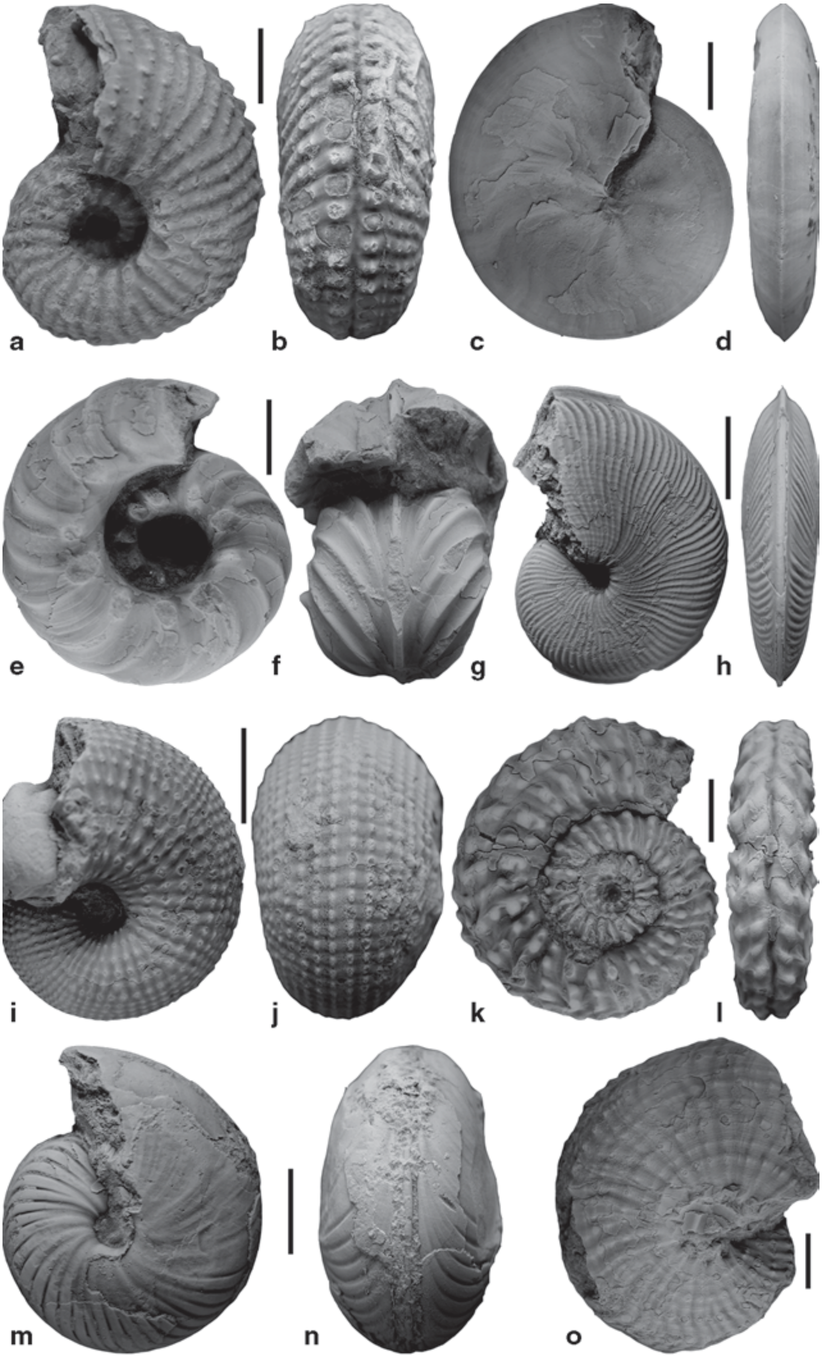

Fig. 13.16 Some characteristic ammonoids of the Carnian (Late Triassic). **a**, **b**, *Trachyceras austriacum* Mojsisovics 1893, JJ338C, Austria. **c**, **d**, *Stolleites tenuis* (Stolley 1911), JJ795C, Spitzbergen. **e**, **f**, *Tropites crassicostatus* Silberling 1959, JJ1330C, Nevada. **g**, **h**, *Discotropites formosus* Smith 1927, JJ566C. **i**, **j**, *Trachysagenites herbichi* Mojsisovics 1893, JJ1336C. **k**, **l**, *Traskites fairbanksi* (Hyatt and Smith 1905), JJ1333C. **m**, **n**, *Pleurotropites gabbi* (Smith 1927), JJ1350C. **o**, *Spirogmoceras shastense* (Smith 1904), JJ1334C. Scale bars = 1 cm. All specimens from JF Jenks coll. **g–o** from N California

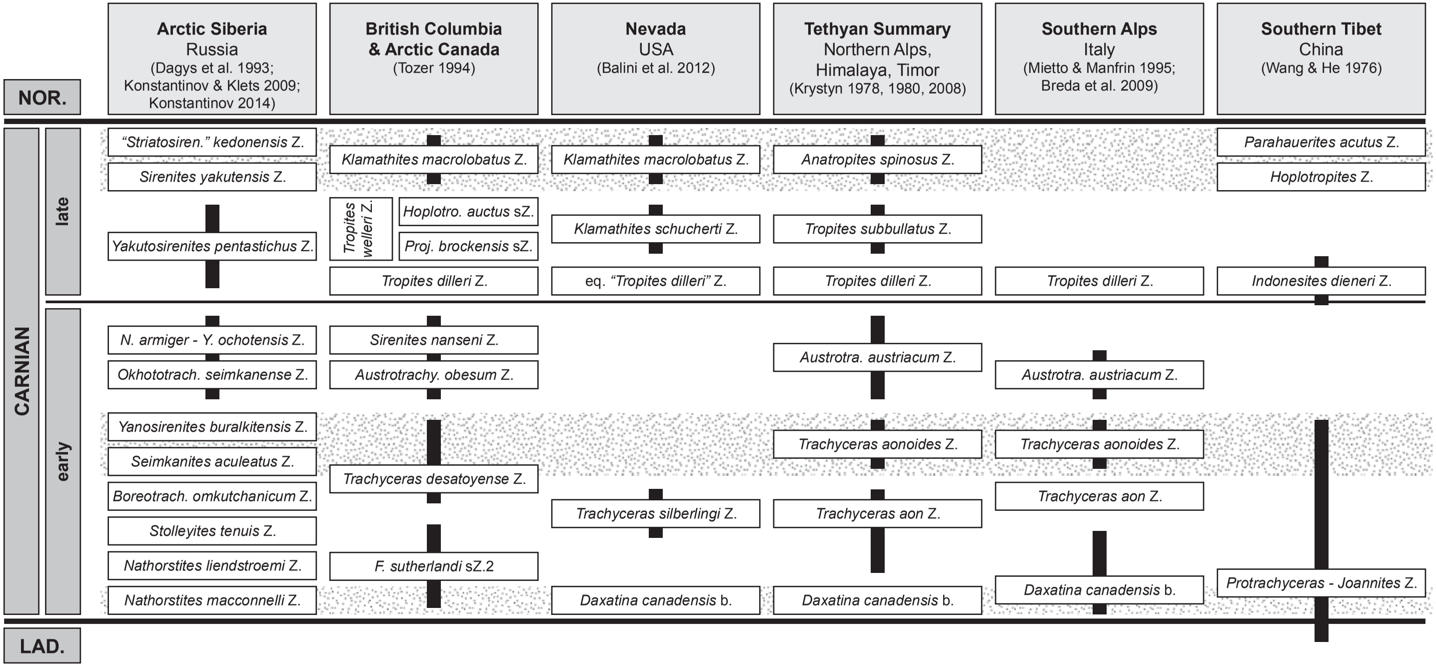

Fig. 13.17 Carnian (Late Triassic) ammonoid zones and correlation (*vertical bars* indicate poorly constrained correlation; *Z* zone, *sZ* subzone, *b* beds)

The biostratigraphic scale that has been most improved in the recent years is surely the Siberian scale (Konstantinov 2014; Konstantinov and Klets 2009; Fig. 13.17). Detailed taxonomic analysis of rather rich collections of Sirenitinae, Trachyceratidae and Arpaditidae (Konstantinov 2006, 2008, 2012) provided support for the subdivision of the Carnian stage into 10 zones. Unfortunately, it is difficult to correlate some of these with the Tethyan and North American zones. In addition, some isolated faunas have also been described (South China: Hao et al. 2003; New Siberian Islands: Bragin et al. 2012; Turkey: Lukeneder and Lukeneder 2014; Japan: Tsujino et al. 2013). Finally, apart from the problems of correlation of the scales from different paleobiogeographic provinces, the least resolved part of the Carnian scale is the Julian/Tuvalian boundary. Thus far, no uncondensed fossil rich sections straddling this boundary have been found. Most of the ammonoid bearing sections have a good Julian or Tuvalian record, but the boundary is often affected by a lithological change.

13.5.2 Norian

The stratigraphic extent of strata assigned to the "Norian" has a contorted history (see Tozer 1984), especially with regard to its stratigraphic relative position with the Carnian. A formal GSSP for the base of the Norian has not yet been designated, but it is commonly placed at the base of the *Stikinoceras kerri* ammonoid zone (Silberling and Tozer 1968) of the North American scale and at the base of the *Guembelites jandianus* zone of the Tethys realm (Krystyn 1980, 1982; Balini et al. 2012b). The leading candidates for the Norian GSSP are Pizzo Mondello in Sicily (Muttoni et al. 2001, 2004; Nicora et al. 2007; Balini et al. 2010a) and Black Bear Ridge on Williston Lake of northeastern British Columbia (Orchard et al. 2001; Orchard 2007a; Zonneveld et al. 2010). Other proposed candidate sections include Silicka Brezova in Slovakia (Channel et al. 2003), Pignola in Italy (Mastandrea et al. 2004), and Kavalaani in Turkey (Gallet et al. 2000).

In terms of ammonoids, the base of the Norian (and of the Lacian) is characterized by the nearly complete disappearance of Tropitidae and the appearance of new members of Juvavitinae (*Dimorphites* and *Guembelites*) and Thisbitidae (*Stikinoceras*). The base of the Alaunian is marked by the appearance of new genera of Cyrtopleuritidae (*Drepanites* and *Cyrtopleurites*). Other members of this family (*Himavatites*, *Mesohimavatites*, *Neohimavatites*) characterize the substage together with certain Haloritinae (*Halorites*) and Thisbitidae (*Phormedites*). The base of the Sevatian is characterized by a decrease in ammonoid diversity and the first occurrence of *Rhabdoceras*, the first heteromorph ammonoid. Other common forms include Haloritinae (*Gnomohalorites* and *Catenohalorites*) and Sagenitidae (*Sagenites quinquepunctatus*). Some characteristic ammonoids of the Norian are illustrated in Fig. 13.18.

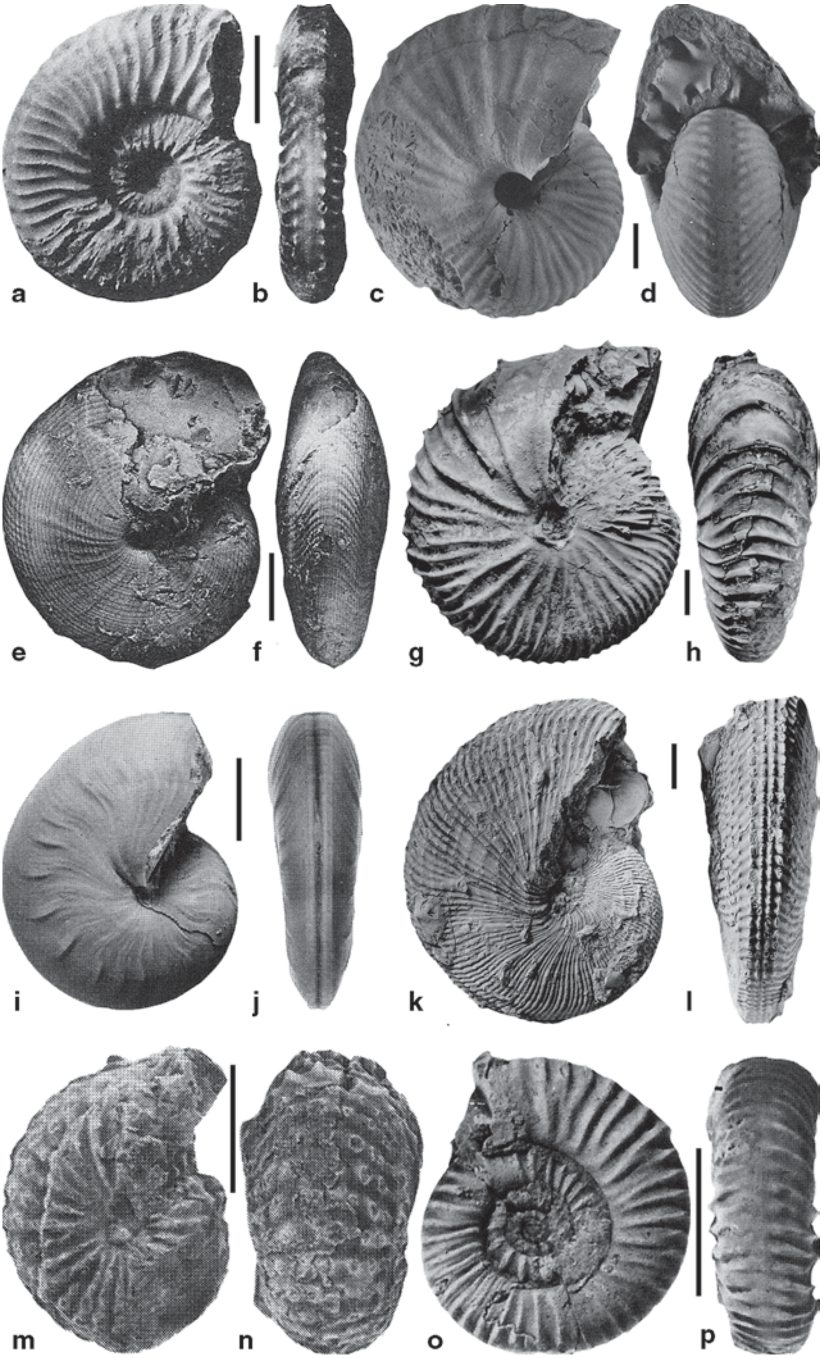

Fig. 13.18 Some characteristic ammonoids of the Norian (Late Triassic). **a**, **b**, *Stikinoceras kerri* McLearn 1930, GSC 9048, holotype (after McLearn 1960, pl. 3, Figs. 2a–c). **c**, **d**, *Guembelites jandianus* Mojsisovics 1896, 05/50/5 (after Krystyn 1982, tab. 13, Figs 1a, b). **e**, **f**, *Malayites daw-*

As with the Carnian, there are relatively few Norian ammonoid zonal schemes (Fig. 13.20), and those possessing the highest resolution are again in Canada (Tozer 1994) and Tethys (Krystyn 1980, 1982, 2008). Correlation of regional scales is often good because of the worldwide distribution of several genera, which often makes faunal composition of coeval zones very similar even though their index taxon may be different. This is also true for Wang and He's (1976) scale (Fig. 13.20), which reflects an independent nomenclature, since it was developed earlier than the Tethyan scale.

The biostratigraphy of the earliest Norian is under study in Sicily, Nevada and Canada (Black Bear Ridge) within the framework of the activities of the Carnian/Norian boundary Working Group of the STS. The twofold subdivision of the *G. jandianus* zone of the Tethys has been formalized by Balini et al. (2012b) as represented by the *Dimorphites noricus* and *D. selectus* subzones. Also of notable interest, an integrated bed-by-bed study of the latest Carnian/earliest Norian transition within the Luning Formation is currently underway in Nevada's Berlin Ichthyosaur State Park (Balini et al. 2014), type locality of the latest Carnian *macrolobatus* zone. Although the rich ammonoid faunas within this interval were described by Silberling (1959), recent studies have also documented never before reported rich conodont faunas as well as numerous occurrences of *Halobia* in these transition beds. These occurrences, together with the rich ammonoid record, permit correlation of the succession with that of British Columbia and hopefully, will contribute to the definition of the GSSP for the Norian stage.

For the most part, because of the long duration of the Norian, sedimentary successions documenting a significant part of this stage are extremely rare. Other than the Pardonet Formation at Williston Lake (northeastern British Columbia; Tozer 1994) all other fossiliferous successions in the world document only relatively small intervals of the Norian. This is also true for the Hallstatt Limestone condensed sections in the Northern Alps, Turkey and Timor (e.g., Tatzreiter 1978, 1981; Krystyn 1980, 2008). In addition to the ammonoid bearing successions shown in Fig. 13.20, some isolated ammonoid faunas have also been described from other areas (e.g., Mexico: González-León et al. 1996; Gómez-Luna and Martinez-Cortés 1997; Lucas and Estep 1999; Iran: Seyed-Emami et al. 2009). Finally, Lucas et al. (2012) reviewed the Carnian/Norian boundary age and marine/terrestrial correlation.

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soni McLearn 1937b, GSC 8836, holotype (after McLearn 1960, pl. 17, Figs. 8a, b). **g**, **h**, *Juvavites magnus* McLearn 1940, GSC 8818, holotype (after McLearn 1960, pl. 9, Figs. 1a–c). **i**, **j**, *Drepanites rutherfordi* McLearn 1937b, GSC 28853, hypotype (after Tozer 1994, pl. 128, Figs. 5a–c). **k**, **l**, *Mesohimavatites columbianus* (McLearn 1939), GSC 9265, hypotype (after McLearn 1960, pl. 5, Figs. 6a, b). **m**, **n**, *Gnomohalorites cordilleranus* Tozer 1979, GSC 32277, holotype (after Tozer 1994, pl. 145, Figs. 4a–c). **o**, **p**, *Lissonites canadensis* Tozer 1979, GSC 28932, holotype (after Tozer 1994, pl. 146, Figs. 1a–c). Scale bars = 1 cm. **c-d** from the Himalayas (Nepal), all others from British Columbia

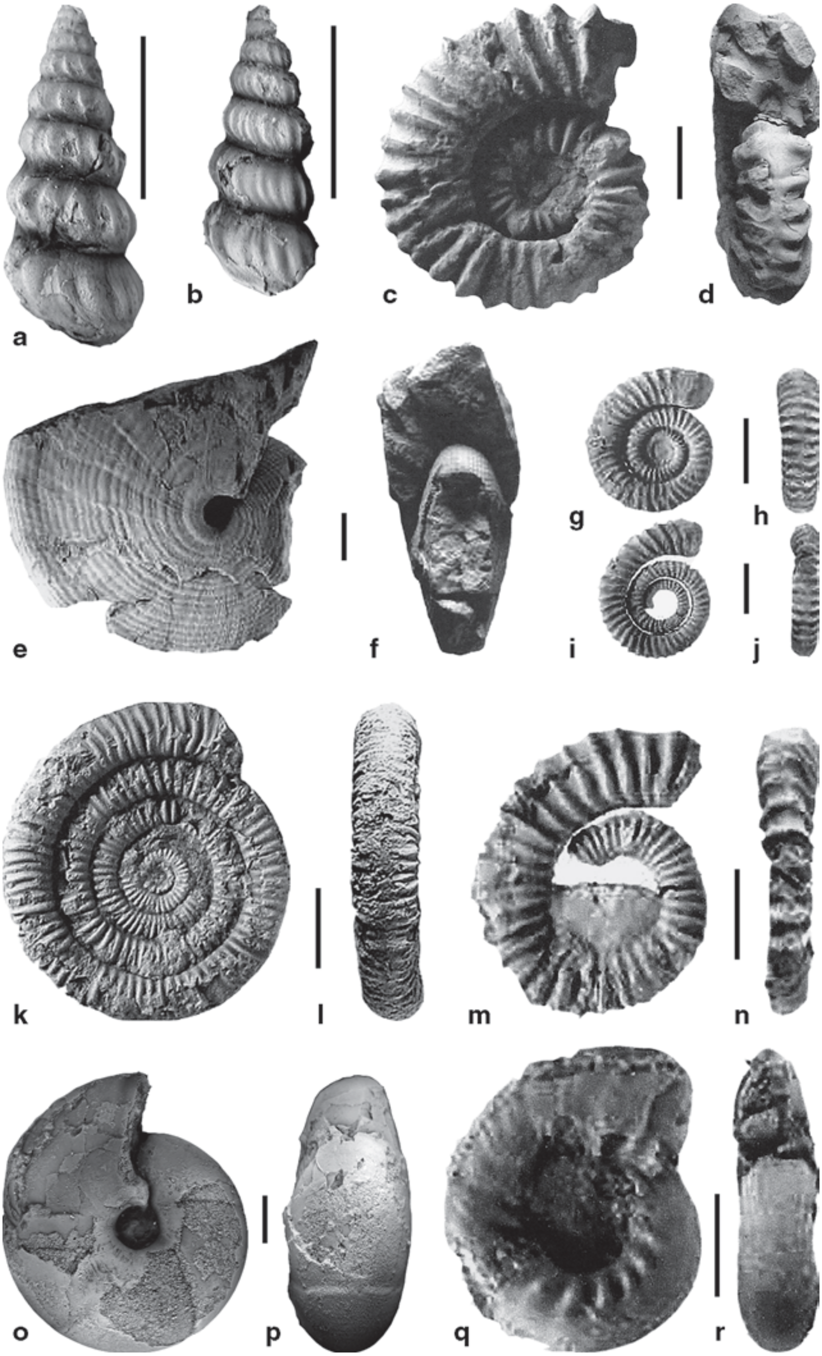

Fig. 13.19 Some characteristic ammonoids of the Rhaetian (Late Triassic) of Nevada. **a**, *Cochloceras amoenum* Mojsisovics 1893, JJ1296C. **b**, *Cochloceras amoenum* Mojsisovics 1893, JJ1297C. **c**, **d**, *Choristoceras robustum* Taylor and Guex 2002, NWMNH No. 25515, holotype (after Taylor and Guex 2002, pl. 4:4–5). **e**, **f**, *Sagenites minaensis* Taylor and Guex 2002, NWMNH No. 25274, holotype (after Taylor and Guex 2002, pl. 3:1–3). **g**, **h**, *Choristoceras shoshonensis* Taylor and

13.5.3 Rhaetian

The youngest Triassic stage, the Rhaetian, has not yet been formally defined by a GSSP, but its base is currently placed at the FAD of the conodont *Misikella posthernsteini* at Steinbergkogel near Hallstatt in Austria (Krystyn et al. 2007b, d; Krystyn 2008, 2010). This placement either coincides with or is very close to the base of the *Paracochloceras amoenum* ammonoid zone, which produces a so-called "long" Rhaetian comprised of two or three ammonoid zones. Consequently, the youngest substage of the Norian, the Sevatian, is thereby reduced to one ammonoid zone. The *posthernsteini* conodont event follows relatively closely above the FO of several ammonoid taxa (*Tragorhacoceras occultus*, *Rhaetites gigantogaleatus*, *Stenarcestes ptychodes*), all common and helpful tools for determining proximity to the Norian/Rhaetian boundary in the Tethys Realm (Krystyn 2008).

Because of its very low ammonoid diversity, the Rhaetian has sometimes been included in the Norian by several workers (e.g., Tozer 1984, 1988; but for an opposite view, see e.g., Ager 1987; Shevyrev 2006). Nevertheless, it is characterized by the appearance of sagenitid ammonoids of the *Sagenites reticulatus* group and the heteromorphic ammonoid *Paracochloceras suessi* and its closely allied genus *Cochloceras*, as well as the disappearance of the genus *Metasibirites* (Krystyn et al. 2007b; Krystyn 2008). Some characteristic ammonoids of the Rhaetian are illustrated in Fig. 13.19.

In view of its poor ammonoid record, there are also very few zonal schemes for the Rhaetian (Fig. 13.20). Important sections occur in Canada (Tozer 1994) and Tethys (Northern Alps: Krystyn 1987, 2008). Additional ammonoid faunas have also been described from Timor (Krystyn and Wiedmann 1986), Mexico (González-León et al. 1996; Gómez-Luna and Martinez-Cortés 1997; Lucas and Estep 1999), Oregon (Taylor and Guex 2002), and southern Tibet (Yin et al. 2007). The best and most complete succession in the world is in New York Canyon (Nevada), where five zones and horizons have been recognized in the same succession (Taylor and Guex 2002) just below the Triassic/Jurassic boundary.

Guex 2002, NWMNH No. 25387, holotype (after Taylor and Guex 2002, pl. 3:14–15). **i**, **j**, *Choristoceras shoshonensis* Taylor and Guex 2002, NWMNH No. 25388, (after Taylor and Guex 2002, pl. 3:16–17). **k**, **l**, *Cycloceltites tozeri* Taylor and Guex 2002, NWMNH No. 25362, holotype (after Taylor and Guex 2002, pl. 4:7–8). **m**, **n**, *Vandaites newyorkensis* Taylor and Guex 2002, NWMNH No. 25412, holotype (after Taylor and Guex 2002, pl. 3:11–13). **o**, **p**, *Arcestes nevadanus* Gabb, 1870, JJ1301C. **q**, **r**, *Gabboceras delicatum* Taylor and Guex 2002, NWMNH No. 25354, holotype (after Taylor and Guex 2002, pl. 3:9–10). Scale bars = 1 cm. **a**, **b**, **o**, **p**: JF Jenks coll.; all others: Northwest Museum of Natural History

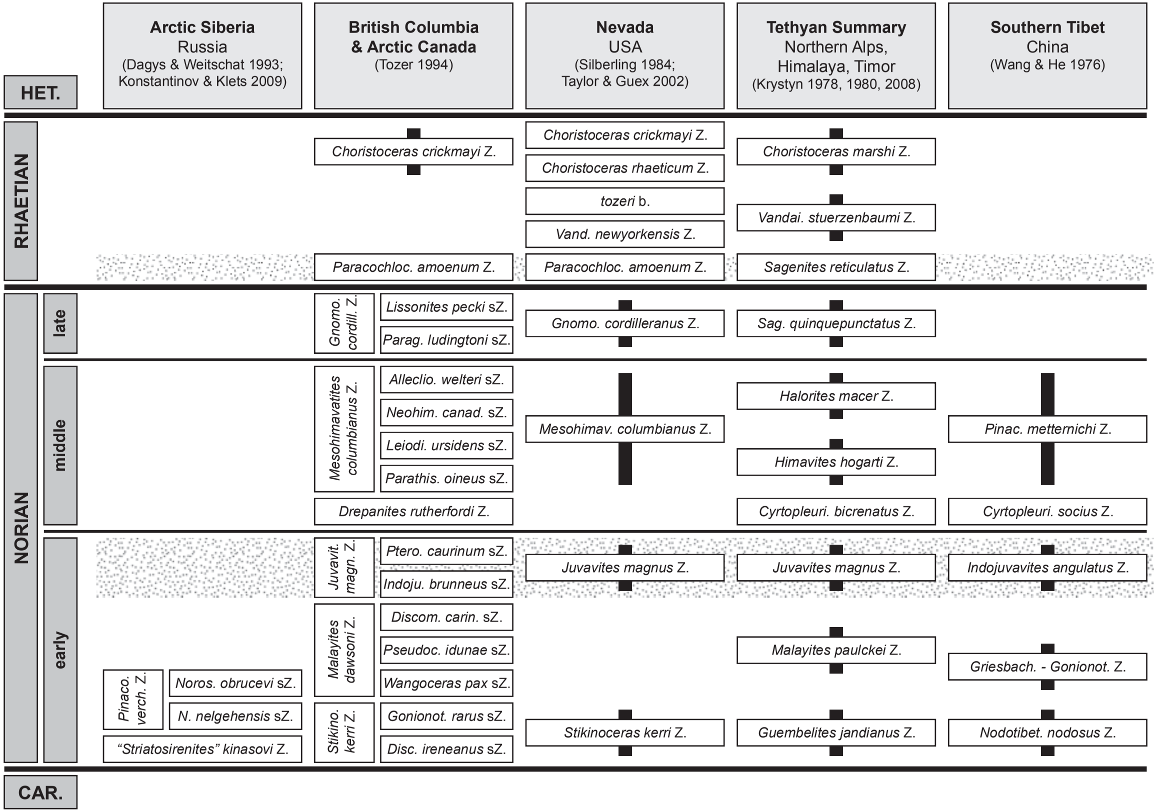

Fig. 13.20 Norian and Rhaetian (Late Triassic) ammonoid zones and correlation (*vertical bars* indicate poorly constrained correlation; *Z* zone, *sZ* subzone, *b* beds)

13.6 Conclusions

Our review of Triassic ammonoid biostratigraphy (historical development and current state of knowledge) demonstrates that the correlation of ammonoid zones through time and space is very irregular. This situation reflects the complex and very long history of Triassic ammonoid biochronology, which has been conditioned by the evolutionary history of ammonoids in space and time, such as biogeographic endemism/ cosmopolitanism. For instance, latitudinal differentiation among ammonoids varied significantly during the Triassic, thus making clear and unambiguous global correlation more difficult at times (for more details, see Dagys 1988; Brayard et al. 2006, 2007b, 2015). Furthermore, the personalities of some ammonoid workers as well as their respective theories and practices regarding taxonomy have produced some rather strongly diverging opinions and approaches (e.g., Brack and Rieber 1996; Mietto et al. 2004), which sometimes may have hindered more accurate and dependable correlation. Famous examples such as *Ceratites binodosus* (Hauer) and *Ceratites reitzi* Böckh have been reviewed by Balini et al. (2010b); Tozer (1971) has also emphasized some of these taxonomic problems.

By tradition, ammonoids have always been regarded as the best marine guide fossils for the Triassic System (Mojsisovics et al. 1895; Tozer 1984; Balini et al. 2010b; Lucas 2010b, 2013). However, in Triassic biostratigraphic studies, there are two different (but not conflicting) approaches to the use of ammonoids (and other fossils) as time markers: one is based on bioevents (FADs and LADs), and the other on coexistences. The former is often linked to a body of strata and it fits well with the concept of GSSPs, which are defined by such bioevents that lead to continuous, interval zones, often focused on a single section. The latter is a more abstract concept, independent of rocks, and characterized by discrete, association (or assemblage) biozones, often encompassing as many sections as possible. This dual concept may sometimes confuse correlation and dating of sections if not clearly defined. Nevertheless, quantitative methods exist for treating both data types that lead to robust biozonation (Monnet et al. 2015). Because bioevents (FADs and LADs) are biased by many factors (preservation, sampling, etc.; see Monnet et al. 2011, 2014), caution should be exercised when using them to define biozones and GSSPs in order to avoid as much as possible the problems related to the non-negligible proportion of diachronic taxa (see e.g., Monnet and Bucher 2002, 2005b, 2007). Because of the tendency that began in the last few decades to define GSSPs by the FADs of conodonts, it is here stressed that such problems hold not only for ammonoids, but for all fossils including conodonts; Shevyrev 2006; Goudemand et al. 2012; Zhang et al. 2014) (see also discussion in Lucas 2013).

The resolution of the various Triassic ammonoid biochronological schemes is highly variable (as is the duration of the stages). This variability is well illustrated by the average duration of ammonoid biochronozones (ca. 0.74 Myr for the zone level), which varies from 60 kyr for the Smithian to over 0.43 Myr for the Anisian to 2.70 Myr for the Norian. Thus, resolution is seen to not only be variable, but it also obviously decreases significantly during the Triassic. Although this decline can be readily correlated with the decreasing turnover of ammonoids during the Triassic (see Brayard et al. 2009), it is also probably influenced somewhat by the relative lack of studies in the Late Triassic. These values are comparable in magnitude with those of Milankovitch cycles (20 kyr for the precession cycles, 100 and 400 kyr for the eccentricity cycles; see Brack et al. 1996; Szurlies 2007; Ikeda et al. 2010; Tanner 2010b) and with the validated magnetozones (mean reversal of 250 kyr for the Early–Middle Triassic; see Hounslow and Muttoni 2010).

The current approach in biochronostratigraphy tends toward global correlation and integrated studies, which is well exemplified by the definition of the GSSPs. Indeed, the definition of GSSPs emphasizes the reproducible correlation of events (e.g., various fossil groups, magnetostratigraphy, and isotope analysis) by cross-comparison (see e.g., Brack et al. 2005; Mietto et al. 2012; Hillebrandt et al. 2013). In this context, the role of ammonoids for the definition of Triassic stages and substages has thus been further corroborated and enlarged. The comparison of ammonoid biostratigraphy to conodont, radiolarian, pelagic bivalve and palynomorph biostratigraphies demonstrates, without doubt, that the ammonoids are the fossil group with the potential to reach the highest temporal resolution within Triassic marine environments.

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Chapter 14
Ammonoid Biostratigraphy in the Jurassic

Günter Schweigert

14.1 Introduction

The diversity of ammonoids in the Jurassic and their rapid changes through time have been recognized early in the history of geology and stratigraphy. Early famous stratigraphers such as William Smith (1769–1839), Alcide d'Orbigny (1802–1857) and, above all, Albert Oppel (1831–1865) subsequently improved and refined the subdivision of the Jurassic System. Since all of them and many of their successors worked in Europe, biostratigraphic studies focused on the Jurassic of this continent. Alcide d'Orbigny and Albert Oppel studied not only ammonites and their successions in selected sections but also created a chronological time scale and introduced the terms "stage" and "zone" which are still used today not only in the Jurassic but throughout the whole Phanerozoic (d'Orbigny 1842–1851, Oppel 1853, 1856–1858). It should be noted here that Oppel's zones are assemblage zones, characterized by a set of taxa indicative for this interval. Later, other definitions of zones such as the first appearance of a species (FAD) besides several others concepts have been used when new zones were added. As a result of these different definitions and the historical process, Jurassic ammonite zones (regional and standard zones as well) a priori must have very different equivalent durations.

Besides a more or less well-established standard chronozonation there exist numerous further independent biostratigraphical successions in almost every faunal province or even in temporarily distinguishable sub-provinces. For a quick overview the comprehensive compilation of Jurassic successions and faunas by Arkell (1956) is still fundamental; however, the knowledge about them has increased enormously since then. The Jurassic standard zonation is basically founded on European successions, due to the long historical tradition resulting in a huge amount of available data and, not the least, the enormous richness of the faunas.

G. Schweigert (✉)
Staatliches Museum für Naturkunde, Rosenstein 1, 70191 Stuttgart, Germany
e-mail: guenter.schweigert@smns-bw.de

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Due to the fact that Jurassic deposits were first described exclusively from Europe, the best refinement was achieved in this region. However, different methods exist on how ammonoid biostratigraphy in the Jurassic can be studied. Some scientists focused on single taxa as guide fossils showing their spatial distribution and their vertical range in sections. This may allow some adequate time correlation, but their ranges in different sections may differ due to palaeoecological, preservational or just collection biases. On generic level, such correlation is easily possible across wider regions, whereas at specific level this is mostly hampered by the provincialism mentioned above.

Today, ammonite faunas are usually studied as a whole, precisely sampled bed-by-bed, with highest possible precision. Even in highly condensed sections like in the Middle Jurassic Inferior Oolite of England and France, or in the Upper Jurassic Ammonitico Rosso of the Calcareous Alps, a succession of faunas can often be recognized. Due to the fact that deposition of sediments—including the fossils—is usually discontinuous, we can achieve a highly precise succession of faunas. The late John H. Callomon (1928–2010) was the founder and master of the method of separating "biohorizons", and he was followed by many Jurassic stratigraphers worldwide (e.g., Callomon 1994, 1995; Dommergues et al 1994; Cariou and Hantzpergue 1997; Page 2003, 2008, Page et al. 2009; Schweigert 2007; Hillebrandt and Krystyn 2009; Meister 2010; Dietze et al. 2012, among numerous others). A biohorizon is defined as the shortest distinguishable biostratigraphic subdivision (see Rogov et al. 2012 for a review). Its time resolution is therefore the highest one based on biostratigraphic grounds; an average duration of 165 ka per biohorizon was estimated for the Late Jurassic (Schweigert 2006). An ammonite biohorizon is basically restricted to a limited area. Combined with the occurrence of widespread well-recognizable guide-fossils it is possible to correlate some of these biohorizons at least with neighbouring faunal provinces and, hopefully, step-by-step worldwide. During the past decades, such high-resolution biostratigraphic studies with the aim of establishing standard chronostratigraphic schemes and correlations focused on the stage boundaries. However, world-standard sections with definite bed markers (GSSP = Global Boundary Stratotype Section and Point) have still not been established for some of the Jurassic stages; therefore the Toarcian, Callovian, Oxfordian, Kimmeridgian and Tithonian stages still lack a proper definition. The reasons for obvious difficulties in finding adequate sections are many and varied. One of the principle difficulties lies in the problems of correlation between distant faunal provinces, e.g. between the Tethyan Realm and the Circum-Pacific (see Westermann 1992 for a comprehensive compilation).

Recently, high-resolution ammonoid biostratigraphy is still the most important tool for correlation in marine Jurassic deposits. Apart from methods of quantitative stratigraphy (see Monnet et al. 2015a for a review), numerous other methods (e.g., magnetostratigraphy, sequence stratigraphy, cyclostratigraphy, geochemical and isotopic data, radiometric dating) and biostratigraphic studies of other groups (dinoflagellates, radiolarians, pollen and spores) provide additional data for calibrations and refinements of the Jurassic standard time scale (e.g., Sadler 2004, Palfy 2007, Ogg and Hinnov 2012). These additional methods may help in dating Jurassic sediments even when there are no ammonoids available, like in terrestrial deposits. In the following, only a brief generalized outline of evolutionary and biogeographically forced trends in Jurassic ammonoid faunas and involved problems is provided.

14.2 Early Jurassic

The Early Jurassic (beginning at 201.3 ± 0.6 Ma after Ogg and Hinnov 2012; for its biozonation see Table 14.1) starts per definition and accordance of the International Stratigraphic Commission with the oldest member of the genus *Psiloceras*, *P. spelae tirolicum* Hillebrandt and Krystyn (Fig. 14.1a), in the ratified GSSP of the Jurassic/Triassic boundary in the Kuhjoch section (Austria) of the Northern Calcareous Alps. *Psiloceras spelae* has been recognized in regions far away from that section, such as Peru and Nevada (Hillebrandt and Krystyn 2009). Rather soon after its appearance the geographically widespread genus *Psiloceras* and its early descendants entered shallower areas along the Tethyan shelves. This conquering of previously unsettled habitats caused both an enormous diversification and provincialism. The ammonite faunas of the oceans and adjacent epicontinental seas are strikingly distinct but occasionally linked by immigrants that migrated in both ways and thus allow correlation (e.g. late Hettangian *Schlotheimia marmorea*). The Sinemurian Stage is well-known worldwide by the abundance of large-sized Arietitinae (*Arietites*, *Coroniceras*: Fig. 14.1e). Sexual dimorphism in ammonoids is poorly studied yet in the Early Jurassic; hence their systematic treatment mainly follows traditional morphological classification. Juraphyllitidae (Fig. 14.1b) become widespread and rather diverse in the Pliensbachian. Juraphyllitidae, Phylloceratidae and Lytoceratidae occasionally settled shelf areas of the Tethys as well (e.g., Meister 1989, Meister and Stampfli 2000). Echioceratidae, Polymorphitidae, Eoderoceratidae and Phricodoceratidae represent important guide forms in the late Sinemurian and early Pliensbachian. A striking long-term event is the spread of the Boreal Amaltheidae (*Amaltheus*, *Pleuroceras*: Fig. 14.1d) far to the South, probably caused by palaeoclimatic reasons and fostered by cold currents (e.g., Braga et al. 1988). A contrary migration is the short-term event in the late Early Pliensbachian, when *Prodactylioceras davoei* (Sowerby) spread over extra-alpine Europe. The first representatives of Boreal Amaltheidae arrived in the earliest late Pliensbachian, when typical Tethyan ammonoids such as lytoceratids were still abundant (Schlatter 1991). Step by step this mixed fauna in Central Europe is replaced by the Boreal immigrants, which at last predominate by far and comprise up to 100 % of the total ammonite fauna. Then, around the beginning of the Toarcian, amaltheids became suddenly extinct and were actually replaced by Dactylioceratidae and Hildoceratidae (Fig. 14.1c), both of Tethyan affinity. Soon later, in the Tethyan Realm the almost worldwide recognizable Falciferum Anoxic Event—best known from the Posidonia Shale Fossil-Lagerstätte of Holzmaden (e.g., Röhl et al. 2001)—affected the Juraphyllitidae, which became extinct. During later Toarcian times, ammonite faunas rapidly recovered and became diverse again, caused by a mixture of elements probably adapted

Table 14.1 Bio/Chronozonation in the Submediterranean Early Jurassic. (modified after Cariou and Hantzpergue 1997) and some selected ammonite taxa, which are used as index species or which are important for long-distance correlations

Stage	European biozonation	Important taxa
Toarcian	Aalensis	*Cotteswoldia aalensis*
	Pseudoradiosa	*Dumortieria pseudoradiosa*
	Dispansum	*Phlyseogrammoceras dispansum*
	Bonarelli	*Esericeras eseri*
	Variabilis	*Haugia variabilis*
	Bifrons	*Hildoceras sublevisoni*
	Serpentinum	*Harpoceras falciferum*
	Tenuicostatum	*Dactylioceras semicelatum*
Pliensbachian	Spinatum	*Pleuroceras solare*
	Margaritatus	*Amaltheus margaritatus*
	Davoei	*Prodactylioceras davoei*
	Ibex	*Tragophylloceras ibex*
	Jamesoni	*Phricodoceras taylori*
Sinemurian	Raricostatum	*Leptechioceras meigeni*
	Oxynotum	*Gleviceras doris*
	Obtusum	*Asteroceras obtusum*
	Turneri	*Caenisites turneri*
	Semicostatum	*Coroniceras lyra*
	Bucklandi	*Coroniceras rotiforme*
Hettangian	Angulata	*Schlotheimia marmorea*
	Liasicus	*Alsatites liasicus*
	Planorbis	*Psiloceras spelae*

to warm (e.g., *Frechiella*, *Porpoceras*, *Hammatoceras*), temperate (e.g., *Grammoceras*, *Pleydellia*, *Cotteswoldia*) and cooler waters (*Pseudolioceras*). Interestingly, in the late Toarcian both lytoceratids and phylloceratids are still widespread and diverse not only in pelagic settings but also in shelf habitats.

70226, diameter 68 mm. **c** *Hildoceras sublevisoni*, early Toarcian, Bifrons Zone, Feuguerolles-sur-Orne, France, SMNS 70228, diameter 70 mm. **d** *Pleuroceras solare* (Phillips), late Pliensbachian, near Pfronten, Northern Calcareous Alps, SMNS 70227, diameter 32 mm. **e** *Coroniceras* aff. *rotiforme* (Sowerby), early Sinemurian, Bucklandi Zone, Wellendingen, S Germany, SMNS 70225, diameter 210 mm. Photograph of Fig. **a** by courtesy of A. v. Hillebrandt, Berlin, all others by G. Schweigert, Stuttgart

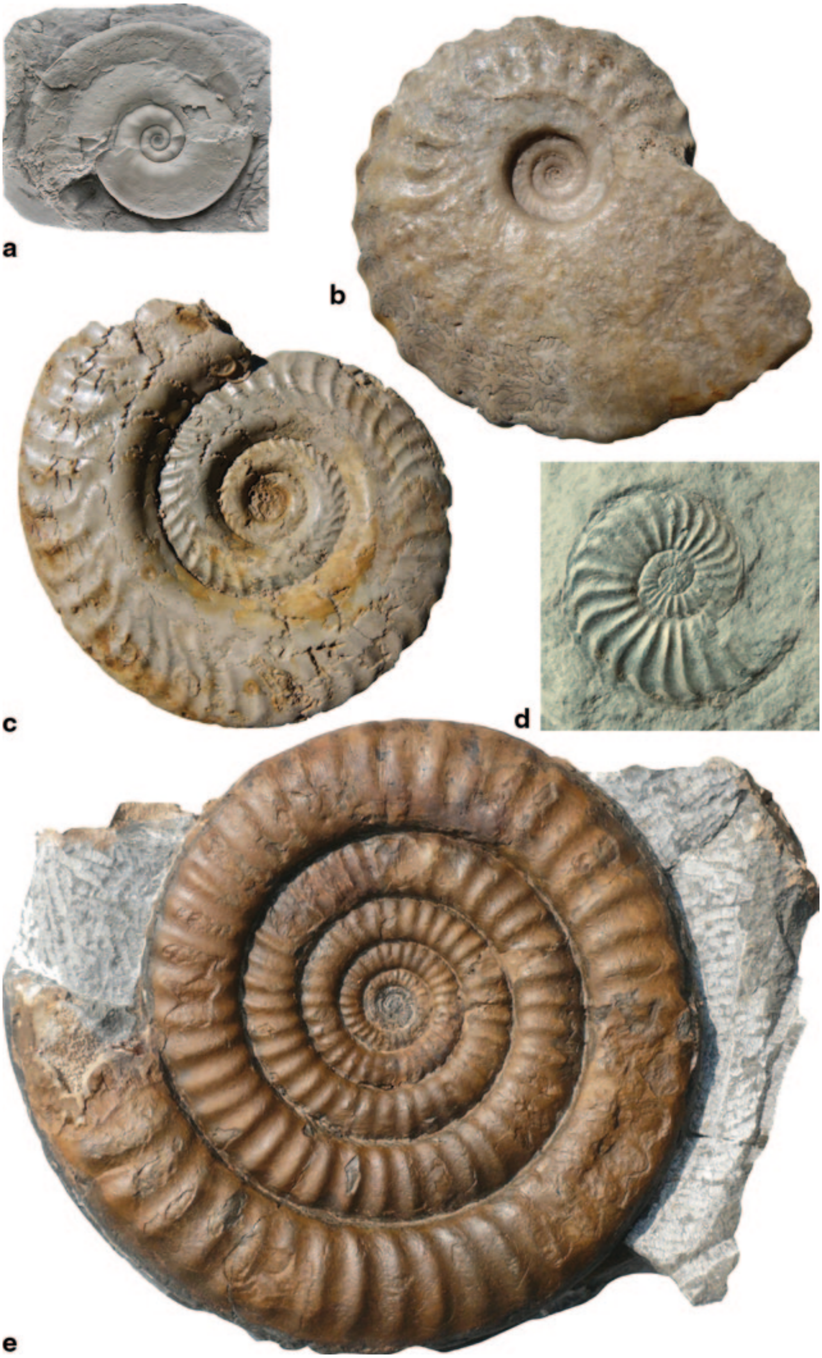

Fig. 14.1 Early Jurassic ammonoids. **a** *Psiloceras spelae tirolicum* Hillebrandt and Krystyn, Kuhjoch, Austria [GSSP of the Triassic/Jurassic boundary], NHMW 2009z0009, diameter 12 mm. **b** *Tragophylloceras ibex* (Quenstedt), early Pliensbachian, Fresney-le-Puceux, France, SMNS

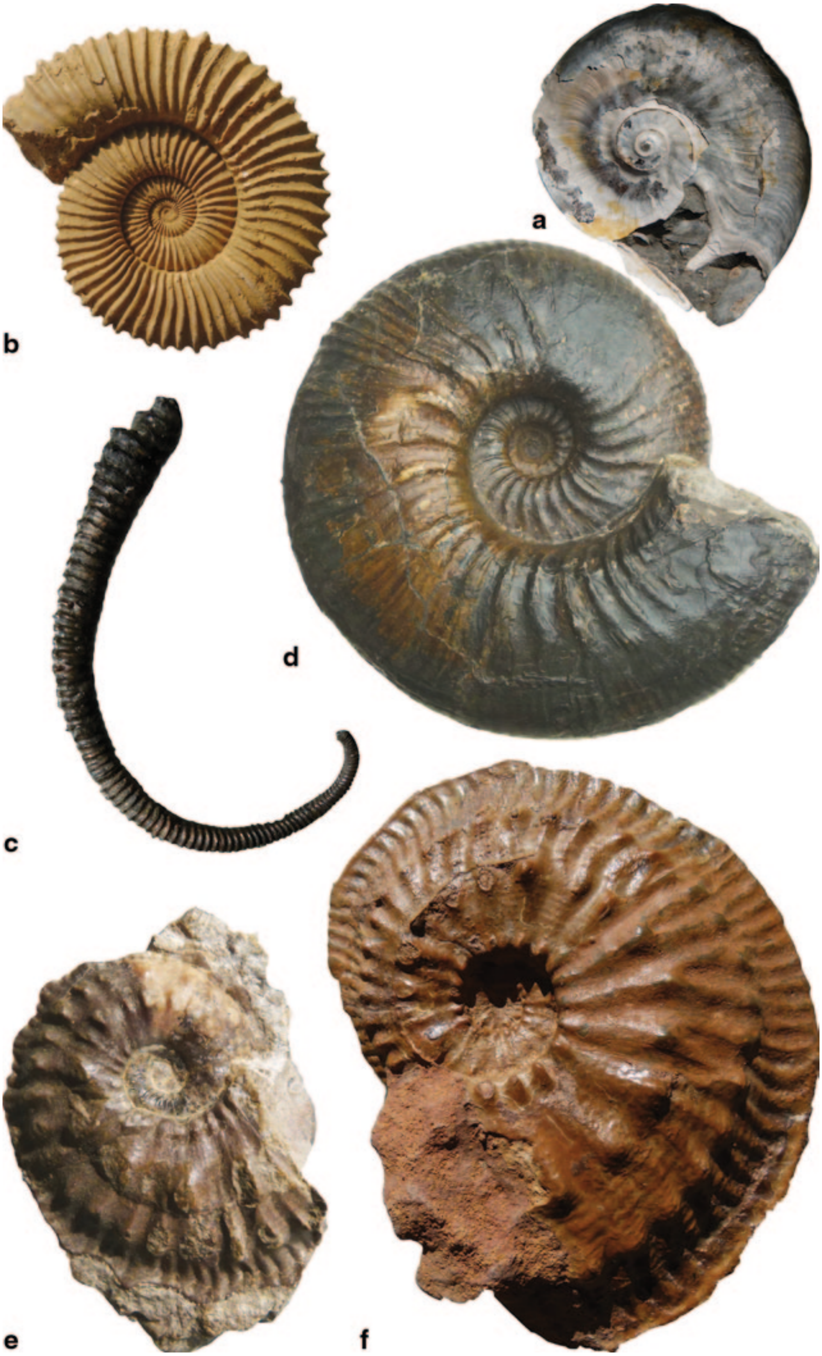

Fig. 14.2 Middle Jurassic ammonoids. **a** *Leioceras opalinum* (Reinecke), microconch, early Aalenian, Opalinum Zone, Heinigen, S Germany, SMNS 60999, diameter 57 mm. **b** *Tmetoceras scissum* (Benecke), middle Aalenian, Murchisonae Zone, Chideock, S England, RBC 509, diameter

14.3 Middle Jurassic

The Middle Jurassic starts with the FAD of *Leioceras opalinum* (Fig. 14.2a) in the GSSP of its lowest stage, the Aalenian, at Fuentelsaz (Spain) (Cresta et al. 2001). Its biozonation is shown in Table 14.2. In the Aalenian, leioceratids are worldwide distributed forming a phyletic lineage which ranges until the earlier Bajocian. Endemism is rare within this family—as an example we mention the diversification of the oxyconic genus *Staufenia* (Rieber 1963). Except for the earliest Aalenian, both lytoceratids and phylloceratids become extremely rare in epicontinental habitats. Hammatoceratids occur mainly in the Tethyan Realm, but some of them temporarily entered Submediterranean and Andean shelves in larger numbers. Hammatoceratids gave rise to sonninids, which diversified in the Bajocian. Spiroceratids (Fig. 14.2c) appear in the late Bajocian Niortense Zone and became extinct in the Parkinsoni Zone. They have uncoiled shells, an almost cosmopolitic distribution, short vertical ranges, and are therefore perfect guide fossils (Dietl 1978). Possible ancestors are represented by the genus *Tmetoceras* (Donovan et al. 1981) (Fig. 14.2b) which shares not only some morphological aspects but also the extremely wide palaeogeographic distribution. According to another theory spiroceratids evolved from *Strenoceras*. A second, apparently independent lineage of uncoiled ammonoids originates in the late Bathonian, represented by *Acuariceras* and *Paracuariceras*. Possibly all of these heteromorphic ammonoids have had a pseudoplanktic life style which caused their worldwide distribution (Dietl 1978).

In the Bajocian, Cardioceratidae evolved in the Arctic and, after the connection of the Arctic Sea with the southern areas by the spreading of the Proto-Atlantic in the late Bathonian, this Boreal family rapidly entered the Submediterranean Province and diversified significantly. One of the most significant ammonite taxa of this family for the base of the Callovian Stage is *Kepplerites keppleri* (Fig. 14.2d). Subsequently, Macrocephalitidae evolved in the western Palaeopacific and spread westwards via the Tethyan Ocean. They reached Central Europe in the late Bathonian and became extremely common in the early Callovian which is why they have long been considered as typical Callovian ammonites (Callomon et al. 1987, 1992). Further Tethyan elements such as strigoceratids, parkinsoniids, stephanoceratids, peltoceratids and reineckeids can be used for biostratigraphic purposes in certain intervals as well. For example, the Bathonian/Callovian boundary is well-marked by the change from the *Phlycticeras scheurlenae* chronospecies into the *Phlycticeras mexicanum* chronospecies (Schweigert and Dietze 1998, Figs. 2E, F). In the field, however, such highly diagnostic forms are too rare to be used successfully, possibly except of the Andean Realm of Chile, where they occur more abundantly. Other

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62 mm. **c** *Spiroceras orbignyi* (Baugier and Sauzé), late Bajocian, Niortense Zone, Aichelberg, S Germany, SMNS 61813/6, length ca. 160 mm. **d** *Kepplerites keppleri* (Oppel), early Callovian, Herveyi Zone, Albstadt-Pfeffingen, S Germany, SMNS 62951, diameter 150 mm. **e** *Phlycticeras mexicanum* Sandoval & Westermann, early Callovian, Sierra de Varas, Chile, SMNS 70229, diameter 35 mm. **f** *Phlycticeras mexicanum* Sandoval & Westermann, early Callovian, Herveyi Zone, Geisingen, S Germany, SMNS 60712, diameter 100 mm. All photographs by G. Schweigert, Stuttgart

Table 14.2 Bio/Chronozonation in the Middle Jurassic showing partly different zonal schemes due to moderate faunal provincialism. (modified after Cariou and Hantzpergue 1997) and some selected ammonite taxa which are used as index species or are important for long-distance correlations

Stage	Tethyan biozonation	Subboreal biozonation	Important taxa
Callovian	Lamberti		*Quenstedtoceras lamberti*
	Athleta		*Peltoceras athleta*
	Coronatum		*Phlycticeras pustulatum*
	Anceps	Jason	*Kosmoceras jason*
		Calloviense	*Sigaloceras calloviense*
		Koenigi	*Proplanulites koenigi*
	Bullatus	Herveyi	*Govericeras toricelli*
			Kepplerites keppleri
Bathonian	Discus		*Clydoniceras discus*
	Retrocostatum	Orbis	*Epistrenoceras histricoides*
	Bremeri	Hodsoni	*Cadomites bremeri*
	Morrisi		*Morrisiceras morrisi*
	Subcontractus		*Tulites subcontractus*
	Progracilis		*Procerites progracilis*
	Aurigerus	Tenuiplicatus	*Parkinsonia convergens*
	Zigzag		*Cadomites exstinctus*
Bajocian	Parkinsoni		*Strigoceras truellei*
	Garantiana		*Spiroceras annulatum*
	Niortense		*Spiroceras orbignyi*
	Humphriesianum		*Stephanoceras macer*
	Sauzei/Propinquans		*Emileia brocchii*
	Laeviuscula		*Witchellia laeviuscula*
	Ovale		*Fissilobiceras ovale*
	Discites		*Euaptetoceras amplectens*
Aalenian	Concavum		*Haplopleuroceras subspinatum*
	Bradfordensis		*Brasilia bradfordensis*
	Murchisonae		*Tmetoceras scissum*
	Opalinum		*Leioceras opalinum*

Haploceratoidea, such as Oppeliidae and Hecticoceratidae, became predominant in the tropical seas of the late Middle Jurassic. Their systematic treatment is likewise chaotic (e.g., Elmi 1967).

In the late Callovian Cardioceratidae became a predominant family both in the extra-alpine European and Circum-Boreal sequences (Callomon 1985), possibly due to palaeoclimatic reasons and/or a noticeable sea-level rise (Wierzbowski and Rogov 2011), somewhat similar to the abovementioned cold pulse in the late Pliensbachian. Species of this family (*Quenstedtoceras lamberti*, *Cardioceras mariae*) are therefore often used as zonal and subzonal index around the Callovian/Oxfordian boundary (e.g., Fortwengler et al. 1997). However, their enormous intraspecific variation (see De Baets et al. 2015 for a more general review of this phenomenon) hampers a secure dating based on cardioceratids alone, which is one of the reasons, why a GSSP for the Oxfordian Stage, with the exact boundary between the Middle and Late Jurassic, has not been ratified yet (Page et al. 2009).

14.4 Late Jurassic

At first glance, ammonoid biostratigraphy in the Late Jurassic (Table 14.3) appears to be well-developed in most parts of Europe, but the highest possible resolution is yet neither reached in the Submediterranean Province nor in the Tethyan Realm nor anywhere else. In general, correlations between provinces are still far from being established. In the Tethyan Realm ammonite faunas still yield numerous phylloceratids and lytoceratids. In adjacent provinces the Late Jurassic ammonoid faunas are mainly characterized by perisphinctids, oppeliids, and aspidoceratids. Among them, oppeliids and aspidoceratids have often surprisingly large geographical distributions and they would thus allow good correlations, but are, on the other hand, rather conservative with respect to their morphology. Exceptions are a few very diagnostic forms such as the microconchiate genera *Epipeltoceras* (late Oxfordian; see Bonnot et al. 2009, Fig. 14.3b) and *Sutneria* (late Oxfordian to early Tithonian) (Fig. 14.3d), or the macroconchiate genera *Hybonoticeras* (late Kimmeridgian to early Tithonian) (Fig. 14.3e) and *Pseudhimalayites* (late Oxfordian to lower Tithonian). Perisphinctids became extremely diverse in the Late Jurassic, with various separate lineages developing in different bioprovinces. Homeomorphism (see Monnet et al. 2015b for its definition) is very common in this family, making determinations extremely difficult, especially when incomplete or poorly preserved material is considered. The same must be said from aspidoceratids. Taking their sexual dimorphism into account, however, the presence or absence of phyletically identical forms can be proven. In the Oxfordian, Boreal areas are still mainly characterized by cardioceratids (*Cardioceras*, *Amoeboceras*), which continue until the late Kimmeridgian, when they finally become dwarfish and disappear. In the adjacent Subboreal Province species of Pictoniinae and Aulacostephaninae (Fig. 14.3c) predominate among perisphinctids. In the Submediterranean Province members of Ataxioceratinae are frequent and diverse, and entered even Cuba and Mexico during the early spreading of the Atlantic Ocean (Villaseñior et al. 2012). Mayaitidae, Katroliceratinae and Virgatosphinctinae characterize the Late Jurassic in the Indo-Madagascan Province (Kachchh, Yemen, Ethiopia, Kenya, Tanzania, Madagascar, see e.g. Spath 1927–1933, Collignon 1959, 1960, Schweigert et al. 2012 and references therein).

Besides some time slices with high rates of endemism like in the early Kimmeridgian there are others with large dispersals and high diversity. Examples are the spread of *Gregoryceras* (Fig. 14.3a) in the Plicatilis and Transversarium zones,

Table 14.3 Bio-/Chronozonation in the Late Jurassic showing parallel zonal schemes due to increased bioprovincialism. (modified after Cariou and Hantzpergue 1997) and some selected ammonite taxa which are either used as index species or which are important for long-distance correlations. Note that Late Jurassic standard stages (in bold) are based on zonal successions of different bioprovinces!

Stage	Tethyal biozonation	Subboreal biozonation	Stage	Important taxa
Tithonian	Durangites	Preplicomphalus	"Portlandian"	
	Microcanthum	[9 further 'zones']		
	Ponti	Pallasinoides		
	Fallauxi	Pectinatus		
	Semiforme	Hudlestoni		
	Darwini	Wheatleyensis		*Pseudhimalayites subpretiosum*
	Hybonotum	Scitulus		
		Elegans		
				Gravesia gigas
Kimmeridgian ("Crussolian")	Beckeri	Autissiodorensis	Kimmeridgian	*Hybonoticeras kachense*
	Cavouri	Eudoxus		*Aulacostephanus eudoxus*
	Acanthicum Divisum	Mutabilis		*Ceratosphinctes rachistrophus*
				Idoceras balderum
	Strombecki	Cymodoce		*Presimoceras herbichi*
	Platynota	Baylei		*Cymaceras guembeli*
				Sutneria platynota
Oxfordian ("Lusitanian")	Planula			*Amoeboceras bauhini*
	Bimammatum	Rosenkrantzi		*Epipeltoceras bimammatum*
	Bifurcatus	Regulare	Oxfordian	*Dichotomoceras bifurcatus* *Larcheria schilli*
	Transversarium	Serratum Glosense		*Proscaphites anar*
	Plicatilis	Densiplicatum		*Dichotomosphinctes antecedens*
	Paturattensis	Cordatum		*Parawedekindia arduennensis*
	Minax	Mariae		*Cardioceras scarburgense*

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48 mm. **c** *Aulacostephanus eudoxus* (Orbigny), late Kimmeridgian, Eudoxus Zone, Tuttlingen, S Germany, SMNS 19699, diameter 63 mm. **d** *Sutneria platynota* (Reinecke), early Kimmeridgian, Platynota Zone, Messstetten-Michelfeld, Germany, SMNS 69477, diameter 24 mm. **e** *Hybonoticeras kachense* (Spath), late Kimmeridian, Beckeri Zone, Blaustein-Lautern, S Germany, SMNS 19426, diameter 155 mm. All photographs by G. Schweigert, Stuttgart

Fig. 14.3 Late Jurassic ammonoids. **a** *Gregoryceras* sp., middle Oxfordian, Transversarium Zone, Blumberg, S Germany, SMNS 70230, diameter 42 mm. **b** *Epipeltoceras bimammatum* (Quenstedt), late Oxfordian, Bimammatum Zone, Albstadt-Laufen, S Germany, SMNS 67719, diameter

reaching even the southernmost margin of the Palaeopacific, but also the Indo-Madagascan Province, besides the Western Tethys and adjacent Submediterranean areas (e.g., Gygi and Hillebrandt 1991, Bert et al. 2009). Kimmeridgian ammonite faunas are quite incompletely known (e.g., Westermann 1992). In some Tethyan and Palaeopacific areas, Kimmeridgian deposits are obscured due to unfavourable environmental conditions like shallow lagoons with evaporites, or by the evolution of endemic ammonite lineages which are not easy to correlate. For example, the perisphinctid genus *Paraboliceras* is considered as being indicative for a Kimmeridgian age (Énay 2009). From the Tithonian Hybonotum Zone and its supposed time equivalents onwards, bioprovincialism significantly increases due to worldwide regressions, thus making long-distance correlations based on ammonites alone extremely difficult (see e.g., Cecca 1999, Zeiss 2001, Parent et al. 2011). This is one of the main reasons why both the bases of the Tithonian Stage and the Cretaceous System are not defined yet in a GSSP. The end of the Jurassic System/Period—at an age of ca. 145 ± 4 Ma (Ogg and Hinnov 2012)—is therefore tentative not only due to the lacking of exact radiometric data but also for theoretical reasons.

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Chapter 15
Ammonite Biostratigraphy of the Cretaceous—An Overview

Jens Lehmann

15.1 Introduction

Ammonites are the most important macrofossils for biostratigraphy in the Cretaceous period (e.g., Kennedy and Cobban 1977; Kennedy 1986). This is due to the world-wide distribution of many species and a fast dispersal of hatchlings that is the main factor controlling distribution (e.g., Scheltema 1977; De Baets et al. 2015b), associated with high evolutionary rates (Kennedy 1977, Ward and Signor 1983). Furthermore, ammonites are facies independent to the greatest possible extent and their calcareous shells have a high preservational potential—at least in shelf deposits. Ammonites are usually common and easy to recognize in the field—even for the non-specialist—and are less facies dependent than other macrofossils. Even small fragments are characteristic enough to be identified. Therefore, ammonites fulfill many preprequisites of "*good index fossils*" and potentially allow high-resolution biostratigraphy in successions otherwise only datable by microfossils, e.g. in drilling cores (Renz 1983; Lommerzheim 1995; Lehmann 2000, 2011). This explains why they are often referred to as ideal index fossils (e.g. Kennedy and Cobban 1977) and why Cretaceous chronostratigraphy is primarily linked to ammonite zonations rather to that of other organisms (Ogg et al. 2012, part of "*The Geological Time Scale 2012*", abbreviated in the following as GTS 2012; Figs. 15.1, 15.2, 15.3 and 15.4).

J. Lehmann (✉)
Faculty of Geosciences, University of Bremen,
Klagenfurter Strasse, 28357 Bremen Germany
e-mail: jens.lehmann@uni-bremen.de

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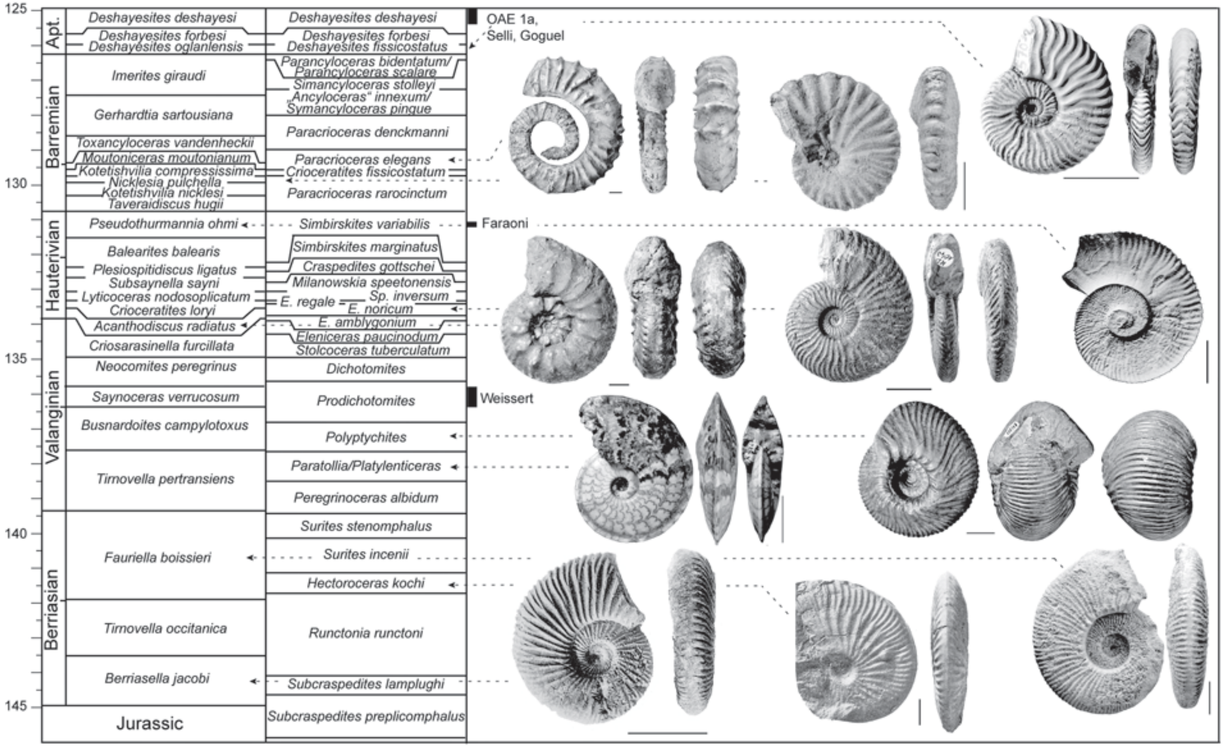

Fig. 15.1 Zonation for the Berriasian to Barremian (Early Cretaceous) used by the GTS 2012 (Ogg et al. 2012) with selected index ammonites. From *left* to *right*: Absolute ages in millions of years, stage terms with *short lines* in the *stage boxes* indicate substage boundaries, zonation for the Boreal faunal realm, zonation for the Tethyan faunal realm; *black bars* indicate the Oceanic Anoxic Events. Scale bar each 2 cm, except for *N. pulchella* and *H. kochi* where it is 1 cm. Photo of *P. elegans* from Kakabadze and Hoedemaeker (2010), *N. pulchella* from Fischer & Gauthier (in Gauthier 2006), *B. jacobi* from Mazenot (1939), *H. kochi* from Casey (1973) and *P. ohmi* from Company et al. (2003); all others by the Geosciences Collection of the University of Bremen

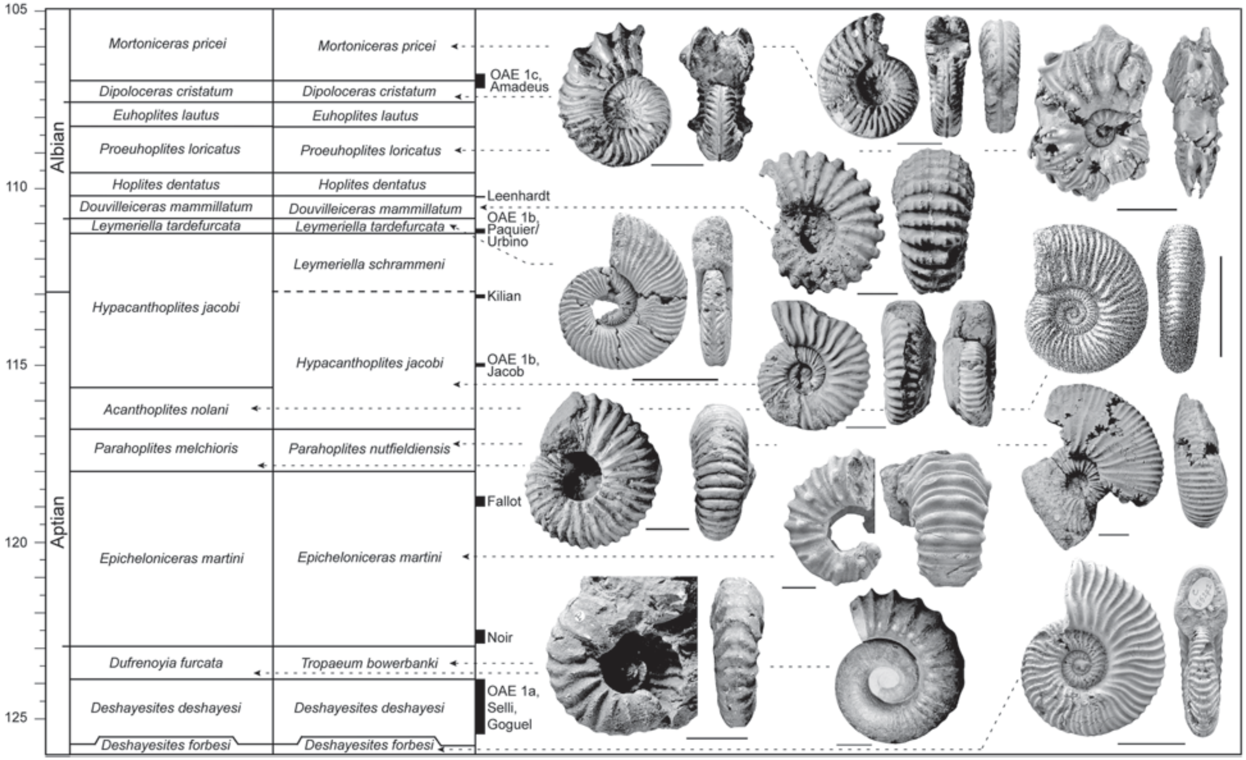

Fig. 15.2 Zonation for the Aptian and Albian (pars, Early Cretaceous) used by the GTS 2012 (Ogg et al. 2012) with selected index ammonites. Further details see caption to Fig. 15.1. Scale bar each 2 cm, except for *E. martinoides* where it is 1 cm and *T. bowerbanki* where the scale corresponds to 10 cm. Photos of *T. bowerbanki*, *P. melchioris*, *D. furcata* and *D. cristatum, M. pricei* by the Geosciences Collection of the University of Bremen, that of *A. nolani* is from Seunes (1887; its use an index should be abandoned: see Bulot et al. 2014) and all others are by the Natural History Museum London. *Short lines* in the *stage boxes* indicate substage boundaries

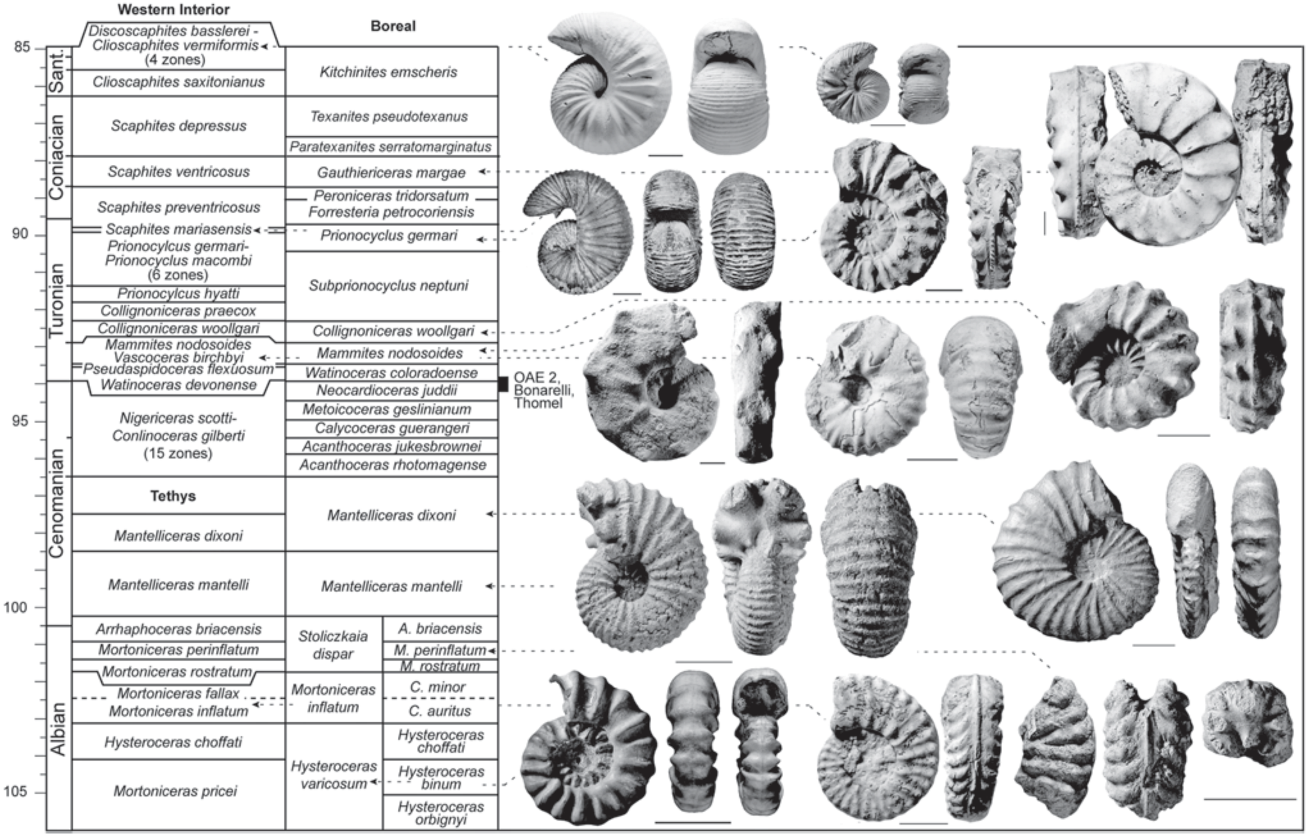

Fig. 15.3 Zonation for the Albian (Early Cretaceous) to Santonian (Late Cretaceous) used by the GTS 2012 (Ogg et al. 2012) and selected index ammonites. Note that the left column of the zonal succession given here adopts the zonation for the Western Interior Basin in North America, this contrasts Fig. 15.1 and

15.2; further details see caption to Fig. 15.1 . The zonation given by Ogg et al. (2012) for the Boreal realm is covering the Upper Albian to Lower Cenomanian only and is identical to that in the column for the Tethys. Here an alternative zonal scheme is added following Owen (2007), Lopez-Horgue et al. (2009) for the Albian, Monnet and Bucher (2007) for the Cenomanian and Kaplan and Kennedy (1996; 2000) for the Coniacian to Santonian. Scale bars: 2 cm (except for *V. birchbyi* where it equals 1 cm). *C. auritus* = *Callihoplites auritus*, *C. minor* = *Cantabrigites minor*. All photos by the Geosciences Collection of the University of Bremen, except for *M. fallax* (from Kennedy et al. 2008, pl 10, Fig. 10 and 11), *V. birchbyi* (from Cobban et al. 1989, Fig. 89 I and J), *P. germari* (from Kennedy et al. 2003, Fig. 2a and b), and *G. margae* from Kennedy (1984). *Short lines* in the *stage boxes* indicate substage boundaries

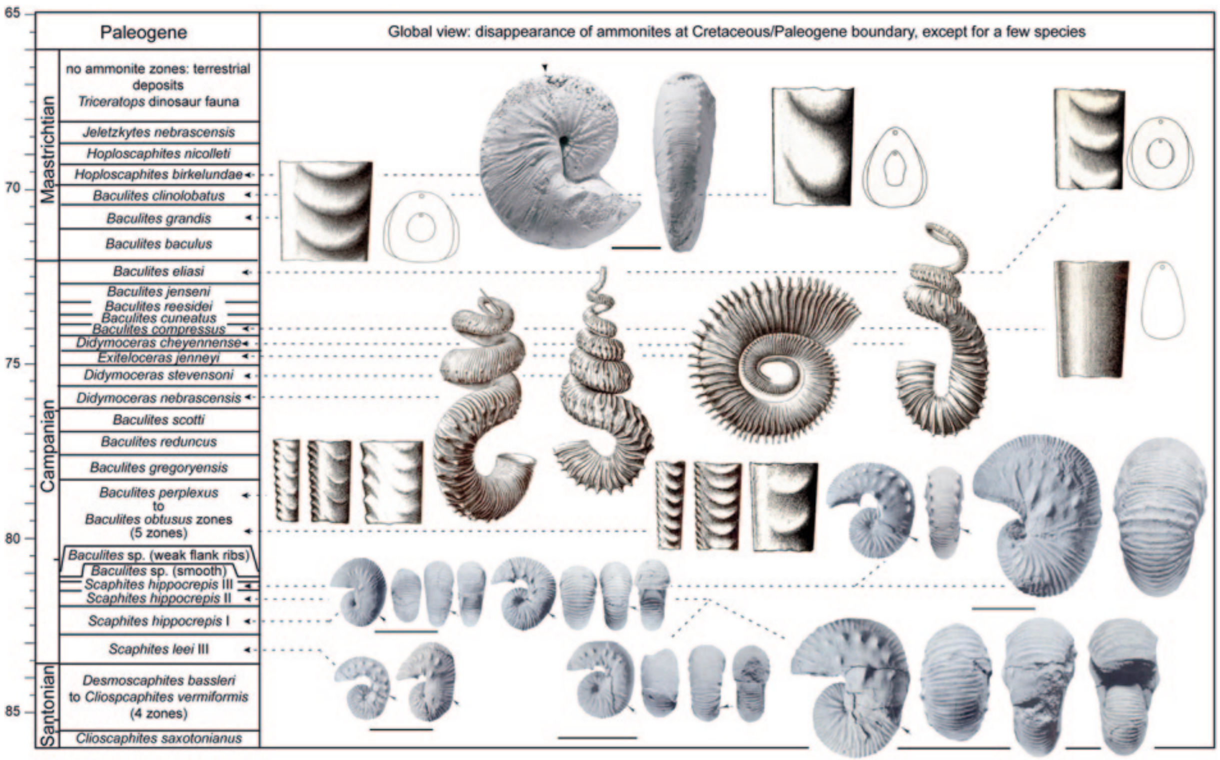

Fig. 15.4 Zonation for the latest Cretaceous (Santonian to Maastrichtian) of North America, used by the GTS 2012 (Ogg et al. 2012) with selected index ammonites. Note that the column of the zonal succession given here was adopted from the zonation for the Western Interior Basin in North America only, thus contrasting Fig. 6.1.51–15.3; further details see caption to Fig. 15.1. *H. birkelundae* after Landman and Cobban (2003, Fig. 20 g, h). Ammonite reconstructions for the *B. obtusus* to *B. clinolobatus* zones after Scott and Cobban (1965). Scale bars: 2 cm. *Short lines* in the stage boxes indicate substage boundaries

15.2 Biostratigraphy and Time

15.2.1 Concepts of Biostratigraphy

In biostratigraphy, the principal approach of subdividing and correlating rock sequences is to refer to a species characteristic for a time interval, usually represented by a bed or an interval (e.g., Kauffman and Hazel 1977; Holland 1990; Salvador 1994; Sturrock 1996; Murphy and Salvador 1999; Rawson 2001). Usually these units are called zones and the principal concept of biozones goes back on the research of Jurassic ammonites. Oppel was the first author to develop a supra-regional comparison using biozones in different countries in his “Juraformation” (Oppel 1856–1858), correlating strata between England, France and Germany (compare Hancock 1977; Rawson 2001). Today, this stratigraphical method is a well-established standard and a subdivision into zones can be applied almost throughout the Cretaceous Period (Figs. 15.1, 15.2, 15.3 and 15.4 herein). However, there are times where ammonites are scarce or absent. In general, an ideal index fossil is widely distributed, easy to identify, fast evolving, readily present, abundant and facies independent (Benton and Harper 2009). Although the latter is true for at least a number of ammonite species, there is often a discrepancy between the time where an index fossil actually lived and the time range where it can be used as a zonal fossil. Ammonites occur in different abundances through time and space. Biozones can be defined in various ways (e.g., Murphy and Salvador 1999; Rawson 2001). Several types of biozones can be distinguished (Fig. 15.5). The first is defined by the range of a single species, called total range zone or taxon range zone. The duration of this zone is limited by the first appearance datum (FAD) and the last appearance datum (LAD), or shortly first appearance (FA) and last appearance (LA). The second type is the concurrent range zone, with the lower, upper, and lateral limits of this zone determined by the concurrent range of two or more taxa. A third type is called interval zone and is defined by a part of the range of a species that can be limited for example by a FA of another species (alternatively LO for first occurrence), a LA (or HO = highest occurrence) of another species or by a partial range of a species that is limited by the appearance/disappearance of other species. A forth type of zones is defined by the lower and upper limit of its maximum abundance, called acme or abundance zone and represents a peak occurrence of a species. Finally, an assemblage zone is defined by overlapping and partial ranges of several species, often not belonging to the same groups of fossils. In the next paragraph (6.1.52.2) examples of some of these general types are given.

Although zonal names should only be used in the area where the fossil actually occurs (e.g., Rawson 2001), particularly ammonite zones are often transferred to other areas, become generalized and deemed to be valid on a global scale. For the Cretaceous, this development is evident by the use of ammonite zones in the various time scales released over the last decades which refer to zonations developed in the Western Tethys, the Western Interior in and the European Boreal (e.g., Obradovich 1993; Gradstein et al. 1995, 1999, 2008; Ogg et al. 2004, 2012). In each region, there are ammonite zonal indices that are strictly endemic, e.g., the succeeding *Did-*

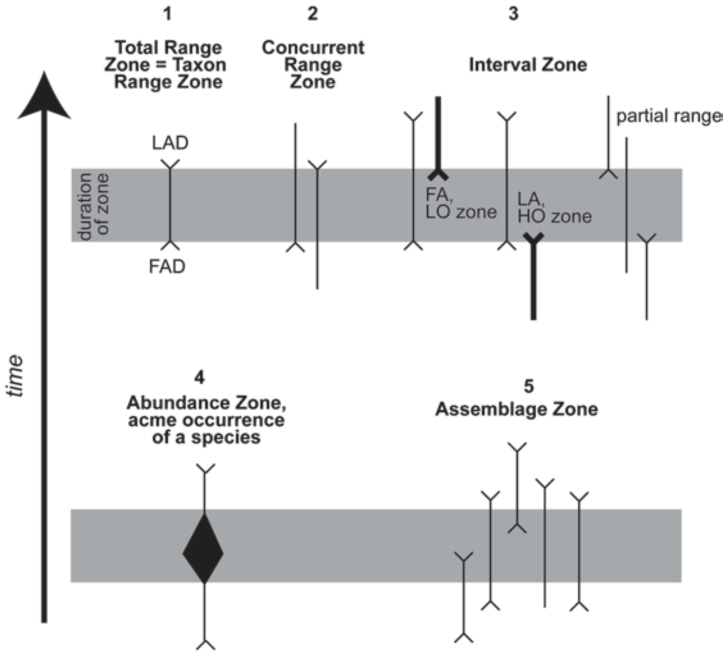

Fig. 15.5 Basic concepts of biozones. The *vertical bars* indicate the range of a taxon through time. Simplified after various sources. (Salvador 1994; Murphy and Salvador 1999). *LAD* latest appearance datum, *FAD* first appearance datum, *LO* lowest occurrence or *FA* first appearance, *HO* highest occurrence or *LA* last appearance

ymoceras spp. zones in the Western Interior (Fig. 15.4 and 15.6a–c) and individual *Baculites* spp. zones typical for North America (e.g., *Baculites anceps pacificus* from the Pacific Realm, see Fig. 15.6f). This hampers the development of a globally valid zonation, and this issue is addressed below with respect to the GTS 2012 in more detail (Ogg et al. 2012, 15.2.3)

15.2.2 Examples of Cretaceous Biozones

Total range zones in the strict sense are rare, particularly on supra-regional scale standard zonations (e.g., Hoedemaeker and Bulot 1990). In the Albian, for example, the *Proeuhoplites loricatus* and *Euhoplites lautus* zones as well as the *Hoplites dentatus* Zone represent zones based on the total range of the individual species (Fig. 15.2). Several zones originally regarded as total range zones have subsequently been redefined as interval zones. An example might be the *Douvilleiceras mammillatum* Zone that has been considered as a total range zone at the top of the Lower Albian (Owen 1988; Hoedemaeker and Bulot 1990). Nevertheless, *D. mammillatum* is a highly variable species with many closely allied forms (Fig. 15.7a–f) and there

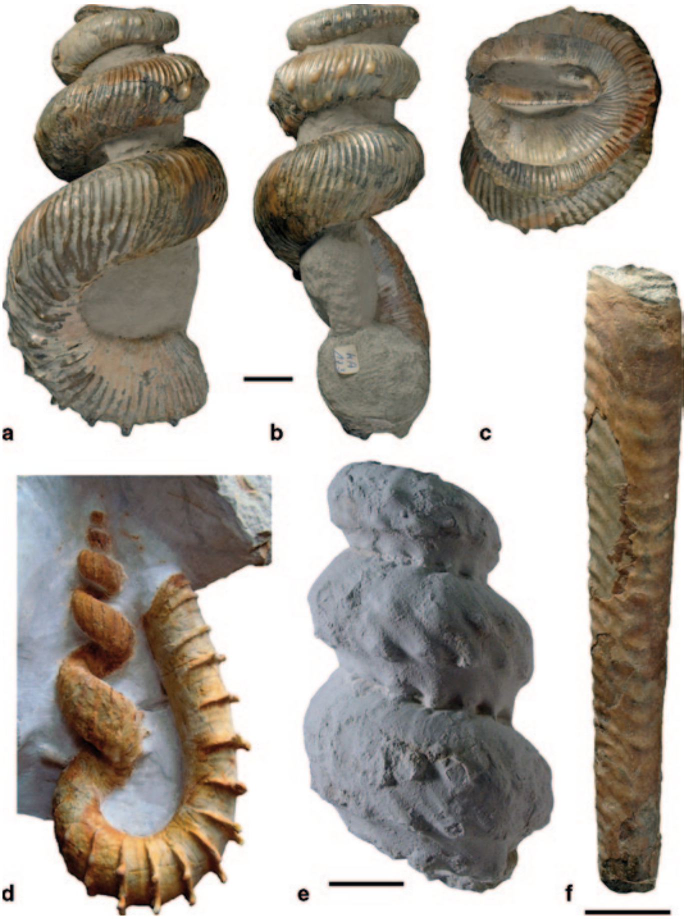

Fig. 15.6 Examples of Late Cretaceous heteromorphic ammonites that have biostratigraphic value on a regional scale. **a–c** *Didymoceras nebrascense*, a basal Late Campanian zonal marker in the Pierre Shale of the U.S. Western Interior. **d** *Hyphantoceras reussianum* characterizing the *Hyphantoceras* Event in the *Subprionocyclus neptuni* Zone, Late Turonian of North Germany. **e** *Mariella* (*Wintonia*) *brazoensis*, an index from uppermost Albian (Main Street Formation) of Texas, USA. **f** *Baculites anceps pacificus* from the Upper Campanian (Spray Formation), *B. rex* and *Baculites anceps pacificus* Zone of British Columbia, Canada. Photos by the Geosciences Collection of the University of Bremen, except for **d** courtesy of U. Resch. Scale bars: 2 cm

has been discussion if a species that is defined quite variably by different authors should actually be used an index (Reboulet et al. 2011; compare Owen 1988 *versus* Amédro 1992). As long as a species in the wider sense is restricted to the eponymous zone there would not be a conflict. However, in the case of *D. mammillatum* there has been some debate about alternative ammonite markers with respect to the correlation to Tethyan sections (Reboulet et al. 2011). This is justifiable since early forms of *D. mammillatum* first appear in the upper *L. tardefurcata* Zone (mid Early Albian), range into the lower *H. dentatus* Zone (early Middle Albian) and, thus,

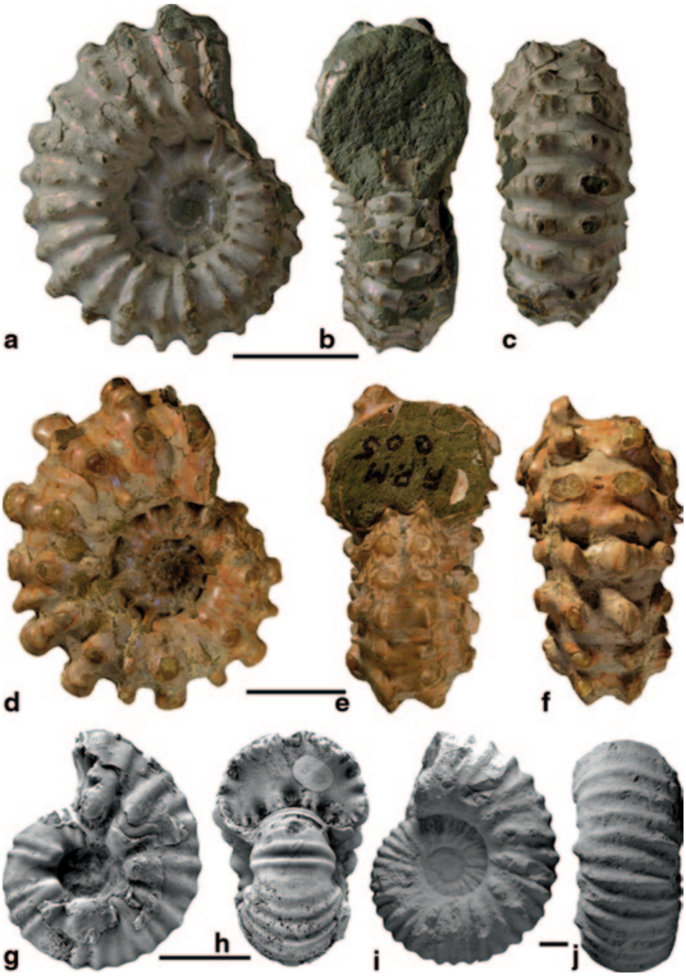

Fig. 15.7 Recoiled heteromorphic ammonites constitute a comparatively small portion of the important index species of the Cretaceous. **a–f** Strong intraspecific variability and a long stratigraphic ranges characterizes *Douvilleiceras mammilatum* sensu lato as an index fossil of the eponymous superzone; **d–f** illustrates a form often separated as a separate species, *D. inaequinodum*. Two examples from the basal Middle Albian of Mahajanga, NW-Madagascar. **g, h** *Roloboceras hambrovi* is characterizing an interval in the Lower Aptian, this example is from the Isle of Wight, S-England. **i, j** *Cheloniceras cornuelianum* is among the most widely distributed and common recoiled heteromorphs of biostratigraphical importance. Lower Aptian from Essaouira, W-Morocco. Photos Geosciences Collection of the University of Bremen, except for **g, h** by Natural History Museum, London. Scale bars: 2 cm

the species straddles the Lower/Middle Albian boundary, in contrast to the original definition of the *D. mammillatum* Zone. The comparatively long range of the index species prompted many authors to impose the *D. mammillatum* total range zone into a higher category zone, referred to as *D. mammillatum* Superzone (e.g., Owen 1988;

Latil 2011; Lehmann et al. 2013). The antithetic concept to superzones are subzones and particularly in the Albian many subzones are used (e.g., Owen 2007; Lehmann 2011) although some authors tended to regard the subzone as a full zone. However, retaining hierarchy may be important as it gives stratigraphers an added value when ammonite material is scarce. The Early Albian *L. schrammeni* Subzone for instance indicates sedimentation in isolated localities since it coincides with a widespread hiatus and is thus useful to indicate an associated major sequence boundary (Mutterlose et al. 2003; Ogg et al. 2012; Fig. 15.2). This approach has been termed "*Lückenstratigraphie*" by Ernst et al. (1996).

Since biozones are valid for a certain area only (see above), the same species can be the index of different types of zones in different parts of the world. An example is the Late Aptian *Hypacanthoplites jacobi* Zone. It is regarded as a total range zone on a regional scale in Sinai (Aly 2006), but on the other hand, *Hypacanthoplites jacobi* is the index of an interval range zone in North Germany, the area where the type specimen originates from. Here, the species ranges into the Lower Albian *Leymeriella schrammeni* Zone (Mutterlose et al. 2003). In this case, the species range of *Hypacanthoplites jacobi* is furthermore critical with respect to the position of the stage boundary, since the *H. jacobi* Zone has been proposed to indicate the highest zone in the Upper Aptian as well as lowest zone of the Lower Albian (for a full discussion see Kennedy et al. 2000; Fig. 15.2). Since Kennedy et al. (2000) synonymized *H. jacobi* and *H. plesiotypicus*, with the latter name having priority, the type of *H. jacobi* (Fig. 15.2) is assigned to *H. plesiotypicus*, but the term *H. jacobi* Zone has been retained.

An example for an abundance or acme zone, which also represents a partial range zone, is that of the large turrilitid *Mariella* (*Wintonia*) *brazoensis* Zone. The zonal index is abundant in the latest Albian Main Street Limestone Formation of Texas only but not beyond (Kennedy et al. 2005). Nevertheless, the index species ranges lower down and higher up in the sequence, its first occurrence is below the zonal index *Mortoniceras perinflatum*. At the upper limit of its occurrence, it is un-

Fig. 15.8 The Late Cretaceous heteromorphic ammonite *Bostrychoceras polyplocum* is characterizing the basal Late Campanian *Bostrychoceras polyplocum*/ *Belemnitella minor*/ *Galerites vulgaris* assemblage zone, Haldem, North Germany. Photos by the Geosciences Collection of the University of Bremen. Scale bar: 2 cm

clear if *M*. (*W*.) *brazoensis* overlaps with *M. rostratum* (Fig. 15.6e). Geographically, this acme zone example is restricted to Texas and northern Chihuahua in Mexico.

Assemblage zones are less used in the Cretaceous. They are usually only used where species of poor biostratigraphic value co-occur, which might even belong to different groups of macrofossils. An example is the *Bostrychoceras polyplocum*/*Belemnitella minor*/*Galerites vulgaris* Zone in the Campanian of North Germany, including an ammonite, a belemnite and an echinoid as index species (Fig. 15.8). Except for *Galerites vulgaris*, these index fossils are only moderately common.

These examples illustrate problems with applying zones as standard or principle. Improved ranges or revised taxonomy might have a major impact on individual zonal concepts and solutions for this dilemma have been discussed repeatly. Hoedemaeker and Bulot (1990) reported about an agreement of a group of Lower Cretaceous ammonite workers to regard the first appearance of an index species as most important to define zones (compare paragraph 15.2.3 below). A few exceptions were allowed for cases that otherwise would endanger the stability of stratigraphic nomenclature. As a recommendation, diagnostic associations of ammonite species should be used in case the index species is rare or absent; this corresponds to an assemblage zone as exemplified above, exclusively defined by ammonites. Such an assemblage of ammonite species is usually not a part of the standard zonation but could support the main zonal subdivision as an additional stratigraphic marker. An example are several pachydiscid species in the Santonian and Campanian of the Pacific region (Ward et al. 2012), among those *Patagiosites arbucklensis* (Fig. 15.9d, e), in an assemblage with other pachydiscids typical for the Santonian *Eubostrychoceras elongatum* Zone. Hoedemaeker and Bulot (1990) further recommended that a detailed definition of the zone should be published, so it can be properly compared with areas outside the type region. Finally, a stable stratigraphic nomenclature is preferable and thus changes in the zonal scheme should be as moderate as possible—in some stages this recommendation found following to some extend among ammonite workers over the past decades (e.g., Berriasian, Cenomanian) but not in others (e.g., Albian).

15.2.3 First and Last Occurrences

Each range of a fossil is defined by the first stratigraphic occurrence (FO) and the last stratigraphic occurrence (LO), alternatively called FA (first appearance) or LA (last appearance). FOs and LOs very often define the zones (compare 15.2.1 and Fig. 15.5). In biostratigraphical correlation, the formal concept of zones is much more applied than that of FOs or LOs and plays an important role in the definition of Cretaceous stage boundaries (including many ammonite datums; Rawson et al. 1996).

In quantitative stratigraphic methods (see Monnet et al. 2015a for a review), like graphic correlation (Miller 1977; Hammer and Harper 2005), LOs and FOs of Cretaceous ammonites are also used as basic data. Graphic correlation is rarely

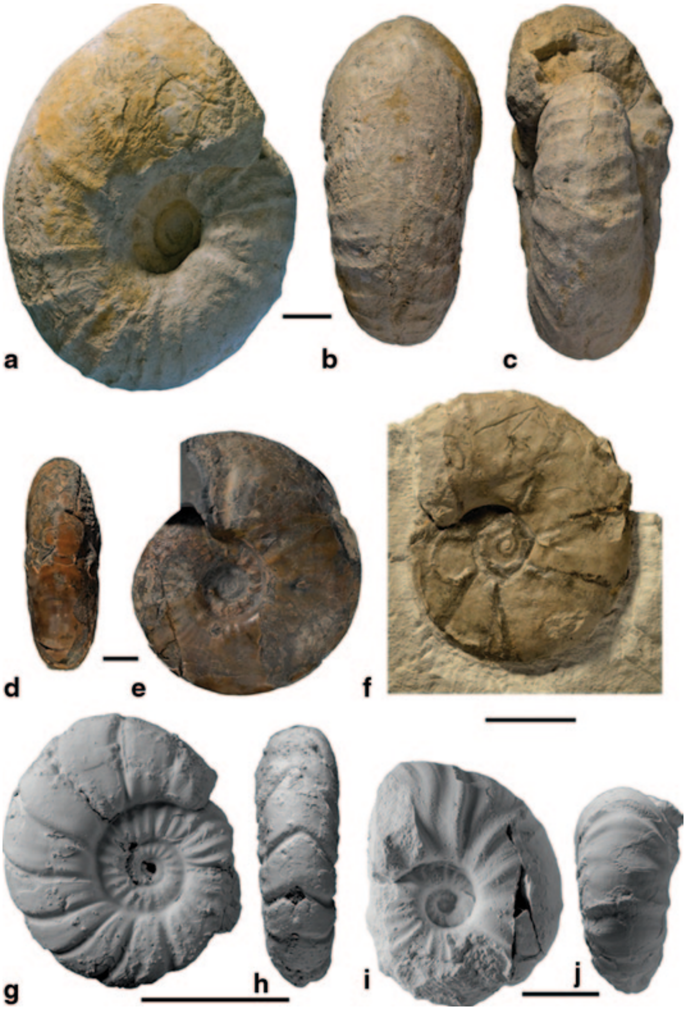

Fig. 15.9 Poorly ornamented (leiostracan) desmoceratid and pachydiscid ammonites of biostratigraphic value. **a–c** *Menuites wittekindi*, lower upper Campanian from Haldem, not used as an index but nevertheless the name has been used in biostratigraphy because of an African species originally believed to be conspecific, North Germany. **d, e** *Patagiosites arbucklensis*, Santonian, a species associated to the *Eubostrychoceras elongatum* Zone in the Sacramento Valley, California, USA. **f** *Patagiosites stobaei,* index of the eponymous Middle Campanian zone (Beckum, North Germany). **g, h** *Wollemanniceras keilhacki*, used earlier as Lower Albian index, after current definition it straddles the Upper Aptian/Lower Albian boundary interval (Immensen, North Germany). **i, j** *Eopachydiscus marcianus*, Late Albian, eponymous zone from the Fort Worth area, Texas, USA. *Scale bar*: 2 cm

based on ammonite data alone, since the combination of different types of stratigraphic data has proven to be the most successful (e.g., Immenhauser et al. 2000; Oboh-Ikuenobe et al. 2007; Scott 2009). Furthermore, more advanced quantitative biostratigraphy methods are still too infrequently used by ammonoid workers (compare Ogg in Gradstein et al. 2012; Monnet et al. 2015a for a review).

15.2.4 Ammonite Events

In addition to biozones, some beds or rock successions with exceptionally abundant or particularly characteristic ammonite occurrences have been recognized, occasionally referred to as events. In some instances the separation of events from biozones is merely nomenclatorial and these events are essentially an acme or an assemblage biozone. An example is the *Hyphantoceras* Event in North Germany, a ca. 3 m thick sequence with an abundance of the heteromorphic ammonite *Hyphantoceras reussianum* (Fig. 15.6d)*,* accompanied by additional typical ammonites and other macrofauna, representing an ecological event in an otherwise monotonous Late Cretaceous limestone succession (Ernst et al. 1983; Dahmer and Ernst 1986; Kosták and Wiese 2002). This type of ammonite event usually occurs regionally and might be related with ammonoid behavior (ecology) or particular sedimentological processes. An example of a widely distributed ammonite event that can be attributed to a sea level lowstand is the *Turrilites* bio-event along the Russian Pacific coast (Jagt-Yazykova 2012). A more generalized ammonite event is described from the same region as *Scaphites* facies bio-event and refers to an enlarged diversity of scaphitid ammonites in the late early–middle Turonian in many regions of the world (Jagt-Yazykova 2012).

In some rare cases, events are named after ammonites although they are not exceptionally abundant within the succession and the event has a primarily non-faunistic background. An example is the "*polyplocum* Event" in the Late Campanian of North Germany, with *Bostrychoceras polyplocum* as a name-giving heteromorph that is occurring simultaneously with a regression (Fig. 15.8; Niebuhr et al. 1997). Here, "*polyplocum* Event" refers to a eustatic (and not to a faunistic) event and a synonymous term for the same event in Western Europe, the "*Catton Sponge Bed*" and "*North Antrim Hardgrounds*", is not related to specific ammonite occurrences (Mortimore et al. 2001).

15.2.5 Biostratigraphy and Geochronology

In paragraphs 15.2.1–15.2.2 we looked at zones merely as rock units "*that you can hit with a hammer*", but on the other side, they represent geological time necessary for their accumulation (McGowran 2005). Biozones also represent time units. In fact many chronostratigraphic units (such as systems and stages) are defined biostratigraphically. Modern time scales favor a holistic approach of integrating geological time, based on absolute age dating with a set of stratigraphic tools (Ogg et al. 2004; 2012). Ammonite zones are in fact a central component of current time scales (Gradstein et al. 2012), but there are several pitfalls: (1) most zones can be valid for certain regions of the world only, (2) integrating biozones is based on different methodological approaches (total range zones, assemblage zones etc., see above; compare Monnet et al. 2015a), and last but not least, (3) in many cases time might be hidden in stratigraphic gaps rather than in the sedimentary record (e.g., Einsele 2000). Thus time is not continuously represented by the biozones, but might be hidden in sedimentary discontinuities within the sequence or at zonal boundaries.

15.2.6 Zonation Used in the GTS 2012

The GTS 2012 indicates a total duration of 79 Ma for the Cretaceous Period (Ogg et al. 2012). The biozones covering this period have been assembled from different parts of the world (see Sect. 15.2.1), generally by tracing areas with shelf deposits that are rich in ammonites. An example in the GTS 2012 is the latest Cretaceous zonal scheme of the Western Interior of North America (Fig. 15.4). Although, the North American record is probably the best for this time interval, it is impossible to refer to it as a general scale, not even for the Western Interior, since a large number of species are endemic. Furthermore, it needs to be emphasized that ammonite zonations used in relation to radiometric time scales not only fail to represent globally valid ammonite successions, but also represent the opinion of the individual authors of parts of this biozonal succession. This entails that the ammonite zonal schemes are a mixture of different types of biozones (total range-, concurrent-, interval-, abundance-, and assemblage zones, see Fig. 15.5). Since the present article intends to give an overview of Cretaceous ammonite successions, the author accepted these inconsistencies for pragmatic reasons and adopted the succession used by Ogg et al. (2012) with minor changes. Despite many critical points in terms of ammonite biostratigraphy, it is accepted that the GTS 2012 is currently a standard in stratigraphy and the most recent approach on the correlation of radiometric ages and biozones. Since Cretaceous Oceanic Anoxic Events (abbreviated OAEs) became important markers for stratigraphic correlation, their position was adopted from the GTS 2012 for completeness sake, but discussing them in detail falls outside the scope of this article. Furthermore, this brief overview is not the place to discuss alternative zonations.

15.3 Accomplishments and Limits of Ammonite Biostratigraphy

On the basis of the GTS 2012, and including a few minor additions, the Cretaceous period can be subdivided into a minimum number of 87 and a maximum number of 113 ammonite zones (Figs. 15.1, 15.2, 15.3 and 15.4). In relation to the duration of the Cretaceous this corresponds to duration of 0.7–0.9 Ma per ammonite biozone. Compared to other groups of fossils this is an average resolution that can be regarded as good. In contrast to ammonites, Cretaceous planktonic foraminifera in the tropics have the best average resolution among microfossils with an average resolution of 2.5 Ma (Sturrock 1996). Nevertheless, ammonite as well as microfossil zones have strongly varying lengths and thus some short ammonite biozones represent an even shorter period of time and thus a higher resolution.

Although ammonites appear as ideal index fossils there are many limits in Cretaceous ammonite biostratigraphy, e.g., with respect to paleobiology and biofacies (compare De Baets et al. 2015a; Lukeneder 2015; Naglik et al. 2015), paleobiogeographic distribution (compare Lehmann et al. 2015), slow evolutionary rates in some groups of ammonites, taxonomy (compare De Baets et al. 2015a; Monnet et al. 2015b; Yacobucci 2015) and preservation (Wani and Gupta 2015). A summary with a focus on a biostratigraphical background can be found in Kennedy and Cobban (1977), but many of these points are also addressed in a different context in multiple other chapters of this book. Thus, I focus on some taxonomic and preservational aspects, which are of specific importance for Cretaceous biostratigraphy.

15.3.1 Biostratigraphic Potential of Index Species

One of the major preconditions for a good index ammonites is a high evolutionary rate resulting in a sequence of multiple species that are morphologically separated. Smooth-shelled, ("*leiostracan*") ammonites developed less characteristic morphologies compared to "*trachyostracan*" (strongly ornamented) species. Nevertheless, in the Cretaceous period, two groups of leiostracan ammonites yielded quite a number of index species—at least on a regional scale: the pachydiscids and the desmoceratids (Fig. 15.9). An examples for the former is *Patagiosites stobaei,* characterizing the Middle Campanian of NW Germany, southern Sweden, southern Belgium and Donbass (Jagt 2002 and references herein; Fig. 15.9f) as well as *Eopachydiscus marcianus* from the Upper Albian of Texas, New Mexico, Colorado and Chihuahua, characterizing an eponymous zone (Fig. 15.9i, j; Kennedy et al. 1983; Lucas et al. 1988). Among desmoceratids only some stronger ornamented forms are of significant biostratigraphic relevance, e.g., *Wollemanniceras keilhacki* which characterizes the Upper Aptian/Lower Albian boundary interval in Germany. This species is distinct from its leiostracan ancestors by numerous constrictions and ribs per whorl (Fig. 15.9g, h) and gave rise to *Proleymeriella* as the earliest representative of the Leymeriellidae. The latter is an important family of index ammonites in the Lower Albian characterized by closely spaced ribs (Fig. 15.2).

One of the striking features of Cretaceous ammonite assemblages are heteromorphic ammonites, including those forms that underwent a recoiling as observed in several individual groups (e.g., Wiedmann 1969). These ammonites display a very dynamic evolutionary history, they have been very successful in many environments across the globe and it has been speculated that this is due to trophic changes induced by global paleogeographic changes (Cecca 1997). The origin of heteromorphic ammonites (earlier separated as suborder Ancyloceratina) is polyphyletic, but since the trend of uncoiling and recoiling is a feature typical for this period they are of great importance for biostratigraphy. Among the 116 index ammonite species used for the standard zonation in Figs. 15.1, 15.2, 15.3 and 15.4, 80% belong to the regularly coiled suborder Ammonitina, 12% are heteromorphs with more or less uncoiled shells and 8% are recoiled heteromorphs like *Douvilleiceras* (Fig. 15.7a, f), *Roloboceras* (Fig. 15.7g, h) and *Cheloniceras* (Fig. 15.7i, j), which had ancestors that were uncoiled. More and more tightly coiled forms gave rise to heteromorph index species in time and thus, the Santonian–Maastrichtian zonal succession exclusively consists of heteromorphic species. The two major ammonite clades of the suborders Phylloceratina and Lytoceratina show conservative morphologies throughout their occurrence (Triassic–Cretaceous) and no significant index species are known from the Cretaceous.

15.3.2 Preservation as Limiting Factor for Biostratigraphy

Chalk deposits are widely distributed in Europe and in other areas of the world in the Late Cretaceous (Ineson et al. 2005). A few decades ago most chalk deposits were attributed to a relatively deep water depth, below the photic zone and below the storm wave base, with quite a number of points raised to support this view (for a review see Zijlstra 1995). Some light-dependent suspension feeders indicate that even very shallow water depth can be inferred for some occurrences (Bathurst 1971; Bromley 1975, 1979) and in fact from a modern point of view most chalk sediments were probably deposited in between both extremes, namely at a moderate water depth (~100–200 m). Although a moderate water depth corresponds to the favorite habitat of most ammonites, they are in fact scarce in many chalk facies successions, including the famous Niobara Chalk in Kansas in the Western Interior (Everhart 2005). This might be largely related with the dissolution of aragonite in chalk deposits below the ACD (Aragonite Compensation Depth). However, the ACD is around 1000–3000 m in the recent ocean (e.g., Berger 1978), and although the ACD might have been significantly shallower in case of some Cretaceous chalk deposits (Hancock 1963), a diagenetic loss appears more likely for chalks deposited at moderate water depth. The ammonite shells could have been dissolved easily, since aragonite is often dissolved during early diagenesis. Therefore, isolated jaw elements of ammonites might be preserved in chalks due to their calcitic mineralogy, whereas the associated ammonite shells are missing. In contrast the selective preservation of cephalopod jaws in the "*Aptychenschichten*" and correlatives in the Late Jurassic and Lower Cretaceous sequences in the Alps and Carpathians (Gasiorowski 1962, 1973), and described from DSDP sites (Renz 1977, 1979), has been related to changes in the sea-water chemistry with increasing depth. Aragonitic cephalopod shells were dissolved below this level leaving only their calcitic jaws. Beyond the observation that ammonoid conchs are usually rare in the Chalk, some chalk sequences contain calcitic fossils, like oysters, that are either directly moulding ammonite shells or that are showing xenomorphic growth (Lewy 1972; Lehmann and Wippich 1995). These calcitic organisms might give ammonite records where no or only poorly preserved ammonite shells give evidence for their existence.

Taphonomic considerations can also have a major impact on biozonation, as in the Late Cretaceous of England. The zonal scheme is only partly based on ammonites, and mostly relies on calcitic macrofossils like bivalves, echinoderms and even

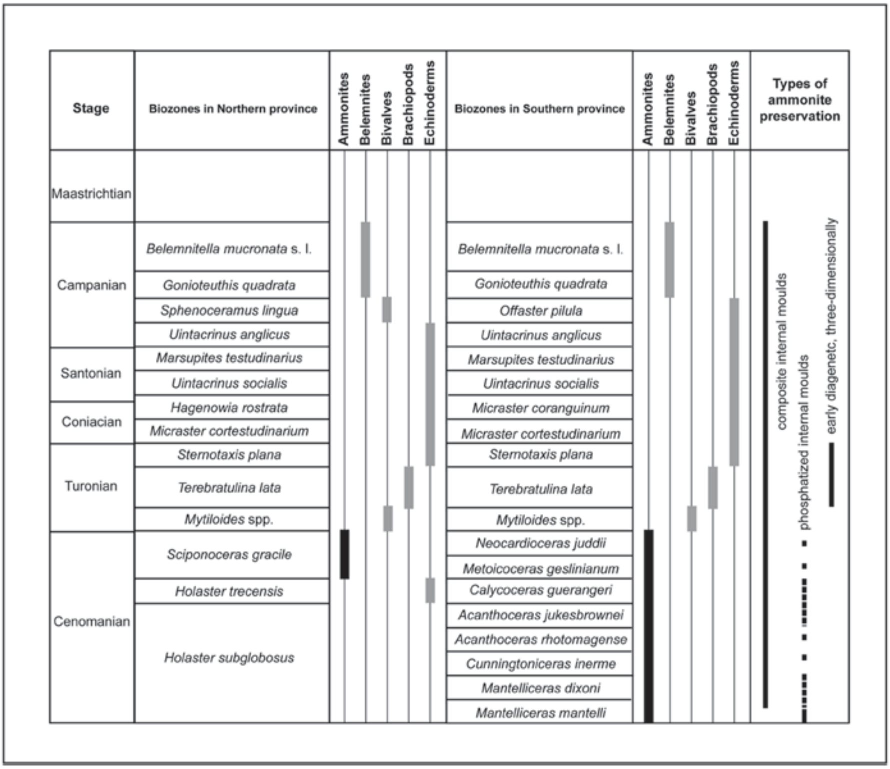

Fig. 15.10 Zonation for the Late Cretaceous Chalk Supergroup of England (following Rawson 2006). Note that the succession of the northern province is mainly distinguished by the virtual lack of index ammonites and that vice versa the dominance of index ammonites in the Cenomanian of the southern province is strongly related to preservation in phosphatic pebble beds. Preservational modes diagrammatic for the southern province, combined from data in Wright and Kennedy (1981); Wright and Kennedy 1984–1996 by; Wright and Kennedy (2002) and Mortimore et al. (2001); *dashed lines* indicate phosphatisation due to scattered event beds in the chalk (e.g., chalk basement beds, diachronous in the area) whereas continuous lines represents chalk preservation as internal moulds

brachiopods (Fig. 15.10; Rawson 2006). In this case there is a strong correlation between preservational modes and the possibility of implementing ammonite zonation. Particularly the diachronous chalk basements beds in southern England yield many well-preserved, phosphatised specimens, and these short-ranged species can be used for (local) biostratigraphy. On the other hand the biostratigraphic control of chalk sequences is often less well-constrained because of poorly preserved or even missing ammonites. An example of different preservational modes from immediately succeeding beds is given in Fig. 15.11. Since the chalk basement beds and generally many of the glauconitic and phosphatic basal beds are controlled by the pre-transgression topography, the sophisticated ammonite biostratigraphy in the Cenomanian of southern England is linked to the morphology of basins and subbasins. In the late Late Cretaceous, the continuously rising sea level (Rawson 2006;

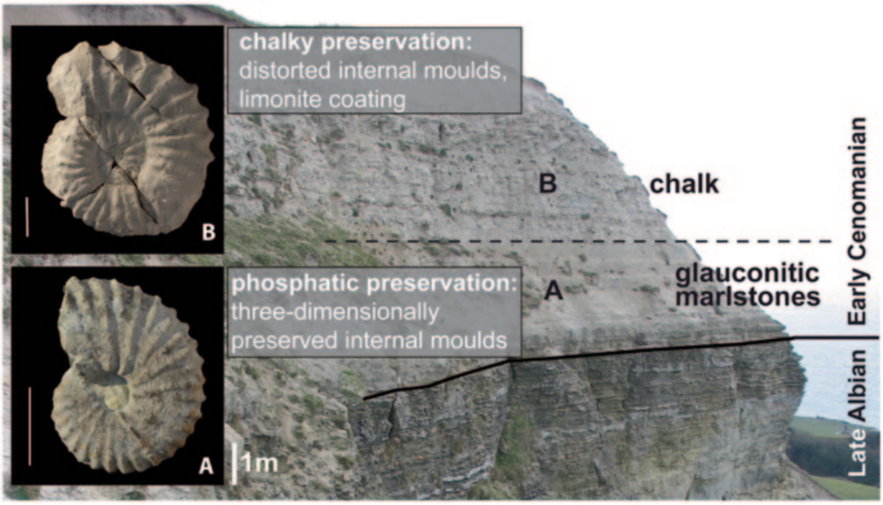

Fig. 15.11 An example of different preservational modes in the Cretaceous. The well preserved ammonite in A (*Mantelliceras saxbii*) contrasts the poor preservational mode in the chalk facies of the Cenomanian in southern England. In the latest Cretaceous, preservation is poorer or ammonites are even absent by complete dissolution of the aragonitic shell before diagenesis. Field photo showing the Gore Cliff, Isle of Wight, southern England. Scale for ammonites each 2 cm. All photos by the Geosciences Collection of the University of Bremen

fig. 15.2) lowered the chance for phosphatisation and thus calcitic index fossils are predominant (Fig. 15.10).

15.3.3 Impact of Taxonomic Difficulties on Biostratigraphy

The analysis of intraspecific variation of a species is one of the challenging missions in paleontology. A principal dilemma in ammonite paleontology is that species discrimination is based on the ammonite shell only, thus the whole species concept relies on shell features. Thus traditionally taxonomy is based on descriptions of morphology and measurements of the shell (Klug et al. 2015) and it suffered from subjective descriptions and an extensive splitting, particularly by many early workers (see De Baets et al. 2015a for a review). A classic example is the monograph by Spath (1923–1943) on the Albian ammonites of the British Gault Clay. Descriptions like these are milestones of biostratigraphy for whole regions of the world and thus, inappropriate taxonomic approaches might have a massive effect. Due to well-exposed ammonite-bearing sections in northern Europe, the Aptian Lower Greensand of southern England constitutes a benchmark for many ammonite workers in other parts of the world. This is based mainly on the monograph of Casey (1960–1980), but the biostratigraphical sequence covered by this diligent piece of work is suffering from taxonomic problems. Recently, Bersac and Bert (2012) challenged the taxonomic concept for many species described from the Lower Greensand, among other aspects questioning their biostratigraphical value. Problems like these might hinder correlation within the same biogeographical domain, separated by not more than a few 100 km only. Correlation of Early Aptian ammonite zones between England and North Germany is less complex than previously believed considering the different taxonomic approach. For example synonymy of the two traditionally used index species *Deshayesites bodei* (Germany) and *Deshayesites fissicostatus* (England) has been assumed for decades (Casey 1964 in Casey 1960–1980; Lehmann et al. 2012), but no biostratigraphic consequences has been drawn resulting in a seemingly different zonal scheme that is still used (Kemper 1967, 1995).

The taxonomic misinterpretation of a zonal index might also have a significant impact on zonal nomenclature and thus hinders a proper stratigraphic correlation. A good example is the zone of *Anapachydiscus wittekindi* and *Eulophoceras jacobi* in the Lower Campanian of Madagascar (Collignon 1969; Besairie and Collignon 1972) that is used for correlation with South Africa (Klinger et al. 2007; Kennedy and Klinger 2012). After introducing *A. wittekindi* as index species in Madagascar, the type species was shown to be from the Upper Campanian of North Germany (Fig. 15.9a–c; Kennedy and Kaplan 1997)—thus occurring in a different stratigraphic level than the Madagascan material. Furthermore, it was re-assigned to the genus *Menuites* (e.g., Kennedy and Kaplan 1997) and this was one reason to revise the taxonomic assignment of the Madagascan records. Cooper and Greyling (1996) renamed *Anapachydiscus wittekindi* of Collignon as *Anapachydiscus collignoni* in accordance with Kennedy and Kaplan (1997) who also felt that the Madagascan species warranted separation from *M. wittekindi* of Schlüter. Cooper and Greyling (1996) restricted usage of the *Anapachydiscus collignoni* Zone to Madagascar, the South African occurrences being recorded from a local *Submortoniceras woodsi* Zone. As a result, an ammonite species supposed to be of great value for long-distance correlation turns out to be two separate species with very restricted distributions and from different biostratigraphical zones.

All species based on qualitative descriptions of shells are subjective to some extent. However, descriptions often incorporate measurements that are reproducible and can be analyzed quantitatively. Some morphometric investigations are defining species using statistical analysis of shell parameters. Such examples mainly cover morphologically variable Cretaceous ammonites (Reyment and Kennedy 1991, 1998; Kennedy et al. 2009; compare De Baets et al. 2015a). A holistic approach incorporating descriptive data and measurements with quantitative methods is the cluster analysis of scaphitids by Crick (1978), but this tool has not yet been widely applied to recognize index species.

15.3.4 Other Cretaceous Index Macrofossils

Cretaceous macrobiostratigraphy mainly relies on ammonites, but a precise stratigraphic subdivision as well as correlation on a supra-regional scale is also possible with inoceramid bivalves (e.g., Kauffman 1978; Tröger 1989; Yazykova 2004). This is surprising since bivalves in general have the disadvantage that they are

Fig. 15.12 *Actinoceramus subsulcatus,* a Late Albian bivalve index from California allowing a much better correlation to Europe than the associated desmoceratid ammonite that is endemic to California. Photo by the Geosciences Collection of the University of Bremen

more strongly influenced by facies and substrate changes compared to ammonites. Inoceramids, however, are remarkably facies independant. Example for superb bivalve index fossils are members of the *Actinoceramus concentricus-A. sulcatus* lineage, characterizing the early Late Albian across Europe, many parts of Asia, South Africa and the Atlantic as well as Pacific coast of North America (Amédro and Robaszynski 2005; Crampton and Gale 2009). Here, *Actinoceramus subsulcatus* is figured from California, allowing a much better correlation with Europe than the associated desmoceratid ammonite that is endemic (Fig. 15.12). The main constraint in inoceramid biostratigraphy—and their major disadvantage compared to ammonites—is that they are usable as zonal fossils from the Albian to Maastrichtian only (e.g., Harries and Crampton 1998). Beyond that, all other groups of macrofossils are less significant on a global scale, usually because they occur in restricted regions only, e.g., buchiid bivalves are typical for the earliest Cretaceous of the northern hemisphere (Grey et al. 2008) and rudist bivalves characterize the carbonate platforms in the circum-equatorial realm (Masse and Philip 1986; Scott and Filkorn 2007). Among the cephalopods, belemnites are another example of a group with limited biostratigraphic application on a global scale; except for the Late Cretaceous in the Northern Temperate realm of Europe where they provide a proper zonal scheme (Doyle and Bennett 1995). Nevertheless, belemnite events provide useful marker beds in the Cenomanian of NW Europe (e.g., Mitchell 2005).

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Chapter 16
Taxonomic Diversity and Morphological Disparity of Paleozoic Ammonoids

Dieter Korn, Christian Klug and Sonny A. Walton

16.1 Introduction

Due to their exceptionally diverse and relatively common fossil occurrences, which are global in distribution and their high rates of speciation, Paleozoic ammonoids are ideal organisms for studying regional and global extinction events such as the end-Frasnian Kellwasser events, the late Famennian Hangenberg Event, and the Permian-Triassic Event. The Ammonoidea are also extremely useful to use when tackling questions in paleobiology; measurements and parameters obtained from the conch as well as from their suture lines allow ammonoid researchers to look at morphological disparity and taxonomic diversity. All of these points mean that ammonoid researchers are blessed with an amazing resource with which they can shed light on past events in earth's history.

Diversity and disparity are two ways in which researchers can observe and quantify changes in organismal groups over time. Diversity measures changes in taxonomic units (species, genus or family) between temporal units (period, stage, time bin etc.). Without question diversity estimates of the fossil record can be greatly affected by preservational biases and thus, actual numbers of species are not reflected in the fossil record for a number of reasons (Foote and Sepkoski 1999; Foote 2000). Therefore analyses can give distorted impressions of diversity changes. These

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D. Korn (✉) · S. A. Walton
Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung,
Invalidenstraße 43, 10115 Berlin, Germany
e-mail: dieter.korn@mfn-berlin.de

S. A. Walton
e-mail: sonny.walton@mfn-berlin.de

C. Klug
Paläontologisches Institut und Museum,
Karl Schmid-Strasse 4, 8006 Zürich, Switzerland
e-mail: chklug@pim.uzh.ch

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distortions can be reduced by also looking at morphological disparity (changes in the morphological range), and charting these changes over time, as a taxonomically restrained group may still be morphologically diverse (Villier and Korn 2004). Also by looking not just at changes in species or genus numbers but also at the variation in morphology one can get a more complete idea as to the drivers behind large scale fluctuations in the history of a clade. Since morphology is linked to the lifestyle or *bauplan* of an organism, it reflects how it breaths, eats, moves, etc. So changes in the *bauplan* of an animal group reflect changes in its habits and habitats to some extent.

In this chapter, the taxonomic history and morphological disparity of the Paleozoic Ammonoidea is examined in detail. The changes in both are tracked through many extinction events, some of these events nearly brought about the end of the ammonoids. Recovery periods after extinction events are also of great importance and these are also discussed. There is often a complicated interplay between taxonomic diversity and morphological disparity during the history of the Paleozoic Ammonoidea and that a reduction or rise in one does not necessarily mean the same response in the other. The curves of diversity and disparity may show similar patterns (Hangenberg Event), but may have dissimilar patterns in other cases (e.g., the Kellwasser and Permian-Triassic events). The Paleozoic ammonoids have a discontinuous disparity curve of conch shapes. There was a rapid increase in conch disparity in the Early Devonian, when the Ammonoidea clade was still young, thereafter were periods of high morphological disparity (middle to late Famennian, late Viséan to Bashkirian, Artinskian to Wordian) and low morphological disparity (earliest Famennian, earliest Tournaisian).

The following summary of Paleozoic ammonoid history is largely obtained from the review by Korn and Klug (2012) with the data mainly deriving from the AMMON database (Korn and Ilg 2007) and the inclusion of post-2007 literature.

16.2 Diversity Dynamics of Paleozoic Ammonoids

A key problem when one uses large-scale diversity curves is that chronostratigraphic stages are of unequal length in the Paleozoic (Fig. 16.1); the Wordian is the shortest interval (2.2 Ma) and Viséan the longest (18.9 Ma). There is also an underlying problem, which is linked to the differing number of occurrences that have produced ammonoids from the various stages. To try and address these concerns the species and genus richness per millions of years and per region is also calculated (Fig. 16.1b, c).

In terms of genera and species richness per chronostratigraphic stage, the interval between the Famennian and Bashkirian is the most diverse, with the Famennian represented by more than 700 species and about 150 genera (Fig. 16.1a). However, this changes when the plot illustrating species per millions of years and stage is

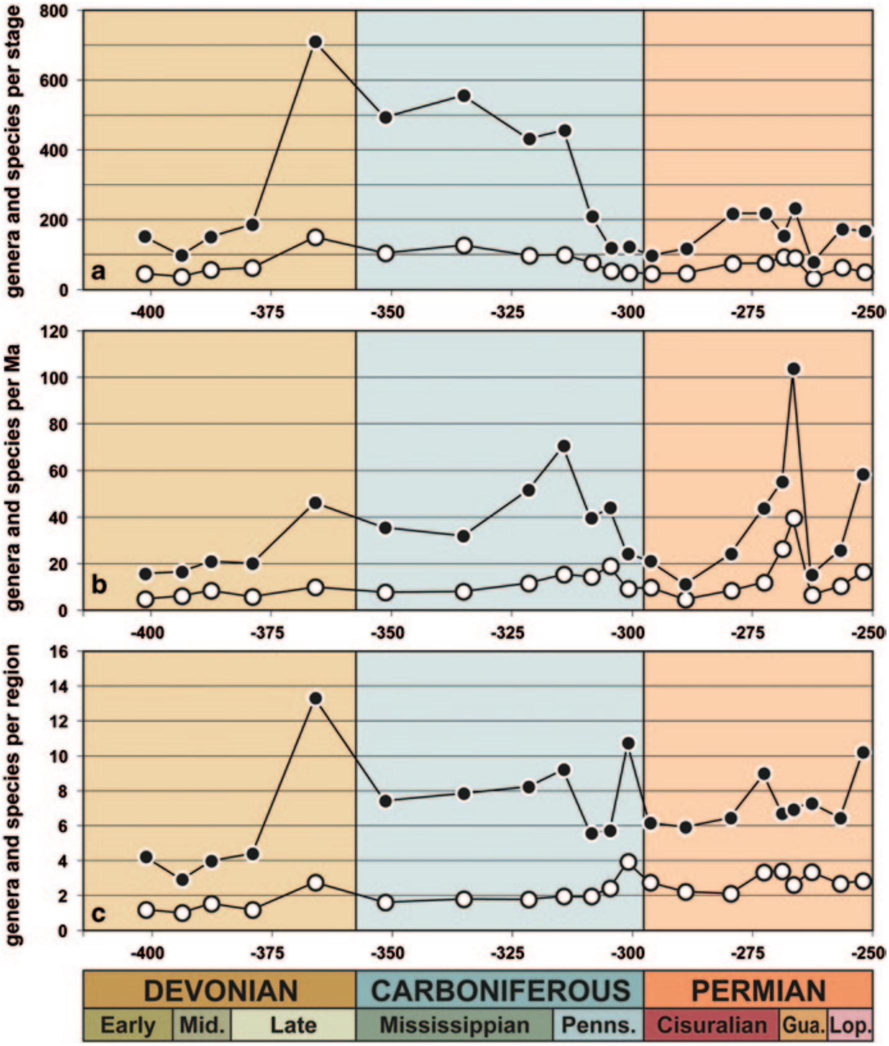

Fig. 16.1 Diversity patterns of Paleozoic ammonoids; data obtained from the AMMON database. **a** Species (*blue dots*) and genus (*white dots*) richness of each stage. **b** Species and genus richness per millions of years in each stage. **c** Species and genus richness per region in each stage (from Korn and Klug 2012)

considered; then, there are several time intervals which are more diverse, namely the Serpukhovian, Bashkirian, Roadian, and Wordian (Fig. 16.1b). When the number of occurrences (regions and areas) is subdivided by the number of species, the Famennian outranks all other stages and stands out in particular when compared with the other Devonian stages (Fig. 16.1c).

16.2.1 Devonian

In the evolutionary history of Paleozoic organisms, the Devonian is a time interval punctuated by several variously severe global events (House 1985, 1989). One of these events, the Upper Kellwasser Event at the Frasnian-Famennian boundary, is one of the so-called 'Big Five' mass extinction events. Although the other Devonian extinction events may not have been as severe, they were still significant global biotic crises (the late Givetian Taghanic Event and the end-Devonian Hangenberg Event). The ammonoids suffered several minor extinctions and almost complete extinctions near the close of the Frasnian and the close of the Famennian, the recovery periods after these events were generally short due to the high speciation rates seen in the Ammonoidea. Korn and Klug (2002) provided an overview of the Devonian ammonoid species and their stratigraphic positions.

The ammonoids originated in the Emsian stage (Early Devonian) from uncoiled or cyrtoconic bactritoids (Schindewolf 1933; Erben 1964). It did not take long for the primitive ammonoids to reach a rather high level in diversity (already from in the early Emsian/Zlíchovian substage, more than 60 species have been described). Locally these primitive ammonoids are abundant and many have a wide geographical range. The richest most diverse occurrences are in Germany (De Baets et al. 2009, 2013), the Czech Republic (Barrande 1865; Chlupáč and Turek 1983), Morocco (Klug 2001a, 2002a), Uzbekistan (Bogoslovsky 1969) and South China (Ruan 1981b). There is a great degree of similarity between many of the species, and therefore the high species number may be an artifact of taxonomic over-splitting (De Baets et al. 2009).

The relatively low number of species (35) in the late Emsian (Dalejan), is most likely explained as a result of the preceding 'Daleje Event' (Ebbighausen et al. 2011). Diversity increased in the next stage (Eifelian) more than doubling to 75 species, followed by a drop in diversity, 55 species, in the early Givetian (the end-Eifelian Kačák Event being the likely driver for this reduction), and 55 in the late Givetian after the Taghanic Event.

These numbers are not absolute, more work must be carried out on the early and middle Devonian time intervals to revise ammonoid taxonomy and as a result of future work, the numbers will undoubtedly change. This is particularly true for the late Givetian, from which assemblages have mainly been documented from Morocco (Petter 1959; Bensaïd 1974; Bockwinkel et al. 2009, 2013).

Diversity increased dramatically in the Frasnian with 200 ammonoid species being described from this stage. However, as in the Emsian, there is a problem with taxonomic practice; the number of species might have been inflated to unrealistic levels due to over-splitting of some of the taxa. One such example of this is seen in the manticoceratid ammonoids (suborder Gephuroceratina) where there are at least 85 species described (Korn and Klug 2002, 2007). These species belong to *Manticoceras* and closely related genera, all within the family Gephuroceratidae. Despite the fact that intraspecific variability in coiling has been known for over a century (Clarke 1899), subsequent authors have neglected to consider this phenomenon when describing assemblages from various regions. This is particularly true in the case of *Manticoceras*, described by Bogoslovsky (1958, 1969), Clarke (1899), Clausen (1969), Glenister (1958), House and Kirchgasser (2008), Miller (1938), Petter (1959) and Wedekind (1913, 1918). These monographs provide an overview of the putative diversity of the Gephuroceratidae. Even if the morphological range of the genus *Manticoceras* s. str. is reduced, for instance by separation of the oxyconic forms like *Carinoceras* and the more globular ones like *Sphaeromanticoceras*, etc. (as done by Becker and House 1993), there are still more than 40 nominal species left over. The very narrow range of variation in the suture lines and the ornamentation of these nominal species leaves a large question mark over the validity of having so many species (Korn and Klug 2007).

The global Kellwasser Event (end-Frasnian) instigated a drastic reduction in ammonoid diversity (e.g., House 1981, 1985, 1989; Becker and House 1994). The event was two-phased, the first phase (lower Kellwasser Event) reduced the diversity to some degree, and the second (upper Kellwasser Event) brought most groups close to extinction (e.g., McGhee 1988; Buggisch 1991). Apart from the problematic archoceratids (suborder Gephuroceratina), of which the survival into the Famennian has been discussed (Korn et al. 2013a), some lineages of the suborder Tornoceratina survived; they became the root stock from which subsequent ammonoids evolved (Becker 1995).

The Tornoceratina (order Goniatitida) diversified in the early Famennian and were widely distributed along the equatorial and subequatorial shelf regions. The Tornoceratina can be split into two major groups, (1) the ‘conservative’ tornoceratids with high apertures and (2) the cheiloceratids with modification of the conch towards more globular forms with lower apertures. A total of 220 ammonoid species have been described from the early Famennian, but this number is probably inflated as many are apparently synonyms (see Bogoslovsky 1971 and Becker 1993b for overviews).

The tornoceratids developed a wider and greater variability in morphology during the mid-Famennian; this evolution of new morphologies gave rise to the clymeniid ammonoids (House 1970; Korn 1992; Gottobrio and Saunders 2005) by shifting the siphuncle from a ventral to a dorsal position. This radical change in the ammonoid *bauplan* drove diversity upwards and 260 species have been reported from this interval. Ammonoids of mid-Famennian age have been reported from many regions and the assemblages are generally dominated by clymeniids (e.g., Wedekind 1914; Bogoslovsky 1971; Czarnocki 1989; Nikolaeva and Bogoslovsky 2005). Diversification of Devonian ammonoids reached its height in the mid-Famennian, the *Prolobites delphinus* and the *Platyclymenia annulata* zones; both contain about 100 species each.

There are about 280 valid species known from the late Famennian ammonoid occurrences of Central Europe, the South Urals, North Africa, etc. The Clymeniida were still the dominant order in communities sporting a wide variety of conch geometries, ornament, and suture lines (for an overview see Wedekind 1914; Petter 1960; Bogoslovsky 1981; Czarnocki 1989; Korn and Klug 2002; Nikolaeva and Bogoslovsky 2005).

The Ammonoidea were nearly exterminated by the end-Devonian Hangenberg Event. The upheaval it caused left only two or three of the various ammonoid lineages; one clymeniid lineage survived the event but then rapidly became extinct without leaving descendants (Korn et al. 2004). One goniatite lineage that survived the Hangenberg Event was the basis for all Carboniferous and subsequent ammonoid evolution. Immediately after the event, faunas were extremely low in diversity (approximately 10 species are known so far), composed only of *Acutimitoceras* and closely related forms as well as a few clymeniids (Schmidt 1924; Korn 1984, 1993).

16.2.2 Carboniferous

Shortly after the almost complete extinction of the Ammonoidea during the Hangenberg Event near the Devonian-Carboniferous boundary, a rather sudden increase in diversity occurred. About 100 species are known from the oldest genus zone of the Carboniferous, the early Tournaisian *Gattendorfia-Eocanites* Genus Zone (e.g., Vöhringer 1960; Ruan 1981b; Korn 1994; Bockwinkel and Ebbighausen 2006; Ebbighausen and Bockwinkel 2007). The most diverse assemblages have been found in the Rhenish and Thuringian Mountains, north-western Africa and South China. More than 90 % of the ammonoid species of the *Gattendorfia-Eocanites* Genus Zone belong to the subfamily Acutimitoceratinae; its descendants probably gave rise to all subsequent Carboniferous and younger ammonoids.

The middle Tournaisian is the least documented interval of Early Carboniferous ammonoid history; the only records are scattered and rather incomplete (e.g., Miller and Collinson 1951; Gordon 1986; Korn et al. 2002). One of the innovations of this interval was subdivision of the external lobe; this occurred in several independent lineages, it is a nice example of convergent evolution, and was perpetuated by almost all of the Ammonoidea. Konovalova (2005) reviewed the ammonoid diversity dynamics of the Tournaisian; she reported approximately 40 species from the “Middle” Tournaisian (*Goniocyclus-Protocanites* Genus Zone).

For a long time the early Late Tournaisian (*Pericyclus-Progoniatites* Genus Zone) was regarded as a low-diversity period with less then 30 species known. However, after the year 2000 new discoveries from Morocco (Korn et al. 2003), Algeria (Korn et al. 2010a, b) and the eastern United States (Work and Mason 2003–2005) increased the number of species to nearly 100.

The subsequent history of the Early Carboniferous ammonoids is markedly discontinuous; high diversity and low-diversity intervals alternate. The first of these periods is the latest Tournaisian (*Fascipericyclus-Ammonellipsites* Genus Zone), an interval from which approximately 220 ammonoid species have been described from various regions including Ireland, Central Europe, the North Urals, the Tyan’ Shan’, North Africa and North America (e.g., Holzapfel 1889; Foord 1901, 1903; Librovitch 1927; Delépine 1940, 1941; Schindewolf 1951; Pareyn 1961; Popov 1968; Kusina 1980; Work et al. 2000; Ebbighausen et al. 2010).

After a rather rapid decrease in the early and middle Viséan to about 50–80 species (Riley 1996; Bockwinkel et al. 2010), diversity increased almost continuously toward the latest Viséan to early Serpukhovian. From this interval (Brigantian to Arnsbergian of the British chronostratigraphical scheme), a high number of species has been described: Brigantian: 280 species, Pendleian: 290 species, Arnsbergian: 205 species (see Gordon 1965 for an overview; Ruzhencev and Bogoslovskaya 1971; Ruan 1981a; Korn 1988). It is the most diverse interval within the history of Palaeozoic ammonoids, possibly caused by increasing provincialism connected with the Variscan Orogeny (Korn 1997a; Korn et al. 2012). By far the most diverse occurrences are in the South Urals (Russia and Kazakhstan). Similar, but impoverished assemblages are known from the Cantabrian Mountains of Spain (Kullmann 1961, 1962, 1963), Algeria (Pareyn 1961) and the Anti-Atlas of Morocco (Korn et al. 1999, Klug et al. 2006). Faunas with a different spectrum of genera are known from other areas, for instance the Subvariscan region (Korn 1988, 1997b; Korn and Ebbighausen 2008), the American West (Korn and Titus 2011) and the American Midcontinent (e.g., Gordon 1965).

A combined total of 150 species has been reported from the Chokieran and Alportian (Ruzhencev and Bogoslovskaya 1978) after an extinction event near the Early-Late Carboniferous (Mississippian-Pennsylvanian) boundary. The most diverse assemblages are again from the South Urals, followed by Central Asia. These two regions retained prime importance through subsequent chronostratigraphic units, i.e., Kinderscoutian, Marsdenian, and Yeodonian. From the last unit, 210 ammonoid species are known, suggesting diversity had recovered to about that of the Serpukhovian. Provincialism may be at the root of this high diversity.

Ammonoid faunas from the succeeding stratigraphic units of the Carboniferous are geographically restricted. From the Desmoinesian stage, for instance, ammonoids have been recorded from only a few places in the world, e.g., the American Midcontinent (Oklahoma, Texas), Canada, Japan and Verkhoyan; only about 30 species are known from the Desmoinesian (Boardman et al. 1994).

The late Carboniferous is characterized by the establishment of two regions in which ammonoids are diverse. The first is again the South Urals area (Ruzhencev, 1950); the second is the American Midcontinent (Boardman et al. 1994). It is mainly from these two regions that 100 species are known from the Kasimovian and 120 from the Gzhelian.

16.2.3 Permian

In contrast to the Devonian and Carboniferous, the evolution of the Permian Ammonoidea was not affected by many crises (for a summary see Leonova 2002, 2011). However, the end-Guadalupian and particularly the end-Permian extinction events were severe, of which the latter almost wiped out the entire clade (for a comparison of diversity and disparity, see Villier and Korn 2004; Brayard et al. 2009).

Transition from the Carboniferous to the Permian was not accompanied by a profound faunal change; the evolutionary lineages from the last two Carboniferous stages were also present in the Early Permian. The South Urals and American Midcontinent remain the most important regions from whence Early Permian (Cisuralian) ammonoid faunas have been recorded, supplemented subsequently by faunas from Central Asia and Timor (Haniel 1915; Smith 1927; Miller and Furnish 1940; Ruzhencev 1951, 1952, 1956; Leonova and Dmitriev 1989; Leven et al. 1992). The approximate numbers of species per Early Permian stage are: Asselian 90, Sakmarian 110, Artinskian 210, and Kungurian 215. The increasing diversity during the Early Permian may be explained by the onset of provincialism with vicariance driving evolution in the various regions (American Midcontinent, Urals, Central Asia, South China) and also by the increasing number of ammonoid-bearing localities (species-area effect).

With the disappearance of shelf areas from the South and Middle Urals at the end of the Early Permian, some ammonoid lineages such as the paragastrioceratid and the metalegoceratid ammonoids (order Goniatitida), which are characteristic for that region, declined dramatically. This was probably the reason for the diversity reduction between the Early and Middle Permian (Guadalupian). Only about 140 ammonoid species are known from the Roadian, but thereafter, the earlier high diversity was re-established with a total of 230 species in the ensuing Wordian. Wordian ammonoids were probably the geographically most widespread during the Permian; diverse and similarly composed assemblages are known from Sicily (Gemmellaro 1887, 1888), Timor (Haniel 1915; Smith 1927), Texas (Plummer and Scott 1937; Miller and Furnish 1940), Arctic Canada (Nassichuk et al. 1965) and elsewhere. The Capitanian then saw another reduction in species numbers to less than 100 species.

The Middle-Late Permian (Guadalupian to Lopingian) transition is marked by a selective extinction event (Villier and Korn 2004; Brayard et al. 2009) that particularly reduced the orders Goniatitida and Prolecanitida; conversely, the Ceratitida apparently were enhanced by the event. The Lopingian is dominated by ceratitid ammonoids representing more than 90 % of the species diversity (e.g., Zhao et al. 1978; Leonova 2002, 2011). Two independent lineages were present, the araxoceratids (Ruzhencev 1959, 1962, 1963) and the xenodiscids (Shevyrev 1965, 1968). The first of these were particularly common in the Wuchiapingian, the second in the Changhsingian. Both lineages survived into the Triassic, but only the xenodiscids proved successful, forming the rootstock for the Mesozoic ammonoids.

16.3 Morphometric Evolution of Paleozoic Ammonoids

16.3.1 Origin of the Ammonoidea and early Diversification

In the early history of the ammonoid clade in the early Emsian (early Zlíchovian substage), there was a limited occupation of the morphospace. The early coiled ammonoid conchs evolved from the straight conchs of their orthocone ancestors. The first ammonoid conchs had incomplete coiling and were widely umbilicate (Erben 1964; Klug 2001a; De Baets et al. 2013); this is highlighted by the fact that they are found in one specific area of the WER-UWI scatter plot (Fig. 16.2a; Korn and Klug 2003). From this humble start, the Ammonoidea quickly spread into unoccupied regions of the morphospace thanks to their high evolutionary rates (Fig. 16.2b–f).

There was a rapid development of conch characters in the late Early and Middle Devonian (morphospace filling) followed by a step back from certain morphs, which were presumably of limited success. This led to canalization within the development of ammonoid conchs during this period. Within the early ammonoids, there arose two independent lineages during the late Emsian, which continued through to the late Devonian.

1. The agoniatitid branch (suborders Agoniatitina and Gephuroceratina) is characterized by a rather slow morphological diversification of conch geometry.
2. The anarcestid branch (suborders Anarcestina and Pharciceratina) evolved rapidly and became the rootstock of most of the subsequent Middle and Late Devonian ammonoid clades.

Conch geometry developments in the Early and Middle Devonian ammonoids occurred in three key ways:

- Changes to conch morphology, which was long lasting: this is particularly common in the early ammonoids, for example the Zlíchovian anetoceratids and mimagoniatitids. The long-term shifts that occurred were the increase in the degree of coiling and, as a result of this, a reduction in the size of the umbilical window until it was phased out due to the ammonitella being tightly coiled.
- Short-term changes to conch morphology and character reversals: this is predominantly seen in the anarcestid lineage. Examples of short term trends include the widening of the umbilicus in the anarcestids and then its narrowing in descendant lineages such as the sobolewiids and pharciceratids.
- Character stasis, which is readily observed in the agoniatitid lineage. In other words the conservation of certain conch morphologies such as the *Agoniatites* conch shape.

Morphospaces are widely used in paleontology to order groups of organisms based on their anatomy. Either discrete data or continuous data can be used. Continuous data is the measurements obtained from body parts or shells or better still the ratios of the anatomical feature with respect to body length or shell diameter (Korn 2012). The latter process has been used successfully in ammonoid research for decades ever since the seminal papers by Raup and Michelson (1965) and Raup (1966). Conch measurements have been converted into conch parameters, the most common ones are those known as the Raupian parameters (Raup 1967) or the modified version of the Raupian parameters developed by Korn (2000); it is the ones developed by Korn, which are used in this chapter. The three cardinal conch parameters used are the conch width index (CWI = relative thickness of the conch), umbilical width index (UWI = relative width of the umbilicus) and the whorl expansion rate (WER = coiling rate of the whorl spiral) (Korn 2000).

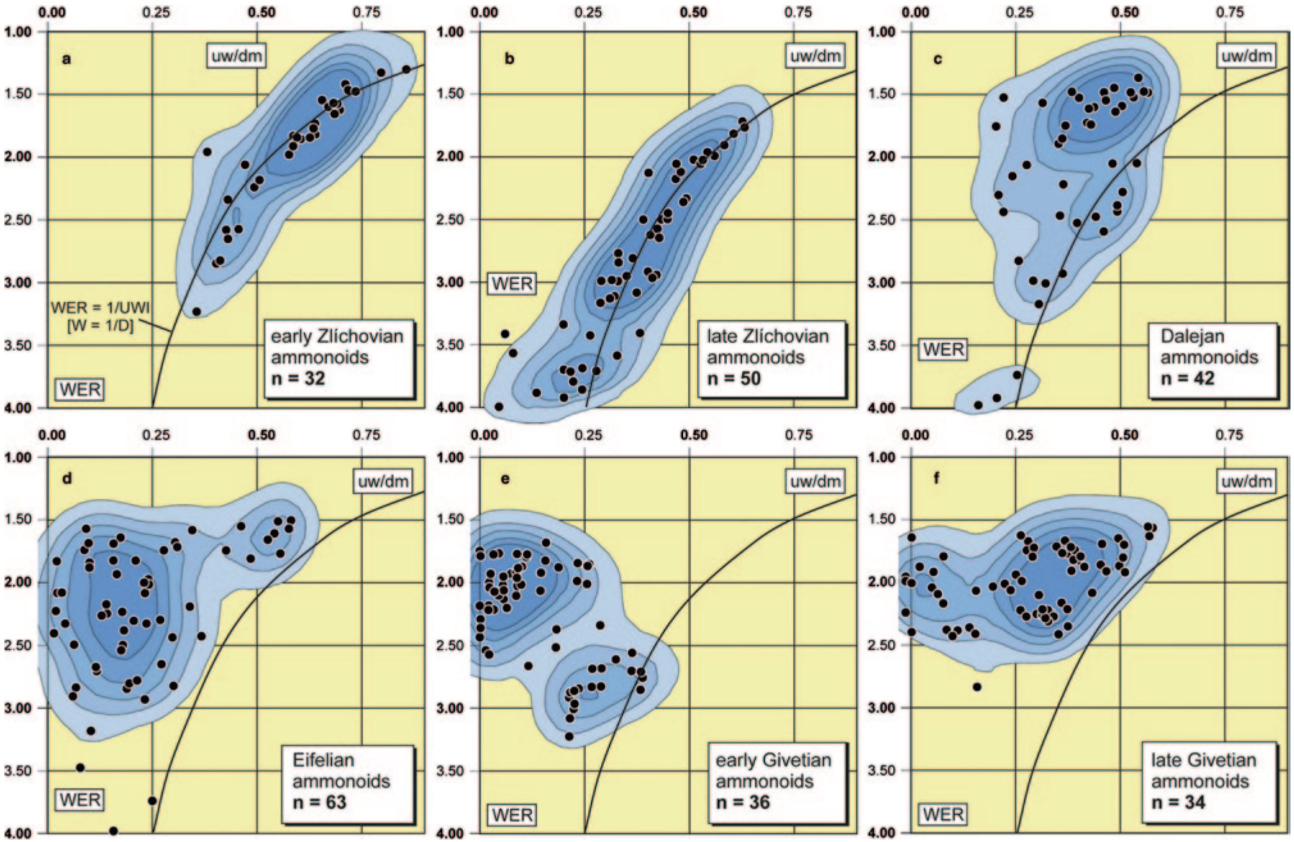

Fig. 16.2 Bivariate plots showing the morphospace occupation of the cardinal conch parameters (WER and UWI) are pair-wise illustrated for six successive Early and Middle Devonian time intervals (from Korn and Klug 2012)

It is a combination of the changes to the parameters, which shapes the conch of an ammonoid. Species that have a high WER show impressive changes in conch diameter and aperture height over just a small number (ca. 5–8) of whorls. Such forms have relatively short but high body chambers, whereas ammonoids with a low WER have long but flattened body chambers (Okamoto 1996; Klug and Korn 2002). Individuals that have a high CWI possess conchs that are rather globular in appearance, and those conchs with a low CWI, are discoidal. Widely umbilicate ammonoids (high UWI) had relatively large umbilical openings. These three cardinal conch parameters have a pronounced effect on the overall conch form, and it is for this reason that they are often used to express morphospaces either in the form of bi-plots or Principal Components Analysis (PCA). An analysis of measurements and their ratios taken from the last intact whorls of ammonoids allows researchers to track any significant changes in the distribution of the data points within a morphospace over time (e.g., Saunders and Swan 1984; Dommergues et al. 2001; Korn and Klug 2003; Klug et al. 2005; McGowan 2007; Moyne and Neige 2007; Saunders et al. 2008; Simon et al. 2010, 2011).

16.3.2 Conch Morphology of Devonian Ammonoids

In the Paleozoic, the greatest range of ammonoid conch morphologies was found in the Devonian. This can be explained by the fact that the Ammonoidea originated in this period, and there was a rapid origination of new and novel conch morphs not previously seen in the Paleozoic (Korn 2000, 2001; Korn and Klug 2002, 2003). Indeed, it has been shown for a number of different animal groups that morphological disparity often reaches a maximum relatively early in a clade's history (Foote 1994; Wills et al. 1994). Also, in this early period of ammonoid evolution, some conch morphologies were quickly replaced by newer forms relegating them to obscurity. These 'defunct' forms, which were replaced, were for a short period novel and competitive. Additionally, these were important steppingstones to more tightly coiled conch morphs with improved hydrodynamic properties (Klug and Korn 2002). Openly coiled conchs are a good example of such a linkage form; they evolved from the straight conchs of the orthocones (De Baets et al. 2013). Additionally, they were obviously more tightly coiled than their predecessors and profited from the greater mobility and as such could occupy new habitats. However, conch evolution continued into the late early Devonian, resulting in more and more tightly coiled ammonoids that probably enhanced greater mobility. As a result of this process, more primitive openly coiled conchs became from an evolutionary perspective less competitive and eventually extinct. Therefore, these conch forms are only found in the Devonian (when concerning only the Paleozoic), leaving an area of ammonoid conch morphospace, which remains empty or only partially filled in proceeding time intervals in the Palaeozoic. Two major ammonoid clades occurred early in the late Emsian (Dalejan) faunas, which had significant differences in conch shape and conch ontogeny. These are the suborders Agoniatitina and Anarcestina (Klug 2002b; Korn and Klug 2002). A characteristic of the agoniatitids is their conservative morphology, which is similar to the ancestral mimagoniatitids (particularly in the laterally compressed subinvolute conchs with a high aperture). The anarcestids had a rapid development towards evolute conchs with a low aperture and a ventrally depressed whorl cross-section.

Differences in the adult conch morphology are also manifested in the ontogenetic trajectories of the main conch parameters. The trajectories can be separated into phases; phases are time intervals that show a certain common trend. The trend can be an increase in a conch parameter or a decrease or increased period of relative stability. Ontogenetic trajectories can thus be described according to the number of phases that they possess, monophasic (one phase), biphasic (two), triphasic (three) and polyphasic (more than three). Similarities in the plots of ontogenetic trajectories such as number of phases, direction of change and extremity of the change can be seen between related groups of ammonoids. This can help ammonoid researchers to infer phylogenetic relationships between different clades; this was the case with the agoniatitids and the gephuroceratids (Korn 2001; Korn and Klug 2001, 2002).

The morphometric analysis of approximately 700 Early Devonian to Early Tournaisian ammonoid (Fig. 16.3) species shows large-scale patterns. Particular interest was paid to the CWI, UWI and the WER. These parameters were computed according to the study by Korn (2000) (compare also Raup 1967).

A PCA was carried out on the data from the three cardinal conch parameters, and a triangular morphospace was plotted based on the results of the PCA (Fig. 16.4). The first two axes of the PCA explain a total of almost 90 % of the variance within the sample (PC1 = 52.6 %; PC2 = 36.9 %). Variations along PC1 are mainly associated with the shape of the body chamber (factor loading: CWI = −0.925, UWI = 0.710, WER = 0.469); PC2 depends mainly on the whorl expansion rate and the umbilical width index (CWI = −0.054, UWI = −0.626, WER = 0.843).

The earliest ammonoids were loosely coiled and had wide umbilici as well as low WERs (anetoceratids); they plot in the bottom to middle right of the morphospace (early Zlichovian). There is a change from these early forms to conch forms (mimagoniatitids), which are more involute and which also possess higher apertures (late Zlichovian to Dalejan), seen by an upwards trend in the data plots and a move to the center (Fig. 16.5).

In the Eifelian the anetoceratids are no longer present (a trimming of the right margin), and despite an extension of the occupied area of the morphospace towards the left there is an overall reduction in the sum of range (SOR).

There is a more extensive trimming of the margins in the early Givetian, resulting in a smaller occupation of the morphospace. The early Givetian has the lowest SOR of all the Early and Middle Devonian intervals (Fig. 16.5) and therefore represents a low disparity period in the evolutionary history of the ammonoids. There is no major transition event of conch forms between the early and late Givetian. Conch morphology, as controlled by the three cardinal conch parameters, was

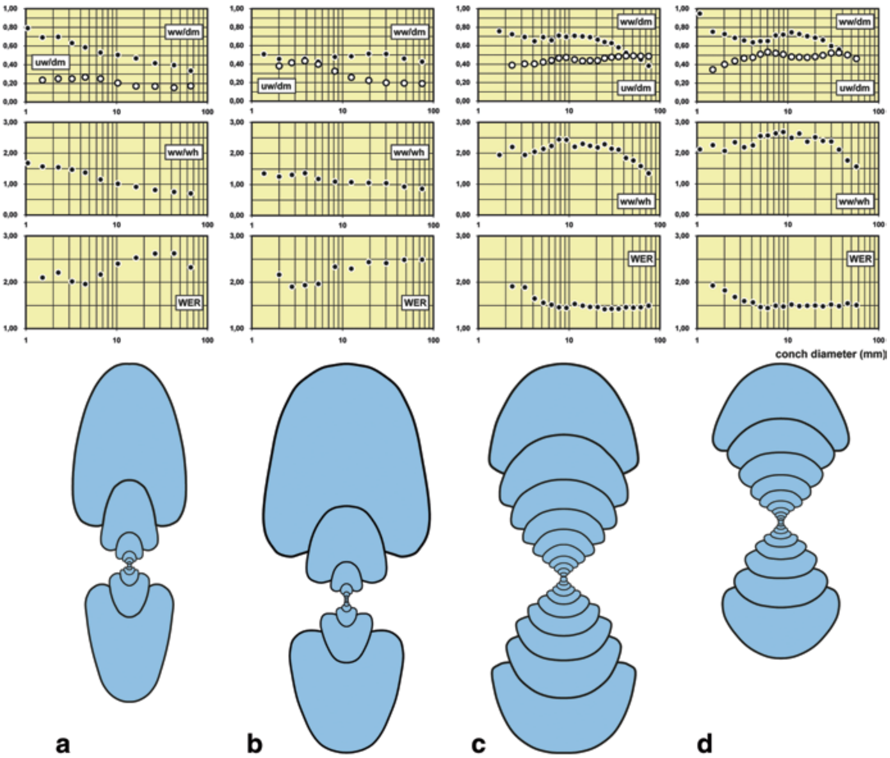

Fig. 16.3 Ontogenetic development of conch geometry in some Devonian ammonoids (Korn and Klug 2001, 2007; Klug 2002a). The diagrams represent (from *top to bottom*) development of the conch width index (ww/dm), umbilical width index (uw/dm), whorl width index (ww/wh), and whorl expansion rate (WER). **a** *Fidelites clariondi* (Petter 1959). **b** *Manticoceras* sp. **c** *Sellanarcestes wenkenbachi* (Kayser 1884). **d** *Pharciceras* sp.

mostly unaffected by the Taghanic Event. although there is an influx of more widely umbilicate forms (morph A) in the late Givetian.

16.3.3 Devonian Extinction Events

The time interval from the Emsian (Early Devonian) to the early Tournaisian (Early Carboniferous) includes a number of geological events (Table 16.2). These events are defined primarily by punctuations in the diversity history of the Ammonoidea (e.g., House 1985, 2002; Walliser 1985, 1996; Table 16.1).

As can be seen from Table 16.2, not every geological event had a discernible effect on the ammonoid conch-shape record (Fig. 16.5). The three events, which had the biggest impact were the Kačák, Upper Kellwasser and Hangenberg events (Fig. 16.6).

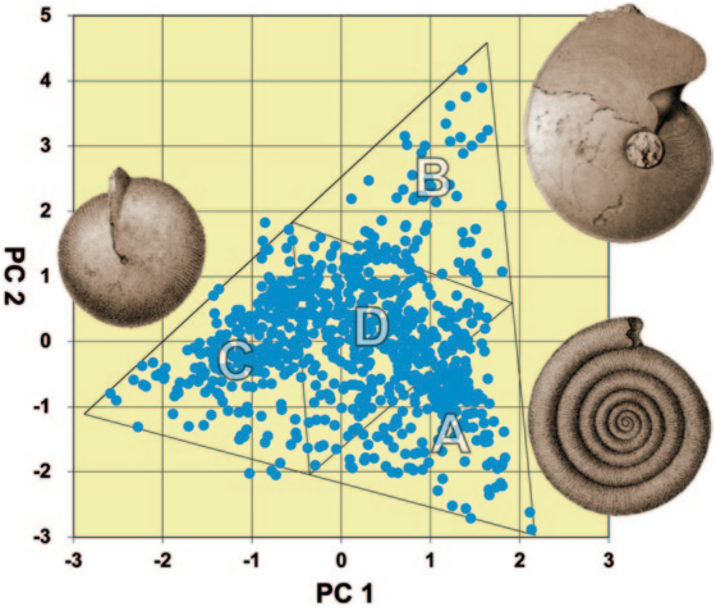

Fig. 16.4 Empirical morphospace of the Devonian ammonoids calculated using the three conch parameters WER, CWI, and UWI, together with representative examples (morphs) of ammonoids and their position within the morphospace segment (from Korn and Klug 2012)

16.3.4 Kellwasser Crisis and Recovery

There was almost no fluctuation in morphological disparity between the late Givetian and the mid-Frasnian; the 'Frasnes Event' is not apparent when one regards ammonoids (Fig. 16.6). In fact, this event, rather than having a negative effect on ammonoids, could be seen as having a positive effect if one looks at species numbers. There is a minor shift towards forms with a high aperture and narrow umbilicus (morph B) in this interval. The margins of the morphospace are reduced as a result of the Lower Kellwasser event resulting in a decrease in disparity. At the same time, some widely umbilicate forms (morph A) reappeared. Morph B is the dominant form; this is due to the evolutionary peak in gephuroceratids. However, morph A does reappear at this time. The disparity measures are inconsequential; the sum of range decreases markedly but the sum of variance is stable (Fig. 16.6c, d).

The Upper Kellwasser Event (Frasnian–Famennian boundary) was a major extinction event for the Ammonoidea (Becker et al. 1989, 1993; Becker and House 1994). The suborder Gephuroceratina became almost extinct and as a result of this, Morph B, which is extensively represented by the suborder, collapsed. If *Archoceras* managed to survive the Kellwasser Event as the last surviving member of the gephuroceratids, it was only the last gasp of the family as they produced no descendants, i.e., a 'Dead Clade Walking' according to Jablonski (2002) or 'failed

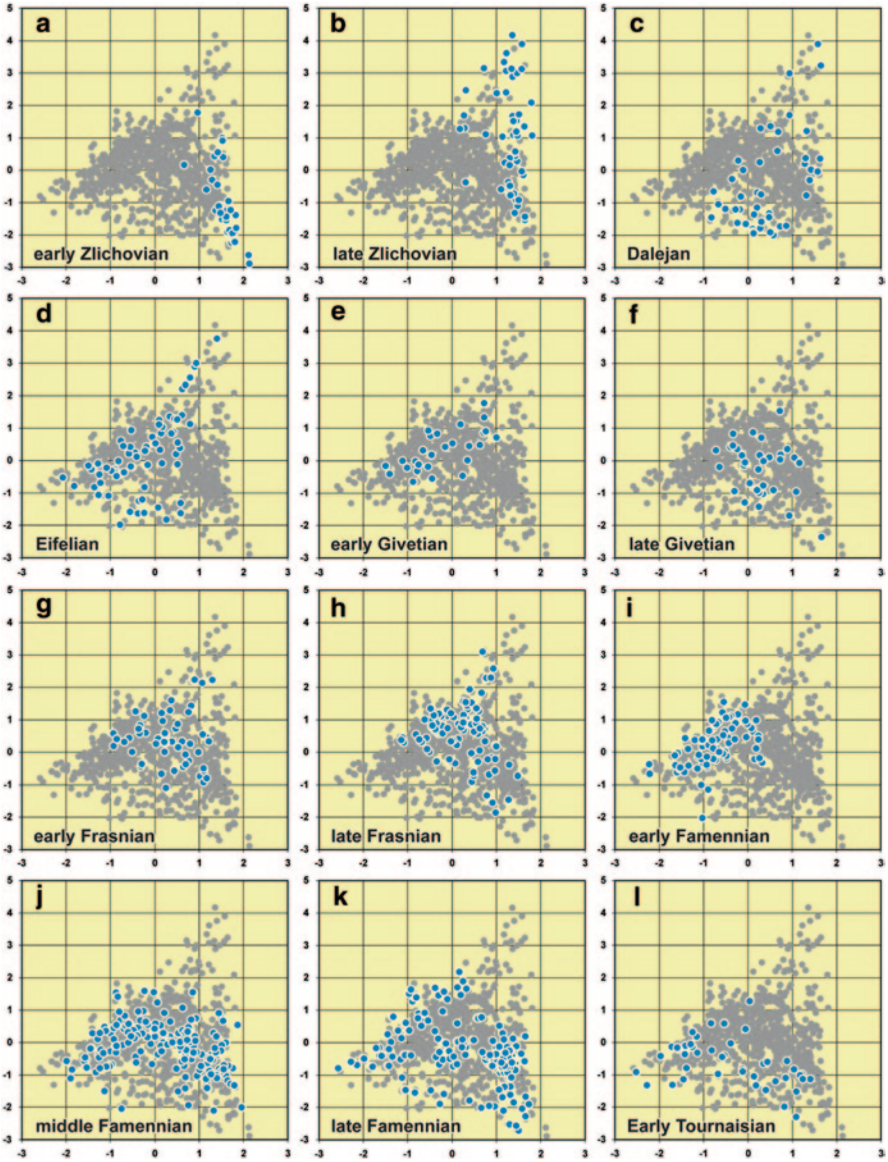

Fig. 16.5 Morphospace occupation of Early to Late Devonian ammonoids and the transition into the earliest Carboniferous by application of the method of a principal component analysis (using conch parameters whorl expansion rate, conch width index, and umbilical width index). From Korn and Klug (2012). *Big circles* are the values from the respective interval, while the *small dots* show values from the entire Paleozoic

survivor' according to Korn et al. (2004). As with the Lower Kellwasser Event, only the sum of range is profoundly affected (and also the range of the middle two quartiles of the occupied morphospace), but the sum of variance is stable.

Table 16.1 Conch characters of the analyzed Devonian ammonoid suborders (Fig. 16.3)

Suborder	Defining characters of the conch ontogeny
Agoniatitina (Emsian to Givetian)	The conch ontogeny is strongly influenced by changing rates of coiling. *Fidelites* (Fig. 16.3a) has a low aperture in the juvenile period (WER = 2.00), there then follows a period (preadult) with an acceleration of the coiling rate, which is then followed by stagnation in the adult stage. There is a strong resemblance to the coiling rates seen in the mimagoniatitids, an in depth analysis of the genus *Rherisites* has been carried out by Klug (2001b)
Gephuroceratina (latest Middle Devonian and Frasnian)	Changes in the WER are quite similar to those seen in the Agoniatitina, although the adult conch shapes can differ. *Manticoceras* for example has a similar conch shape to *Fidelites* and shares the postembryonic tripartite ontogeny in the WER (Fig. 16.3b). Close phylogenetic relationships between the agoniatitids and the gephuroceratids have been proposed due to the strong resemblance of their conch ontogenies and the similar sizes of their ammonitella (Korn 2001, Korn and Klug 2001, 2002)
Anarcestina (Emsian to Givetian)	They are characterized by an ontogeny, which shows only minor changes in the main conch parameters. The CWI and WWI are relatively stable over long periods of growth (Fig. 16.3c), in the example specimen the UWI increases continuously but slowly, the aperture remains low throughout the entire growth period (Klug 2002a)
Pharciceratina (Givetian and early Famennian)	These multilobate ammonoids possess a conch ontogeny comparable to that of the anarcestids (Fig. 16.3d). Despite developing an increased variation in conch morphology, their ontogenetic trajectories closely resemble Emsian to Eifelian anarcestids. Our example (*Pharciceras*) virtually shows the same conch ontogeny as *Sellanarcestes*. Advanced pharciceratids differ from our example in having a closed umbilicus, but the ontogeny of their coiling rate is still characteristic for the anarcestid–pharciceratid lineage (Korn 2001). The main difference from their anarcestid ancestors is the increase in sutural complexity in pharciceratids (Saunders et al. 1999, 2008; Korn and Klug 2002)

There was a slow recovery after the Upper Kellwasser Event in the early Famennian ammonoid zones. The Tornoceratina survivors suffered a severe reduction in their morphospace occupation. In the early Famennian, however, the cheiloceratids diversified and managed to fully occupy the area of morph C, a first in the history of the ammonoids. The empty space resulting in the loss of the gephuroceratids was not filled for about 8 Ma; it was not until the mid-Famennian (*Pernoceras dorsatum* and *Pseudoclymenia pseudogoniatites* Zones) that parts of this area were repopulated by the tornoceratids. This instigated a change in morphospace occupation and House (1985) named this the 'Nehden Event'. Nevertheless, this event should be interpreted more as an innovative period in the evolution of the tornoceratid ammonoids rather than as a crisis.

The *Prolobites delphinus* Zone saw the introduction of the clymeniids, and with this rapidly diversifying group, the ammonoids reached a point of recovery after the devastation of the Upper Kellwasser event. Indeed, a peak in morphological range can be seen at this point. There is no true innovation in conch forms by the tornoceratids and cheiloceratids; they maintained their morphospace occupation (mainly

Table 16.2 Devonian geological events and their effect on ammonoid evolution

Devonian geological events	Effect on ammonoid morphology
Daleje Event	Disappearance of crioconic shells
Choteč Event (close to the Emsian–Eifelian boundary)	Disappearance of the umbilical window in the embryonic shell
Kačák Event (close to the Eifelian–Givetian boundary)	Major effect on ammonoid evolution seen by a reduction in occupied area of morphospace (SOR is reduced)
Taghanic Event (mid-Givetian)	Minor extinction event, but with recovery and dispersal of surviving lineage (pharciceratids)
Frasnes Event (Middle–Late Devonian boundary)	No discernible effect on the Devonian ammonoid morphospace
Lower Kellwasser Event (late Frasnian)	Minor extinction event, but with recovery and dispersal of surviving lineage (archoceratids)
Upper Kellwasser Event (Frasnian–Famennian Boundary)	Major effect on ammonoid evolution seen by a reduction in occupied area of morphospace (SOR is reduced)
Enkeberg Event (early Famennian)	No discernible effect on the Devonian ammonoid morphospace
Annulata Event (middle Famennian)	No discernible effect on the Devonian ammonoid morphospace
Dasberg Event (late Famennian)	No discernible effect on the Devonian ammonoid morphospace
Hangenberg Event (close to the Devonian–Carboniferous Boundary)	Major effect on ammonoid evolution seen by a reduction in occupied area of morphospace (SOR is reduced), almost the entire morphospace range was affected

morph C); the clymeniids quickly diversified spreading over a wide range in the morph A and morph D areas.

The Annulata Event and the Dasberg Event had no discernible effect on the morphometric evolution of the Ammonoidea (Becker 1993a), which can be seen by a lack of any major difference in the disparity indices over the following zones (Fig. 16.6c, d). In the middle *Wocklumeria* Stufe, the clymeniids instigated a marked change in the occupation of the morphospace by dispersing over most of the morph A field and evolving conch forms similar to goniatitid morphology (morph C).

16.3.5 Hangenberg Event and its Aftermath

The Hangenberg Event had the biggest impact on the Ammonoidea out of all of the Devonian extinction events (Korn 1993, 2000; Korn et al. 2013b). As a result of the massive loss of species, especially in the Clymeniida and the Goniatitida, there was a dramatic drop in taxonomic diversity and morphological disparity. The survival of a few clymeniid species produced no descendant species, and the lineage terminated

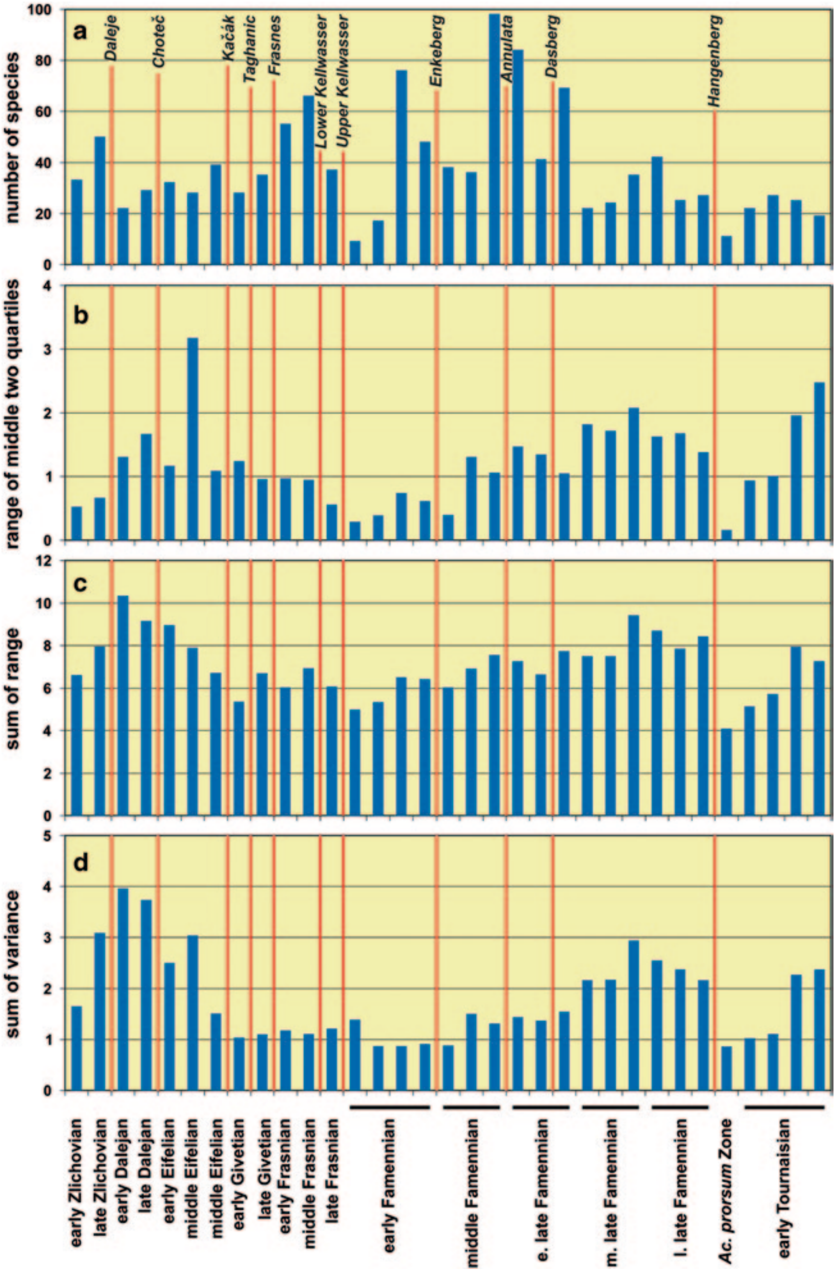

Fig. 16.6 Diversity and disparity fluctuations of Early to Late Devonian ammonoids and the transition into the earliest Carboniferous illustrating the impact of the various geological events (from Korn and Klug 2012)

shortly after the extinction event (Korn et al. 2004). One goniatite lineage, the Goniatitida, survived the Hangenberg Event and managed to flourish in the new world order filling niches that were once occupied by the clymeniids.

Before the Hangenberg Event, in the *Wocklumeria sphaeroides* Zone, the ammonoid morphs (A-D) were all represented, albeit in a dispersed manner. The Hangenberg Event affected all morphs; there was a drastic reduction in the sum of range and sum of variance evident in the post-event *Acutimitoceras prorsum* Zone. The goniatites conch morphology is rather restricted and therefore plots in a narrow area in the morphospace (Fig. 16.7).

A partial refilling of areas in the morphospace, vacated by the clymeniids and tornoceratids, occurred over the following Carboniferous *Acutimitoceras acutum* to *Paragattendorfia patens* Zones. However, the range of morphospace occupation during the Early Tournaisian did not reach previous levels found in the Late Devonian.

16.3.6 The Basal Carboniferous Recovery

Morphometric analyses of Carboniferous ammonoids have been undertaken several times (Saunders and Swan 1984; Nikolaeva and Barskov 1994; Saunders and Work 1997; Saunders et al. 1999). Previous stratophenetic studies of the ammonoid assemblages from the latest Devonian to earliest Carboniferous cephalopod limestone succession of the Rhenish Mountains (Korn 1986, 2000) revealed some telling changes in the morphological evolution of the Ammonoidea. The investigation concentrated on the WER and the UWI, two conch characters, which are very important in ammonoids since they indicate body-chamber length (and hence orientation in the water column) and mobility as well as the shape of the body chamber. The main findings were that the Hangenberg Event caused an almost complete change in the morphological spectrum adopted by ammonoids. As already stated, the clymeniids and tornoceratids became extinct at or immediately after the Hangenberg Event; the morphospace area they once occupied was refilled by the surviving prionoceratid ammonoids (Fig. 16.7), albeit not completely.

Although the Hangenberg Event was devastating, there was a rapid rate of recovery afterwards; eight species of prionoceratids, with an open umbilicus in their juvenile stage are present in the latest Devonian *Acutimitoceras prorsum* Zone, which is the first post-event zone. *Acutimitoceras* and *Nicimitoceras* seem to appear in next to no time with a new conch geometry, which was probably developed earlier.

There was no major increase in conch diversity over the four earliest Carboniferous zones from the *Acutimitoceras acutum* Zone to the *Paragattendorfia patens* Zone (Fig. 16.8). A group of widely umbilicate goniatites became well established, but intermediates were not important as can be seen by their absence.

It is remarkable that the goniatites of the '*Gattendorfia* Stufe' differ so conspicuously in their WER/UWI proportions from the clymeniids of the Late Devonian '*Wocklumeria* Stufe'. The bivariate plot of the WER/UWI values of all the clyme-

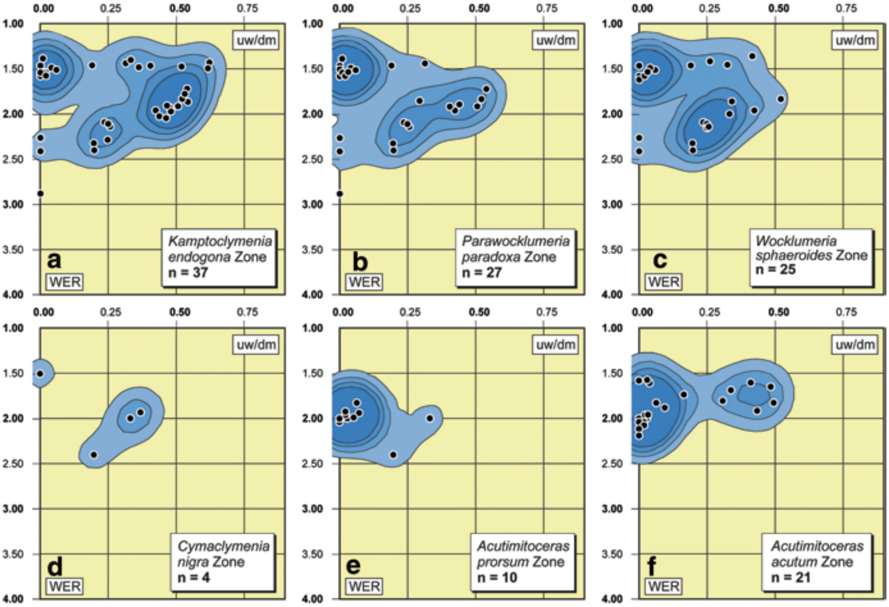

Fig. 16.7 Morphospace occupation using the example of WER–UWI couplet across the Devonian-Carboniferous Boundary (after Korn 2000). Note the sharp decrease in the *Cymaclymenia nigra* Zone (Hangenberg Event) and the subsequent recovery

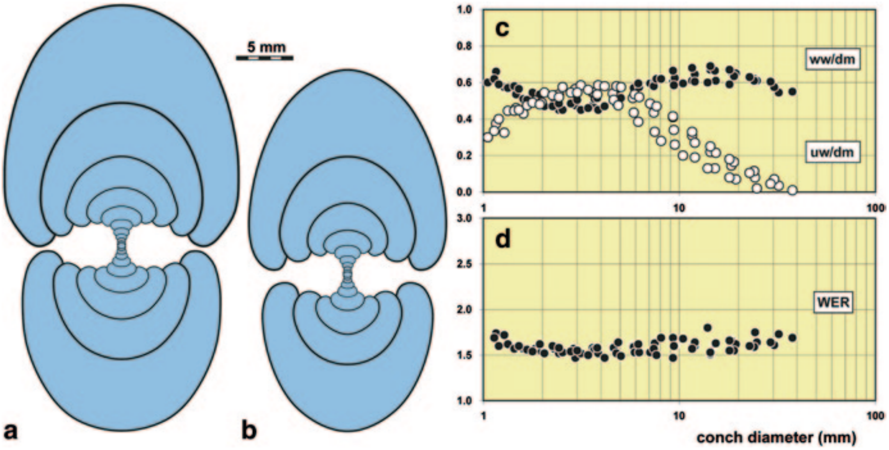

Fig. 16.8 Conch ontogeny of the latest Devonian *Acutimitoceras hilarum* Korn, 2004 from Lalla Mimouna (Anti-Atlas, Morocco) on the basis of cross-sections. **a, b** Cross sections, x 2.0. **c** Ontogenetic development of the whorl width index (ww/dm) and umbilical width index (uw/dm). **d** Ontogenetic development of the whorl expansion rate (WER)

niids from the '*Wocklumeria* Stufe' and goniatites from the '*Gattendorfia* Stufe' demonstrates the significant differences in position of the morphospace occupied by these groups (Fig. 16.7).

16.3.7 Conch Morphology of Carboniferous Ammonoids

Nearly all Carboniferous ammonoids can be assigned to a single monophyletic clade, which originated in the earliest Tournaisian prionoceratids. This clade gave rise to two subclades, the Carboniferous and Permian representatives of the Goniatitida and the Prolecanititida. The genus *Acutimitoceras* is a good candidate for being close to the initial radiation of the two subclades; its conch ontogeny has been intensively studied (Bockwinkel and Ebbighausen 2006) on the basis of material from the Rhenish Mountains and the Anti-Atlas.

Acutimitoceras hilarum is a Late Devonian species with strikingly allometric conch growth and can thus be used as a characteristic example for many Carboniferous and Permian ammonoids (Korn et al. 2004, 2007). Its conch ontogeny consists of three stages, which are mainly driven by changes in the proportions of the whorl width (a triphasic ontogenetic trajectory) and by a biphasic change in the umbilical width (Fig. 16.8). The first growth stage (which may be called serpenticonic) is characterized by slowly expanding, ventrally depressed whorls embracing the preceding whorl to a minor degree only. During the second stage, the whorl cross-section becomes more circular and increasingly embraces the preceding volution; as a result of these changes, the conch developed a stouter form. The adult stage is marked by an almost complete closure of the umbilicus and lateral compression of the whorls.

Korn and Vöhringer (2004) analyzed the ontogeny of *Gattendorfia crassa* from the early Tournaisian (Mississippian) Hangenberg Limestone of the Rhenish Mountains. It is well placed, due to its basal position in the Carboniferous ammonoids, to be used as a model for many lineages. There is a general similarity between the ontogenies of *Gattendorfia* and *Acutimitoceras*, with the obvious exception that the umbilicus is not completely closed off in the adult stage of *Gattendorfia*. The conch ontogeny closely resembles that of other Carboniferous species, such as *Cravenoceras leion* from the basal most Serpukhovian strata of Derbyshire, in which the adult morphology as well as several ontogenetic trajectories are similar to *Gattendorfia* (Korn and Tilsley 2002). The ontogenetic changes affecting the outline of the whorl cross-section are striking; this reflects a rearrangement of soft parts in the body chamber of the animal.

The aforementioned examples can be regarded as ontogenetic models for many of the Carboniferous ammonoids, which usually possess a triphasic postembryonic conch ontogeny. The three phases can, however, show a remarkable degree of variability in the strength of the expression and in their length.

16.3.8 Permian Extinction Events

Using the four cardinal conch parameters (WER, UWI, WWI and IZR), Villier and Korn (2004) ran a PCA and plotted an empirical morphospace for Permian and earliest Triassic ammonoids (Fig. 16.9). The resulting scatter plot resembles that of the Devonian ammonoids in its triangular field. The major conch morphologies, of this time interval are pictured (Fig. 16.9):

- Morph A—represented by *Paragastrioceras* (with a widely umbilicate, slender conch and low coiling rate);
- Morph B—represented by *Artinskia* (with a narrowly umbilicate, slender conch and high coiling rate);
- Morph C—represented by *Almites* with a narrowly umbilicate, globular conch and low coiling rate).

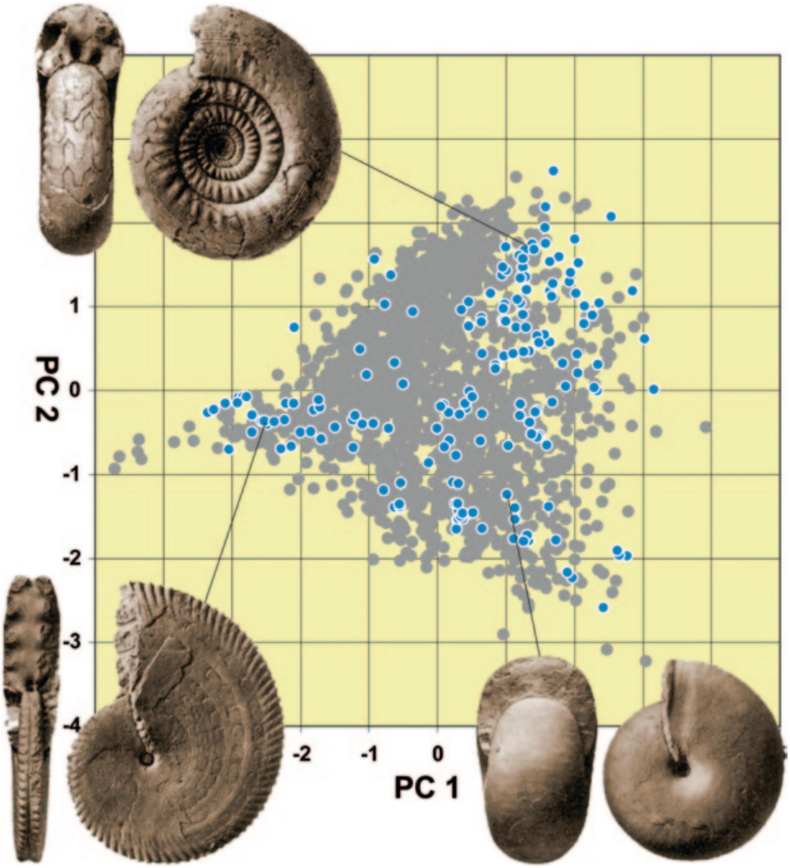

Fig. 16.9 Morphospace occupation using conch parameters: whorl expansion rate, umbilical width index, whorl width index, and imprint zone rate of the ammonoids from the latest Carboniferous to Early Triassic. After Villier and Korn (2004). Examples of the extreme morphologies are shown at the sides of the morphospace triangle

The disparity indices sum of variance and sum of range were calculated from the empirical morphospace. The temporal changes in disparity (variance and range) generally follow the pattern of the diversity curve for superfamilies, but at low taxonomic levels, diversity and morphological disparity are independent. There was an increase in disparity from the Late Carboniferous to the Early Permian. It then remained relatively stable for the first three stages of the Permian. From the Artinskian to the end of the Permian (approximately 30 Ma), there is a general decreasing trend in disparity; this is briefly interrupted by an increase in the Wordian. There is a substantial difference in the patterns of the two disparity estimates; fluctuations in variance are more pronounced, whereas the decreasing trend of the range occurs more regularly. Due to their diversification, an increase in the disparity of three groups (Neoicoceratacea, Adrianitaceae, and Cyclolobina) helped to drive the brief increase that is observed in the Wordian. The end-Capitanian crisis is characterized by the loss of a large number of genera (Glenister and Furnish 1981). The downward trend in disparity continued during the two last stages of the Permian; the lowest value occurred just before the end-Permian mass extinction in the Changhsingian. The early Triassic is marked by stagnation in variance and only the morphospace occupation increased.

The end-Capitanian and the end-Changhsingian are two distinct mass extinction events, the latter standing out due to its intensity. There are three major patterns to be seen in the morphological disparity through time of the Permian ammonoids: a long-term reduction in disparity, a high level of selective extinction at the end of the Capitanian, and a non-selective extinction at the end of the Permian (Korn et al. 2013c). The end-Capitanian event shows, despite the high level of extinction, a pattern that corresponds to a model of background extinction. The pattern of the end-Permian extinctions are in agreement with the model of a 'mass extinction regime' (Jablonski 1986, 2005), consisting of a major event, which is relatively brief in duration, has a global effect, is independent of earlier variations in diversity, and which is random in nature in terms of the taxa, which are killed off.

16.4 Ammonoid Morphospace Over the Paleozoic and Triassic

The Paleozoic and early Mesozoic represents an interesting interval in the history of the Ammonoidea; it contains not only the origin of the Ammonoidea but it also includes numerous extinction and diversification events. These periods of evolutionary upheaval will be reflected in the development of the ammonoids and are best seen in the changes that occur to their suture lines and conch shapes. The three cardinal conch parameters provide an excellent basis on which to analyze the changes in conch morphology. A Principal Components Analysis (PCA) based on the CWI, UWI and WER parameters obtained from the last measurable half whorl of 4834 ammonoid species from the Devonian through to the Triassic was performed (Fig. 16.10). The first two principal components explain 85.5 % of the

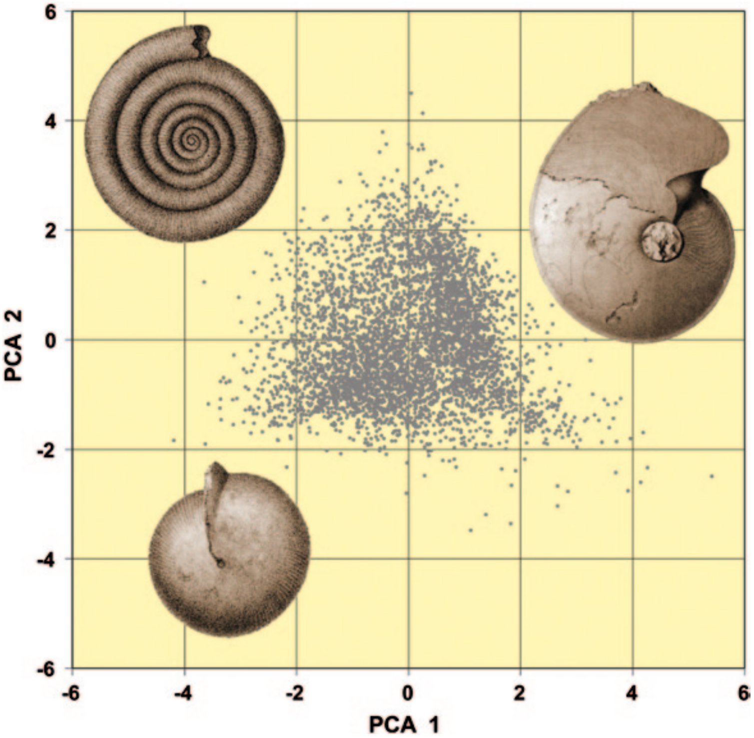

Fig. 16.10 The occupation of morphospace analyzed by a principal components analysis of the cardinal conch parameters conch width index, umbilical width index and whorl expansion rate. Examples of the extreme morphologies are shown at the sides of the morphospace triangle

Table 16.3 The disparity indices, sum of variance, sum of range and range of the middle two quartiles (RMQ) in the Principal Components Analysis of the morphometric data from Devonian to Triassic ammonoids

PC	Eigenvalue	% variance
1	1.387	46.23
2	1.177	39.25
3	0.436	14.52

variance (Table 16.3). The disparity indices, sum of variance (SOV), sum of range (SOR) and range of the middle two quartiles (RMQ) were calculated for the first two principal components for each of the four periods (Table 16.4).

The filled area of the morphospace for all of the specimens is triangular in shape, with the three end points representing extreme morphotypes (Fig. 16.10). In order to see the differences in morphospace occupation over the time periods, the data points for each period are plotted against the complete dataset.

The Devonian shows a high density of taxa on the right side of the total occupied morphospace. There are a number of specimens in the bottom right point of the

Table 16.4 Disparity indices of the first two principle components of the analyzed time intervals

Period	SOR	RMQ	SOV
Devonian	15.16	3.31	2.73
Carboniferous	12.41	2.75	2.07
Permian	13.44	3.51	2.75
Triassic	14.15	2.89	2.06

SOR sum of range, *RMQ* range of the middle two quartiles, *SOV* sum of variance

triangle, representing more extreme conch forms which are sub-involute, discoidal and with very high WER values. Another extreme conch form also represented is in the top point of the triangle. These morphs are very evolute, extremely discoidal and have a very low WER (Fig. 16.11a). The Devonian has a high range in disparity, both overall and in the RMQ. This is representative of the fast evolutionary rates of the Ammonoidea, showing how they quickly radiated not just in terms of number of species but also in terms of morphological disparity. With the second highest variance, the Devonian also represents a time with less clustering around a small number of conch morphs (Table 16.4).

There is a dramatic change between the positions of the Carboniferous taxa with that of the Devonian; the Carboniferous species populate mainly the left and middle of the empirical morphospace with a marked move away from the area representing the two conch morph forms mentioned above (Fig. 16.11b). The large shift in morphospace occupation was probably instigated by the mass extinction events that took place at the end of the Devonian, especially the Hangenberg Event. The densely populated areas of the Carboniferous morphospace are representative of ammonoids with globular and pachychonic conch forms they are sub-involute and with low apertures. The Carboniferous has the smallest SOR out of all of the periods at 12.41. This reflects the reduction in the morphospace occupation especially with the absence of any species in the more extreme morph ranges around the top and bottom right points of the empirical morphospace triangle. A low variance value also matches the changes in conch forms as there is a reduction in the variety of conch morphs in this period of ammonoid evolution (Table 16.4).

The changeover from the Carboniferous to the Permian is not marked by a major ammonoid extinction event as is indicated by the fact that there no dramatic changes in morphology at the boundary of the two periods (see Figs. 16.7 and 16.11). The area occupied during the Carboniferous is still filled in the Permian, although not as densely. There is an increase in taxa towards the far right of the overall morphospace, which was unoccupied in the Carboniferous. More species are now seen again in the morphospace area in the bottom right. In the Permian there is an increase in the RMQ, it reaches its highest value of 3.51, and the SOV also reaches its highest level at 2.75 (Table 16.4). This shows a return to taxa being more spread around a greater number of conch morph forms, as was seen in the Devonian.

The Permian-Triassic mass extinction event hit the Ammonoidea hard. Only a few genera survived this period of instability, and this explains the massive reduction in globular ammonoid conchs and the abandonment of the extreme left side of

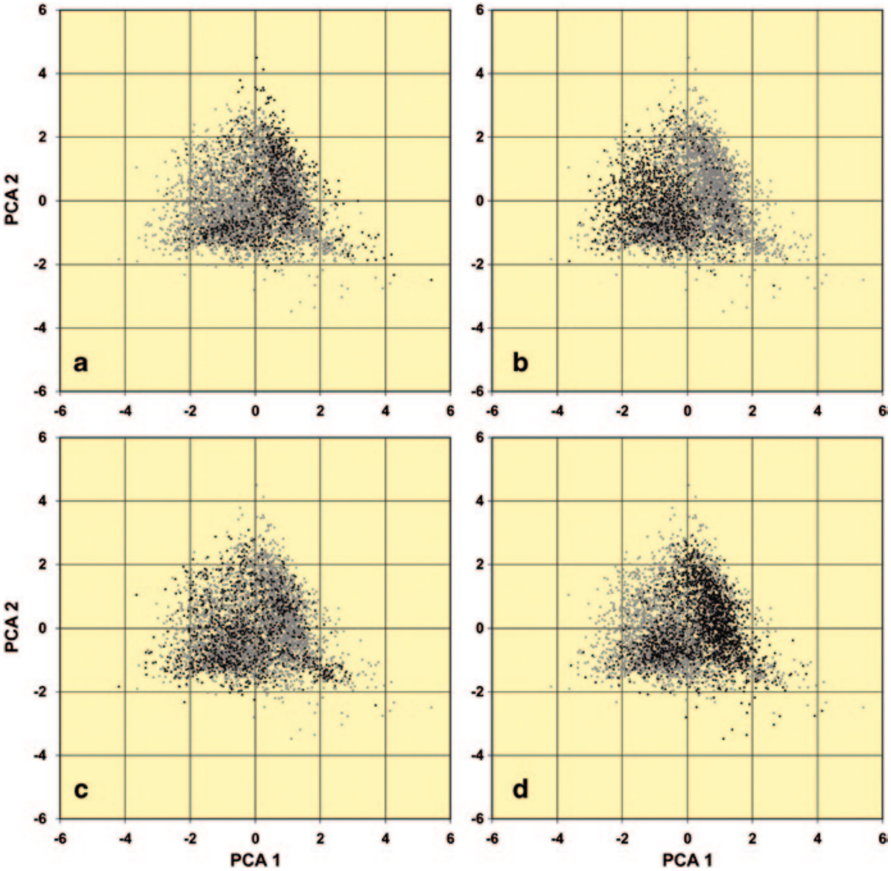

Fig. 16.11 Changes in the occupation of ammonoid morphospace through time **a** Devonian, **b** Carboniferous, **c** Permian and **d** Triassic ammonoids

the overall morphospace area in the Triassic plot. The RMQ is greatly reduced from that of the Permian, and the variance is the lowest of all four periods, this shows another move towards a strong concentration on a reduced number of conch morph forms similar to the Carboniferous, but this time towards narrower conchs (discoidal) with high apertures (WER = 2.00 − 2.50).

16.5 Conclusions

When looking at the extinction and diversification patterns of ammonoids during the Paleozoic, it is not enough to look solely at the taxonomic diversity (number of taxa preserved). Other analyses are needed to complete the picture such as morphological disparity, which is a particularly useful tool. By looking at changes in conch morphology over time researchers are able to test hypotheses about the severity and nature of extinction events.

Taxonomic diversity is often independent of morphological disparity, and because of this morphological disparity can help to mitigate the sampling bias of the fossil record. By focusing on differences in shape of the ammonoid conchs, morphological disparity can achieve a degree of independence from taxonomy. It is this independence that makes it possible to compare samples with varying degrees of taxa, which is obviously not possible if one only uses taxonomic diversity. Disparity analyses consider the spread of taxa and the areas of occupied morphospace occupied during successive time intervals.

The Ammonoidea are excellent candidates for analyzing extinction dynamics. They show a wide variability in their taxonomic diversity over time and they survived many extinction episodes. The diversity dynamics of ammonoids analyzed by the distribution patterns of over 4000 species obtained from the AMMON database and ranging from the Emsian stage (Early Devonian) to the Triassic gives us a deep insight into the evolutionary history of the clade.

The results of these analyses allowed for a comparison of the effects of extinction events as well as subsequent radiations. It turned out that only the Kellwasser Events, the Hangenberg Event and the Permian-Triassic Event had major effects on the ammonoid morphospace. The end-Eifelian Kačák Event had a more intense effect than the end-Givetian Taghanic Event. Due to the complex nature of ecosystems and how they are brought towards a point of collapse, it would be unlikely that these events all had identical courses, causes and effects. The Hangenberg Event was the most severe of the Paleozoic extinctions for the Ammonoidea, because all but one group became extinct. Despite more than one group surviving the other events, however, only one clade would last long enough to provide the rootstock for subsequent ammonoid evolution. The other clades can be considered as cases of 'dead clades walking'. The random reduction in morphospace that occurs at some of the events (e.g., end-Permian) would indicate that they were non-selective in nature in terms of conch morphology. In contrast, the Kellwasser and Hangenberg extinctions were morphologically selective, with distinct forms preferentially eliminated (e.g., Korn et al. 2013b).

The extinction-processes during the Paleozoic seem to have differed. However, due to preservational and sampling biases ('Signor-Lipps effect': Signor and Lipps 1982) this is hard to assess. Bearing this in mind, current data would indicate that the Kačák and Hangenberg Events occurred rather suddenly, but the end-Permian and the end-Frasnian events were played out over longer periods of time in a more stepwise fashion.

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Chapter 17
Permian-Triassic Extinctions and Rediversifications

Arnaud Brayard and Hugo Bucher

17.1 Introduction

At the boundary between the Paleozoic and Mesozoic eras (~252 myr), the end-Permian mass extinction was the most devastating global-scale event ever recorded, resulting in the loss of more than 90 % of marine species (Raup 1979) and the disappearance or severe reduction in diversity of typical Paleozoic organisms (e.g., trilobites, tabulate and rugose corals, brachiopods). The ecological recovery of the benthos is traditionally assumed to have spanned the entire Early Triassic (i.e. ~5 myr), thus strikingly contrasting with that of pelagic environments and their dwellers. Whether or not this difference is the result of a selective preservation bias against the benthos cannot be excluded. However, extreme diversity fluctuations of nekto-pelagic organisms (e.g., ammonoids and conodonts) during the entire Early Triassic indicate major environmental upheavals in the ocean in the wake of the end-Permian extinction(s). In support of markedly unstable Early Triassic times, several major events are known from the sedimentary, geochemical and palynological records (e.g., Payne et al. 2004, 2010; Galfetti et al. 2007a, b, c; Hermann et al. 2011, 2012; Sun et al. 2012; Grasby et al. 2013; Romano et al. 2013; Fig. 17.1a), suggesting profound global changes in climate, sea-level and oceanic geochemistry (e.g. anoxia, euxinia, acidification). The initial low resolution time frames of these recurrent environmental deterioration events after the Permian-Triassic boundary (PTB) crisis were therefore first lumped into a "delayed recovery" model which is still the standard in effect in some recent reviews (e.g., Chen and Benton 2012).

A. Brayard (✉)
UMR CNRS 6282 Biogéosciences, Université de Bourgogne, 6 boulevard Gabriel,
21000 Dijon, France
e-mail: arnaud.brayard@u-bourgogne.fr

H. Bucher
Paläontologisches Institut und Museum, Universität Zürich, Karl-Schmid Strasse 4,
8006 Zürich, Switzerland
e-mail: hugo.fr.bucher@pim.uzh.ch

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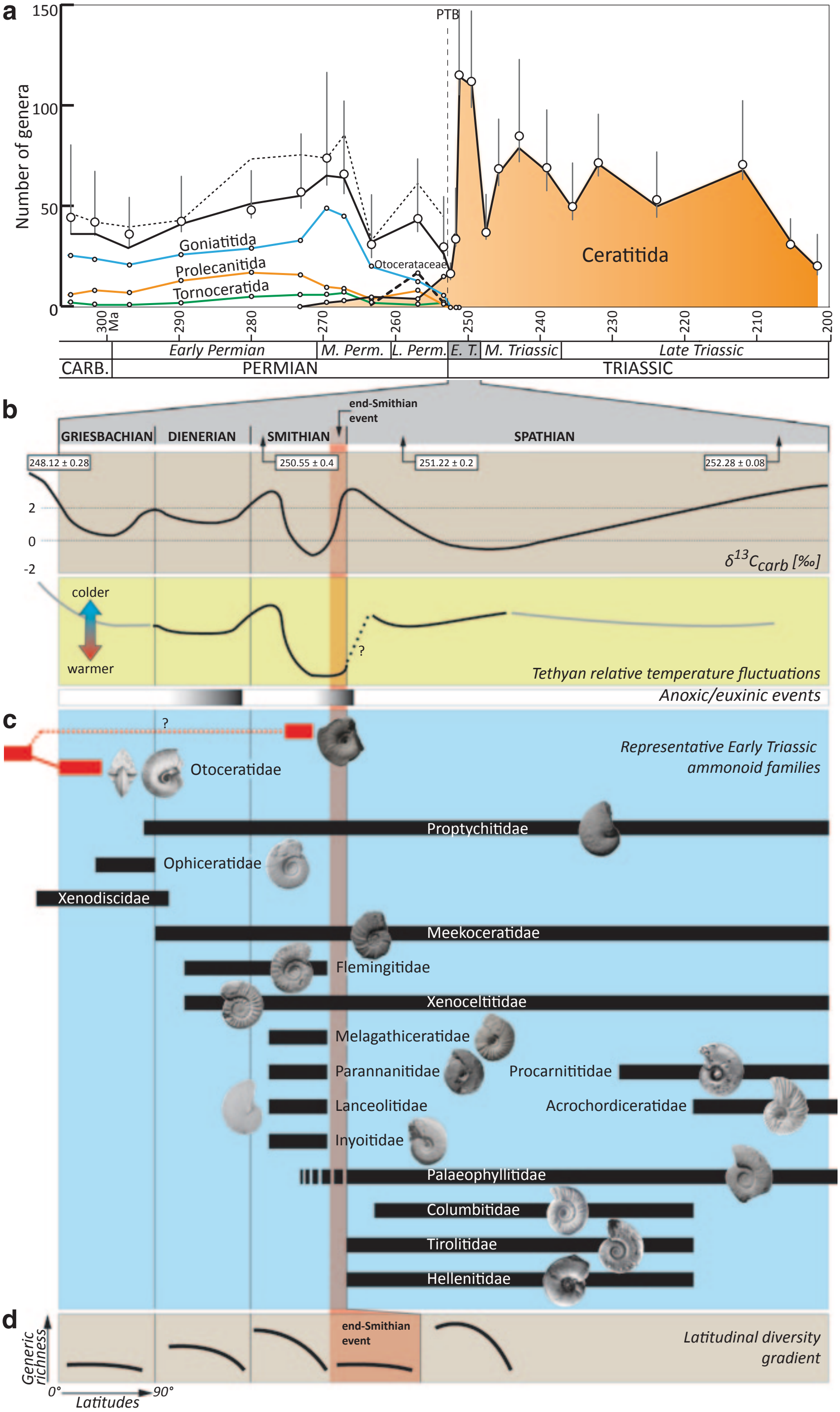
a
150
100
50
0
Number of genera
PTB
Goniatitida
Prolecanitida
Tornoceratida
Otocerataceae
Ceratitida
300 Ma
290
280
270
260
250
240
230
220
210
200
Early Permian
M. Perm.
L. Perm.
E. T.
M. Triassic
Late Triassic
CARB.
PERMIAN
TRIASSIC
b
end-Smithian event
GRIESBACHIAN
DIENERIAN
SMITHIAN
SPATHIAN
248.12 ± 0.28
250.55 ± 0.4
251.22 ± 0.2
252.28 ± 0.08
2
0
-2
δ13Ccarb [‰]
colder
warmer
?
Tethyan relative temperature fluctuations
Anoxic/euxinic events
c
?
Representative Early Triassic ammonoid families
Otoceratidae
Proptychitidae
Ophiceratidae
Xenodiscidae
Meekoceratidae
Flemingitidae
Xenoceltitidae
Melagathiceratidae
Parannanitidae
Procarnititidae
Lanceolitidae
Acrochordiceratidae
Inyoitidae
Palaeophyllitidae
Columbitidae
Tirolitidae
Hellenitidae
d
end-Smithian event
Generic richness
0°
90°
Latitudes
Latitudinal diversity gradient

Contrasting with this early view, recent analyses of nekto-pelagic taxa such as ammonoids and conodonts document an explosive Early Triassic rediversification (Orchard 2007; Brayard et al. 2009c). Indeed, although ammonoids were among the organisms most affected by the PTB mass extinction, Triassic ammonoids actually reached levels of diversity much higher than in the Permian less than ~1.5 myr after the PT boundary (Brayard et al. 2009c). In this chapter, we provide a brief overview of the present state of our knowledge of the ammonoid record around the PTB crisis and during the recovery interval.

17.2 Late Permian Events

Four major clades of Permian ammonoids (Goniatitida, Prolecanitida, Tornoceratida and Ceratitida; Fig. 17.1a; e.g., Ruzhencev 1960; Glenister and Furnish 1981; Leonova 2002, 2011) are globally characterized by relatively slow and uncoupled origination and extinction dynamics (Brayard et al. 2009c). Goniatitida were the dominant group during the Early-Middle Permian interval (e.g., Ruzhencev 1960; Glenister and Furnish 1981; Leonova 2002, 2011). Following a diversity peak during the Middle Permian, all ammonoid groups show a protracted, two-step decline in diversity during the Late Permian (Capitanian and Changhsingian extinctions; Glenister and Furnish 1981; Stanley and Yang 1994; Zhou et al. 1996). The first extinction event in the Capitanian is now generally agreed to have been triggered by the eruption of the Emeishan flood basalts (Bond et al. 2010). Remarkably, Ceratitida did not follow this trend and flourished during the Wuchiapingian with the notable rapid diversification of the morphologically-singular Otoceratаceae (Brayard et al. 2009c; Leonova 2002, 2011; Zakharov and Abnavi 2013). This time interval also corresponds to a marked restriction of global ammonoid morphological disparity (e.g., Saunders et al. 2008; Villier and Korn 2004; Leonova 2005). With blossoming Xenodiscidae and Pseudotirolitidae, Ceratitida also largely embodied the taxonomic diversity of Changhsingian ammonoids. The PTB mass extinction was most probably triggered by eruption of the Siberian traps (Reichow et al. 2009; Svensen et al. 2009).

Fig. 17.1 **a** Total ammonoid generic richness (*black bold line*: all ammonoids; *color lines*: major ammonoid groups; *Permian bold line*: data from Goniat.org; *Permian dotted line*: alternate data from the Ammon database (Korn and Ilg 2007); *Triassic bold line* modified after Brayard et al. (2009c) based on an updated database) and mean Chao2 estimate of the overall generic richness with its 95 % Confidence Interval (large circles with vertical bars; see Brayard et al. 2015). PTB: Permian-Triassic boundary. E.T.: Early Triassic. Note that the end-Smithian ammonoid extinction event discussed in the text is not illustrated here due to its short time duration. **b** Chronostratigraphic subdivisions of the Early Triassic (radiometric ages by Ovtcharova et al. 2006; Galfetti et al. 2007b and Shen et al. 2011) with simplified trends of geochemical ($\delta^{13}C_{carb}$; data from Galfetti et al. 2007b) and Tethyan relative temperature fluctuations during this period (data from Romano et al. 2013 [*black line*] and Sun et al. 2012 [*grey line*]). **c** Temporal distribution of some Early Triassic representative families (modified after Tozer 1981; Brayard et al. 2006, 2009c). Ammonoid illustrations from Brayard and Bucher (2008), Brayard et al. (2013) and Guex et al. (2010). **d** Simplified trend of the formation of a latitudinal diversity gradient during this period (modified after Brayard et al. 2006, 2007b, 2009b)

The Goniatitida and Tornoceratida completely disappeared with this event (Glenister and Furnish 1981; Tozer 1981; Leonova 2002, 2011) and apparently, only one Prolecanitida genus (*Episageceras*) survived the crisis (Kummel 1972; Tozer 1981; Dagys and Ermakova 1996; Leonova 2011; Zakharov and Abnavi 2013). Among the Ceratitida, only two main ammonoid clades survived across the PT boundary: the Otoceratidae and Xenodiscidae. *Otoceras* rapidly disappeared after the mass extinction, before the end of the Griesbachian. However, after a gap spanning the entire Dienerian, Otocerataceae probably had their final appearance with *Proharpoceras* in the Smithian (Brayard et al. 2007a). Thus, with very exceptions (*Episageceras*, *Otoceras*, *Proharpoceras*) and a still ambiguous case (Sagecerataceae) (e.g., Glenister and Furnish 1981; Tozer 1981; Becker and Kullman 1981; Brayard et al. 2007a; McGowan and Smith 2007), Triassic ammonoids are usually agreed to root into a single and morphologically very simple clade, the Xenodiscidae and are therefore interpreted as a monophyletic clade (Tozer 1981; Brayard et al. 2006; McGowan and Smith 2007). Following this hypothesis, all Mesozoic ammonoids are consequently derived from the xenodiscids, which went unscathed across the PTB mass extinction.

17.3 Early Triassic Events

Early Triassic times are commonly divided into four stages or substages of highly uneven duration (Griesbachian, Dienerian, Smithian and Spathian), which are very well defined by ammonoid zones and events (Fig. 17.1b; see Jenks et al. 2015 and Monnet et al. 2015). Based on ammonoids, the PTB is traditionally defined by the first occurrence of *Otoceras* (e.g., Tozer 1994, 2003; Dagys and Ermakova 1996; Zakharov 2002; Shevyrev 2006). Although knowledge of Griesbachian and Dienerian ammonoids is still limited, proptychitids and meekoceratids originated during the Dienerian. In their first steps, these Dienerian originations did not lead to any spectacular taxonomic diversification (e.g., Tozer 1974; Shevyrev 2001; Brühwiler et al. 2008; Ware et al. 2011; Fig. 17.1c). The beginning of the Smithian is defined by the origination of new families such as the highly speciose Flemingitidae and Kashmiritidae. Ammonoid richness first peaked during the middle Smithian through the evolution of extremely short-lived species (Brayard et al. 2009c; Brühwiler et al. 2010). The beginning of the Spathian witnessed an explosive radiation rooted in the latest Smithian *Xenoceltites*. Tirolitidae first quickly diverged from *Xenoceltites* and formed the basal group of from which the next radiation that began in the early Spathian and continued onward at a very high pace.

The tempo of recovery after the PTB mass extinction has recently been estimated thanks to new U-Pb radiometric ages allowing for more accurate and precise time calibrations (Ovtcharova et al. 2006; Galfetti et al. 2007b; Shen et al. 2011). The rediversification was explosive for some marine groups such as the ammonoids (Brayard et al. 2009c) and conodonts (Orchard 2007), spanning less than ~1.5 myr (Fig. 6.21a). Ammonoids reached levels of taxonomic richness in the Smithian that were already much higher than those of the Permian (see also Tozer 1981; Leonova 2002). Their recovery did not follow Sepkoski's (1978) classical logistic diversification model, for which major assumptions are required about the carrying capacity of the environment, but it instead has been re-interpreted as a hierarchical model periodically interrupted by brief but significant extinction events (e.g., end-Smithian; Brayard et al. 2009c).

The global first-order trend in increasing ammonoid diversity was accompanied by a progressive change from cosmopolitan to latitudinally-restricted distribution during the Early Triassic with the formation of a clear latitudinal diversity gradient during most of the Smithian and Spathian sub-stages (Fig. 17.1d; Brayard et al. 2006, 2015). Marked intertropical faunal exchanges across the Tethys and Panthalassa are obvious at that time with the occurrence of identical ammonoids on opposite sides of Panthalassa, illustrating latitudinally-restricted faunal exchanges during the Smithian (Brayard et al. 2007b, 2009a, b, 2013; Jenks et al. 2010), and the Spathian (Galfetti et al. 2007b; Guex et al. 2010; Monnet et al. 2013).

The global recovery trend was not a continuous process. It was interrupted at least once during a brief episode of ammonoid cosmopolitanism combined with a marked extinction event during the end-Smithian (e.g., Tozer 1982; Dagys 1988; Brayard et al. 2006). This extinction event was the most important one within the entire Triassic and its intensity compares with that of the PTB extinction. Only four species-poor families (the xenoceltitids and the sageceratids, but also virtually the palaeophyllitids and the proptychitids) survived the late Smithian extinction.

Similarly, conodonts reached their highest Triassic generic diversity during the middle Smithian, but only a very few species went through the end-Smithian crisis. On land, floras underwent a drastic ecological turnover with a middle Smithian spore peak comparable to the end-Permian one, followed by an early gymnosperm recovery during the late Smithian (Hermann et al. 2011). An abrupt, global change from hygrophytic to xerophytic associations characterizes the Smithian-Spathian boundary (Galfetti et al. 2007c; Hermann et al. 2011). The global carbon isotope record also reached a marked negative peak during the middle Smithian, followed by an abrupt positive shift in the late Smithian (e.g., Payne et al. 2004; Galfetti et al. 2007b). In the Tethys, the oxygen isotope record from biogenic phosphate tends to track the carbon isotope record and indicates a temperature drop of ca. 7.5 °C close to the Smithian-Spathian boundary (Romano et al. 2013).

It is well known by ammonoid workers (e.g., Kummel and Steele 1962) that the Early Triassic ammonoid radiation is represented by numerous homeomorphic taxa. Trends in morphological disparity and richness were especially decoupled during the Griesbachian and Dienerian with persisting low disparity values in the Dienerian whereas richness shows a weak increase (McGowan 2004, 2005; Brosse et al. 2013). The first disparity peak occurred early in the Smithian (Brosse et al. 2013). The end-Smithian extinction had obvious consequences with a marked contraction of the previously occupied morphospace. The Spathian corresponds to a second disparity peak with a morphospace analogous to the early-middle Smithian. However, Spathian superfamilies occupied more restricted portions of the morphospace (Brosse et al. 2013).

Ammonoid recovery during the Early Triassic therefore appears as the combined outcome of (i) the classical rapid refilling of a vacated ecospace after the mass extinction, and (ii) the successive extinction events and recurrent stressful environmental conditions that may have enhanced their high turnover rates. Most likely explanations for the end-Smithian extinction call upon the combined consequences of the concentration of carbon dioxide of volcanic origin (e.g., Galfetti et al. 2007b) and sea-level changes. Whatever the precise cause(s), it had a deep impact on the biotic rediversification, especially for ammonoids, conodonts and plant ecological assemblages as well. We cannot exclude the possibility that a few other Early Triassic biotic events are still hidden due to the insufficient knowledge of intervals such as the Griesbachian and Dienerian. However, significant results and new questions on the Early Triassic recovery will certainly arise from further studies of ammonoids and their spectacular evolutionary rebounds, which are hardly reconcilable with the alleged persistence of globally devastated ecosystems.

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Chapter 18

Ammonoids at the Triassic-Jurassic Transition: Pulling Back from the Edge of Extinction

Louise M. Longridge and Paul L. Smith

18.1 Introduction

The mass extinction at the end of the Triassic is one of the "big five" extinctions in the Phanerozoic and one of four that directly affected the evolutionary history of the ammonoids. At the Triassic-Jurassic (T-J) transition, approximately 22 % of marine families, 53 % of genera and 80 % of species became extinct (Pálfy 2003; Sepkoski 1996) but the event is of particular significance to the ammonoids because of their near demise. Left hanging by a thread, the group managed to pull back from the brink of extinction and, in spectacular fashion, re-establish itself as a dominant presence throughout the rest of the Mesozoic. As a result of the exceptionally low eustatic sea-level at the time, a situation that almost certainly contributed to the dynamics and severity of the extinction, there are only a very small number of marine stratigraphic sections that are reasonably continuous across the T-J boundary. The list includes an exposure in Austria that was recently designated Global Stratotype Section and Point for the base of the Jurassic (Hillebrandt et al. 2013). Studying the precise details of the T-J event horizon is therefore difficult, but a clear picture of the scale of the ammonoid near extinction and a sense of the dynamics of recovery can be obtained by considering high level taxonomic changes, broad patterns of generic diversity and differences in morphospace occupation across the entire Late Triassic to Middle Jurassic interval. This is the purpose of our brief review.

Interpreted environmental changes over the T-J interval include initial cooling, longer term global warming, widespread aridification, a global regression/transgression couplet, oceanic anoxia and a biocalcification crisis brought on by lower seawater pH (Hallam 1997, 2001; Hallam and Wignall 1997, 2000; Hesselbo et al.

L. M. Longridge (✉) · P. L. Smith
Earth, Ocean and Atmospheric Sciences, University of British Columbia, 2207 Main Mall,
Vancouver, BC V6T 1Z4, Canada
e-mail: llongridge@eos.ubc.ca

P. L. Smith
e-mail: psmith@eos.ubc.ca

C. Klug et al. (eds.), *Ammonoid Paleobiology: From macroevolution to paleogeography,*
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2004; Hillebrandt 2014; McElwain et al. 1999; Schootbrugge et al. 2007; Tanner et al. 2004; Tucker and Benton 1982). There was also a significant perturbation to the global carbon cycle with negative isotope anomalies identified in marine strata in British Columbia, Nevada, England, Austria, Italy, China and Hungary (Bachan et al. 2012; Galli et al. 2005; Guex et al. 2003, 2004, 2007; Hesselbo et al. 2002; Hillebrandt et al. 2013; Kuerschner et al. 2007; Lucas et al. 2007; McRoberts et al. 1997; Pálfy et al. 2001; Ward et al. 2001, 2004, 2007; Williford et al. 2007; Yin et al. 2006) and in terrestrial strata in Greenland and China (Hesselbo et al. 2002, 2006). Tanner et al. (2004) suggest that the T-J turnover may have been caused by a combination of gradual and catastrophic environmental changes. This could include long term ecological degradation from sea-level fluctuation or climate change in addition to more abrupt events such as flood basalt volcanism or possibly even bolide impact (Fowell and Olsen 1993; Fowell et al. 1994; Olsen et al. 1987, 2002a, b), although the latter is unlikely.

Flood basalt volcanism of the Central Atlantic Magmatic Province (CAMP) is currently considered the most likely cause of environmental perturbations and biotic crisis at the end-Triassic (Blackburn et al. 2013; Golonka 2007; Guex et al. 2004; Hesselbo et al. 2002, 2007; Hillebrandt et al. 2013; Knight et al. 2004; Marzoli et al. 1999, 2004, 2006, 2008, 2011; Pálfy 2003). These eruptions were caused by Pangean rifting prior to breakup producing basaltic lavas that extended over an area of 7×10^6 km^2 and had an estimated volume of $2–3 \times 10^6$ km^3 (Blackburn et al. 2013; Marzoli et al. 1999). The lavas were mostly produced by four major eruptive pulses in the first 600 Ka of extrusive activity, but the magmatic province as a whole had a duration of approximately 1.5 Ma or possibly longer in Morocco where volcanic activity began first (Blackburn et al. 2013; Nomade et al. 2007; Verati et al. 2007). The first of the four pulses probably triggered the extinction at 201.6 Ma (Blackburn et al. 2013; Schaltegger et al. 2008). Environmental change may have been caused by volcanic outgassing of CO_2 and SO_2, or perhaps more indirectly by the release of methane from shallow marine clathrate deposits, which acted as a positive feedback on global warming (Blackburn et al. 2013; Hesselbo et al. 2002; Pálfy et al. 2001).

18.2 Taxonomic Turnover

High level T-J ammonoid taxonomy is currently based principally on a stratophenetic rather than a cladistic approach. There are numerous stratophenetic phylogenies and taxonomic classifications, some that are more conservative and others that are less so (Dommergues and Meister 1999; Donovan et al. 1981; Page 1996, 2008; Tozer 1981, 1994; Venturi and Bilotta 2008). Figure 18.1 shows the ranges of 23 ammonoid superfamilies plotted at the resolution of age/stage. The superfamilies are based primarily on the approaches of Tozer (1981, 1994) for the Triassic and Page (2008) and Venturi and Bilotta (2008) for the Jurassic. A geographically restricted superfamily, the Aequiloboidea has recently been recognized by Bilotta

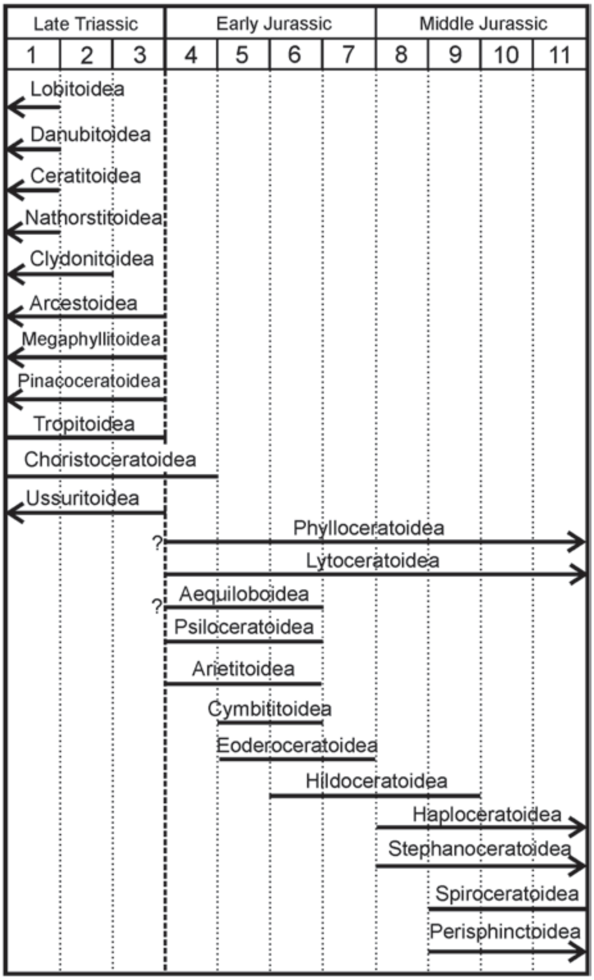


Fig. 18.1 Ammonoid superfamilies in the Late Triassic through Middle Jurassic. *1* = Carnian, *2* = Norian, *3* = Rhaetian, *4* = Hettangian, *5* = Sinemurian, *6* = Pliensbachian, *7* = Toarcian, *8* = Aalenian, *9* = Bajocian, *10* = Bathonian, *11* = Callovian. Resolution is at the stage level. Modified from Tozer (1981) and Page (2008) using data from Bilotta (2010), Hoffmann (2010), Howarth (2013), and Tozer (1994)

(2010). We include the Analytoceratoidea in the Lytoceratoidea following the work of Hoffman (2010).

Whatever classification is adopted, there is consensus that the order Phylloceratida is the only group to cross the T-J boundary and play a central role in the Early Jurassic recovery of the ammonoids. The Triassic phylloceratid superfamily Ussuritoidea is ancestral to the Early Jurassic phylloceratid superfamily Phylloceratoidea, although Pálfy and Dosztály (2000) have reported a very early occurrence of the Phylloceratoidea in the Rhaetian of Hungary. In addition, Bilotta (2010) speculates that the geographically restricted Aequiloboidea also had its origin in the latest Triassic but this is not proven and, anyway, the superfamily does not play a major role in the Early Jurassic radiation.

Of the nine superfamilies ranging upward from the Middle into the Late Triassic (Fig. 18.1), four are restricted to the Carnian with the Clydonitoidea ranging into the Norian and four ranging into the Rhaetian (Arcestoidea, Megaphyllitoidea, Pinacoceratoidea, Ussuritoidea). The Tropitoidea and the Choristoceratoidea are restricted to the Late Triassic ranging into the Rhaetian with rare Early Jurassic occurrences of Choristoceratoidea reported from the basal part of the Hettangian in North and South America (Guex 1995; Guex et al. 2012; Hillebrandt 2000a; Longridge et al. 2007). Basal Hettangian Choristoceratoidea have also been reported in Tibet (Yin et al. 2007) although Hillebrandt et al. (2013) recently questioned the Hettangian age of the co-occurring ammonoid based on his assessment of its septal suture. The long ranging Lytoceratoidea and Phylloceratoidea are present in the Hettangian together with the Psiloceratoidea (derived from the Phylloceratida), which gives rise to the Arietitoidea that is the source of much of the great Early Jurassic recovery. In addition, appearance of the Eoderoceratoidea, and, to a lesser extent, the Cymbitoidea in the Sinemurian add to the momentum of the recovery. In summary, at the superfamily level, the Carnian shows the greatest diversity followed by a decline through the Norian and Rhaetian with almost everything terminated at the T-J boundary. Although there may be some minor overlap of typically Triassic with typically Jurassic forms, it is negligible. The Psiloceratoidea was the rootstock of the Jurassic recovery which, at this taxonomic level, was relatively rapid such that the number of co-existing superfamilies from the Norian in the Late Triassic to the Callovian at the end of the Middle Jurassic was fairly consistent, averaging somewhat over six per stage with a Triassic minimum of six in the Rhaetian and a Jurassic minimum of four during the Toarcian.

At the lower end of the taxonomic hierarchy, we can consider generic data but, of course, estimates of the number of genera will contain errors based on synonyms and omissions. During the Late Triassic, which, according to Gradstein et al. (2012) had a duration of 35.7 million years, there existed in excess of 225 ammonoid genera whereas during the Early Jurassic, with a duration of 27.2 million years, there existed in excess of 325 genera. During the Middle Jurassic with a supposed duration of 10.6 million years there existed in excess of 325 genera (Smith et al. 2014).

When moving to a finer resolution, problems with time scale calibrations become significant. Gradstein et al. (2012) decided to abandon U-Pb dates based on Zr populations requiring that only single Zr crystal data be used in time scale calibration work. As a result, the 2012 Mesozoic time scale (Gradstein et al. 2012) is considerably less well constrained than the time scale produced in 2004 (Gradstein et al. 2004). The revised duration of Middle Jurassic ages seem particularly questionable but the problem can only be resolved by more field work integrating biochronology with samples for single crystal Zr analysis. However, if we accept the more recently produced time scale and plot the number of ammonoid genera per million years by geological age (Fig. 18.2), we see a steady decline during the Late Triassic followed by a significant jump in the Hettangian to levels exceeding those in the Late Triassic. A downward readjustment in the Sinemurian is followed by a steady increase in standing diversity throughout the rest of the Early and Middle Jurassic. The anomalously high value for the Bajocian (Fig. 18.2) could be an artifact

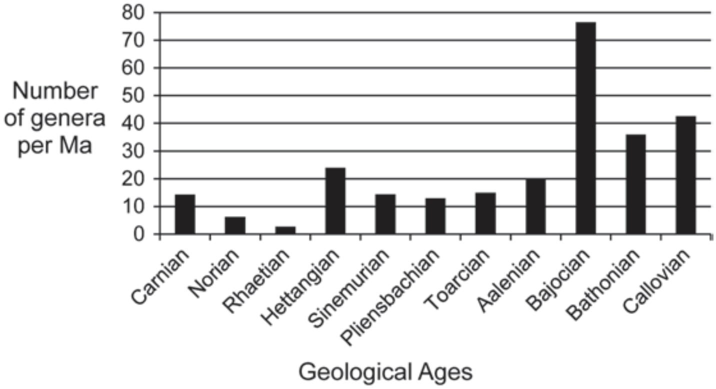


Fig. 18.2 Ammonoid genera per million years plotted at the level of geological age for the Late Triassic to Middle Jurassic interval. Diversity data from Smith et al. (2014); time scale data from Gradstein et al. (2012)

of time scale calibration problems, although the morphospace data discussed below also suggests that the Bajocian marked the time of full recovery for the ammonoids.

18.3 Changes in Morphospace Occupation

Another perspective on the magnitude of the T-J extinction and the dynamics of ammonoid recovery can be obtained by using a morphospace model. The advantage of this approach is that it is somewhat more objective than a taxonomic approach because it is not based on taxa definition and the interpretation of phylogenetic relationships. A recent study by Smith et al. (2014) employed Raup's accretionary growth model (Raup 1966, 1967) to develop a simple morphospace concept describing planispiral shell geometry and whorl shape using three variables to define a universal space. The occupation of this space before and after the event offers insights into the dynamics of the near extinction and the evolutionary, functional and ecological constraints that might have influenced recovery. The three variables of the Raup model, as used here, are based on six parameters which, using the terminology of Smith (1986), are defined as follows (Fig. 18.3a, b):

- 1. The expansion rate [$W=(r_2/r_1)^2$].
- 2. The relative distance between the generating curve and the axis of coiling [$U=UD/D$ where UD is the umbilical diameter and D is the shell diameter].
- 3. The whorl width (WW) divided by whorl height (WH), which is a box model used to approximate the relative compression or depression of the specimen [WWWH = WW/WH].

The parameters W and U are used to generate a W-U coordinate system defining 'morphospace' for ammonoid shell geometry. Measurements from individual genera

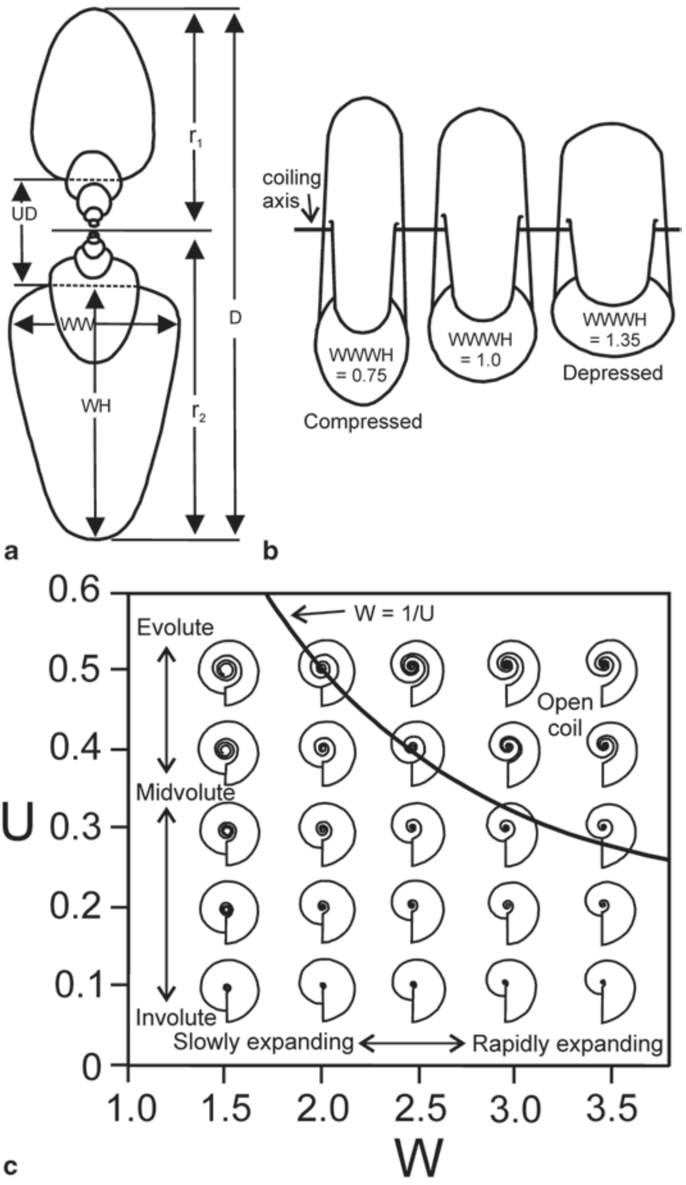


Fig. 18.3 **a** Linear dimensions used to characterize ammonoid shell morphology. *D* = shell diameter; *UD* = umbilical diameter; *WW* = whorl width; *WH* = whorl height. *Lower case letters* = shell radii. Ratios used are: relative width of umbilicus *U* = *UD*/*D* (equivalent to *D* of Raup 1966, 1967); expansion rate W = $(r_2/r_1)^2$; and whorl shape, *WWWH* = *WW*/*WH* (equivalent to S of Raup 1966, 1967). **b** Ventral view of ammonoids illustrating changes in whorl compression as measured by *WWWH*. **c** Schematic of ammonoid shell morphology in the *W*-*U* morphospace (modified from Raup 1967). Figure 1 and 2b of Smith et al. (2014); Figure was originally modified from Raup (1966), following the terminology of Smith (1986) and Liang and Smith (1997)

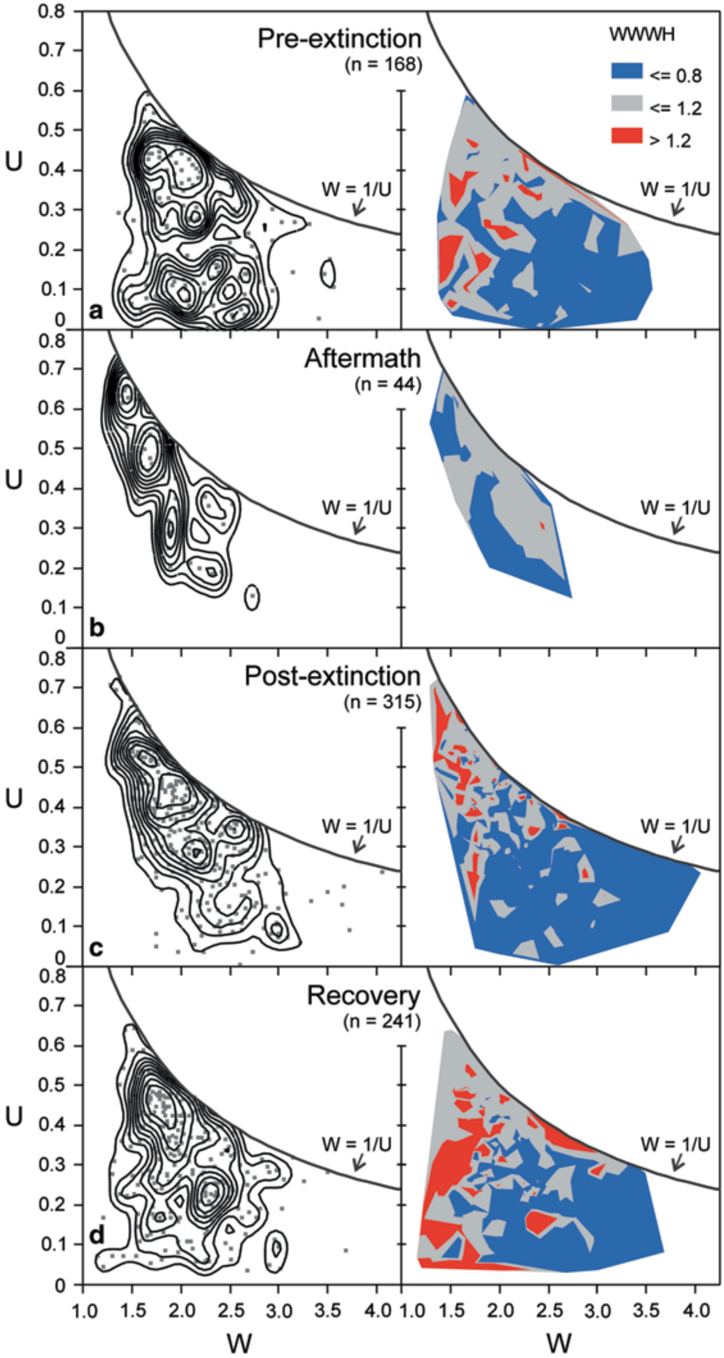
are plotted on the W-U graph and then contoured based on frequency of occurrence per unit area. Figure 18.3c provides illustrations of hypothetical shell geometries for several different W-U coordinates. The curved line on Fig. 18.3c, called the off-lap line (equation $W = 1/U$), marks the boundary between coiled forms with whorl overlap and shells that have an open coil. These open coiled forms belong to the heteromorphs, which are part of a broader group the rest of which cannot be accommodated in the W-U Raup model. Consequently, the heteromorphs are commented upon separately. In the planispires, there is a persistent covariation between coiling geometry and whorl shape such that W-U morphospace can be used to explore all basic aspects of shell geometry. Different whorl shapes and their associated WWWH values are illustrated in Fig. 18.3b. Based on a stage-by-stage analysis across the T-J event, Smith et al. (2014) recognised four intervals, namely the pre-extinction (Carnian to Rhaetian), aftermath (Hettangian), post-extinction (Sinemurian to Aalenian) and recovery (Bathonian to Callovian) as shown in Fig. 18.4, which illustrates both shell coiling geometry and whorl shape. On the right side of Fig. 18.4, the same specimens are shown as for the contoured plot shown on the left side of the figure but the whorl shape is color coded. The blue color represents low WWWH values (less than 0.8) indicating the compressed end of the whorl shape spectrum. The red color represents high WWWH values (more than 1.2) indicating the depressed end of the whorl shape spectrum. The intermediate, more equidimensional whorl shapes are denoted by the silver-grey color.

It is clear that there is a core area of the W-U morphospace centred on the values $U = 0.4$–0.45 and $W = 1.75$–2.0 that remains occupied throughout the Late Triassic to Middle Jurassic interval. This represents midvolute forms that are slowly expanding and with whorl sections that are equidimensional to slightly depressed.

The Late Triassic pre-extinction interval (Fig. 18.4a) shows a W-U landscape that is broadly occupied in the planispire region and characterized by a multi-peaked density distribution. An overall linear correlation between W and U is not evident although rapidly expanding forms are consistently compressed. The pre-extinction interval is also characterized by the greatest diversity of heteromorph ammonoids with spherocone, open-coiled, straight, helicoid, and high-spired (gastropod-like) morphologies all represented.

There are two major changes in morphospace occupation that occur across the T-J boundary. Firstly, the Hettangian aftermath interval (Fig. 18.4b) is characterized by a significant contraction of morphospace occupation. This represents a significant loss of involute ammonoids including slowly and rapidly expanding forms and those that are compressed and depressed. Secondly, the aftermath witnesses the first appearance of very evolute, slowly expanding forms ($U > 0.6$; $W < 1.7$) with equidimensional (slightly compressed to slightly depressed) whorl sections. There is now a strong negative linear correlation between W and U. Apart from local, brief holdovers of open coiled ammonoids, there are no heteromorphs in the aftermath interval.

During the post-extinction interval (Fig. 18.4c) there is a partial reversal of the pattern established in the aftermath. The very evolute forms wane but there is a rapid reappearance of involute compressed forms (low U, high W, low WWWH).


Pre-extinction
(n = 168)
Aftermath
(n = 44)
Post-extinction
(n = 315)
Recovery
(n = 241)
WWWH
<= 0.8
<= 1.2
> 1.2
W = 1/U
U
W
a
b
c
d
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1.0
1.5
2.0
2.5
3.0
3.5
4.0

The linear correlation between W and U in the sample as a whole weakens and is less negative than in the aftermath landscape. Apart from sporadic and minor appearances of spherocones in the Sinemurian to Toarcian (Cymbitoidea and *Onychoceras*), there are no heteromorphs in the post-extinction interval.

The recovery interval (Fig. 18.4d) for the planispires sees a morphospace topography that is very similar to, but not exactly the same as the pre-extinction interval. The taxa are distributed broadly, and for the first time since the extinction, the area representing the involute, slowly expanding forms with equidimensional to depressed whorl sections ($U<0.2$; $W<1.7$) is also occupied. There are multi-peaks in the density distribution but a weak W-U covariation persists. All the heteromorph geometries have now reappeared except for the high-spired torticones, which are unknown throughout the Jurassic.

In his comprehensive summary of research on the modes of life and habitat of the ammonoids, Westermann (1996) makes the point that the majority seem to have been pelagic, divided equally amongst active swimmers (nekton), planktonic drifters and planktonic forms involved in vertical migration (Ritterbush and Bottjer 2012; Westermann 1996; Westermann and Tsujita 1999). All the remaining ammonoids he describes as demersal (benthopelagic or nektobenthonic). His conclusions concerning modes of life are based on a review of faunal associations and biofacies as well as shell architecture as it relates to poise, stability and mobility. Smith et al. (2014) pointed out that Westermann's correlation between shell shape and the habitats the ammonoids exploited could be plotted on the Raup morphospace model as shown in Fig. 18.5. Planktonic drifters are evolute, slowly expanding forms with subcircular to depressed whorl sections (high U, low W and $WWWH \geq 1$). Planktonic vertical migrants tend to be involute and slowly expanding with depressed whorl sections (low U, low W and $WWWH>1$). Nektonic forms are involute and rapidly expanding with compressed whorl sections (low U, high W and $WWWH<1$). Demersal forms occupy the area of overlap (Fig. 18.5) between nektonic and planktonic forms (average U values around 0.45, average W values around 2, and a range of WWWH values from somewhat compressed to somewhat depressed).

The demersal mode of life is at the core of the adaptive landscape, and it is this region that is never relinquished, including during the immediate aftermath of the T-J extinction (Fig. 18.4b). The demersals probably exploited a variety of food resources including bottom scavenging and predation of the lie-in-wait variety. The extinction aftermath is also characterized by a proliferation of ammonoids that were

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Fig. 18.4 Contoured frequency of occupation of the *W* (expansion rate) and *U* (umbilical ratio) morphospace together with (*right panel*) the associated whorl shapes plotted for the following intervals: **a** Pre-extinction (Carnian-Rhaetian), **b** Aftermath (Hettangian), **c** Post-extinction (Sinemurian-Aalenian) and, **d** Recovery (Bajocian-Callovian). The $W=1/U$ lines indicated on the figure are the off-lap lines (Raup 1967). The morphospace defined by the shell expansion rate (*W*) and the looseness of coil (umbilical ratio *U*) shows points representing genera whose density of occurrence is contoured (increment is 10%, with 90% of the sample enclosed by the outer contour). Only planispiral, non-heteromorph shell occurrences are plotted. Colours in the *right panels* denote occurrences of compressed ($WWWH \leq 0.8$), equidimensional ($WWWH>0.8<1.2$), and depressed ($WWWH \geq 1.2$) whorl shapes (see Fig. 18.3b). Modified from Fig. 4 of Smith et al. (2014)

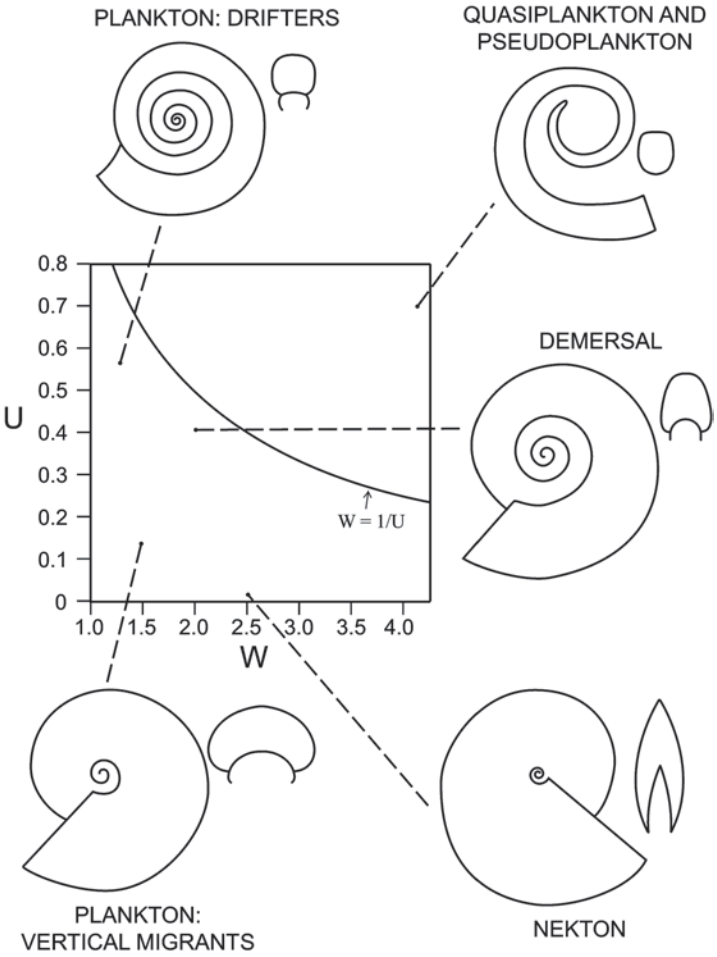

Fig. 18.5 Shell geometry related to the mode of life of ammonoids, as interpreted by Westermann (1996). Figure 9 of Smith et al. (2014)

planktonic drifters, a mode of life that assists with dispersal and recolonization. This dominance of demersal and planktonic forms in the Hettangian has also been pointed out by Ritterbush and Bottjer (2012). The evolute planktonic forms fade quickly during the Early Jurassic while at the same time the nektonic forms proliferate (Figs. 18.4b-c, 18.5). These were presumably the more active carnivores occupying roles at a higher level within the trophic structure. The Middle Jurassic saw a recovery of the involute, somewhat depressed, slowly expanding planispires, which were planktonic and may have migrated vertically in the water column (lower left parts of Figs 18.4c and 18.5). The open coiled planispire heteromorphs that reappeared in the Bajocian were probably drifters or pseudoplankton (very high W and U values in Fig. 18.5). The straight shelled heteromorphs that reappeared in the

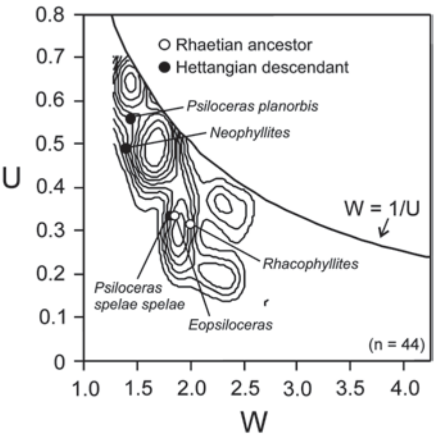

Fig. 18.6 The contoured occupation of W-U morphospace in the aftermath of the Triassic-Jurassic extinction (Hettangian) showing the prevalence of evolute, slowly expanding geometries, which dominate the succeeding, post-extinction interval. The Late Triassic genera *Eopsiloceras* and *Rhacophyllites* are indicated along with the oldest *Psiloceras, P. spelae spelae* and the slightly younger more evolute, more slowly expanding descendants *P. planorbis* and *Neophyllites*. Modified from Fig. 7 of Smith et al. (2014)

Bathonian were either planktonic or perhaps demersal with the ability to escape rapidly from benthic threats.

In summary, the T-J extinction resulted in the disappearance of nearly all planispiral ammonoid modes of life except the generalist demersals, which persist throughout the Late Triassic to Middle Jurassic interval. In the immediate aftermath of the extinction, the readily dispersed evolute drifters evolved for the first time but waned as the nektonic forms re-established themselves. It was not until the Bajocian and later that the full spectrum of modes of life was re-established. The greatest diversity of heteromorph ammonoids existed in the Late Triassic when partially uncoiled, open-coiled, straight-shelled, helicospires and torticones all existed. The aftermath and post-extinction intervals (Hettangian to Aalenian) are notable for the absence of heteromorphs. Minor exceptions include local occurrences of open coiled forms in the earliest part of the aftermath and the occurrence of partially uncoiled forms beginning in the Sinemurian. It was not until the recovery interval beginning in the Bajocian that a breadth of heteromorph shell geometry was established that was similar to the pre-extinction interval. An exception is the gastropod-like torticone geometry, which did not appear again until the Cretaceous (Arkell et al. 1957).

The consensus is that the Early Jurassic ammonoid genus *Neophyllites* and the significantly more important genus *Psiloceras* had their origins in the Late Triassic genera *Rhacophyllites* and *Eopsiloceras* (Fig. 18.6) (Guex 1982, 1987, 1995, 2006; Guex and Rakús 1991; Hillebrandt and Krystyn 2009). *Psiloceras spelae*, the very earliest species of *Psiloceras*, is similar in shell geometry to *Eopsiloceras* but subsequent species are considerably more evolute and slowly expanding (Fig. 18.6)

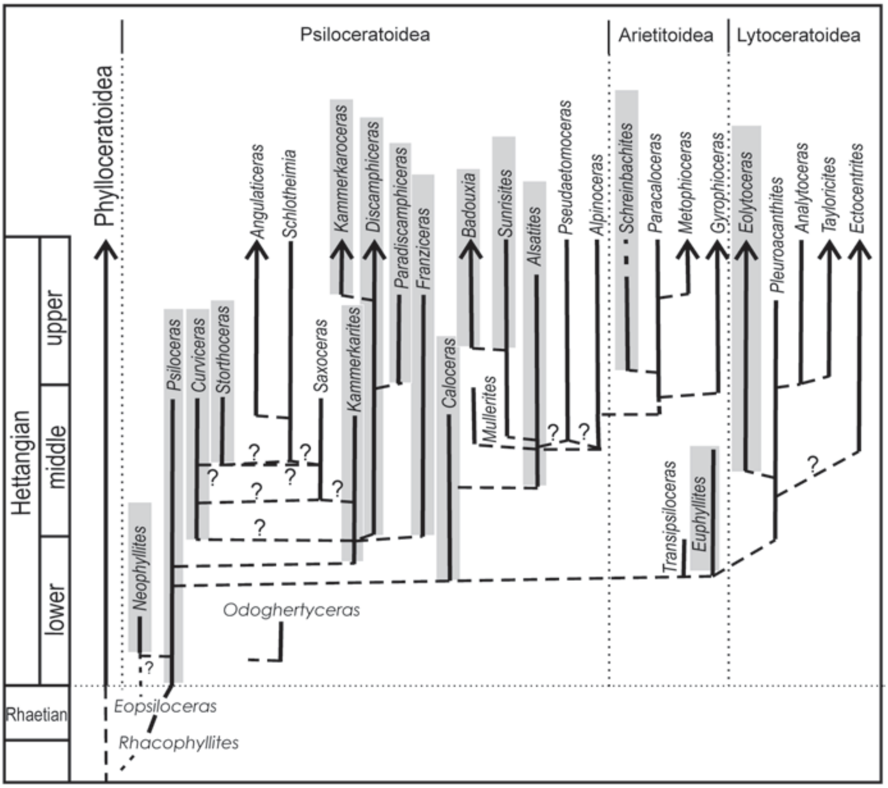

Fig. 18.7 Partial phylogeny of Hettangian ammonoids mostly including genera found in the Eastern Pacific. Genera where some or all species have an asymmetric siphuncle are indicated in *grey*. The *dashed* part of the range of Phylloceratoidea indicates an evolutionary relationship with the Ussuritoidea. Adapted from Guex (1995), Hillebrandt (2000a), Rakús (1993b); also including data from Bloos (1994), Efimova et al. (1968), Guex (1987, 2006), Guex et al. (1998, 2000), Hillebrandt (2000a-c), Longridge et al. (2006, 2007, 2008a, b), Meister et al. (2002) and Taylor (1998)

(Guex et al. 1998; Hillebrandt and Krystyn 2009; Smith et al. 2014). Similarly, *Neophyllites* is evolute and slowly expanding.

18.4 Siphuncle Offset and Septal Face Asymmetry

In most ammonoids the siphuncle runs ventrally along the shell's plane of bilateral symmetry but in many members of the Early Jurassic ammonoid radiation, individuals from groups that are not directly taxonomically related show asymmetry in the disposition of the siphuncle, which is offset from the venter (Fig. 18.7). This is accompanied by a corresponding asymmetry in the septa (Fig. 18.8a, b) whereby the septal suture line has the ventral lobe shifted to one side of the whorl as shown

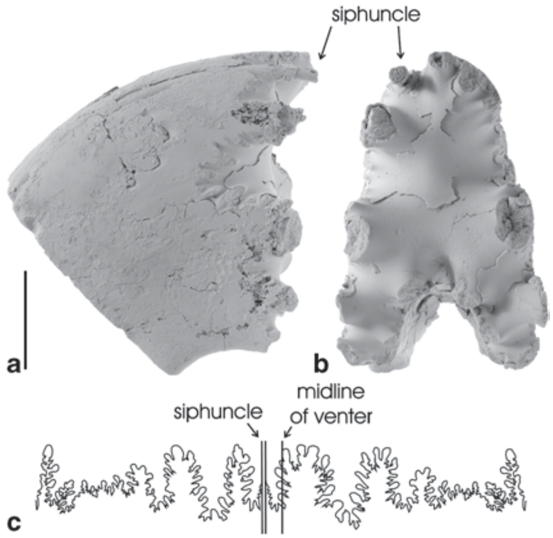

Fig. 18.8 Scanned fragment of *Badouxia columbiae*, **a**, Lateral view, **b**, Frontal view, scale bar = 2 cm, **c**, septal suture line from *B. columbiae*, scale bar = 4 cm. Modified from Fig. 1 of Longridge et al. (2009). © The Palaeontological Association

in Fig. 18.8c. There are no quantitative data but qualitative observations allow some general statements. Offset can be to the left or right of the line of symmetry but the magnitude remains consistent throughout ontogeny. Sometimes this general asymmetry (siphuncle offset and accompanying septal asymmetry) is characteristic of virtually all members of a species whereas in other cases it is only displayed in some individuals. The asymmetry is prevalent in many Hettangian genera including *Neophyllites*, *Psiloceras*, *Euphyllites*, *Eolytoceras*, *Caloceras*, *Alsatites*, *Sunrisites*, *Badouxia*, *Kammerkarites*, *Franziceras*, *Discamphiceras*, *Paradiscamphiceras*, *Kammerkaroceras*, *Curviceras* and *Storthoceras* (Bilotta 2010; Bloos 1981, 1994, 1996, 1999; Bloos and Page 2000; Böhm et al. 1999; Canavari 1882; Frebold 1951, 1967; Guérin-Franiatte 1990; Guex 1989, 1995; Guex and Rakús 1991; Hengsbach 1986a, b; Hillebrandt 2000a-c; Hillebrandt and Krystyn 2009; Lange 1941, 1952; Longridge et al. 2006, 2008a, b; Neumayr 1879; Rakús 1993b; Schlegelmilch 1976; Spath 1919, 1924; Taylor 1988; Wähner 1882–1898; Wiedmann 1970; Yin et al. 2007). Asymmetry is also recognized in some younger Early Jurassic genera such as *Arctoasteroceras*, *Aequilobus* and *Dudresnayiceras* in the Sinemurian, and *Sinuiceras* in the Pliensbachian (Bilotta 2010; Frebold 1960). We suspect that with close observation, the phenomenon will be discovered in additional Jurassic genera.

There are two main hypotheses for the cause of this asymmetry. The first, proposed by Hengsbach (1979, 1986a, b, 1991, 1996), favors a parasite infestation shortly after hatching. He suggests that parasites located in the soft body, at or near the siphuncle, caused a constant displacement of the root of the siphuncle and thus, of the ventral lobe of the suture. He claims that the degree and direction of offset were controlled by the location and size of the site of infestation and further suggests that after the death of the parasite, the asymmetry would have been too well established to be corrected in subsequent growth. The second hypothesis is that of Guex (2001, 2006) who suggests that environmental stress in the earliest Jurassic may have generated genetic changes in the ammonoid root stock, leading to offset of the siphuncle and corresponding asymmetry in the suture. Guex highlights work showing that in taxa other than ammonoids, external environmental stress can increase the rate of gene mutation and recombination as well as initiate asymmetries (Alméras and Elmi 1987; Hoffman and Parsons 1991; Williamson 1981). Furthermore he cites the work of Rutherford and Lindquist (1998) who show that external stresses can alter a protein that influences an organism's development thereby producing more morphological variants that, under the influence of natural selection, can accelerate evolutionary radiation. In sum, Guex argues that stress induced genetic or biochemical changes are potentially responsible for the offset siphuncle phenomenon.

Both hypotheses are plausible and it is difficult to decide which is correct based on the limited data currently available. Some of the evidence favors the hypothesis of Hengsbach. Offset is not consistently present even in closely related, contemporaneous genera. For example, siphuncle offset is only intermittently expressed at the generic level in the Psiloceratina (Fig. 18.7). It occurs in species of *Schreinbachites* (Bloos 1994, 1996) but has not been recognized in species of *Alpinoceras* or *Paracaloceras*, which are currently considered to be the ancestral genera (Fig. 18.7). Similarly, siphuncle offset is also sporadic at the species level whereby even contemporaneous species from a single genus may not consistently show asymmetry. Once again, if the cause of the offset was related to genetic changes, it seems reasonable to expect that all closely related forms would be affected. In contrast, it is easier to see how only some animals might be infested by a parasite.

Other evidence seems to better support the hypothesis of Guex. Firstly, single species often show siphuncle offset across extensive biogeographic ranges. For example, specimens of the Late Hettangian ammonoid *Badouxia canadensis* are found throughout the eastern Pacific and almost invariably have an offset siphuncle (Hall and Pitaru 2004; Hillebrandt 2000b; Longridge et al. 2006). It seems improbable that a parasite could cause siphuncle offset in virtually 100 % of individuals of a single species, spread over such a wide geographic range. Secondly, external influences can affect the position of the siphuncle. For example, in a specimen of *Eolytoceras* from Taseko Lakes (GSC 127429 in Longridge et al. 2008b), the external lobe and siphuncle switch sides from right to left of the median line between a shell diameter of c. 2.1 cm and 2.3 cm. The position then begins to 'correct' as growth continues and by the end of the preserved specimen, the siphuncle is nearly central. This disturbance was probably caused by an injury to the animal, but the fact that the position begins to correct suggests that it may have been influenced by genetics rather than an external influence such as parasites. This also suggests that the assertion of Hengsbach (1986a), that the siphuncle would continue to be displaced even after death of the parasite, could be incorrect.

Other patterns of siphuncle offset currently apparent in the fossil record could be equally well explained by either Hengsbach's hypothesis of parasite infestation or Guex's hypothesis of genetic influence. Triassic genera that are immediately ancestral to the Jurassic ammonoids (Tozer 1994; Yin et al. 2007) as well as the Hettangian Phylloceratoidea (Böhm et al. 1999; Hillebrandt 2000c; Longridge et al.

2008b; Neumayr 1879; Rakús 1993a, 1999; Wähner 1882–1898; Fig. 18.7) do not have the asymmetry. Furthermore, in many species where siphuncle offset occurs, the pattern of offset is not consistent. For example, over 40 specimens of *B. canadensis* come from a single locality in the Taseko Lakes area of British Columbia (Section D, bed 2 in Longridge et al. 2006). All members of this collection possess an offset siphuncle although the position varies. In some specimens, the siphuncle is shifted to the right of the plane of bilateral symmetry while in others it is shifted to the left. The degree of offset is also highly variable between individuals. Hengsbach (1996) claims that the side of the organism on which the malformation occurs should vary with a parasitic cause whereas it should not vary with a genetic cause. At the present time we do not have sufficient data to negate either the Hengsbach or the Guex hypothesis.

18.5 Discussion and Conclusions

According to Kauffman and Harries (1996), ecological generalists are one of the common survivors of mass extinctions. These groups tend to have broad geographical ranges, large niche sizes, relatively primitive morphology, and species with long stratigraphic ranges. Also, they usually occur consistently, but rarely, in great numbers over broad paleogeographic areas and often show limited post-extinction diversification (Kauffman and Erwin 1995; Kauffman and Harries 1996). An example is the Phylloceratina, a group that perhaps survived the end-Triassic mass extinction by persisting in the open oceans (Hillebrandt and Krystyn 2009). We suggest that the ammonoids generally follow a model of adaptive radiation whereby recovery represents a refilling of empty niches and a return to pre-extinction equilibrium (Erwin 2000, 2001; Sepkoski 1984). In the initial aftermath, biodiversity is low and geographically widespread taxa prevail. This survival interval is followed by the rapid appearance of new taxonomic groups that may show significant regional differences. Repopulation follows an exponential curve and the greater the extinction the longer the recovery interval. This pattern may be evident in the ammonoids where the earliest *Psiloceras* are widespread and morphologically variable. Later *Psiloceras* and descendant taxa show considerable regional differences (Hillebrandt and Krystyn 2009).

The T-J extinction occurred at 201.6 Ma (Blackburn et al. 2013; Gradstein et al. 2012; Schaltegger et al. 2008) and the effect on the ammonoids was profound. Demersal modes of life seem to be the most resistant to extinction. The immediate aftermath of the extinction is also characterized by forms interpreted to be planktonic drifters, which perhaps aided dispersal and recolonization. Determining the point at which full recovery was achieved is difficult and depends on the metric. Superfamilies proliferated and standing generic diversities increased fairly quickly but it was not until the Middle Jurassic that generic diversity per million years reached levels in excess of those seen in the Late Triassic. Similarly, by the Bajocian much of the planispire and heteromorph morphospace had been reoccupied, but it was not until the Bathonian-Callovian that shell disparity comparable to that of the Late Triassic was achieved. The Bajocian began at 170.3 Ma and the Callovian ended at 163.5 Ma. The time to full recovery of the disparity seen in Triassic ammonoid shell geometry was therefore between 30 and 40 million years (Smith et al. 2014).

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Chapter 19
Ammonites on the Brink of Extinction: Diversity, Abundance, and Ecology of the Order Ammonoidea at the Cretaceous/Paleogene (K/Pg) Boundary

Neil H. Landman, Stijn Goolaerts, John W.M. Jagt, Elena A. Jagt-Yazykova and Marcin Machalski

19.1 Introduction

Ammonite shells are common fossils in marine Mesozoic deposits. Their disappearance in Cenozoic strata has intrigued naturalists from the early nineteenth century onward, and the cause of their extinction has been the subject of lively debate. Following the seminal publication of Alvarez et al. (1980), paleontologists have considered that the most plausible explanation for their disappearance was the impact of an asteroid, and its ensuing consequences (Gould 1995; Ward 1996). Today, the evidence for the Chicxulub impact in the Yucatán Peninsula, Mexico, is overwhelming (Schulte et al. 2010). Indeed, the stratigraphic layer of debris associated with the

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N. H. Landman (✉)
Division of Paleontology (Invertebrates), American Museum of Natural History, New York, NY 10024, USA
e-mail: landman@amnh.org

S. Goolaerts
Department of Paleontology, OD Earth & History of Life,
Royal Belgian Institute of Natural Sciences (IRSNB-KBIN), 1000 Brussels, Belgium
e-mail: stijn.goolaerts@naturalsciences.be

J. W. M. Jagt
Natuurhistorisch Museum Maastricht, 6211 KJ Maastricht, The Netherlands
e-mail: john.jagt@maastricht.nl

E. A. Jagt-Yazykova
Zakład Paleobiologii, Uniwersytet Opolski, 45-052 Opole, Poland

St. Petersburg State University (SPbGU), 199034 St. Petersburg, Russia
e-mail: eyazykova@uni.opole.pl

M. Machalski
Instytut Paleobiologii, Polska Akademia Nauk, 00-818 Warsaw, Poland
e-mail: mach@twarda.pan.pl

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impact serves as the official base of the Danian Stage (= base of Cenozoic Erathem) (Molina et al. 2006). Yet, the diversity and geographic distribution of ammonites just prior to and at the moment of impact are still not well documented. Kiessling and Claeys (2002) provided an overview of localities where ammonites occur near or at the K/Pg boundary (KTBase project). However, only a handful of sections were described, leaving many blind spots. Thanks to renewed collecting efforts during the past decade to recover ammonites from close to the boundary, it is now possible to assemble a much more detailed picture of the health of this group at the brink of extinction.

19.2 Methods

We examined the stratigraphic distribution of ammonites at a total of 29 sites encompassing 14 regions around the world to tabulate the generic and specific diversity of these animals just prior to and at the K/Pg boundary. These sites include the Atlantic Coastal Plain of North America (New Jersey and Maryland); the Gulf Coastal Plain of North America (Missouri, Mississippi, and Texas); the La Popa Basin, northeastern Mexico; Denmark (Stevns Klint, Kjølby Gård, and the "*Dania*" Quarry); the Maastrichtian type area (the Netherlands and northeast Belgium); Poland (Nasiłów, Mełgiew, and Lechówka); Kyzylsay, Kazakhstan; the Sumbar River, Turkmenistan; the Bay of Biscay (Zumaya, Hendaye, and Bidart); Bjala (= Byala), Bulgaria; Tunisia (Kalaat Senan, El Kef, and Garn Halfaya) and Egypt (Dababiya Quarry Corehole); the Naiba River Valley, Sakhalin, Far East Russia; the Poty Quarry, Brazil; Lomas Colorados, Bajada de Jagüel, the Neuquén Basin, Argentina; and Seymour Island, Antarctica (Fig. 19.1, Appendix). We have arbitrarily focused on the last 0.5 million years of the Maastrichtian at each site (our target interval) because this is the shortest interval of time that still yields enough ammonite data from different environmental settings and geographic areas. However, it is worth noting that taphonomic bias and collection failure play a much larger role in the recovery of ammonite data than they do in the assembly of, for example, microfossil data.

We demarcated our target interval using biostratigraphy, magnetostratigraphy, and cyclostratigraphy, as well as data on fossil occurrences in relation to the K/Pg boundary in sections without any physical sign of a sedimentary break between the highest ammonites and the K/Pg boundary. In terms of biostratigraphy, many of our sites belong to, or can be correlated with, Calcareous Nannofossil Zone CC26b of Perch-Nielsen (1985), which is approximately equivalent to Zone UC20dTP of Burnett (1998), and extends from the FO of *Micula prinsii* to the LO of unreworked, non-survivor Cretaceous taxa, which starts 750 kyr (Hennebert 2012) to 530 kyr (Dinarès-Turell et al. 2013) before the end of the Cretaceous (see also Gardin et al. 2012). This interval is approximately equivalent to geomagnetic polarity Chron 29r, which starts 0.3 myr prior to the K/Pg boundary according to recent calculations (e.g., Husson et al. 2011). For planktic foraminifera, our 0.5 myr interval corresponds to the combined *Plummerita hantkeninoides* CF1 Zone, *Pseudoguembelina*

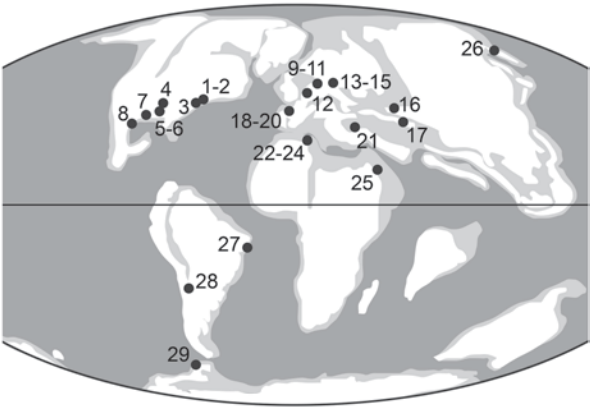


Fig. 19.1 Distribution of localities described in the text plotted on a paleogeographic map of the Earth at the K/Pg boundary (after Blakey 2011). *1* Central Monmouth County, New Jersey, *2* Northeastern Monmouth County, New Jersey, *3* Anne Arundel County, Maryland, *4* Stoddard and Scott Counties, Missouri, *5* Tippah County, Mississippi, *6* Chickasaw County, Mississippi, *7* Falls County, Texas, *8* Northeastern Mexico, *9* Stevns Klint, Denmark, *10* Kjølby Gård, Denmark, *11* Dania Quarry, Denmark, *12* Maastricht, the Netherlands, *13* Nasiłów, Poland, *14* Mełgiew, Poland, *15* Lechówka, Poland, *16* Kyzylsay, Kazakhstan, *17* Sumbar River, Turkmenistan, *18* Zumaya, Spain, *19* Hendaye, France, *20* Bidart, France, *21* Bjala, Bulgaria, *22* Kalaat Senan, Tunisia, *23* El Kef, Tunisia, *24* Garn Halfaya, Tunisia, *25* Dababiya Quarry core, Egypt, *26* Sakhalin Island, Russia, *27* Poty Quarry, Brazil, *28* Bajada de Jagüel, Argentina, *29* Seymour Island, Antarctica. (See Appendix for a description of the localities)

palpebra CF2 Zone, and possibly also the upper part of the *Pseudoguembelina fructicosa* CF3 Zone. The base of CF1 is approximately 0.23 myr prior to the K/Pg boundary, according to Hennebert and Dupuis (2003).

In evaluating the record of ammonites at the K/Pg boundary, it is important to distinguish between complete and incomplete sections. For example, in complete sections, e.g., in Tunisia, all of the impact markers are present, including a layer of fine clay (the so-called K/Pg boundary clay) with elevated concentrations of iridium. In such sections, the timescale of deposition is constrained by two points: the impact layer, which represents the same moment everywhere (isochronous), and the base of the highest biostratigraphic zone, which is possibly diachronous. This timescale can be further refined using cyclostratigraphic data, as in the Bay of Biscay, the Tunisian Trough Basin, and the Maastrichtian type area. In incomplete sections, e.g., at Nasiłów, central Poland, in contrast, the fallout layer (boundary clay) is not preserved, although it was undoubtedly deposited, and instead the boundary is marked by an erosional unconformity. The amount of time this unconformity represents is difficult to estimate using biostratigraphic indices and can include parts of the latest Maastrichtian and earliest Danian.

The authors of the ammonite species mentioned in the text are listed in Table 19.1. Some of the ammonites documented are in open nomenclature because the specimens are worn or consist of only fragments. For example, specimens of

Table 19.1 List of species that occur near the K/Pg boundary and the according localities (for abbreviations see Appendix).

	ATLANTIC COAST			GULF COAST					DENMARK			MA	POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMERICA		AN
Taxon/Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
PHYLLOCERATINA																													
Hypophylloceras (Neophylloceras) velledaeforme (Schlüter, 1872)									1		1																		
Hypophylloceras (Neophylloceras) ramosum (Meek, 1858)																		1	1	1						1			
Hypophylloceras (Neophylloceras) hetonaiense Matsumoto, 1942																										1			
Hypophylloceras (Neophylloceras) surya (Forbes, 1846)											1								1										
Hypophylloceras (*Neophylloceras*) sp. of Goolaerts, 2010																						1							
Phyllopachyceras forbesianum (d'Orbigny, 1850)																		1	1	1		1							
LYTOCERATINA																													
GAUDRYCERATIDAE																													
*Gaudryceras kayei**																		1											

Table 19.1 (continued)

	ATLANTIC COAST			GULF COAST					DENMARK			MA	POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMERICA		AN
Taxon/Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
(Forbes, 1846)																													
Gaudryceras hamanakense (Matsumoto and Yoshida, 1979)																										1			
Gaudryceras venustum Matsumoto, 1984																										1			
Anagaudryceras matsumotoi Morozumi, 1985																										1			
Anagaudryceras seymouriense Macellari, 1986																													1
Anagaudryceras politissimum (Kossmat, 1895)																		1	1	1	1								
Anagaudryceras cf. *politissimum* (Kossmat, 1895)																						1							
Anagaudryceras sp. of Ward and Kennedy, 1993																		1											
Zelandites varuna (Forbes, 1846)																						1	1			1			1

Table 19.1 (continued)

	ATLANTIC COAST			GULF COAST					DENMARK			MA	POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMERICA		AN
Taxon/Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Zelandites japonicus Matsumoto, 1938																										1			
Zelandites sp. of Ward and Kennedy, 1993																		1											
*Vertebrites kayei** (Forbes, 1846)																					1								
TETRAGONITIDAE																													
Tetragonites (*Tetragonites*) sp. of Goolaerts, 2010																						1	1						
Saghalinites cala (Forbes, 1846)																						1							
Saghalinites wrighti Birkelund, 1965																				1									
Saghalinites n. sp. of Birkelund, 1993									1		1																		
Pseudophyllites indra (Forbes, 1846)																				1	1	1	1	1					
Pseudophyllites sp. of Goolaerts, 2010																							1	1					
Pseudophyllites loryi (Kilian and Reboul, 1909)																													1

Table 19.1 (continued)

	ATLANTIC COAST			GULF COAST					DENMARK			MA	POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMERICA		AN
Taxon/Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
AMMONITINA																													
Desmophyllites larteti (Seunes, 1891)																		1											
Hauericeras rembda (Forbes, 1846)																						1	1	1					
Pseudokossmaticeras duereri (Redtenbacher, 1873)																				1									
Brahmaites (Brahmaites) brahma (Forbes, 1846)												1							1			1	1	1					
Grossouvrites gemmatus (Hupé, 1854)																													1
Maorites densecostatus (Kilian and Reboul, 1909)																													1
Kitchinites laurae Macellari, 1986																													1
Desmoceratoidea sp. of Goolaerts, 2010																						1	1						
Pachydiscus (*P.*) *riccardii* Macellari, 1986																													1
Pachydiscus (P.) neubergicus (von Hauer, 1858)																											1		

Table 19.1 (continued)

	ATLAN-TIC COAST			GULF COAST					DEN-MARK			MA	POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMER-ICA		AN
Taxon/Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Pachydiscus (P.) neubergicus dissitus Henderson and McNamara, 1985																		1	1										
Pachydiscus (P.) gollevillensis (d'Orbigny, 1850)																			1										
Pachydiscus (*P.*) *ultimus* Macellari, 1986																													1
Pachydiscus (*P.*) *jacquoti jacquoti* (Seunes, 1890)							1					1	1					1		1									
Pachydiscus (*P.*) *armenicus* Atabekian and Akopian, 1969																		1	1	1									
Pachydiscus (*P.*) *noetlingi* Kennedy in Fatmi and Kennedy, 1999												1																	
Pachydiscus (P.) flexuosus Matsumoto, 1979																										1			
Pachydiscus (*P.*) sp. A of Goolaerts, 2010																						1	1	1					

Table 19.1 (continued)

	ATLANTIC COAST			GULF COAST					DENMARK			MA	POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMERICA		AN
Taxon/Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Pachydiscus (*P.*) sp. indet. of Goolaerts, 2010																						1							
Pachydiscus (*P.*) sp. indet. of Ivanov and Stoykova, 1995																					1								
P.(*Neodesmoceras*) *snamensis* (Pervinquière, 1907)																						1	1	1					
P.(*Neodesmoceras*) *mokotibensis* Collignon, 1952	1			1																									
P. (Neodesmoceras) gracilis Matsumoto, 1979																										1			
Menuites terminus (Ward and Kennedy, 1993)									1		1	1	1					1	1	1	1								
Menuites sp. A of Goolaerts, 2010																						1	1	1					
Menuites sp. B of Goolaerts, 2010																						1		1					
Sphenodiscus binckhorsti Böhm, 1898												1	1																

Table 19.1 (continued)

	ATLANTIC COAST			GULF COAST					DENMARK			MA	POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMERICA		AN
Taxon/Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Sphenodiscus lobatus (Tuomey, 1856)	1			1	1	1																							
Sphenodiscus pleurisepta (Conrad, 1857)		1		1	1	1		1																					
Sphenodiscus spp. of Landman et al., 2004b		1																											
ANCYLOCERATINA																													
NOSTOCERATIDAE																													
Nostoceras sp. of Van der Tuuk and Zijlstra, 1979												1																	
DIPLOMOCERATIDAE																													
Glyptoxoceras rugatum (Forbes, 1846)												1																	
Glyptoxoceras cf. *G. rugatum* (Forbes, 1846)							1																						
Glyptoxoceras sp. of Jagt, 1995												1																	
Glyptoxoceras sp. 1 of Jagt, 2012												1																	

Table 19.1 (continued)

	ATLANTIC COAST			GULF COAST					DENMARK			MA	POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMERICA		AN
Taxon/Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Diplomoceras cylindraceum (Defrance, 1816)									1		1	1							1	1		1	1	1		1			
Diplomoceras lambi Spath, 1953																													1
Diplomoceras sp. of Stinnesbeck et al., 2012																											1		
Phylloptychoceras cf. *P. sipho* (Forbes, 1846) of Jagt et al., 2006												1																	
Phylloptychoceras cf. *P. sipho* (Forbes, 1846) of Goolaerts, 2010																						1	1	1					
Phylloptychoceras sp. of Birkelund, 1993									1																				
BACULITIDAE																													
Baculites anceps Lamarck, 1822												1	1																
Baculites ovatus Say, 1821								1																					
Baculites vertebralis Lamarck, 1801									1	1	1	1																	
Baculites cf. *B. vertebralis* Lamarck, 1801																	1												

Table 19.1 (continued)

	ATLANTIC COAST			GULF COAST					DENMARK			MA	POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMERICA		AN
Taxon/Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Baculites cf. *B. claviformis* Stephenson, 1941 of Kennedy and Cobban (2000)					1																								
Baculites cf. *B. undatus* Stephenson, 1941 of Kennedy and Cobban, 2000					1																								
Baculites sp. A of Goolaerts, 2010																						1	1	1					
Baculites sp. C of Cobban and Kennedy, 1995				1	1	1																							
Baculites sp. of Naidin, 1987																1													
Baculites sp. of Machalski, 2005a														1															
Baculites sp. of Racki et al., 2011															1														
Baculitidae indet. of Goolaerts and Dupuis, 2012																									1				
Eubaculites carinatus (Morton, 1834)	1	1	1	1	1	1	1					1																	

Table 19.1 (continued)

	ATLANTIC COAST			GULF COAST					DENMARK			MA	POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMERICA		AN
Taxon/Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Eubaculites cf. *E. carinatus* (Morton, 1834) of Landman et al., 2004a			1																										
Eubaculites latecarinatus (Brunnschweiler, 1966)	1	1		1	1	1						1																	
Eubaculites sp. ex. gr. *E. simplex* (Kossmat, 1895)																												1	
Fresvillia paradoxa (Pervinquière, 1907)																						1	1	1					
SCAPHITIDAE																													
Indoscaphites cunliffei (Forbes, 1846)																						1	1	1					
Indoscaphites pavana (Forbes, 1846)																						1	1	1	1				
Hoploscaphites constrictus (J. Sowerby, 1817)																1													
Hoploscaphites constrictus crassus Łopuski, 1911													1																

Table 19.1 (continued)

	ATLANTIC COAST			GULF COAST					DENMARK			MA	POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMERICA		AN
Taxon/Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Hoploscaphites constrictus johnjagti Machalski, 2005b									1	1	1	1		1			1												
Hoploscaphites constrictus subsp. indet. of Racki et al., 2011															1														
Hoploscaphites felderi Kennedy, 1987									1			1																	
Hoploscaphites pungens (Binkhorst van den Binkhorst, 1862)												1																	
Hoploscaphites sp. ex gr. *waagei-angmartussutensis*												1	1																
Acanthoscaphites? sp. of Kennedy, 1987												1																	
Discoscaphites cf. *D. conradi* (Morton, 1834) of Kennedy and Cobban, 2000					1																								
Discoscaphites gulosus (Morton, 1834)	1	1																											

Table 19.1 (continued)

	ATLAN-TIC COAST			GULF COAST					DEN-MARK			MA	POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMER-ICA		AN
Taxon/Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Discoscaphites cf. *D. gulosus* (Morton, 1834) of Kennedy et al., 2001							1																						
Discoscaphites iris (Conrad, 1858)	1	1	1	1	1	1	1																						
Discoscaphites cf. *D. iris* (Conrad, 1858) of Landman et al., 2004a			1																										
Discoscaphites jerseyensis Landman et al., 2007	1																												
Discoscaphites minardi Landman et al., 2004a	1	1		1	1	1																							
Discoscaphites cf. *D. minardi* Landman et al., 2004a of Landman et al., 2004a			1																										
Discoscaphites sphaeroidalis Kennedy and Cobban, 2000	1	1		1	1	1	1																						

Geographic distribution of ammonite species at 29 sites in the last 0.5 myr of the Cretaceous. Abbreviations: MA: Maastrichtian type area, The Netherlands and Belgium; KA: Kazakhstan; TR: Turkmenistan; BU: Bulgaria; EG: Egypt; FER: Far East Russia; AN: Antarctica; * = the two species may be synonymous, but further research is required.

Phylloptychoceras from Tunisia are small pyritic fragments of shafts and can, therefore, only be referred to as *Phylloptychoceras* cf. *P. sipho*. Similarly, specimens of *Baculites* from this region are too incomplete and lack details of ornamentation and suture to permit species identification. On the Atlantic and Gulf Coastal plains, the poor state of preservation of some specimens of *Glyptoxoceras* and *Discoscaphites* also precludes their identification to species level. Even in sections that have been studied for decades, such as those in Denmark, some material is too crushed or incomplete to be assigned to a particular species with any certainty (e.g., *Saghalinites* n. sp. of Birkelund 1993).

19.3 Results

19.3.1 Atlantic Coastal Plain of North America

(Sites 1–3: New Jersey and Maryland). The *Discoscaphites iris* Zone, the highest ammonite zone in North America, is present in this area and has yielded nine species, four (sub)genera, and four families distributed among the Ammonitina (*Pachydiscus* (*Neodesmoceras*) and *Sphenodiscus*) and Ancyloceratina (*Eubaculites* and *Discoscaphites*) (Landman et al. 2004a, b, 2007; Figs. 19.2, 19.3; Tables 19.1, 19.2). This zone corresponds to Calcareous Nannofossil Zone CC26b, representing approximately the last 0.5 myr of the Maastrichtian. At offshore sites (~100 m deep) containing ammonites, the section is demonstrably incomplete with an unconformity at the K/Pg boundary. At more nearshore sites (~40 m deep) containing ammonites, the sequence is apparently more complete. The upper part of the section consists of a very fossiliferous unit (called the *Pinna* Layer) that yields numerous specimens of *Discoscaphites* and *Eubaculites*. The *Pinna* Layer is overlain by the Burrowed Unit, which bears many fewer ammonites, almost all of which are *Eubaculites*. However, the *Pinna* Layer occurs above a horizon with a weak iridium anomaly (520 pg/g). The crucial question is whether this iridium anomaly represents the record of the bolide impact and, if so, whether it is in place or has migrated downward (Landman et al. 2007, 2012b; Miller et al. 2010; for additional discussion about the remobilization of iridium, see Racki et al. 2011). For example, if the iridium anomaly is in place, then the ammonites in the *Pinna* Layer and the Burrowed Unit may have been short-term survivors of the bolide impact, possibly persisting into the earliest Danian. However, even if the iridium anomaly has migrated downward from the top of the *Pinna* Layer, a more conservative interpretation favored here and elsewhere (Landman et al. 2014), the species of *Eubaculites* in the Burrowed Unit are still Danian survivors (see 19.4.1).

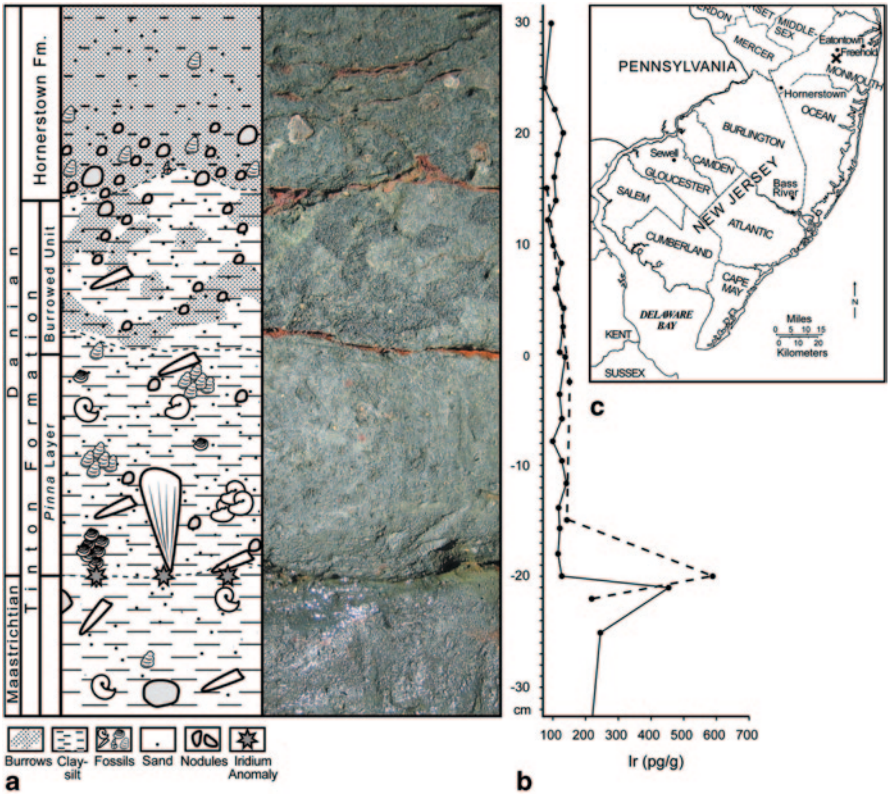


Fig. 19.2 Stratigraphic section of the upper Maastrichtian and lower Danian in Monmouth County, New Jersey, Atlantic Coastal Plain, USA. **a** The top of the Tinton Formation consists of the *Pinna* Layer overlain by the Burrowed Unit, which is overlain, in turn, by the Hornerstown Formation. An enriched concentration of iridium occurs at the base of the *Pinna* Layer (indicated by the stars). The position of the K/Pg boundary is based upon the assumption that the enriched concentration of iridium has been remobilized. **b** Iridium profile from two sites (represented by the solid and dashed lines) (Landman et al. 2007). **c** Map of part of New Jersey with the locality marked by an X

19.3.2 Gulf Coastal Plain of North America

(Sites 4–7: Missouri, Mississippi, and Texas). The *Discoscaphites iris* Zone is present on the Gulf Coastal Plain in Missouri (Stephenson 1955), Mississippi (Cobban and Kennedy 1995; Kennedy and Cobban 2000), and Texas (Kennedy et al. 2001) and contains as many as 15 species, although not all of them are present at every site (Fig. 19.4; Tables 19.1, 19.2). In Stoddard and Scott Counties, southeastern Missouri, the Owl Creek Formation consists of clayey sands, which were probably deposited at depths of less than 100 m, and is unconformably overlain by the Clayton Formation (Campbell et al. 2008). In Tippah County, northeastern Mississippi, the Owl Creek Formation consists of micaceous clays, which were probably deposited at similar depths. The Owl Creek Formation at this site is also unconformably

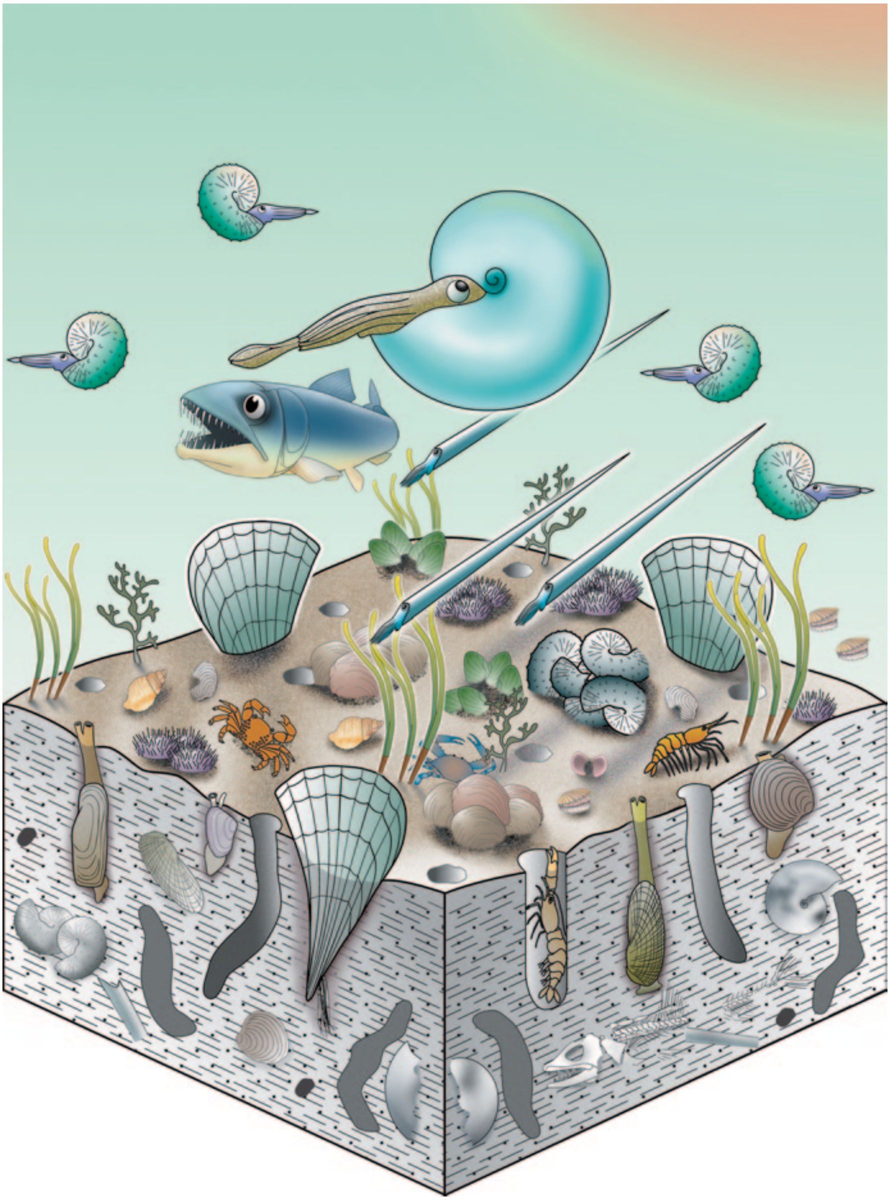


Fig. 19.3 Hypothetical reconstruction of the sea bottom on the Atlantic Coast at the end of the Maastrichtian just before the meteor impact, as inferred from sections in Monmouth County, New Jersey. The ammonites include *Sphenodiscus lobatus*, *Discoscaphites iris*, and *Eubaculites latecarinatus* (from Landman et al 2007)

Table 19.2 Geographic distribution of 31 ammonite genera at 29 sites in the last 0.5 my of the Cretaceous

		ATLAN-TIC COAST			GULF COAST					DEN-MARK			MA	POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMER-ICA		AN	
	Taxon/Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	N occur-rences
1	*H.* (*Neophylloceras*)									1		1							1	1	1		1				1				7
2	*Phyllopachyceras*																		1	1	1		1								4
3	*Gaudryceras*																		1								1				2
4	*Anagaudryceras*																		1	1	1	1	1				1			1	7
5	*Vertebrites*																					1									1
6	*Zelandites*																		1				1	1			1			1	5
7	*Tetragonites*																						1	1							2
8	*Saghalinites*									1		1									1		1								4
9	*Pseudophyllites*																				1	1	1	1	1					1	6
10	*Desmophyllites*																		1												1
11	*Hauericeras*																						1	1	1						3
12	*Pseudokossmaticeras*																				1										1
13	*B.* (*Brahmaites*)												1							1			1	1	1						5
14	*Grossouvreites*																													1	1

Table 19.2 (continued)

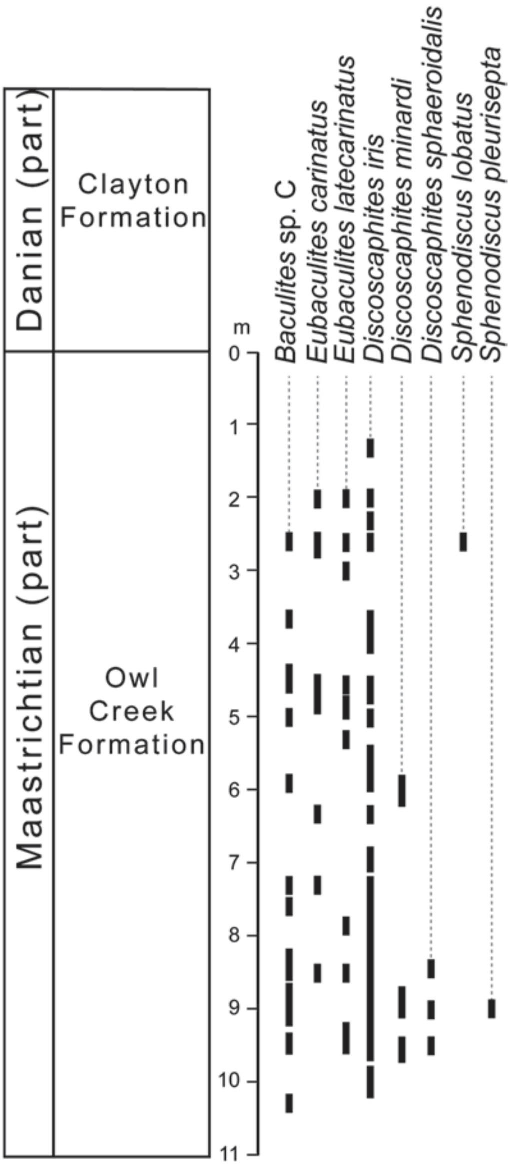
		ATLANTIC COAST			GULF COAST					DENMARK			MA	POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMERICA		AN	
	Taxon/Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	N occurrences
15	*Maorites*																													1	1
16	*Kitchinites*																													1	1
17	*P.* (*Pachydiscus*)							1					1	1					1	1	1	1	1	1	1		1	1		1	13
18	*P.* (*Neodesmoceras*)	1			1																		1	1	1		1				6
19	*Menuites*									1		1	1	1					1	1	1	1	1	1	1						11
20	*Sphenodiscus*	1	1		1	1	1		1				1	1																	8
21	*Nostoceras*												1																		1
22	*Glyptoxoceras*							1					1																		2
23	*Diplomoceras*									1		1	1							1	1		1	1	1		1	1		1	11
24	*Phylloptychoceras*									1			1										1	1	1						5
25	*Baculites*				1	1	1		1	1	1	1	1	1	1	1	1	1					1	1	1	1					16
26	*Eubaculites*	1	1	1	1	1	1	1					1																1		9
27	*Fresvillia*																						1	1	1						3
28	*Indoscaphites*																						1	1	1	1					4
29	*Hoploscaphites*									1	1	1	1	1	1	1	1	1													8

Table 19.2 (continued)

		ATLANTIC COAST			GULF COAST					DENMARK			MA	POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMERICA		AN	
	Taxon/Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	N occurrences
30	*Acanthoscaphites*												1																		1
31	*Discoscaphites*	1	1	1	1	1	1	1																							7

The genera represent all four orders of Cretaceous Ammonoid: Phylloceratina (1-2), Lytoceratina (3-9), Ammonitina (10-20), and Ancyloceratina (21-31). For a description of localities, see Appendix. Abbreviations: *AT*: Atlantic Coast; *MA*: Maastrichtian type area, The Netherlands and Belgium; *KA*: Kazakhstan; *TR*: Turkmenistan; *BU*: Bulgaria; *EG*: Egypt; *FER*: Far East Russia; *S.Am*: South America; AN: Antarctica; N.occ: Number of occurrences.

Fig. 19.4 Stratigraphic range chart of the ammonites in the Owl Creek Formation in Tippah County, north-eastern Mississippi, Gulf Coastal Plain, USA (Larina et al. 2012). The Owl Creek Formation is unconformably overlain by the Clayton Formation, with no evidence of impact debris. Ammonites extend to approximately 1 m below the unconformity, which presumably contains the K/Pg boundary



overlain by the Clayton Formation, without any evidence of impact debris. Ammonites extend to approximately 1 m below the unconformity, which presumably contains the K/Pg boundary, and the absence of ammonites above this level may be due to dissolution (Larina et al. 2012). Towards the southeast in Chickasaw County, Mississippi, the Owl Creek Formation passes into the Prairie Bluff Chalk, which contains the same assemblage of ammonites. However, the base of the Clayton Formation in this area consists of a 30-cm-thick unit filled with impact spherules and reworked Maastrichtian fossils (Boas et al. 2013a, b).

On the other side of the Mississippi Embayment, ammonites are present in the upper Corsicana Formation along the Brazos River, Falls County, Texas. The erosional surface at the top of this formation has been interpreted as the K/Pg boundary (Hansen et al. 1987; for further discussion of this interpretation see Hart et al. 2012). The ammonites are the same as those in Mississippi with the addition of *Pachydiscus* (*P.*) *j. jacquoti* and *Glyptoxoceras* cf. *G. rugatum*. Two ammonite species (*Eubaculites carinatus* and *Discoscaphites* cf. *D. gulosus*) extend into the uppermost 1 m of the formation (Kennedy et al. 2001). In addition, Keller et al. (2009, p. 54) reported a single specimen of *D. iris* at the base of the *Pseudoguembelina palpebra* CF2 Zone in the Brazos River Mullinax-1 Core.

19.3.3 La Popa Basin, Northeastern Mexico

(Site 8). In northeastern Mexico, Stinnesbeck et al. (2012: table 1) reported *Sphenodiscus pleurisepta* and *Baculites ovatus* from Planktic Foraminifera Zone CF3. The highest occurrence of *S. pleurisepta* is 3 m below an erosional unconformity marking the K/Pg boundary.

19.3.4 Denmark

(Sites 9–11: Stevns Klint, Kjølby Gård, and the "*Dania*" Quarry). The ammonite record in Denmark has been extensively studied because these sections exhibit nearly continuous deposition across the K/Pg boundary (Birkelund 1979, 1993; Schiøler et al. 1997; Machalski 2005a, b; Machalski and Heinberg 2005; Rasmussen et al. 2005; Surlyk et al. 2006; Hart et al. 2011; Damholt and Surlyk 2012; Gravesen and Jakobsen 2013). The environment is interpreted as a shelf sea ranging from the euphotic zone to several hundred meters deep (Surlyk 1997; Surlyk et al. 2006; Schulte et al. 2010). The stratigraphy along the 14.5 km long classic section at Stevns Klint is complex, with the upper, but not uppermost, Maastrichtian Sigerslev Member separated by one or two closely spaced hardgrounds from the uppermost Maastrichtian Højerup Member (Fig. 19.5). These hardgrounds were probably produced by early diagenetic cementation during shallowing events (Hansen 1990; Surlyk 1997; Surlyk et al. 2006). Correlation of these events with those in the upper part of the Nekum and Meerssen members in the Maastricht area (Hart et al. 2011) suggests that the hardgrounds developed in the last 240 kyr of the Maastrichtian (Schiøler et al. 1997). The Højerup Member corresponds to the uppermost Maastrichtian *Stensioeina esnehensis* Foraminifera Zone.

The Højerup Member is internally organized into a series of low asymmetrical bryozoan bioherms alternating with basins, producing a relief of as much as 4 m. The K/Pg transition is continuous in the basins with the Højerup Member conformably overlain by the basalmost Danian Fiskeler Member (Fish Clay), which is overlain, in turn, by the Cerithium Limestone Member (Rødvig Formation; Surlyk et al. 2006). The uppermost Højerup Member is rich in ammonites, especially on

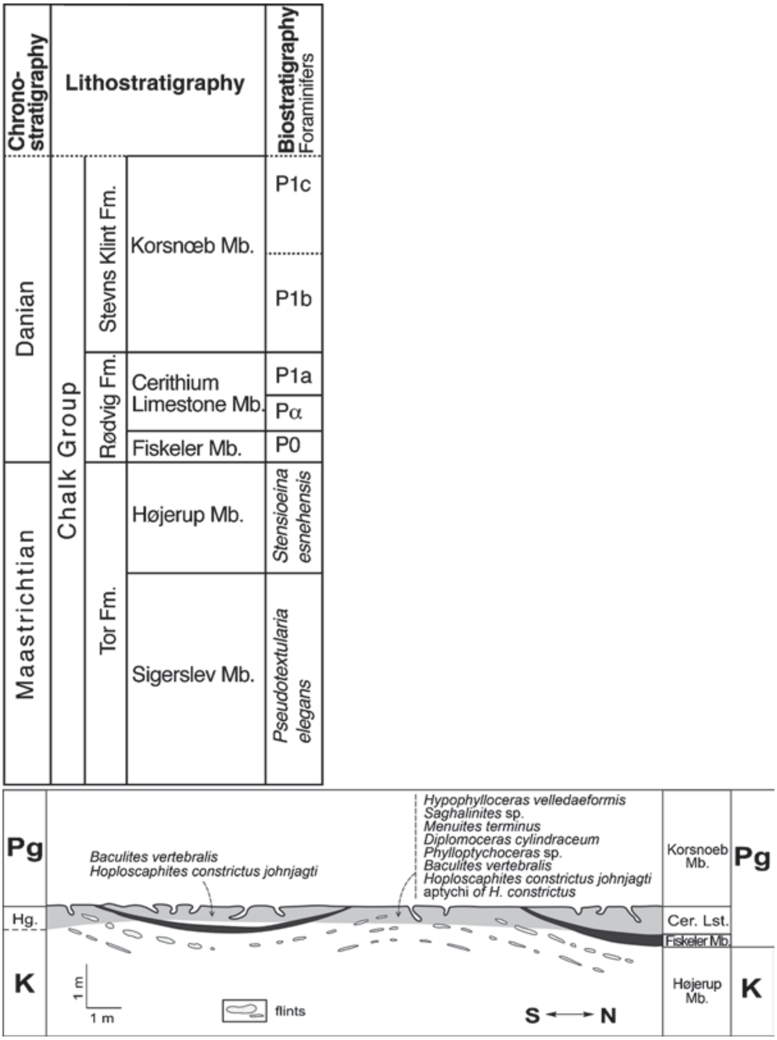


Fig. 19.5 *Top*. Stratigraphic chart of the K/Pg section at Stevns Klint, Denmark (modified from Surlyk et al. 2006). *Bottom*. Diagram of the boundary interval. Hg = Hardground (modified from Machalski and Heinberg 2005)

the crests of the bioherms, which are incorporated into a Danian hardground that truncates both the Højerup Member and Cerithium Limestone (Birkelund 1993; Machalski 2005a). In total, the fauna consists of eight species, seven genera, and six families distributed among the Phylloceratina (*Hypophylloceras* (*Neophylloceras*)), Lytoceratina (*Saghalinites*), Ammonitina (*Menuites*), and Ancyloceratina (*Phylloptychoceras*, *Diplomoceras*, *Baculites*, *Hoploscaphites*) (Tables 19.1, 19.2). Specimens of *B. vertebralis* and *H. constrictus johnjagti* also occasionally occur in the basal Danian Cerithium Limestone Member (Birkelund 1979, 1993; Surlyk and Nielsen 1999; Machalski 2002). These specimens have generally been interpreted

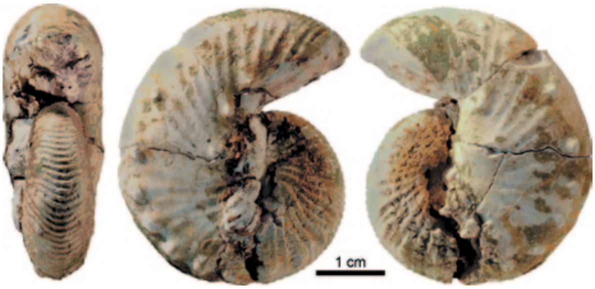


Fig. 19.6 *Hoploscaphites constrictus johnjagti* from the Cerithium Limestone Member at Stevns Klint, Denmark (modified from Machalski and Heinberg 2005)

as reworked material, but Machalski and Heinberg (2005) argued that they may represent early Danian survivors (Fig. 19.6).

At Kjølby Gård, ammonites occur up to 20 cm below the K/Pg boundary (Birkelund 1993). The "*Dania*" Quarry, northern Denmark, has also been thoroughly studied and represents the *stevensis-chitoniformis* brachiopod Zone, which correlates with the *Palynodinium grallator* dinoflagellate Zone (Hansen 1977; Håkanssan and Hansen 1979; Birkelund 1993; Machalski 2005a, b; Gravesen and Jakobsen 2013). The sequence at "*Dania*" is unique among Danish boundary sequences in containing the uppermost Maastrichtian zonal species *Micula prinsii*. This nannofossil is present in one of the marl layers low in the sequence (Håkansson and Hansen 1979), which implies that the "*Dania*" succession occurs within Calcareous Nannofossil Zone CC26b of Perch-Nielsen (1985).

19.3.5 Maastrichtian Type Area

(Site 12: the Netherlands and northeast Belgium). Several outcrops and quarries near Maastricht on both sides of the border between the Netherlands and Belgium that expose the uppermost Maastrichtian are treated together. This area has been extensively studied because of its importance for biostratigraphy (Zijlstra 1994; Smit and Brinkhuis 1996; Schiøler et al. 1997; Jagt 1996, 2002; Jagt et al. 2003, 2006; Jagt and Jagt-Yazykova 2012; Mai 1998). The clay beds just above the Berg en Terblijt Horizon at the base of the IVf-7 interval (Meerssen Member) are assigned to Planktic Foraminifera Zone P0. Our targeted interval of 0.5 myr was bracketed by reference to this horizon and by using the cyclostratigraphic interpretation of Zijlstra (1994) and Schiøler et al. (1997) to define the lower part of our interval. According to them, the Nekum and Meerssen members (upper part of the Maastricht Formation) represent the last 300 kyr of the Maastrichtian. This part of the formation is interpreted as having been deposited on a shallow carbonate platform (Kennedy and Jagt 1998; Jagt 1996, 2002, 2005, 2012; Jagt et al. 2006).

We examined the record of ammonites from the Meerssen and Nekum members. In terms of dinoflagellate zonation, this interval (upper Nekum and Meerssen members) corresponds to the *Palynodinium grallator* dinoflagellate Zone, and the Meerssen Member to the *Thalassiphora pelagica* dinoflagellate Subzone (e.g., Mai 1998). A total of 19 species, 12 genera, and seven families of ammonites are present near or at the K/Pg boundary distributed among the Ammonitina (*Brahmaites*, *Pachydiscus*, *Menuites*, and *Sphenodiscus*) and Ancyloceratina (*Nostoceras*, *Glyptoxoceras*, *Diplomoceras*, *Phylloptychoceras*, *Baculites*, *Eubaculites, Hoploscaphites,* and *Acanthoscaphites*?) (Fig. 19.7; Tables 19.1, 19.2). The most common ammonites are *Baculites* and *Hoploscaphites*.

Several scaphitids and baculitids have also been recorded from Unit IVf-7 of the Meerssen Member above the Berg en Terblijt Horizon in the section exposed at the former Curfs quarry near Geulhem, southern Limburg, southeast Netherlands (Jagt et al. 2003; Machalski et al. 2009; Jagt 2012; Fig. 19.8). As stated above, this horizon is generally interpreted as marking the K/Pg boundary (although there is no evidence of impact debris) and these specimens are assigned to Planktic Foraminifera Zone P0. Because the species of *Baculites* are different from those below this

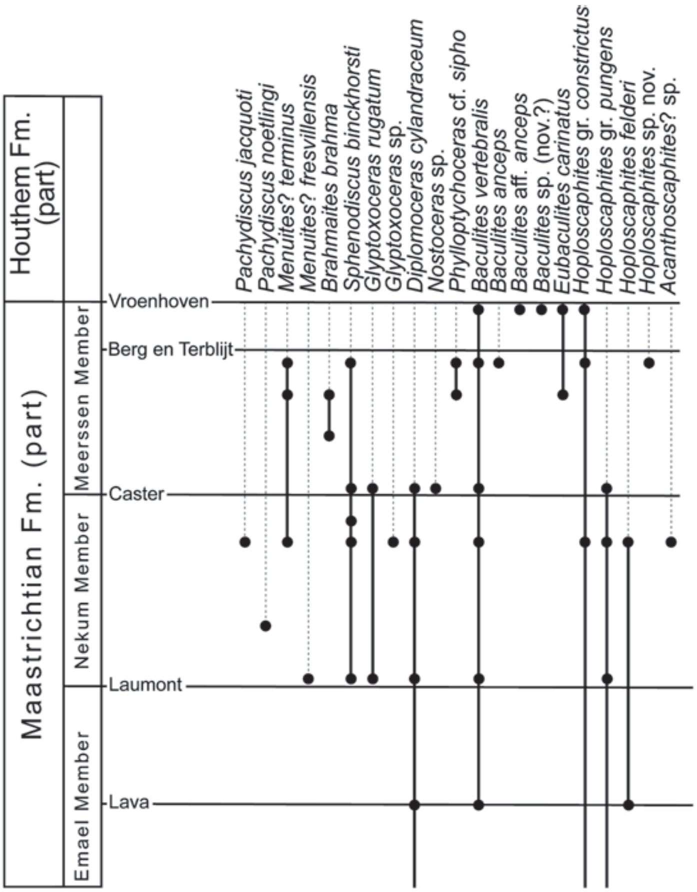


Fig. 19.7 Stratigraphic range chart of the ammonites at the K/Pg section in the Maastrichtian region, the Netherlands and northeast Belgium (modified from Jagt et al. 2006). The Berg en Terblijt Horizon, which forms the base of section IVf-7, is interpreted as the K/Pg boundary. The dots indicate isolated occurrences and the lines indicate "more or less" complete ranges

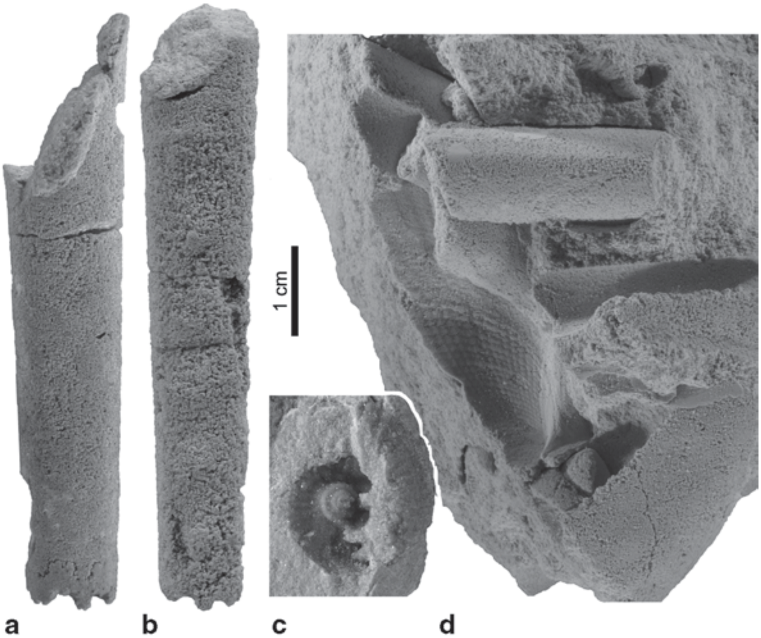


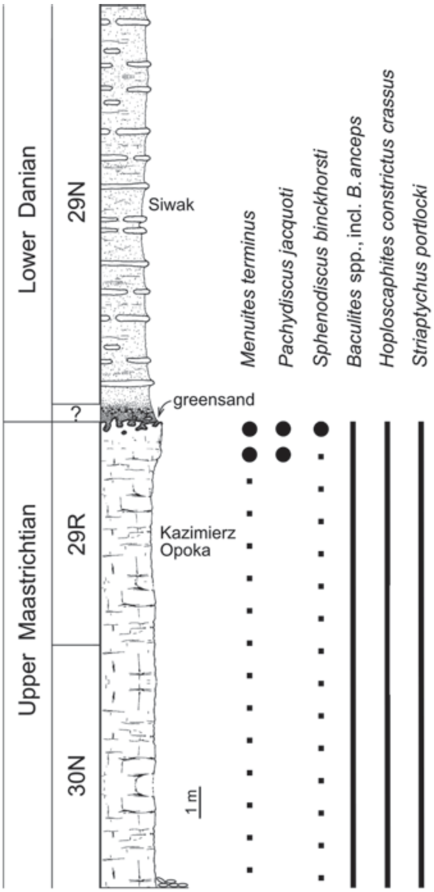
Fig. 19.8 Ammonites from the top of Unit IVf-7 of the Meerssen Member above the Berg en Terblijt Horizon in the section exposed at the former Curfs quarry near Geulhem, southern Limburg, southeast Netherlands (Jagt et al. 2003; Jagt 2012; Machalski et al. 2009). **a**, **b**, **d** *Baculites* aff. *anceps* (Jagt Collection, NHMM). The mature apertures are preserved in **a** and **b**. The empty spaces in **d** are voids left by dissolution of the original aragonite. **c** *Hoploscaphites constrictus*, with incomplete filling of the phragmocone (Jagt Collection, NHMM). All of these features indicate that the ammonites in this unit were buried with their shells intact without significant reworking or transport, which would have otherwise destroyed the delicate apertural features. In addition, the shells must have been buried rapidly enough to prevent complete infilling of the phragmocones

horizon and because many of them are preserved with their apertures intact, they may represent early Danian survivors (Smit and Brinkhuis 1996; Jagt et al. 2003).

19.3.6 Poland

(Sites 13–15: Nasiłów, Mełgiew, and Lechówka). The K/Pg boundary is exposed in Nasiłów in the Kaziemerz Dolny area, Poland (Hansen et al. 1989; Machalski 2005a). According to Abdel-Gawad (1986), the upper part of the section represents deposition in an inner shelf environment. However, the section is incomplete with a hiatus that spans the topmost Maastrichtian and the lowermost Paleocene encompassing as much as 500 kyr, but possibly much less. This inference is based in part on the absence of *H. constrictus johnjagti*, the terminal Maastrichtian chrono-subspecies of the *H. constrictus* lineage, which characterizes the uppermost Maastrichtian of Denmark (Højerup Member) and the Netherlands and northeast

Fig. 19.9 Stratigraphic range chart of the ammonites at the K/Pg section in Nasiłów, Poland (Machalski and Walaszczyk 1987, 1988; Machalski 2005a). Reworked specimens are present in the greensand



Belgium (top Nekum-Meerssen members) (Machalski and Walaszczyk 1987, 1988; Machalski 2005a).

Ammonites occur in the *Belemnella kazimiroviensis* belemnite Zone, Magnetic Chron 29r, and lower part of the *Palynodinium grallator* dinoflagellate Zone. They are preserved in a hard limestone layer at the top of the Kazimierz Opoka (silicious chalk) (Figs. 19.9, 19.10). This unit passes into a thin layer of soft opoka, with both layers penetrated by crustacean burrows filled with sediment derived from the overlying Danian glauconitic sandstone. A total of six species, five genera, and four families are present (Tables 19.1, 19.2). The fauna is dominated by *Baculites* spp., including *Baculites anceps*, followed by *Hoploscaphites constrictus crassus*. The rest of the ammonite fauna consists of *Menuites terminus*, *Pachydiscus* (*P.*) *j. jacquoti*, and *Sphenodiscus binckhorsti.*

A K/Pg boundary interval similar to that of Nasiłów is exposed nearby, on the opposite side of the Wisła River at Bochotnica. The section at Mełgiew, Poland, is more complete than that at Nasiłów with a hiatus of only a few thousand years at the K/Pg boundary (Machalski 2005a), as indicated by the presence of the chrono-subspecies *Hoploscaphites constrictus johnjagti*. The only additional ammonites include *Baculites* spp., but this section has not been as thoroughly studied

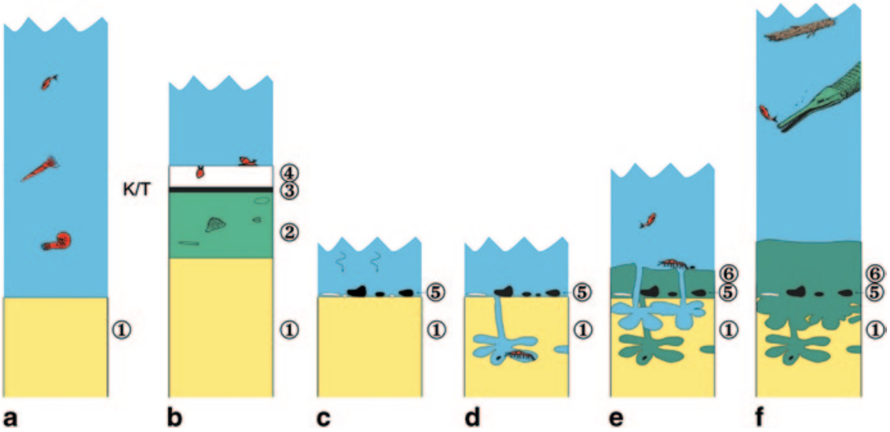


Fig. 19.10 Depositional and erosional history at the K/Pg boundary in the Kazimierz Dolny region, Poland (from Machalski 1998). Stage **a**: Sedimentation of the siliceous chalk (Kazimierz Opoka) of late Maastrichtian age (*1*). Stage **b**: Sedimentation of a slightly glauconitic carbonate mud unit (*2*) of late Maastrichtian age, followed by a clay layer (*3*) and a carbonate unit (*4*), both of Danian age. Stage **c**: Erosion or dissolution (?) episode in early Danian leading to the destruction of the top of unit 1 and total destruction of units 2–4, and to the formation of a residual lag (*5*) composed of reworked nodules, early diagenetic molds, and other fossils of Maastrichtian and Danian age. Stage **d**: Omission conditions on the sea floor and the development of burrowing leading to the formation of the first generation of visible burrows during the Danian. Stage **e**: Start of sandy-glauconitic sedimentation (*6*) of Danian age, filling of earlier burrows and formation of the next generation, origin of pseudobreccia at the top of the Kazimierz Opoka, and additional reworking of the residual lag. Stage **f**: Continuation of Danian sedimentation

as the Nasiłów section. At Lechówka, Poland, ammonites occur just below the iridium spike in the top of the *Guembelitria cretacea* planktic foraminifera Zone *sensu* Peryt (1980) (Racki et al. 2011).

19.3.7 Kyzylsay, Kazakhstan

(Site 16). The uppermost Maastrichtian of the Mangyshlak Peninsula contains rare and poorly preserved specimens of *Baculites* sp. and *Hoploscaphites constrictus* (see Naidin 1987; Herman et al. 1988; Jeffrey 1997; Tables 19.1, 19.2). They occur in white chalks that were deposited at depths of less than 100 m. The specimens of *H. constrictus* occur in the *Belemnella kazimiroviensis* belemnite Zone immediately below the boundary clay, which is marked by an anomalous concentration of iridium, with no signs of any sedimentary breaks.

19.3.8 Sumbar River, Turkmenistan

(Site 17). An apparently complete boundary section occurs in the Sumbar River area, western Kopet Dagh, southwest Turkmenistan (Machalski et al. 2012). The boundary is marked by a clay layer with an anomalous iridium concentration. The area is interpreted as a relatively deep-water environment on the outer shelf, based on the high percentage of planktic species in the foraminiferal assemblages. Two ammonite species, *Hoploscaphites constrictus johnjagti* and *Baculites* cf. *B. vertebralis*, have been recovered from the *Pseudotextularia elegans* Planktic Foraminiferal Zone as high up as 5 cm below the boundary clay (Moskvin 1959; Alekseev et al. 1988; Machalski et al. 2012; Tables 19.1, 19.2). These records represent the southeasternmost extent of these two (sub)species, which are otherwise known from northwest and central Europe. In addition, a single specimen of what appears to be *H. constrictus* is present in the Danian part of the section in an interval 22–24 cm above the base of the boundary clay. However, it is currently unclear if this specimen is reworked from the Maastrichtian or dates from the Danian.

19.3.9 Bay of Biscay

(Sites 18–20: Zumaya, Hendaye, and Bidart). This region of southwestern France and northeastern Spain encompasses many K/Pg sections that are apparently continuous and complete (Wiedmann 1987, 1988a, b; Kennedy 1993; Ward and Kennedy 1993; Ten Kate and Sprenger 1993; Rocchia et al. 2002). The strata consist of massive marls with rare turbidites deposited in an outer-shelf setting with water depths of 100–500 m (Mathey 1982; Schulte et al. 2010). In Zumaya, using the cyclostratigraphic studies of Batenburg et al. (2012) and Dinarès-Turell et al. (2013), our targeted interval (last 0.5 myr of the Maastrichtian) appears to correspond to the top few meters of Member IV and the entire Member V of Ward and Kennedy (1993). This is a conservative estimate as due to small differences in measured thicknesses between Ward and Kennedy (1993), Dinarès-Turell et al. (2013), and Batenburg et al. (2012), the exact position of the base of our 0.5 myr interval cannot be situated more precisely than 1 m. The base of Member V is approximately 15 m below the K/Pg boundary in Ward and Kennedy (1993), 12 m below the K/Pg boundary in Batenburg et al. (2012), and 10.2 m below the K/Pg boundary in Dinarès-Turell et al. (2013). The base of our 0.5 myr interval thus equates to approximately 20 and 18 m below the K/Pg boundary on the Batenburg et al. (2012) and the Dinarès-Turell et al. (2013) logs, respectively. Thus, being conservative, only ammonite records from Member V and the top few meters of Member IV were included in our tally. Unit V of Ward and Kennedy (1993) falls within the *Micula prinsii* Zone (= Calcareous Nannofossil Zone CC26b of Perch-Nielsen 1985).

Ammonites are rare throughout most of the section in the Bay of Biscay (Fig. 19.11). They are present in the uppermost few meters of Member IV and the entire Member V of Ward and Kennedy (1993). In total, they consist of 13 species, representing 11 genera belonging to the Phylloceratina (*Phylloceras*, *Phyllopachyceras*), Lytoceratina (*Anagaudryceras*, *Zelandites*, *Pseudophyllites*), Ammonitina (*Desmophyllites*, *Brahmaites*, *Pachydiscus*, *Pseudokossmaticeras*, *Menuites*), and Ancyloceratina (*Diplomoceras*). The top 1.5 m in the combined sections at Zumaya, Hendaye, and Bidart contain approximately 40 specimens representing ten species, although only one of these specimens is present in the highest 10–15 cm of the section (Ward

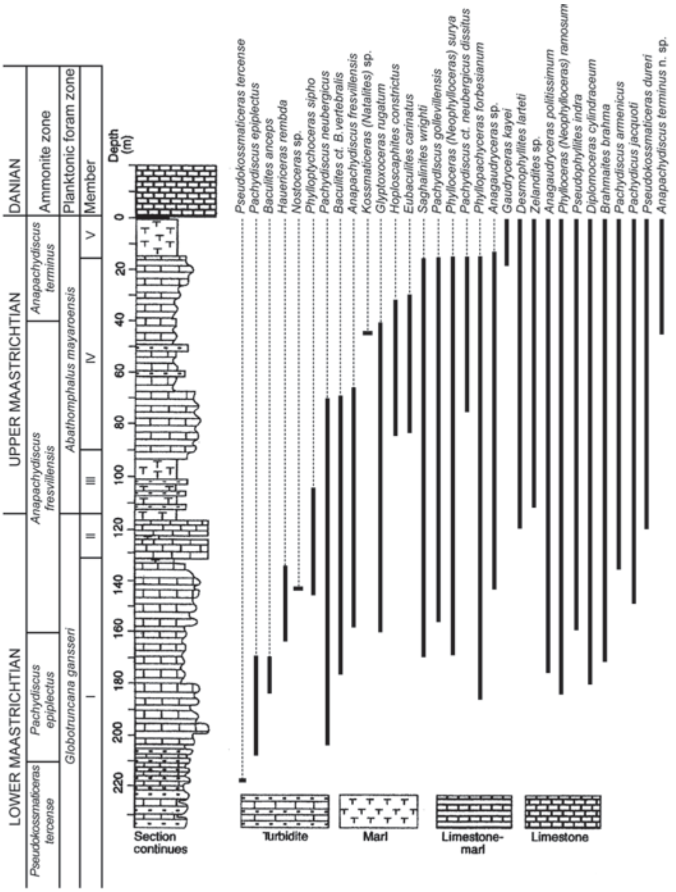


Fig. 19.11 Composite stratigraphic range chart of the ammonites at the K/Pg section in the Bay of Biscay plotted on the measured section at Zumaya, Spain (modified from Marshall and Ward 1996)

and Kennedy 1993). In addition, Rocchia et al. (2002) reported the occurrence of a poorly preserved specimen from 5 cm below the boundary clay at Bidart, which contains Ni-rich spinel crystals and an anomalously high concentration of iridium.

Marshall and Ward (1996) also used statistical methods (confidence intervals) to examine the ranges of ammonite species in the top 1.5 m of the composite section in the Bay of Biscay to determine the likelihood that the actual ranges extended above the observed ranges. Using a 50 % confidence range interval, they concluded that at least two of these species could have persisted to the K/Pg boundary, even though they are not actually preserved at this level.

19.3.10 Bjala (= Byala), Bulgaria

(Site 21). In the area of Bjala (= Byala), eastern Bulgaria, along the shores of the Black Sea, several sections of the Bjala Formation contain a complete K/Pg boundary succession (Preisinger et al. 1993; Ivanov and Stoykova 1994; Ivanov 1995; Stoykova and Ivanov 2004, 2005). The formation consists of marls in the lower part of the section and marls alternating with marly limestones in the upper part, which were deposited on the outer shelf and inner slope. The section is capped by a 1–3-cm thick clay bed marked by an anomalous concentration of iridium. Five species occur in Calcareous Nannofossil Zone CC26b (Preisinger et al. 1993; Ivanov and Stoykova 1994; Ivanov 1995; Stoykova and Ivanov 2004, 2005): *Pseudophyllites indra*, *Anagaudryceras politissimum*, *Vertebrites kayei*, *Menuites terminus,* and *Pachydiscus* sp. indet. (Tables 19.1, 19.2). Two of these species (*P. indra* and *A. politissimum*) occur 40 cm below the iridium enriched layer of clay.

19.3.11 Tunisia and Egypt

Tunisia (Sites 22–24: El Kef, Kalaat Senan, and Garn Halfaya); Egypt (Site 25: Dababiya Quarry Corehole). Several of the most complete K/Pg boundary sections are located in the Tunisian Trough Basin (Goolaerts et al. 2004; Goolaerts 2010a). Indeed, the reddish layer at the base of the Boundary Clay near El Kef (the KS locality) is the Global Stratotype Section and Point (GSSP) for the K/Pg boundary (Molina et al. 2006). Ammonites occur as high as 1–2 m below the boundary at El Kef (GSSP section), Kalaat Senan (Aïn Settara, Tabet Zaara, and Oued Raïne sections), and Garn Halfaya (Garn section), although almost all of the specimens occur as surface float and may have moved slightly downslope. The highest ammonite occurs 1 m below the boundary at Garn Halfaya, which is approximately equivalent to 50 kyr prior to the end of the Cretaceous based on the cyclostratigraphic data of Hennebert and Dupuis (2003). All of the reported ammonites occur in the highest ammonite zone, the *Indoscaphites pavana* Assemblage Zone, which represents approximately the last 420 kyr of the Maastrichtian based on the cyclostratigraphy of Hennebert and Dupuis (2003) and Hennebert (2012). In the Dababiya Quarry Corehole, specimens occur within Calcareous Nannofossil Zone CC26b (Goolaerts and Dupuis 2012; Berggren and Ouda 2013; Berggren et al. 2012).

The ammonite assemblage in the ultimate 0.5 myr of the Maastrichtian in the Tunisian Trough Basin consists of 22 species, 17 genera, and 10 families (Fig. 19.12; Tables 19.1, 19.2). This assemblage is the taxonomically most diverse terminal Maastrichtian fauna discovered to date. However, because the specimens consist of small septate inner whorls less than 20 mm in diameter, they are sometimes difficult to identify to species or even genus level. They are distributed among the Phylloceratina (*Neophylloceras* and *Phyllopachyceras*), Lytoceratina (*Anagaudryceras*, *Zelandites*, *Tetragonites*, *Pseudophyllites*, and *Saghalinites*), Ammonitina (*Hauericeras*, *Brahmaites*, *Menuites*, *Pachydiscus*, *Neodesmoceras*, and Desmoceratoidea gen. indet.), and Ancyloceratina (*Diplomoceras*, *Phylloptychoceras*, *Fresvillia*, *Baculites*, and *Indoscaphites*) (Tables 19.1, 19.2).

The ammonite fauna is dominated by scaphitids (*Indoscaphites*), baculitids (*Baculites*), and pachydiscids. The environment is interpreted as outer neritic to bathyal (Schulte et al. 2010), but the variation in the abundance of *Indoscaphites* suggests a depth gradient. The abundance increases from a minimum of 48 % at El

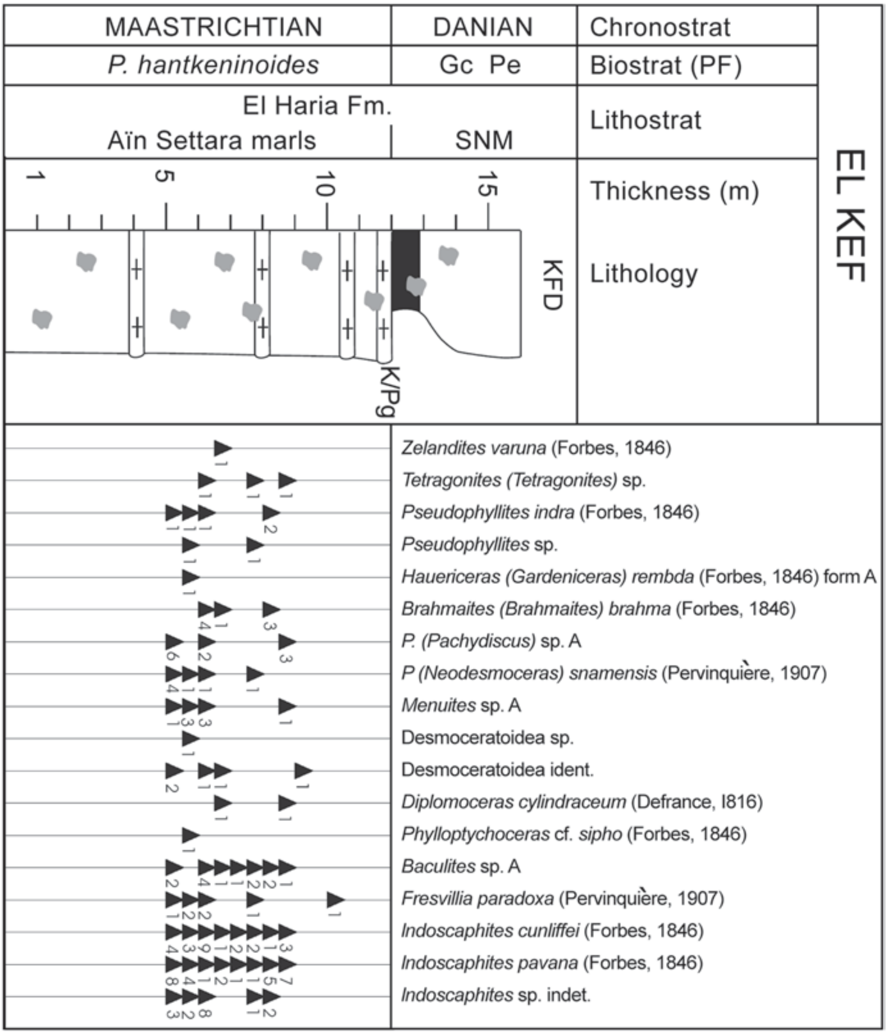


Fig. 19.12 Stratigraphic distribution of ammonite species by number of specimens in the upper part of the El Haria Formation at the El Kef GSSP section for the base of the Paleogene Period (modified from Goolaerts 2010a)

Kef to 60 % at Garn Halfaya to a maximum of 76 % at Kalaat Senan. Correlatively, the abundance of Lytoceratina decreases along this same transect. Phylloceratina are extremely rare, and have only been found at Kalaat Senan, which is probably due to the greater number of specimens collected at this site (643) compared to that at El Kef (145) and Garn Halfaya (108). The dominant elements of the fauna, the scaphitids and baculitids, are also reported from the uppermost Maastrichtian of Egypt (Dababiya Core; Berggren et al. 2012; Goolaerts and Dupuis 2012). The absence of other species in this region is probably due to the paucity of specimens collected from this site (10).

19.3.12 Naiba River Valley, Sakhalin, Far East Russia

(Site 26). The latest Maastrichtian ammonites at this site are not very well constrained in terms of biostratigraphy. Numerous well-preserved specimens of *Zelandites*, and a few specimens of *Gaudryceras* and *Hypophylloceras* (*Neophylloceras*) have been recovered from a concretionary horizon approximately 2 m below a 20-cm-thick green clay marking the K/Pg boundary (Yazykova in Zonova et al. 1993; Yazikova 1994; Yazykova 1991, 2004; Jagt-Yazykova 2011, 2012; *contra* Kodama et al. 2000; Kodama 2003; Hasegawa et al. 2003). The next lower concretionary horizon is 4–5 m below the K/Pg boundary and contains seven ammonite (sub)genera: *Hypophylloceras* (*Neophylloceras*), *Zelandites*, *Gaudryceras*, *Anagaudryceras*, *P.* (*Pachydiscus*), *P.* (*Neodesmoceras*), and *Diplomoceras*.

19.3.13 South America

(Site 27: Poty Quarry, Brazil; Site 28: Lomas Colorados, Bajada de Jagüel, Neuquén Basin, Argentina). In the Poty quarry in northeastern Brazil, ammonites are rare but *Pachydiscus* (*P.*) *neubergicus* and *Diplomoceras* sp. have been collected in the *Plummerita hantkeninoides* CF1 Zone at 100 and 80 cm, respectively, below the erosional unconformity containing the K/Pg boundary (Stinnesbeck and Keller 1996; Stinnesbeck et al. 2012; Tables 19.1, 19.2). In the Neuquén Basin, near Bajada de Jagüel (Argentina), a single specimen of *Eubaculites* sp. (ex gr. *E. simplex*) is present in the *Pseudoguembelina palpebra* CF2 Zone (Stinnesbeck et al. 2012).

19.3.14 Seymour Island, Antarctica

(Site 29). The section at Seymour Island has been extensively studied (Macellari 1986, 1988; Elliot et al. 1994; Zinsmeister and Feldmann 1996; Zinsmeister 1998; Zinsmeister et al. 1989; Tobin et al. 2012). The sequence consists of mid-shelf clastic to inner-shelf concretionary siltstones and silty sandstones of the López de Bertodano Formation. The K/Pg boundary is defined as the first occurrence of Paleogene dinocyst fossils, which coincide with the presence of an enhanced concentration of iridium. The *Pachydiscus* (*P.*) *ultimus* Zone is the highest ammonite zone and contains the lower part of Magnetic Chron 29r. It contains nine species, eight genera, and six families distributed among the Lytoceratina (*Zelandites*, *Anagaudryceras*, *Pseudophyllites*), Ammonitina (*Maorites*, Grossouvrites, *Kitchinites*, and *Pachydiscus*), and Ancyloceratina (*Diplomoceras*) (Fig. 19.13; Tables 19.1, 19.2). According to Zinsmeister (1998), five ammonite species are present at 50 cm below the K/Pg boundary: *Zelandites varuna*, *Pseudophyllites loryi*, *Maorites densicostatus*, *Kitchinites* (*K.*) *laurae*, and *Diplomoceras maximum* (for a discussion of the taxonomy of *Diplomoceras lambi, D. maximum*, and *D. cylindraceum*, see Machalski 2012).

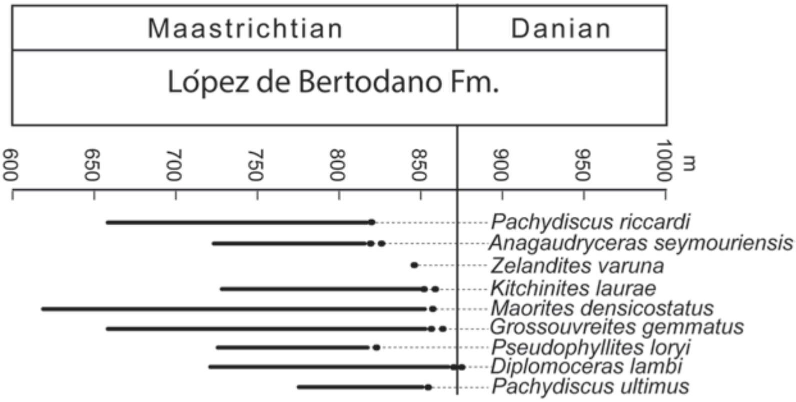


Fig. 19.13 Stratigraphic range chart of the ammonites at the K/Pg section in Antarctica (modified from Tobin et al. 2012). The solid bars indicate actual ranges (Zinsmeister et al. 1989). The dots indicate 20 % range extensions based on a statistical analysis of confidence intervals. (Wang and Marshall 2004)

Wang and Marshall (2004) used statistical methods to examine the stratigraphic ranges of the highest ammonite species on Seymour Island. Using 50 % range extensions, they estimated that the fossil record is consistent with the possibility that all of the species actually extended to the K/Pg boundary. More recently, Tobin et al. (2012) analyzed additional occurrence data using the same techniques as those of Wang and Marshall (2004) and reached a similar conclusion.

19.4 Discussion

19.4.1 Ammonite Diversity at the K/Pg Boundary

Based on the above compilation, ammonites are abundant and diverse in the last 0.5 million years of the Maastrichtian. They are distributed across all four Cretaceous suborders, the Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina, comprising six superfamilies (Phylloceratoidea, Tetragonitoidea, Desmoceratoidea, Acanthoceratoidea, Turrilitoidea, and Scaphitoidea) and 31 (sub)genera (*Hypophylloceras* (*Neophylloceras*), *Phyllopachyceras*, *Gaudryceras*, *Anagaudryceras*, *Zelandites*, *Vertebrites*, *Tetragonites, Saghalinites*, *Pseudophyllites*, *Desmophyllites*, *Hauericeras*, *Kitchinites*, *Pseudokossmaticeras*, *Brahmaites* (*Brahmaites*), Grossouvreites, *Maorites*, *P.* (*Pachydiscus*), *P.*(*Neodesmoceras*), *Menuite*s, *Sphenodiscus*, *Nostoceras*, *Glyptoxoceras*, *Diplomoceras*, *Phylloptychoceras*, *Baculites*, *Eubaculites*, *Fresvillia*, *Indoscaphites*, *Hoploscaphites*, *Acanthoscaphites*, and *Discoscaphites*) (Table 19.2). They comprise 57 species (Figs. 19.14, 19.15, 19.16, 19.17; Table 19.1). If the specimens in open nomenclature are also included in the count, the tally increases to 93 species.

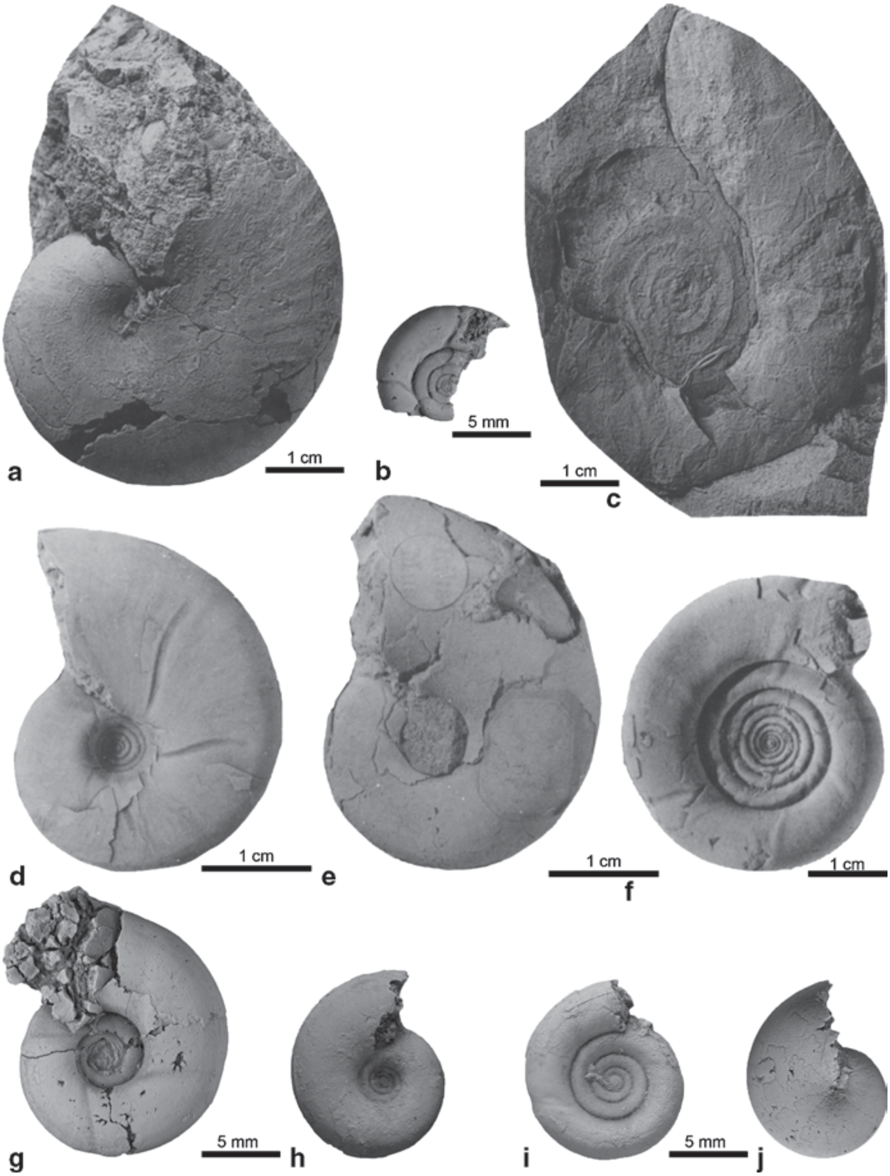


Fig. 19.14 Illustration of some of the youngest ammonites belonging to the Phylloceratina and Lytoceratina at the close of the Maastrichtian. **a** *Phyllopachyceras forbesianum,* Bay of Biscay (Ward and Kennedy 1993, Fig. 18.6). **b** *Saghalinites cala,* Tunisia (Goolaerts 2010b, pl. 1, Fig. 24). **c** *Anagaudryceras politissimum,* Bay of Biscay (Ward and Kennedy 1993, Fig. 17.12). **d** *Zelandites varuna,* Antarctica (Macellari 1986, Fig. 11.11). **e** *Pseudophyllites loryi,* Antarctica (Macellari 1986, Fig. 11.1). **f** *Anagaudryceras seymouriense,* Antarctica (Macellari 1986, Fig. 9.3). **g** *Tetragonites sp.,* Tunisia (Goolaerts 2010b, pl. 2, Fig. 4). **h** *Pseudophyllites indra,* Tunisia (Goolaerts 2010b, pl. 2, Fig. 18). **i** *Anagaudryceras* cf. *A. politissimum,* Tunisia (Goolaerts 2010b, pl. 1, Fig. 20). **j** *Phyllopachyceras forbesianum,* Tunisia. (Goolaerts 2010b, pl. 1, Fig. 9)

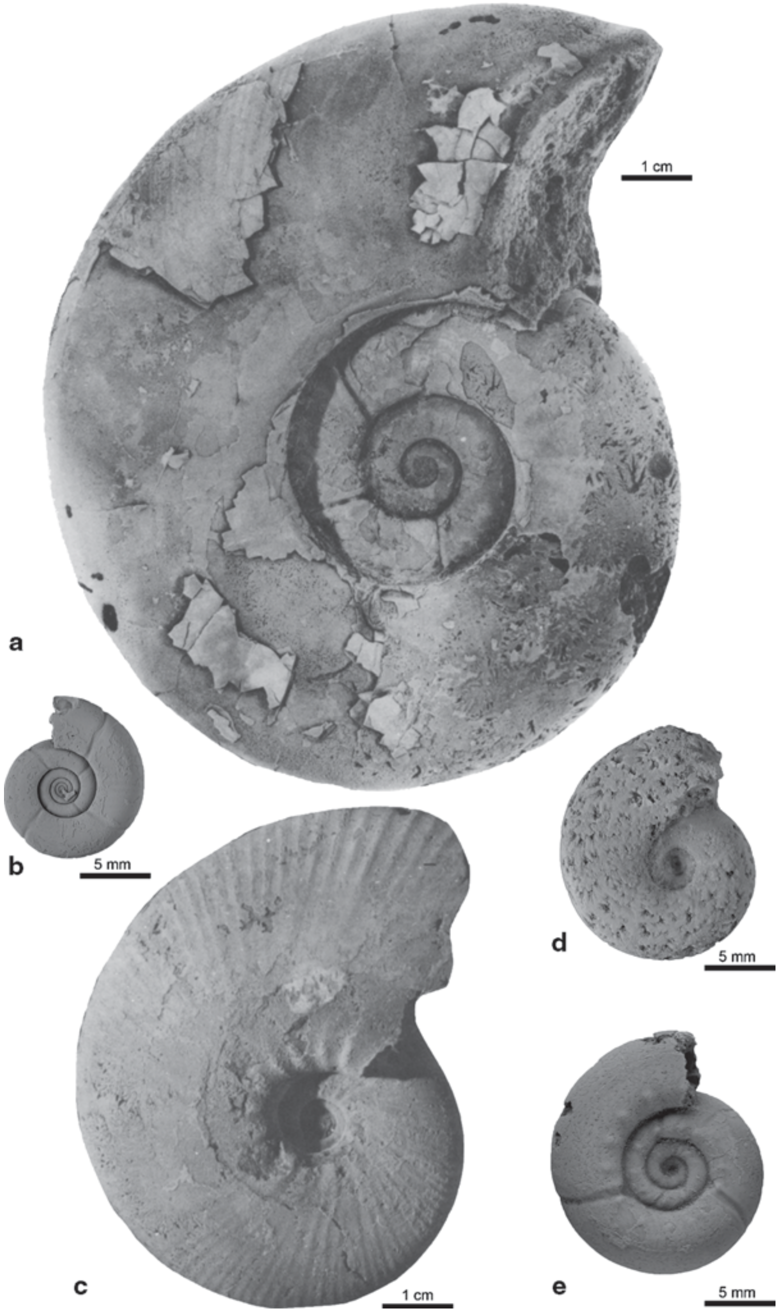


Fig. 19.15 Illustration of some of the youngest ammonites belonging to the Ammonitina at the close of the Maastrichtian. **a** *Kitchinites laurae,* Antarctica (Macellari 1986, Fig. 20.3). **b** *Hauericeras rembda,* Tunisia (Goolaerts 2010b, pl. 3, Fig. 19). **c** *Pachydiscus (P.) riccardi,* Antarctica (Macellari 1986, Fig. 37.4). **d** *Pachydiscus (Neodesmoceras) snamensis,* Tunisia (Goolaerts 2010b, pl. 7, Fig. 16). **e** *Brahmaites brahma,* Tunisia. (Goolaerts 2010b, pl. 4, Fig. 14)

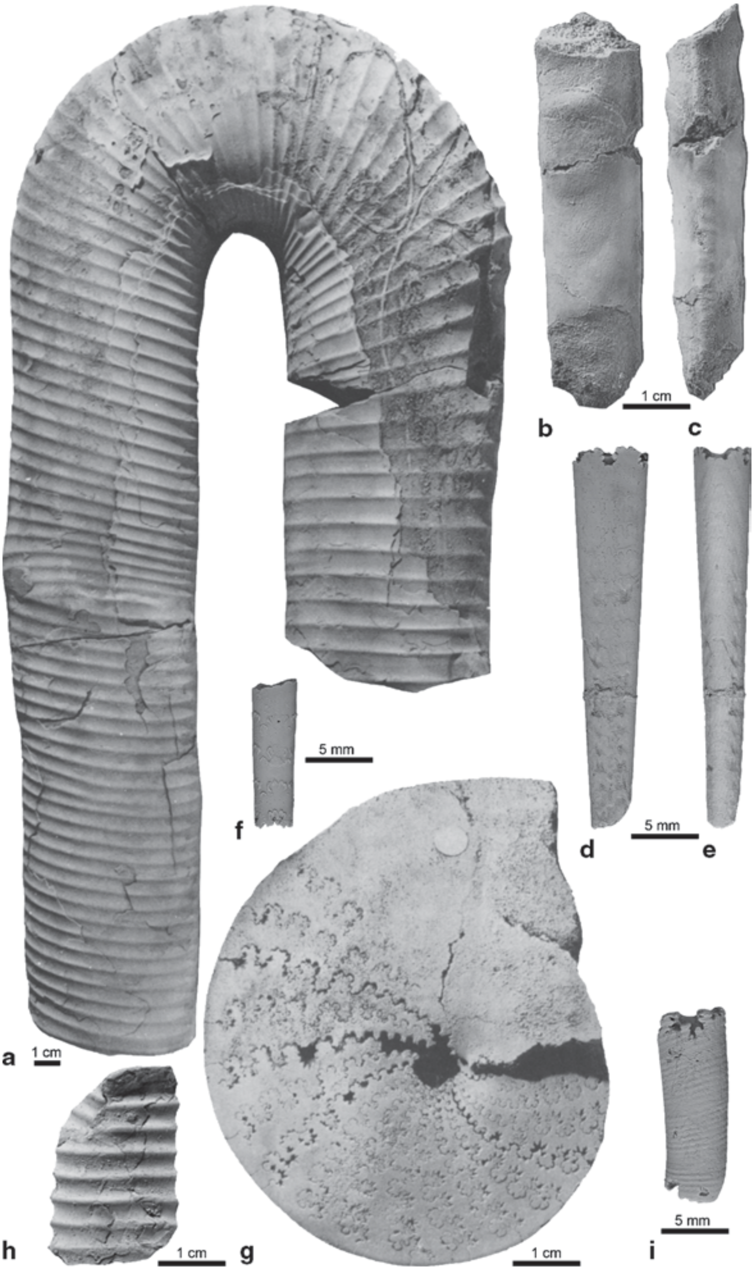


Fig. 19.16 Illustration of some of the youngest ammonites belonging to the Ammonitina and Ancyloceratina at the close of the Maastrichtian. **a** *Diplomoceras lambi,* Antarctica (Macellari 1986, Fig. 14.1). **b**, **c** *Eubaculites carinatus,* lateral and dorsal views, New Jersey (Landman et al. 2007, Figs. 32O, Q). **d**, **e** *Baculites* sp. A, lateral and dorsal views, Tunisia (Goolaerts 2010b, pl. 9, Figs. 2, 3). **f** *Fresvillia paradoxa,* Tunisia (Goolaerts 2010b, pl. 8, Fig. 22). **g** *Sphenodiscus binckhorsti,* the Netherlands (Kennedy 1986, Fig. 9C). **h** *Glyptoxoceras* cf. *G. rugatum,* Texas (Kennedy et al. 2001, Fig. 4d). **i** *Diplomoceras cylindraceum,* Tunisia (Goolaerts 2010b, pl. 8, Fig. 11)

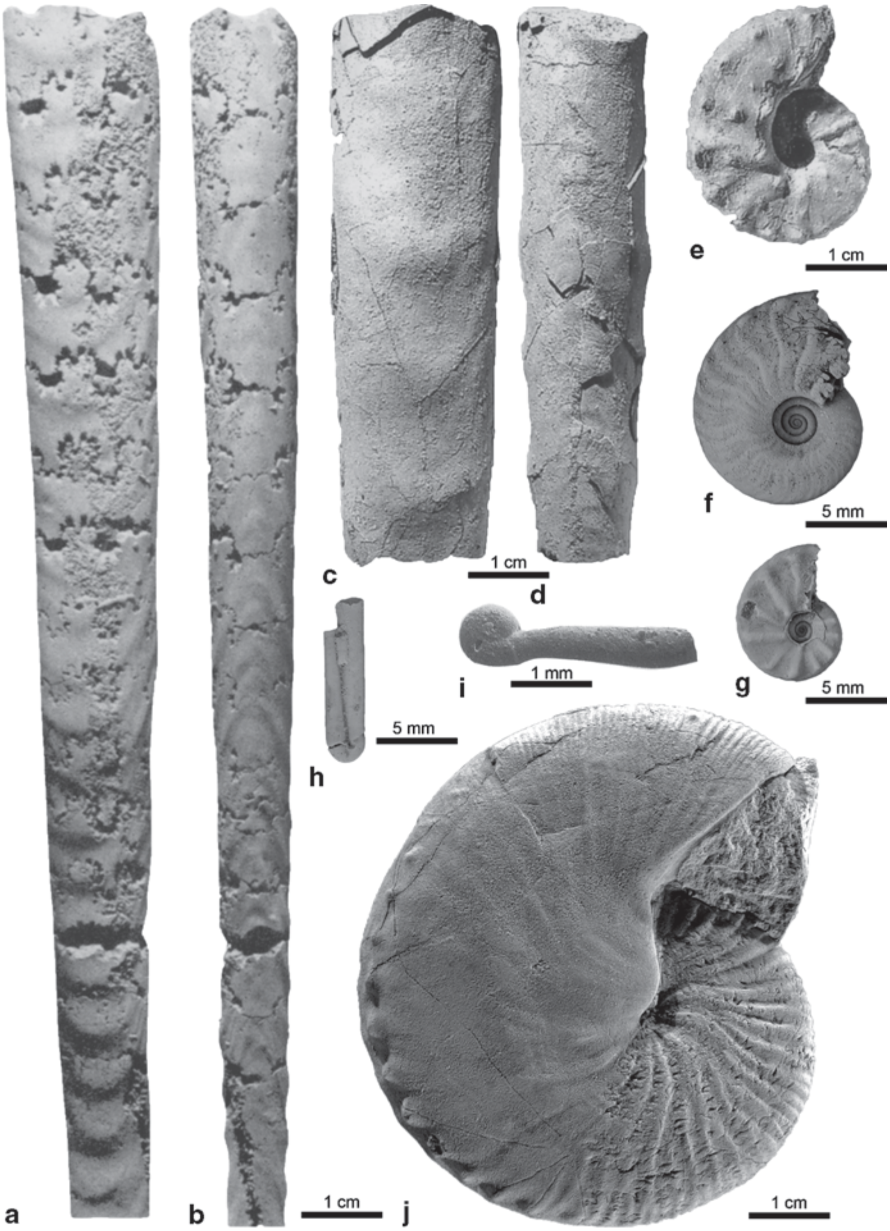


Fig. 19.17 Illustration of some of the youngest ammonites belonging to the Ancyloceratina at the close of the Maastrichtian. **a**, **b** *Baculites anceps,* lateral and dorsal views, the Netherlands (Kennedy 1986, Figs. 10N, O). **c**, **d** *Baculites* cf. *B. undatus,* lateral and dorsal views, Mississippi (Kennedy and Cobban 2000, pl. 2, Figs. 29, 30). **e** *Discoscaphites iris,* microconch, Mississippi (Kennedy and Cobban 2000, pl. 3, Fig. 14). **f** *Indoscaphites pavana*, Tunisia (Goolaerts 2010b, pl. 15, Fig. 10). **g** *Indoscaphites cunliffei,* Tunisia (Goolaerts 2010b, pl. 14, Fig. 19). **h** *Phylloptychoceras* cf. *P. sipho,* Tunisia (Goolaerts 2010b, pl. 8, Fig. 15). **i** *Baculites vertebralis,* early ontogenetic stage, Denmark (Birkelund 1993, Fig. 6A). **j** *Hoploscaphites constrictus crassus,* Poland (Machalski 2005a, Fig. 8D)

The stratigraphic distribution of these species demonstrates that ammonites are present in the uppermost part of the Maastrichtian just below or at the K/Pg boundary. For example, in northeastern Mississippi, eight species extend to approximately 1 m below an unconformity, which presumably encompasses the K/Pg boundary. The absence of ammonites above this level may be due to dissolution (Larina et al. 2012). In Denmark, eight species occur in the upper part of the Maastrichtian Højerup Member (Birkelund 1979, 1993; Surlyk and Nielsen 1999), and two of *them* extend into the overlying Danian Cerithium Limestone Member (Machalski and Heinberg 2005). In Turkmenistan, two species have been recovered from as high up as 5 cm below the boundary clay and a single specimen is present in the Danian part of the section (Machalski et al. 2012). In Bulgaria, Ivanov and Stoykova (1994) and Ivanov (1995) recorded five specimens comprising at least two species at 40 cm below the boundary clay, which is marked by an anomalous concentration of iridium. In northeastern Brazil, two species have been collected in the uppermost 1 m of the section below an erosional unconformity encompassing the K/Pg boundary (Stinnesbeck et al. 2012). In Antarctica, five species are present in the López de Bertodano Formation at 50 cm below the K/Pg boundary, as indicated by an enriched concentration of iridium (Zinsmeister 1998). In addition, based on a statistical analysis of the range data of these five species, they may even have persisted into the early Danian (Wang and Marshall 2004). In Sakhalin, Jagt-Yazykova (Yazikova 1994; Jagt-Yazykova 2011, 2012) reported three species from a concretionary horizon approximately 1.5 m below a 20-cm-thick green clay marking the K/Pg boundary.

How does stratigraphic distance below the K/Pg boundary translate into years before the asteroid impact? In stratigraphically complete K/Pg sections, the time can be estimated by taking into account the thickness between the impact layer (time zero) and the base of the highest biostratigraphic zone (estimated, for example, at 300 kyr before impact), assuming a constant rate of sedimentation. A better approach is to use cyclostratigraphy, which permits the construction of a high-resolution time scale that takes into account variation in the rate of sedimentation and the degree of completeness of the section. For example, in the Tunisian Trough Basin, the highest ammonites occur 1 m below the boundary (Goolaerts 2010a). Based on a cyclostratigraphic study of the alternation of limestones and marls at this site (Hennebert and Dupuis 2003), these ammonites were probably deposited at approximately 50 kyr prior to the K/Pg boundary. In the Bay of Biscay, ten species are present in the top 1.5 m of the section, and one species is present in the top 10–15 cm of the section (Ward and Kennedy 1993). Rocchia et al. (2002) also noted the occurrence of a poorly preserved specimen filled with iridium debris at 5 cm below the boundary clay. Based on the temporal interpretation of the alternation of limestone and marl beds in this area, the two highest specimens were buried at less than 500–800 years prior to the boundary (Rocchia et al. 2002). Near Maastricht, in the Netherlands and northeast Belgium, 19 species are present near or at the K/Pg boundary in the upper part of the Nekum Member and overlying Meerssen Member. According to interpretations of the short-term cyclicity (centimeter-meter scale) of the beds in this area, the highest Maastrichtian ammonites were deposited at less than 20 kyr before the K/Pg boundary (Zijlstra 1994; Schiøler et al. 1997).

The stratigraphic distribution of ammonites at or near the K/Pg boundary has been examined using statistical methods (confidence intervals) to estimate the degree to which their observed ranges underestimate their actual ranges. In Antarctica, the highest ammonite zone contains nine species, five of which extend to 50 cm below the K/Pg boundary. Using 50 % range extensions, Wang and Marshall (2004) estimated that five of these species actually persisted to the K/Pg boundary. Using a more conservative approach (20 % range extensions), they estimated that only one of these species persisted to the boundary. In the Bay of Biscay, ten species are present in the top 1.5 m of the section. Using a statistical method employing 50 % confidence intervals, Marshall and Ward (1996) argued that at least two of these species persisted to the boundary. Indeed, in both areas, recent, intense collecting has yielded additional specimens in the uppermost Maastrichtian, consistent with the previously noted statistical predictions (Rocchia et al. 2002; Olivero 2012; Tobin et al. 2012).

The paucity of specimens in the uppermost Maastrichtian in some sections, and their absence altogether in the uppermost Maastrichtian of other sections, is probably due to taphonomic bias, collection failure, or local environmental changes rather than to their actual disappearance. For example, in the Tunisian Trough Basin, the species that occur in the highest levels are the most common species, suggesting that the likelihood of fossilization correlates with species abundance. The best explanation for the observed decrease in species richness in the uppermost Maastrichtian in this area is either collection failure or local environmental change rather than extinction (Goolaerts 2010a). In addition, as noted for the Bay of Biscay, Antarctica, and the classic area of Maastricht, ongoing research has yielded additional specimens in the uppermost part of the section, emphasizing the importance of renewed collecting efforts even in well-studied areas (Machalski et al. 2009; Jagt 2012). Thus, it is likely that the commonly cited decline in ammonite diversity at the end of the Maastrichtian (Stinnesbeck et al. 2012) is related more to local environmental changes or collection failure rather than to global extinction.

It is possible that ammonites not only persisted to the K/Pg boundary, but survived for days to tens of thousands of years later, according to various estimates. Most of this evidence comes from shallow-water settings. In New Jersey, nine ammonite species are present in a 20-cm-thick unit (the *Pinna* Layer) above a horizon with a weak iridium anomaly (Landman et al. 2012b; Figs. 19.2, 19.3). The mode of occurrence of the fossils in this layer indicates an autochthonous accumulation with little or no time-averaging. Fewer ammonites are present above this layer in the so-called Burrowed Unit and consist of broken specimens of *Eubaculites carinatus* associated with isolated jaws (aptychi) of this species. Because such jaws are absent in the underlying *Pinna* Layer, it suggests that these fossils were not reworked from below but were fossilized during the deposition of the Burrowed Unit. If the horizon with iridium marks the K/Pg boundary, it implies that ammonites persisted and perhaps even initially thrived in the early Danian (as shown by the ammonites in the *Pinna* Layer), followed by a brief appearance of a more impoverished fauna (as shown by the ammonites in the Burrowed Unit). Even if the iridium anomaly was displaced downward from the top of the Pinna Layer, as previously noted, it still implies that the ammonites in the Burrowed Unit would have survived. In the

Maastrichtian type region, Jagt et al. (2003) reported several dozen specimens of *Baculites* and *Hoploscaphites* in Unit IVf-7 of the Meerssen Member above the Berg en Terblijt Horizon, which is generally interpreted as marking the K/Pg boundary, rather than the overlying Vroenhoven Horizon. The fact that many of the baculitids are preserved with their apertures intact suggests that they may have survived into the early Danian (Planktic Foraminiferal Zone P0) (Fig. 19.8). In Denmark, Machalski and Heinberg (2005) reported *B. vertebralis* and *H. constrictus johnjagti* in the lower Danian Cerithium Limestone Member (Fig. 19.6). These specimens have generally been interpreted as reworked material. However, the mode of occurrence of these specimens suggests that they were fossilized at the same time as the deposition of the Cerithium Limestone Member. In addition, the most common fossils in the underlying Maastrichtian chalk are virtually absent in the Cerithium Limestone, which is inconsistent with a hypothesis of reworking. Thus, both these lines of evidence suggest that the ammonites in the Cerithium Limestone Member represent early Danian survivors (Machalski and Heinberg 2005).

19.4.2 Depth Distribution of Ammonites at the K/Pg Boundary

At the end of the Maastrichtian, shallower water settings (<100 m) are represented by deposits in northern and central Europe and North America. In northern and central Europe, the most abundant ammonites are *Baculites* followed by *Hoploscaphites* (Figs. 19.16, 19.17) In addition, the fauna contains a few species of desmoceratoids, including *Menuites terminus*, and a few species of diplomoceratids including *Glyptoxoceras rugatum* and *Diplomoceras cylindraceum*. In North America, the most abundant ammonites are also baculitids, represented by *Eubaculites* and *Baculites,* followed by scaphitids, represented by *Discoscaphites*. Sphenodiscids are relatively common but desmoceratoids and diplomoceratids (e.g., *Glyptoxoceras*) are rare, and phylloceratids and lytoceratids are absent.

Deeper-water settings (>100 m) at the end of the Maastrichtian are represented by deposits in the Bay of Biscay, the Tunisian Trough, Antarctica, and Sakhalin. In the Bay of Biscay, the fauna is characterized by several species of phylloceratids and lytoceratids, many of which are endemic to the area (Fig. 19.14). In addition, the fauna contains a high diversity of desmoceratoids. In contrast, only one species of *Diplomoceras* is present and *Eubaculites* and *Hoploscaphites* are absent in the upper part of the section. Several of the same species of phylloceratids and lytoceratids (*Hypophylloceras* (*Neophylloceras*) *ramosum* and *Anagaudryceras politissimum*) are present in Bulgaria. The fauna in the Bay of Biscay also has several species in common with the fauna in Tunisia, including phylloceratids and lytoceratids (e.g., *Phyllopachyceras forbesianum* and *Pseudophyllites indra*) and desmoceratoids (e.g., *B.* (*Brahmaites*) *brahma*). The most distinctive elements of the Tunisian fauna, however, are species of *Indoscaphites*, suggesting a strong connection with southern India. In Antarctica, phylloceratids are absent but lytoceratids are present, including *A. seymouriense* and *Pseudophyllites loryi*, both of which are endemic to the area. The fauna is also characterized by five endemic species of desmoceratoids including *Maorites densecostatus*, *Kitchinites laurae*, and *Pachydiscus* (*P.*) *riccardii*. Surprisingly, few species are shared with South America, especially with the slightly older Quiriquina Formation in central Chile (Salazar et al. 2010), which contains two species of phylloceratids but no lytoceratids. In Sakhalin, the fauna is dominated by phylloceratids and lytoceratids, with a few genera and species in common with Tunisia, Bulgaria, and the Bay of Biscay. It is also characterized by two species of pachydiscids that are endemic to the area.

19.4.3 Ecology of Ammonites at the K/Pg Boundary

The phylloceratids and lytoceratids, although never abundant in terms of individuals, are well represented in deeper-water settings (>100 m deep) at the end of the Maastrichtian (Fig. 19.14). A total of seven genera are each present in Tunisia and the Bay of Biscay, and three each in Bulgaria and Antarctica. They are characterized by relatively compressed shells without much ornament, and comprise the traditional Leiostraca, and are restricted to the distal shelf and upper continental slope based on paleoenvironmental data. This habitat is consistent with depth estimates based on studies of the strength of the siphuncular tube and septa (Hewitt 1996). The buccal apparatus of these forms is different from other ammonites at the end of the Cretaceous in featuring a calcareous deposit at the apical end of the lower jaw, possibly permitting them to feed on hard material, like crustacean carapaces (Tanabe and Landman 2002; Tanabe et al. 2013). Depending on the genus, Westermann (1996) interpreted the mode of life of these forms as demersal swimmers, planktic vertical migrants, or nektic swimmers. However, an analysis of the isotopic composition of the outer shell of several species of Late Cretaceous *Hypophylloceras*, *Phyllopachyceras*, and *Gaudryceras* from Japan suggests that these forms lived close to the sea floor (Moriya et al. 2003).

The desmoceratoids at the end of the Maastrichtian also favored deeper-water settings, with five genera each in Tunisia and the Bay of Biscay, and four in Antarctica (Fig. 19.15). With their relatively thick septa, narrow but thick-walled siphuncular tubes, and long septal necks, desmoceratoids are well adapted to deeper-water settings. They possess moderately compressed, involute shells with a rounded venter and relatively smooth surface. The hydrodynamic properties of desmoceratoids are, thus, similar to those of other Mesozoic ammonites with low shell-thickness ratios (Seki et al. 2000). These forms are considered to have been demersal swimmers, which lived on the distal shelf and upper continental slope (Westermann 1996). This interpretation is consistent with isotopic analyses of the outer shell, which suggest a mode of life near the bottom (Moriya et al. 2003). It is notable that desmoceratoids appear to have modified their aptychus-type jaw, reducing the aptychus to only a thin covering (Tanabe and Landman 2002; Tanabe et al. 2013). This may have permitted them to broaden their diet to include carrion from the sea floor.

Scaphitids at the close of the Cretaceous occur in shallow-water settings such as the Gulf and Atlantic Coastal Plains of North America and northern and central Europe, although they occasionally occur in deeper-water settings such as

Turkmenistan (Fig. 19.17). In terms of numbers of individuals, they are probably the most abundant ammonites after baculitids. The mode of life and habitat of Late Cretaceous scaphitids has been investigated by Landman et al. (2012a) based on analyses of the functional morphology of the shell and buccal apparatus, light stable isotopes, facies distributions, faunal associations, and the mechanical strength of the septa, shell, and siphuncle. Based on this evidence, scaphitids were probably sluggish swimmers that preferred well-oxygenated water just above the bottom. They may have exploited a low-energy lifestyle, remaining at a single site for an extended period of time. As members of the Aptychophora Engeser and Keupp 2002, scaphitids possessed an aptychus-type lower jaw and may have preyed upon small organisms in the water column, such as decapod crustaceans, copepods, and newly hatched ammonites.

Sphenodiscids were also relatively common in the same facies as scaphitids in North America and northern and central Europe at the end of the Maastrichtian (Fig. 19.16). Based on their streamlined, oxyconic shells and distribution in nearshore facies, sphenodiscids have been interpreted as inhabitants of shallow-water environments ranging from around wave base to slightly below (Ifrim and Stinnesbeck 2010). They may have been capable of brief spurts of relatively rapid swimming permitting ambush predation (Westermann 1996). However, they are equipped with aptychus-type lower jaws without sharp cutting edges, precluding the likelihood of a diet of hard-shelled prey.

The diplomoceratids (*Glyptoxoceras*, *Diplomoceras*, and *Phylloptychoceras*) and baculitids are nearly cosmopolitan at the end of the Cretaceous, suggesting that they were facies-independent. The diplomoceratids occur at eight regions ranging from deeper-water (Bay of Biscay) to shallower-water settings (the Netherlands and northeast Belgium) (Fig. 19.16). The baculitids (*Baculites*, *Eubaculites*, and *Fresvillia*) are even more widespread than the diplomoceratids and occur in ten regions (Figs. 19.16, 19.17). Indeed, baculitids are probably the most abundant ammonites at the end of the Cretaceous in terms of number of individuals. The wide distribution of these forms with respect to environmental settings suggests that they may have lived high in the water column, well above the bottom. This is consistent with the fact that they are occasionally preserved even in areas with dysoxic bottom water that excluded benthic fauna. Baculitids have generally been interpreted as sluggish swimmers (Klinger 1981) hovering in the water column at an inclined angle to the vertical (Fig. 19.3), but this requires a counterbalance at the adapical end. Based on studies of the morphology of the radula and the presence of prey remains in the buccal apparatus, it is possible that baculitids preyed on small micro-organisms in the water column, such as tiny crustaceans (Kruta et al. 2011). This interpretation may also have applied to the diplomoceratids with their upturned aperture at maturity, which is also consistent with a microphagous mode of life.

19.4.4 Causes of Ammonite Extinction

Following the Alvarez hypothesis, it is now generally accepted that the disappearance of ammonites in the latest Maastrichtian/earliest Danian was due to the asteroid impact. However, the exact killing mechanism is still unknown. The most plausible explanation is perhaps a transient episode of surface water acidification on the heels of the asteroid impact (Alegret et al. 2012; Arkhipkin and Laptikhovsky 2012; Hönisch et al. 2012). According to these arguments, the gypsum-rich deposits at the impact site would have vaporized, producing sulfuric acid. In addition, the heating of the atmosphere would have generated nitric acid due to the oxidation of N_2, resulting in acid rain. The alternative hypothesis of a global collapse in primary productivity (called the Strangelove Ocean) or export productivity (called the Living Ocean) lacks support because the benthic foraminifera in the deep sea did not suffer a severe extinction at the time, unlike the planktic foraminifera (Alegret et al. 2012). Darkness due to the fine dust in the atmosphere following the collision may also have been a contributing factor, blocking solar radiation and leading to a short-lived cold spell (Vellekoop et al. 2014).

Surface ocean acidification would have had disastrous consequences for planktic calcifiers, including calcareous nannofossils, planktic foraminifera, and ammonites. All the ammonites at the end of the Cretaceous, irrespective of their mode of life at maturity, probably followed a planktic mode of life immediately after hatching (Landman et al. 1996; Westermann 1996; Arkhipkin and Laptikhovsky 2012). This hypothesis is based on two functional arguments: the small size of the embryonic shell (ammonitella), which ranges from 0.5 to 1.5 mm in diameter, and its near-spherical shape, both of which are presumably adaptations to life in the plankton (Fig. 19.18). The newly hatched ammonites may have been passive vertical migrators, drifting with surface currents. This interpretation is consistent with a number of observations on the mode of occurrence of ammonites preserved at this stage of development. For example, the Late Cretaceous Sharon Springs Member of the Pierre Shale in Wyoming contains small specimens of newly hatched ammonites. These sediments are interpreted to have been deposited on an anaerobic bottom with oxygenated water above, implying that the newly hatched ammonites were planktic or at least nektic (Landman 1988). This mode of life may have been very ‘effective’ during background times, but it may have proved to be an Achilles Heel for ammonites during stressful times (Arkhipkin and Laptikhovsky 2012).

Variation in the degree of surface ocean acidification can help explain the fact that all of the evidence for the short-term survival of ammonites in the early Danian is from relatively shallow-water settings (the Atlantic Coastal Plain, the Netherlands and northeast Belgium, and Denmark). The ammonites in these areas may have survived for days to tens of thousands of years after the impact. It is possible that these coastal areas may have been buffered from transient surface water acidification due to the burning of plants on the land, and the resultant increase in riverine run-off. As a consequence, some planktic organisms that secreted calcium carbonate, including ammonites, may have persisted for a brief interval of time in these regions. Ironically, this kill mechanism apparently favored scaphitids and baculitids, which are characterized by short-term species longevities, rather than phylloceratids and lytoceratids, which are characterized by long-term species longevities (for a discussion of the evolutionary mode and tempo of Cretaceous ammonites, see Ward and Signor 1983). Thus, this kill mechanism was independent of the evolutionary success of particular ammonites, as least as measured by their species longevity.

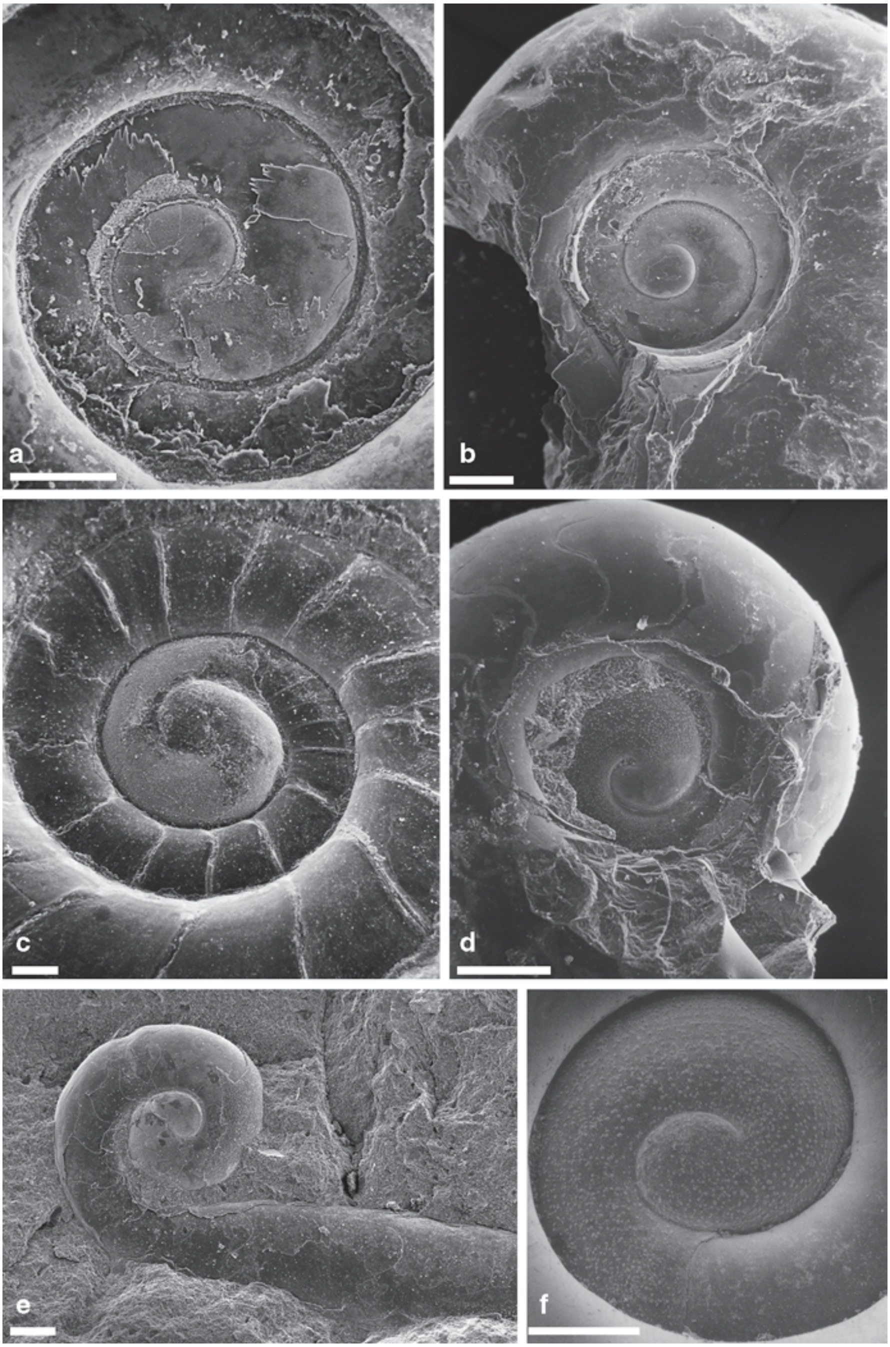


Fig. 19.18 Illustration of the embryonic shells of six species of Late Cretaceous ammonites (**a**–**e**, with kind permission of K. Tanabe, University of Tokyo). The embryonic shell consists of the protoconch and approximately one whorl ending in the primary constriction, and is ornamented

The geographic distribution of ammonite genera may also have played a role in their pattern of extinction. Landman et al. (2014) compiled a database of all ammonite genera in the last 0.5 myr of the Maastrichtian. They also incorporated data on ammonite genera that appear to have briefly survived into the Paleocene (Jagt et al. 2003; Jagt 2012; Machalski and Heinberg 2005; Machalski et al. 2009; Landman et al. 2012b). Using two metrics to evaluate the geographic range of each genus (first, a convex hull encompassing all of the occurrences of each genus and, second, the maximum distance between occurrences for each genus), they documented that most ammonite genera at the end of the Maastrichtian were restricted in their geographic distribution, possibly making them vulnerable to extinction. However, the geographic distribution of those genera that may have briefly survived into the Paleocene is significantly greater than that of 'non-surviving' genera, implying that more broadly distributed genera were more resistant to extinction. Similar geographic patterns of survivorship have been observed in other molluscs at the K/Pg boundary. For example, Jablonski (2008) noted that it terms of marine bivalve genera, survivors were significantly more broadly distributed than victims. However, even the most widely distributed ammonites eventually succumbed to extinction. Evidently, a broad geographic distribution may have initially protected some ammonites against extinction, but it did not guarantee their survival.

19.5 Conclusions

Ammonites are abundant and diverse in the last 0.5 million years of the Maastrichtian. They are distributed across all four Cretaceous suborders, the Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina, comprising six superfamilies, 31 (sub)genera, and 57 species. The distribution of ammonites is dependent on the environmental setting. In shallow-water environments (< 100 m deep), almost all of the ammonites are ancyloceratines, including scaphitids, baculitids, and diplomoceratids. In fact, baculitids and diplomoceratids are the most widespread ammonites at the end of the Cretaceous. In deeper-water settings (> 100 m deep), almost all taxa comprise phylloceratids, lytoceratids, and ammonitids (especially desmoceratoids). The commonly cited decline in ammonite diversity at the end of the Maastrichtian is related more to local environmental changes or collection failure rather than to global extinction. Indeed, ongoing research has yielded additional specimens even in well-studied areas. In addition, recent data from shallow water settings (Atlantic Coastal Plain, the Netherlands and northeast Belgium, and Denmark) suggest

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with a microtuberculate ornamentation. **a** *Hypophylloceras subramosum* (Phylloceratina), middle Campanian, Hokkaido, Japan (refigured from Tanabe 1989, Fig. 2D). **b** *Phyllopachyceras ezoense* (Phylloceratina), middle Campanian, Hokkaido, Japan (refigured from Tanabe 1989, Fig. 2C). **c** *Gaudryceras denseplicatum* (Lytoceratina), Coniacian, Hokkaido, Japan (refigured from Tanabe 1989, Fig. 2A, B). **d** *Menuites* sp. (Ammonitina), middle Campanian, Hokkaido, Japan (refigured as *Anapachydiscus* sp. in Tanabe 1989, Fig. 1A, B). **e** *Baculites compressus* (Ancyloceratina), late Campanian, South Dakota, USA. **f** *Hoploscaphites* sp. (Ancyloceratina), upper Maastrichtian, South Dakota (Refigured from Landman and Waage 1993, Fig. 13D). Scale bar = 200 um that not only did ammonites persist to the boundary, but some species may even have survived for as much as tens of thousands of years afterward. The most likely explanation for ammonite extinction is a brief episode of surface water acidification immediately following the Chixculub impact, which caused the decimation of the calcareous plankton including, possibly, the planktic post-hatching stages of ammonites. However, the geographic distribution of ammonites may also have played a role in the events at the end of the Cretaceous, with more broadly distributed genera more resistant to extinction.

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Appendix of Localities

1: Manasquan River Basin, Monmouth County, New Jersey, U.S.A., 40°12′30″N, 74°17′30″W
2: Northeastern Monmouth County, New Jersey, U.S.A., 40°17′30″N, 74°7′14″W
3: Round Bay, Anne Arundel County, Maryland, U.S.A., 39°2′13″N, 76°33′28″W
4: Stoddard and Scott counties, Missouri, U.S.A., 37°00′17″N, 89°51′02″W
5: Tippah County, Mississippi, U.S.A., 34°44′55″N, 88°54′47″W
6: Chickasaw County, Mississippi, U.S.A., 33°58′04″N, 89°00′05″W
7: Brazos River, Falls County, Texas, U.S.A.,31°8′11″N, 96°49′40″W
8: La Popa Basin, Northeastern Mexico, 26°12′44″N, 101°4′25″W
9: Stevns Klint, Denmark, 55°16′45″N, 12°26′47″E
10: Kjølby Gård, Denmark, 57°3′15″N, 8°44′55″E
11: “Dania” Quarry, northern Denmark, 56°39′42″N, 10°1′56″E
12: Maastrichtian Type Area, The Netherlands and Belgium, 50°49′18.41″N, 5°41′39.54″E
13: Nasiłów, Poland, 51°20′39″N, 21°57′35″E
14: Mełgiew, Poland, 51°13′30″N, 22°47′8″E
15: Lechówka, Poland, 51°10′17″N, 23°14′43″E
16: Kyzylsay, Kazakhstan, 44°20′1″N, 52°26′10″E
17: Sumbar River, Turkmenistan, 38°27′18″N, 56°12′41″E
18: Zumaya, Bay of Biscay Area, 43°17′54″N, 2°16′16″W
19: Hendaye, Bay of Biscay Area, 43°23′1″N, 1°49′26″W
20: Bidart, Bay of Biscay Area, 43°26′25″N, 1°35′41″W
21: Bjala (=Byala), Bulgaria, 42°52′44″N, 27°53′57″E
22: Kalaat Senan, Tunisia, 35°47′15″N, 8°27′21″E
23: El Kef, Tunisia, 36°9′15″N, 8°38′55″E
24: Garn Halfaya, Tunisia, 36°0′40″N, 8°33′23″E

25: Dababiya Quarry Corehole, Egypt, 25°30′10″N, 32°31′27″E
26: Naiba River Valley, Sakhalin, Far East Russia, 47°28′34″N, 142°24′10″E
27: Poty Quarry, Brazil, 7°53′95″S, 34°51′14″W
28: Lomas Colorados, Bajada de Jagüel, Neuquen Basin, Argentina, 37°59′24″S, 68°47′38″W
29: Seymour Island, Antarctica, 64°16′50″S, 56°43′23″W

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Chapter 20
Ammonoid Taphonomy

Ryoji Wani and Neal S. Gupta

20.1 Introduction

Ammonoids have been thought to maintain almost neutral buoyancy and therefore had nektic, nektoplanktic, or nektobenthic habits in the water column (e.g., Jacobs and Chamberlain 1996; Westermann 1996), so that they never could be preserved *in situ* (= autochthonous; for the definition, see Kidwell et al. 1986) (Maeda and Seilacher 1996). Therefore, we cannot neglect the taphonomic history, by which the information obtained from a fossil had or had not been biased during the taphonomic history, when we try to reconstruct the paleoecology and habitats of ammonoids from fossil evidence. There exists no ammonoid that does not carry a taphonomic overprint that must be intellectually removed before paleobiological analysis can begin (Maeda and Seilacher 1996). Therefore, the reconstruction of taphonomic history is the first step to precisely elucidate the paleobiology and paleoecology of ammonoids.

In the first edition of "*Ammonoid Paleobiology*", Maeda and Seilacher (1996) have comprehensively reviewed ammonoid taphonomy. Numerous studies of ammonoid taphonomy, which applied various methodologies (including experimental techniques with modern analogues), however, have been published after 1996. Therefore, this study mainly reviews the recent studies related to ammonoid taphonomy and summarizes our current knowledge about this topic. Finally, future researches of ammonoid taphonomy are briefly viewed and discussed.

R. Wani (✉)
Faculty of Environment and Information Sciences, Yokohama National University,
Yokohama 240-8501, Japan
e-mail: wani@ynu.ac.jp

N. S. Gupta
Lab for Terrestrial Environments, Bryant University, Smithfield, RI, USA

Geophysical Laboratory, Carnegie Institution of Washington, Washington, DC, USA
e-mail: sgupta3@bryant.edu; ngupta@ciw.edu

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20.2 Taphonomic Processes Affecting Ammonoids

Ammonoid taphonomy can be generally classified into two stages: biostratinomy and diagenesis (e.g., Boston and Mapes 1991; Maeda and Seilacher 1996). Biostratinomy is the study of the processes that take place after an organism's death but before its final burial, and diagenesis is any chemical, physical, or biological change undergone by sediments after their initial deposition and during and after their lithification. In the taphonomic study of ammonoids, recognition and reconstruction of their biostratinomic process is more important than those in benthic animals (e.g., bivalves, gastropods, arthropods), because ammonoids have been thought to have nektic, nektoplanktic, or nektobenthic habits (e.g., Jacobs and Chamberlain 1996; Westernmann 1996). Therefore, we should address and examine whether or not the place that ammonoid specimens occur is identical with the place where ammonoids once lived before starting the examination and reconstruction of ammonoid paleobiology and paleoecology. In modern nautili, their empty shells sometimes float on the sea surface, get transported by water currents for a long distance, and then appear in areas far outside of their habitat area (House 1987). Ammonoid empty shells, consisting of multi-chambered phragmocone and subsequent body chamber as those in modern nautili (e.g., Jacobs and Chamberlain 1996), might have floated on the sea surface and drifted by water currents for a long distance, just as modern nautilus shells. After dead shells sank on sea bottom, the bottom transport by water current possibly made the shells break and become filled by sediments, sometime with a preferred orientation to the water current. The sediment filling, in case, processed without shell breakage, but through the siphunclular openings on septa. The material filling ammonoid septate phragmocone (e.g., sediments, precipitation of carbonates) probably played important roles the following diagenetic processes (e.g., shell dissolution, compaction, subsequent reworking).

The diagenetic processes of ammonoids are thought to be basically similar to those of other organism (e.g., bivalves, gastropods). Selective cementation of sediments filling the phragmocones, bacterial pyrite coating inside phragmocones, and/or precipitation of carbonates within phragmocones would enhance the possibility of three-dimensional preservation of ammonoid shells. Without such reinforcement, shells would easily become flattened by sediment compaction. Additionally, some unique diagenetic processes (e.g., selective destruction and/or dissolution of shells) are supposedly unique to ammonoids due to their shell structure of ammonoids (i.e., septate phragmocone with a penetrating siphuncle). Moreover, ammonoids consist of several materials with different chemical and physical properties: shells of calcium carbonate (outer shell walls and septa), chitinous and calcareous (calcite and aragonite) jaw elements, organic components of soft parts. These different physicochemical properties are intimately linked with special diagenetic processes and therefore special preservation modes within ammonoids.

20.3 Aspects on Necrosis and Fossil Diagenesis of Organic Components

The jaws of modern cephalopods are composed mainly of a chitin-protein complex (Saunders et al. 1978; Hunt and Nixon 1981; Lowenstam et al. 1984; Kear et al. 1995). They consist of upper and lower jaws. The jaws and the radula constitute the feeding apparatuses within the buccal mass. Fossil jaws are not uncommon and are known from strata as old as Devonian (Korn and Klug 2002). They provide information on the phylogeny and functional morphology of extinct cephalopods. However, they can also shed light on the fate of organic components over geologic time.

Arthropod cuticles, like the jaws and radulae of cephalopods, consist of a chitin-protein complex and are abundant as cuticular remains in the fossil record. Decay experiments on crustacean cuticle demonstrated that the chitin component is more resistant than the protein (Baas et al. 1995; Stankiewicz et al. 1998a). Nonetheless, cuticles of arthropods that are older than Tertiary show no trace of the original chitin or protein (Briggs et al. 2000). Maturation experiments and chemical analysis have shown that such cuticles are transformed over time to a geopolymer with significant aliphatic content, likely as a result of the incorporation of lipids. Some cuticles show a degree of aromatization, which is possibly a reflection of their higher thermal maturity (Gupta et al. 2007c). Previous analysis of animal fossils, including eurypterids (Gupta et al. 2007c), graptolites (Gupta et al. 2006b) and beetles (Gupta et al. 2007a) have indicated the presence of ester linkages in the macromolecule, indicating that such functional groups are important in crosslinking the geopolymer, possibly sterically protected by alkyl chains rendering the geopolymer immune to hydrolytic attack. Additionally, ether linkages have been shown to play a role in crosslinking the macromolecule in fossil algae (Versteegh et al. 2004).

In this paper we compare the jaw compositions of two modern cephalopods, *Dosidicus gigas* and *Nautilis belauensis*, with those of four extinct cephalopods from the Upper Cretaceous of North America and Japan. The fossil jaws are composed of a coarsely crystalline black material with a honeycomb-like texture. X-ray diffraction analysis indicated that the material is amorphous and includes organic compounds (Landman et al. 2006b). The jaws are preserved in shale and are slightly distorted due to post-depositional compaction of the sediments.

We sampled the lower jaws of two modern cephalopods, the Humboldt squid (*Dosidicus gigas*) from California and *Nautilus belauensis* from Palau (Tables 20.1, 20.2). These represent the coleoid and nautiloid cephalopods, respectively. We also sampled the lower jaws of four extinct cephalopods from the Upper Cretaceous (Campanian–Maastrichtian) of North America and Japan: the ammonoids *Placenticeras meeki/costatum*, *Hoploscaphites landesi* and *Anagaudryceras limatum*, and the coleoid *Nanaimoteuthis jeletzkyi* (Table 20.1). All the fossils are preserved in limestone or siderite-cemented concretions in shale. The jaws from South Dakota, British Columbia and Japan are associated with ammonoid shells that preserve their original microstructure. In contrast, the jaws from Alberta are associated with shells

Table 20.1 Description of modern and fossil cephalopods

Taxon	Description	Specimen no.	Age	Ammonoid zone	Locality
Placenticeras meeki/costatum	Lower jaw	BHMNH 5041[a]	Campanian	*Baculites compressus—B. cuneatus* Zone, Pierre Shale	Meade County, South Dakota[b]
Placenticeras meeki/costatum	Lower jaw	AMNH 47277[d]	Campanian	*B. cuneatus* Zone, Bearpaw Shale	Welling, Alberta[e]
Placenticeras meeki/costatum	Lower jaw	TMP 92.42.21[f]	Campanian	*B. compressus—B. cuneatus* Zone, Bearpaw Shale	Welling, Alberta[e]
Hoploscaphites landesi	Lower jaw	AMNH 53351[g]	Campanian	*B. compressus—B. cuneatus* Zone, Pierre Shale	Meade County, South Dakota[h]
*Nanaimoteuthis jeletzky*i	Lower jaw	CDM 2006.1.1[i]	Campanian		Vancouver Island, British Columbia
Anagaudryceras limatum	Lower jaw	UMUT[j]	Coniacian		Hokkaido, Japan
Dosidicus gigas	Lower jaw	–	Modern		California
Nautilus belauensis	Lower jaw	–	Modern		Palau

[a] Black Hills Museum of Natural History; Landman et al. (2006b, pp. 20–21, Fig. 20.15)
[b] locality 2a of Landman et al. (2006b)
[c] Landman et al. (2006b, p. 36) report that it is strongly convex—i.e. not compacted
[d] American Natural History Museum; Landman et al. (2006b, p. 11)
[e] locality 3 of Landman et al. (2006b)
[f] Royal Tyrrell Museum; Landman et al. (2006b, pp. 14–17, Fig. 20.11)
[g] American Natural History Museum
[h] locality 2a of Landman et al. (2006b)
[i] Cortenay and District Museum and Paleontology Center
[j] University Museum of the University of Tokyo. See also Gupta et al. (2008)

that have been transformed into the gemstone ammolite, presumably as a consequence of elevated temperature and pressure (Mychaluk et al. 2001).

Samples of the jaws of the modern Humboldt squid (*Dosidicus gigas*) and *Nautilus belauensis* were broken off for analysis. Aliquots were analyzed using pyrolysis-gas chromatography-mass spectrometry (Py-GC-MS), with neither chemical treatment nor organic solvent extraction, in order to evaluate the entire molecular distribution. Model compounds (Sigma-Aldrich)—chitin, D-tryptophan, D-alanine, D-tyrosine, D-phenylalanine and D-proline—were analyzed to help interpret the origin of moieties released from thermal fragmentation of the samples.

Fossil samples were mechanically removed from the surrounding matrix. They were transferred to glass vials and washed using ultrasonication in deionized water

Table 20.2 Major products in pyrolyzates of modern Humboldt squid jaw and *n*-alkyl component in fossils. (Letters refer to compounds characteristic of chitin and numbers to pyrolysis products of proteins; ions in descending order of abundance after base peak (adapted from Gupta et al. 2008)

Peak	MS characteristics (*m/z*) (M+. underlined)	Compound name	Origin
1	$\underline{92}$ (base), 91, 65	Toluene	Phenylalanine
2	$\underline{81}$, 80 (base), 52	C$_1$-Pyrroles	Proline, hydroxyproline
3	$\underline{106}$, 91 (base)	C$_2$- benzene	Phenylalanine
4	$\underline{104}$ (base), 78, 51	Styrene	Phenylalanine
5	$\underline{95}$, 94 (base), 80	C$_2$-Pyrrole	Hydroxyproline?
6	$\underline{94}$ (base), 66	Phenol	Tyrosine
7	$\underline{108}$ (base), 107, 77	C$_1$-Phenol	Tyrosine
8	$\underline{117}$ (base), 90, 116	Ethylcyanobenzene	Phenylalanine
9	$\underline{131}$, 91 (base), 65	Propylcyanobenzene	Phenylalanine
10	$\underline{131}$, 130 (base), 77	C$_1$-Indole	Tryptophan
11	$\underline{168}$, 70 (base), 97, 125, 165	2,5-Diketopiperazine derivatives	Proline-alanine
12	$\underline{186}$, 138 (base), 93, 54, 58	Diketodipyrrole	Hydroxyproline
13	$\underline{194}$, 70 (base), 154, 54, 86	2,5-Diketopiperazine derivative	Proline-proline
a	$\underline{125}$, 83 (base), 54, 42, 53	3-Acetamidofuran	Chitin
b	$\underline{139}$, 97 (base), 69, 42, 53	3-Acetamido-5-methylfuran	Chitin
c	$\underline{153}$, 111 (base), 82, 42, 83	3-Acetamido-4-pyrone	Chitin
d	185, 84 (base), 55, 83, 42	Oxazoline structure	Chitin
+	57, 71, 85, 99	*n*-Alkane	*n*-Alkyl component
−	55, 69, 93, 97	*n*-Alkene	*n*-Alkyl component
●	74 (base), 87	Fatty acid methyl ester	Ester bound component of macromolecule
MeK	58 (base)	Methyl ketone (alkan-2-one)	Ether bound component of macromolecule
?a	152 (base), 111, 125, 137	Unknown	Unknown
?b	191 (base), 182	Unknown	Unknown

(10 min) to remove any adhering sedimentary particles. After being dried overnight in a fume hood they were extracted ultrasonically (×2, 15 min each) with CH_2Cl_2:CH_3OH (2:1) to remove any soluble organic component not chemically bound within the fossil macromolecules. This residue was analyzed using Py-GC-MS to obtain the distribution of the soluble, low molecular weight products. Samples were also analyzed using thermochemolysis [pyrolysis in the presence of tetramethylammonium hydroxide (TMAH); Challinor 1991; de Leeuw and Baas 1993] for structural analysis of the macromolecules and particularly ester moieties. The sediment that hosted *Nanaimoteuthis jeletzkyi* was crushed with a mortar and pestle and analyzed with Py-GC-MS in order to compare the products with those from the

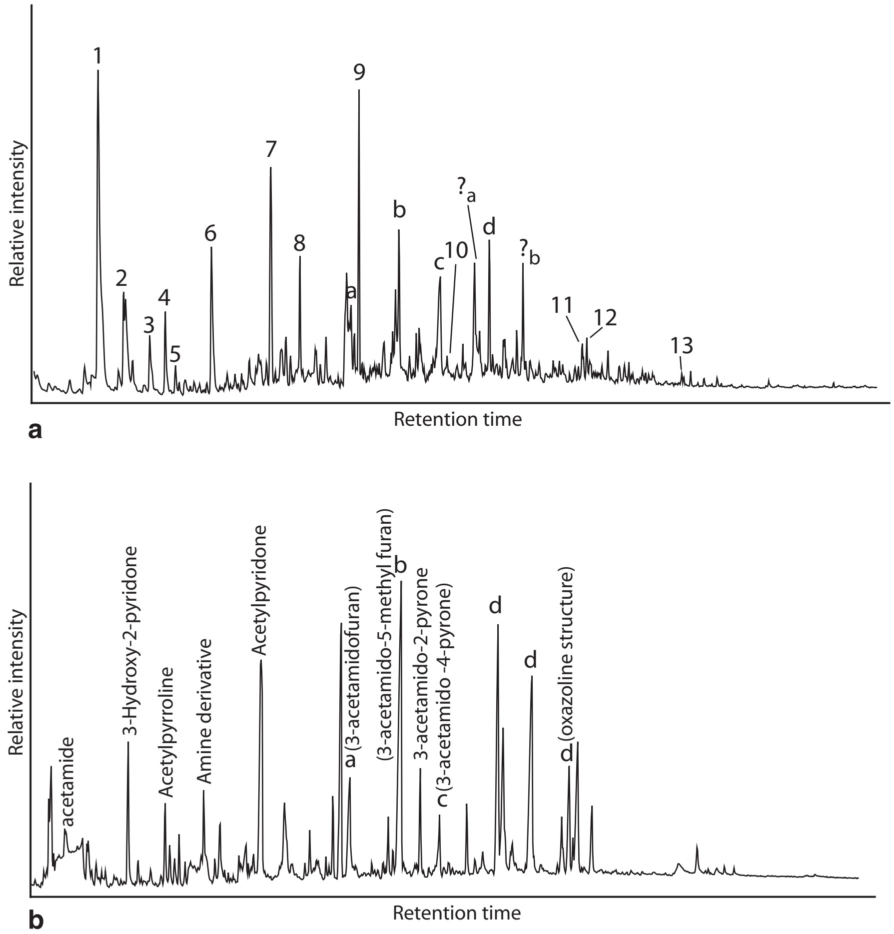

Fig. 20.1 Pyrolysis-GC-MS analysis of **a** modern Humboldt squid jaw indicating a chitin-protein composition and **b** model compound Chitin. Table 20.2 provides a key to numbers and letters used to annotate the peaks that are derived from proteins and chitin (adapted from Gupta et al. 2008)

entrained fossil. The sediment was analyzed without solvent extraction in order to evaluate the composition of both the soluble and insoluble organic component.

For thermally assisted hydrolysis and methylation (THM), an aliquot of the lipid-extracted residue was transferred to a fresh vial and 1 ml TMAH solution (25 w%) added. The sample was soaked in TMAH solution (3–4 h) prior to ensure that sufficient TMAH was available during on-line pyrolysis, which was conducted under conditions identical to analytical pyrolysis. Appropriate blanks were also analyzed to exclude contamination from prior samples and the TMAH solution.

Analysis of the modern Humboldt squid (Fig. 20.1a) and *Nautilus* jaws revealed the presence of 3-acetamidofuran, 3-acetamido-5-methylfuran, 3-acetamido-4-pyrone, oxazoline structures. Aromatic compounds included alkyl benzenes and al-

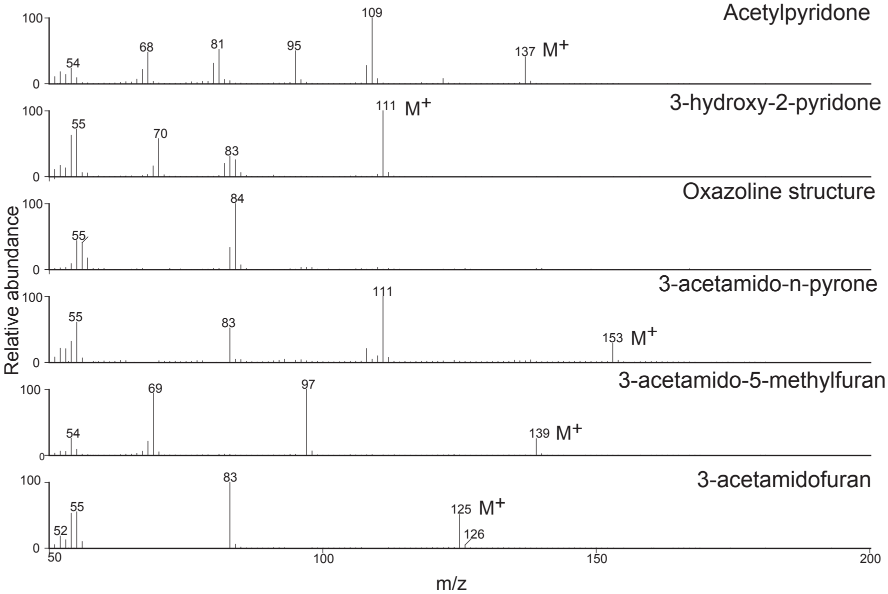

Fig. 20.2 Mass spectra of compounds used for identification of moieties detected both in chitin model compound and in the Humboldt squid beak; n in 3 acetamido-n-pyrone can be either 2 or 4 (adapted from Gupta et al. 2008)

kyl phenols. Indoles, cyanobenzenes, diketodipyrrole and 2, 5 diketopiperazine structures were also detected. Analysis of model compound chitin revealed several products that were produced from the jaw of the modern Humdoldt, squid confirming the presence of the biopolymer chitin (Fig. 20.1b). Figure 20.2 shows the mass spectra of compounds used for identification of those detected both in chitin model compounds and in the squid beak.

Analysis of a jaw of *Placenticeras* from Alberta (AMNH 47277) revealed a dominant aliphatic character and the breakdown product of an aliphatic component represented by a series of *n*-alkane and *n*-alkene homologues, with chain length extending from $<C_9$ to C_{24} (Fig. 20.3, *m*/*z* 83+85) and methyl ketones (*m*/*z* 58) extending from C_7 to $C_{120.}$ Aromatic compounds such as benzene and alkyl derivatives, and phenols and their alkyl derivatives, were also detected.

Py-GC-MS analysis of the jaw of *Placenticeras* from South Dakota (BHI 5041) also revealed a significant aliphatic component that was evident through the presence of *n*-alkane and *n*-alkene homologous series, with chain length extending from $<C_9$ to C_{23} (Fig. 20.4a). Those $<C_9$ were not detected as they probably eluted during the thermal hold time and prior to the commencement of MS aquisition. Methyl ketones (alkan-2-ones, *m*/*z* 58) were also detected up to C_{17}, the C_7 to C_{10} components being the most abundant. Aromatic compounds, including benzene and its alkyl derivatives, and phenols and their alkyl derivatives, were detected in minor quantities. Analysis of the jaw of *Anagaudryceras limatum*, in contrast, revealed a dominant aromatic component that consists of

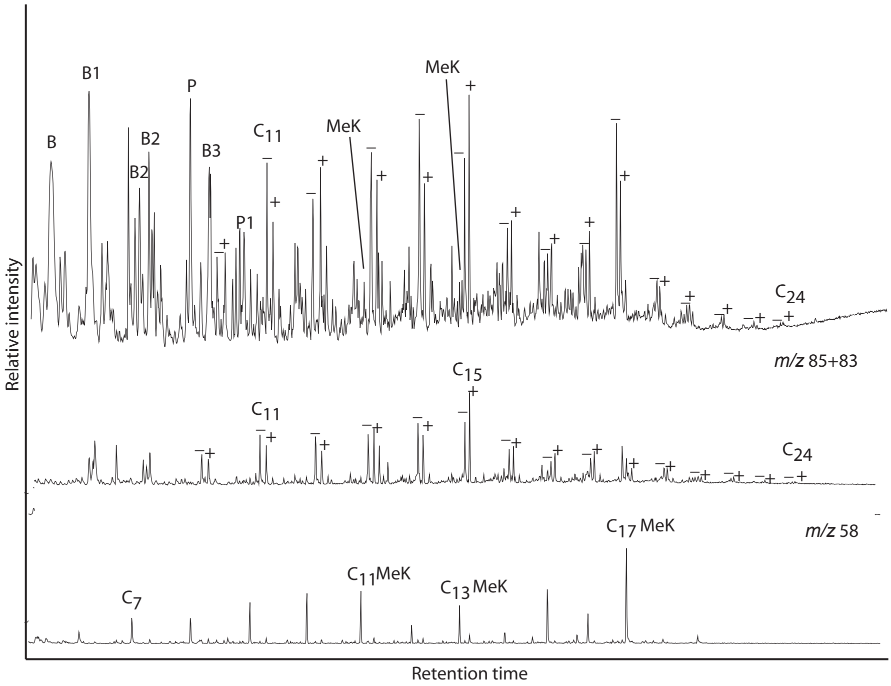

Fig. 20.3 Analysis of fossil *Placenticeras* jaw (AMNH 47277) using py-GC-MS, including *m*/*z* 85+83 chromatograms showing distribution of alkane/alkene homologues, and *m*/*z* 58 showing the distribution of methyl ketones (alkan-2-ones). B = Benzene; Bn = alkyl benzene derivative; P = Phenol; Pn = alkyl phenol derivative; CnMeK = methyl ketone; +=n-alkane; −=n-alkene; n represents the chain length (adapted from Gupta et al. 2008)

alkyl benzenes (*m*/*z* 78+91+92+105+106+119+120+134), alkyl phenols (*m*/*z* 66+94+107+108+121+122+136), and polyaromatics such as naphthalenes and phenanthrene (*m*/*z* 128+141+142+156+178+192; Fig. 20.5).

The data shown in Fig. 20.6 demonstrate macromolecular compositions that are intermediate in nature between aliphatic and aromatic. A second jaw of *Placenticeras* from Alberta (TMP 92.42.21; Fig. 20.6a) and the jaw of *Nanaimoteuthis jeletzkyi* (Fig. 20.6b) reveal aliphatic chain length up to $C_{18–19}$, along with significant aromatic components. No organic compounds were detected during pyrolysis of the sediment hosting the *Nanaimoteuthis jeletzkyi* jaw. The jaw of *Hoploscaphites* also showed an intermediate aliphatic + aromatic hydrocarbon composition.

TMAH pyrolysis/thermochemolysis of the *Placenticeras* jaw (BHI 5041) (Fig. 20.4b) and the *Anagaudryceras limatum* jaw (UMUT MM 30877; data not shown) yielded fatty acid methyl esters (FAMEs) with chain length from C_6 to C_{18}, indicating that ester bonds are important in fossils that are predominantly both aromatic and aliphatic. The most abundant fatty acyl moieties were those with chain length C_{16}, C_{14}, C_9 and C_8. No sulfur-bearing compounds, such as thiophenes, were detected in the pyrolysate.

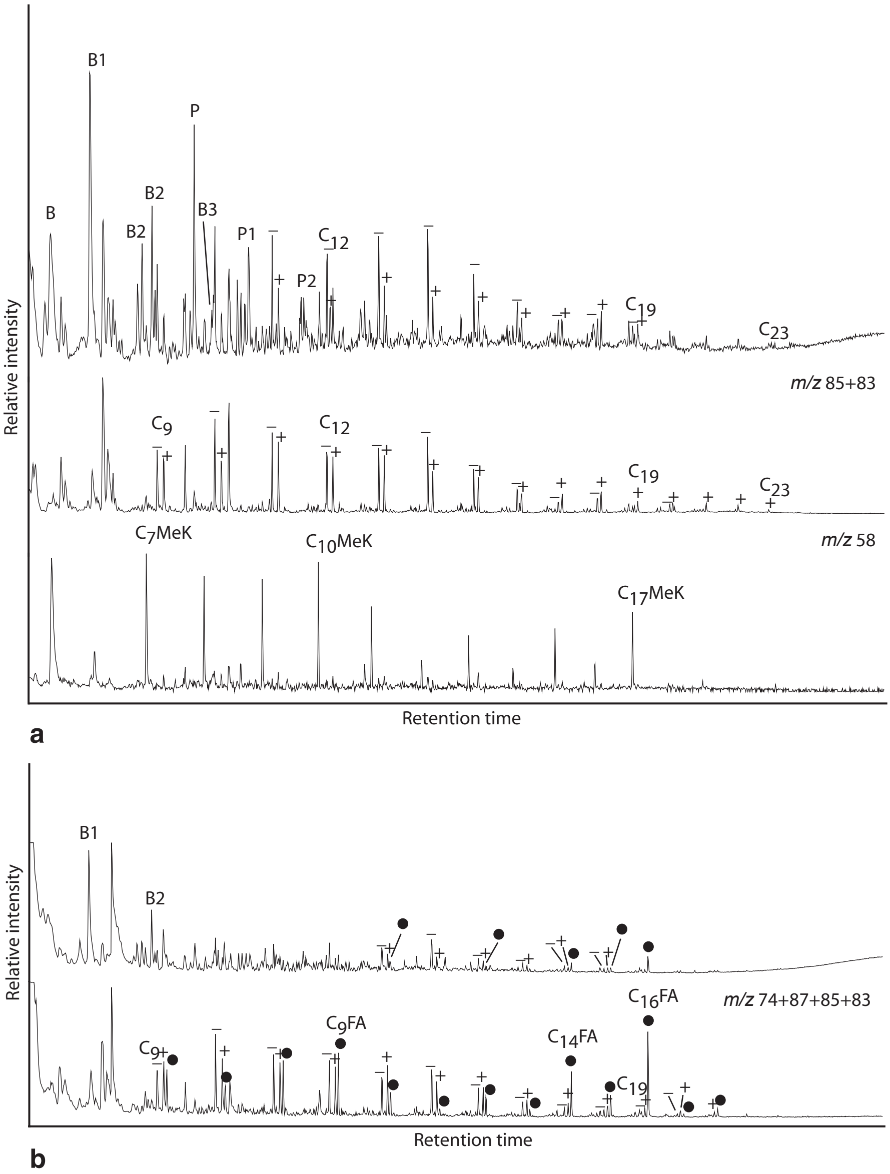

Fig. 20.4 Analysis of fossil *Placenticeras* jaw (BHI 5041) using **a** py-GC-MS, including *m*/*z* 85+83 chromatograms showing distribution of alkane/alkene homologues, and *m*/*z* 58 showing distribution of methyl ketones (alkan-2-ones), **b** TMAH- py-GC-MS (thermochemolysis), revealing distribution of fatty acyl moieties with respect to the alkane/alkene homologues in *m*/*z* 74+87+85+83 chromatogram; CnFA = fatty acid (represented by ●). Other symbols are as in Fig. 20.3 (adapted from Gupta et al. 2008)

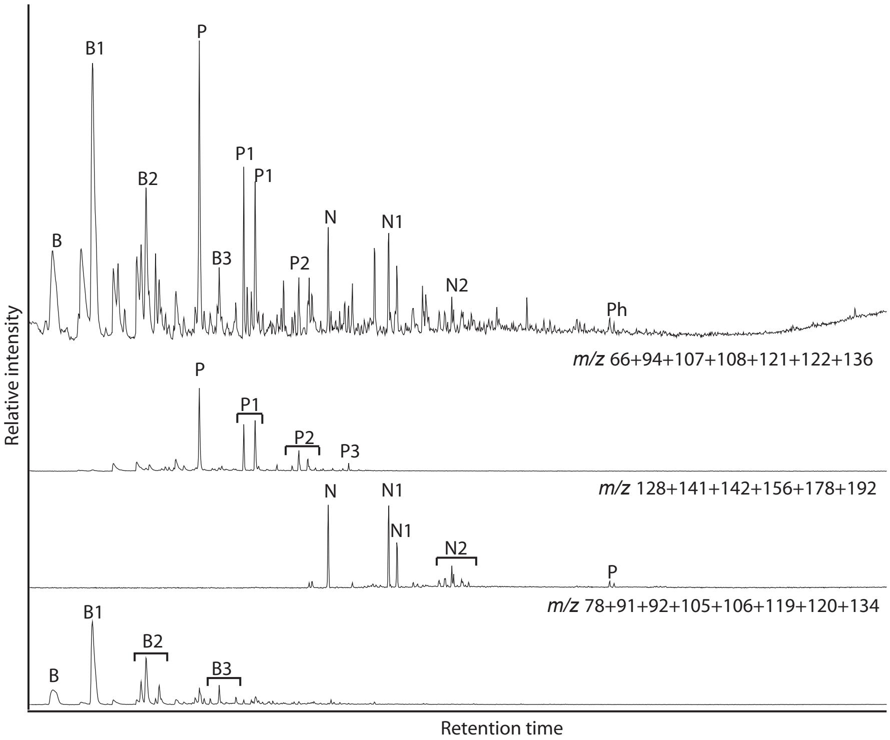

Fig. 20.5 Py-GC-MS analysis of fossil jaw of *Anagaudryceras limatum* revealing its aromatic rich nature. N = naphthalene; N1 = methylnaphthalene; N2 = C2 naphthalene; P = phenanthrene. The *m*/*z* 66+94+107+108+121+122+136 chromatogram highlights the distribution of phenols and alkyl derivatives, *m*/*z* 128+141+142+156+178+192 that of polyaromatics and *m*/*z* 78+91+92+105+106+119+120+134 the benzene and alkyl derivatives. Other symbols are as in Fig. 20.3 (adapted from Gupta et al. 2008)

The specimens from Alberta, Canada were obtained from the St. Mary River area where the Bearpaw Formation is mined for ammolite, a semiprecious mineral formed from the shells of ammonites. Mychaluk et al. (2001) estimated that the sedimentary sequence was buried to a depth of ~4 km in this area on the basis of vitrinite reflectance values of 0.6 % Ro, corresponding to high volatile bituminous rank (England and Bustin 1986).

Table 20.1 summarizes the chemical moieties detected in the modern Humboldt squid jaw during thermal cleavage and their likely precursors. It is clear that the bulk of the material consists of the biopolymer chitin associated with proteins. The fossils on the other hand display no moieties diagnostic of the chitin biopolymer (as detected in the modern sample) possibly as it is prone to degradation by chitinophosphatic bacteria as well as by oxidation and hydrolysis (Stankiewicz et al. 1998b). The aliphatic rich fossils are similar in composition to Type II kerogen, even though such a non-hydrolyzable aliphatic component is absent from the living

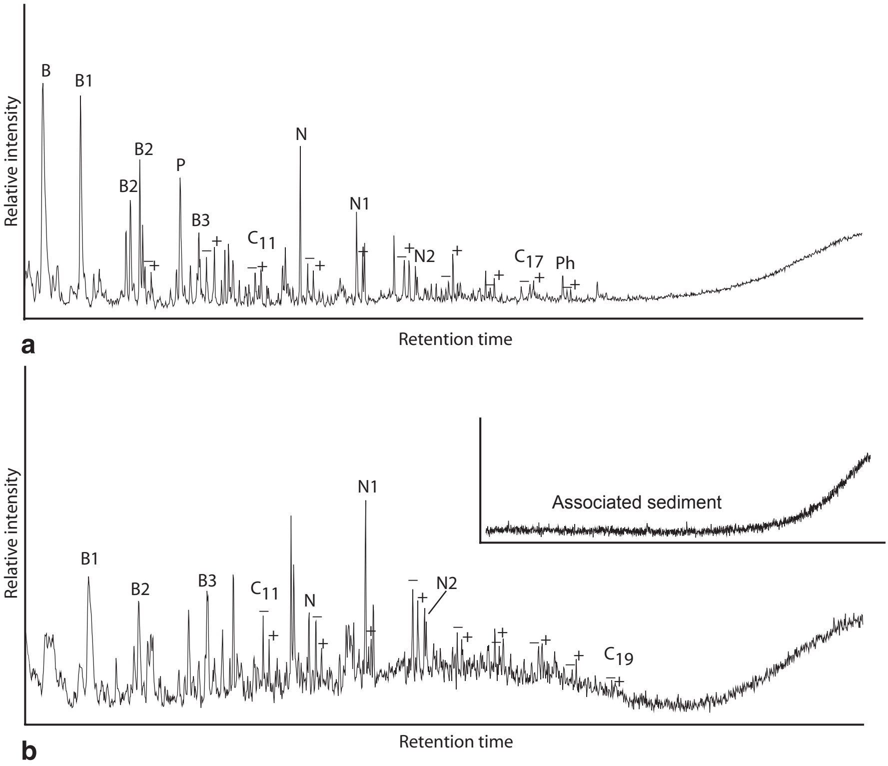

Fig. 20.6 Py-GC-MS analysis of **a** fossil jaw of *Placenticeras* (TMP 92.42.21) revealing an intermediate nature, **b** fossil jaw of *Nanaimoteuthis jeletzkyi*, also intermediate (inset–analysis of host sediment, revealing organic-lean nature). Other symbols are as in Fig. 20.3 and 20.4 (adapted from Gupta et al. (2008)

squid jaw, indicating that it is a product of diagenesis (Briggs 1999). The sediment did not contain any detectable components that were observed in the products from the fossils. Accordingly, post-depositional migration cannot account for their composition (see Gupta et al. 2007a).

Thermochemolysis of the fossil jaws yielded FAMEs from C_6 to C_{18} from transmethylation of ester functional groups in the macromolecules, thereby revealing the distribution of incorporated fatty acyl moieties. Such incorporation of lipids via in situ lipid incorporation (Briggs 1999; Stankiewicz et al. 1998b; Stankiewicz et al. 2000) has been observed for fossil leaves (Gupta et al. 2007b), graptolites (Gupta et al. 2006b), and arthropods (Gupta et al. 2007a). The aliphatic rich fossil jaws also yielded methyl ketones, indicating ether cross links in the macromolecules (Hartgers et al. 1995; Gelin et al. 1994). Thus, the fossil geopolymer is likely formed from aliphatic moieties bound by a combination of ether as well as ester linkages. The present results suggest, for the first time, that such a process is prevalent in animal fossils as well as algae.

Analysis of squid pens from the Jurassic Sölnhofen Limestone (Germany) and the Oxford Clay Formation (England) yielded pyrolysates dominated by aromatic compounds that included alkyl benzenes, naphthalene and thiophenes (Stankiewicz et al. 1997). A subsidiary *n*-alkyl component included homologues up to C_{18} without any trace of chitin or protein products. Artificial maturation of chitin (Gupta et al. 2006a) revealed the presence of alkyl phenols and indenes. Thus the phenols in the fossil material could have arisen from diagenetically altered chitin (and not the chitin biopolymer per se) that may have survived degradation, and were present in a chemically altered state as a component of the fossil geopolymer. The aromatic compounds, including alkyl benzenes are common in pyrolysates of most fossilized organic materials, so their biological provenance is difficult to establish (Hartgers et al. 1994). Elevated pressure and temperature conditions associated with deep burial have been shown to increase the aromaticity of fossil eurypterids (Gupta et al. 2007c). The *Placenticeras* jaw fossils from Canada (likely subjected to elevated P-T conditions) show the presence of an aliphatic component together with a significant proportion of aromatic components. The *Placenticeras* jaw from South Dakota is primarily aliphatic and the *Anagaudryceras limatum* jaw from Japan is primarily aromatic. Neither was subjected to deep burial and elevated P-T conditions. Thus, it is difficult to establish a direct correlation here between aromaticity and the P-T conditions experienced by the samples.

The aliphatic component in cephalopod fossils does not show the long chain components (i.e. *n*-alkanes/*n*-alkenes $>C_{25}$) that are present in terrestrial fossils such as leaves and beetles (Gupta et al. 2007a, 2007b), presumably reflecting the absence of the longer chain plant waxes that are present in the cuticles of terrestrial organisms. In addition, the cephalopod fossils reported here and by Stankiewicz et al. (1997) contain a much greater aromatic component than terrestrial fossils; the dominance of aliphatic components in the latter is a reflection of the lipid content in surface waxes in terrestrial taxa.

The methyl ketones revealed here in fossil cephalopod jaws have also been recorded in microalgal 'dinoclasts' using similar analytical techniques (Versteegh et al. 2004). Just as the jaws of living cephalopods contain no chemically-resistant, non-hydrolysable aliphatic polymer, nor do living dinoclasts contain an aliphatic component like the modern or fossil macromolecule known as algaenan, Versteegh et al. (2004) and de Leeuw et al. (2006) concluded that the macromolecule comprised ether linked C_{16} and C_{18} alkyl chains and was formed by oxidative polymerisation of fatty acid equivalents. Thus, the macromolecular building blocks were derived from the common components of cellular membranes and storage vesicles.

20.4 New Approaches for Ammonoid Taphonomy: Experimental Techniques With Modern Analogues

From the first edition of "Ammonoid Paleobiology" in 1996 onward, experimental analyses with modern analogues (e.g., experimental approaches with modern nautilus shells or plastic models, hydrostatic calculations) have been attempted to better understand processes involved in ammonoid taphonomy, especially biostratinomy. This is because most of their biostratinomic processes (waterlogging, implosion, post mortem surfacing, transport on the seafloor, deformation after sedimentation in soft sediments, shell fragmentation, transportation of jaws) can hardly be recognized from the fossil record only.

20.4.1 Waterlogging

The timing when dead shells with soft parts attached to the shells start to be waterlogged had been ambiguous even in modern nautili, although it is crucial to consider the post-mortem surfacing and drift on sea surface by water currents in ectocochleate cephalopods. In live specimens of modern nautili, mantle tissue is tightly attached to the shell at the scars of the paired cephalic retractor muscles, the unpaired middorasal scar, the scar of the mantle myoadhesive band, the scar of septal myoadhesive band, and the scar of the palliovisceral ligament (Doguzhaeva and Mutvei 1996). These attachments continuously surround the entire inner surface of the shell. Based on experiments carried out in the Philippines, Wani et al. (2005) demonstrated that waterlogging of the phragmocone in modern nautili does not occur until the mantle tissue detaches from the shell due to decomposition (Fig. 20.7). This finding contradicts the previous assumption that shells are always passively waterlogged even in live and also in dead specimens under the high water pressure (e.g., Ward 1987; Maeda and Seilacher 1996). The direct application of this finding to ammonoids, however, might be problematic, because the mantle tissue attachments in ammonoids appear to not continuously surround the entire inner surface of shells in most of the examined specimens (Doguzhaeva and Mutvei 1996). For the further consideration of the transfer of the knowledge about the waterlogging process in modern nautili, the muscle attachment in ammonoids, especially whether or not the muscle attachments continuously surround the entire inner surface of shells, should be examined and demonstrated with extremely well-preserved specimens.

Direct observations of waterlogged and therefore submerged empty shells of modern nautili have been first reported from New Caledonia by Mapes et al. (2010a, 2010b). Mapes et al. (2010a) concluded that the length of time the shell is unburied will not control the degree of epizoan encrustation or the external shell appearance, given the limited sample available for study and assuming equal conditions where shells rested on the seafloor. They cautioned, however, that fossil cephalopods may have differed considerably in their post-mortem behavior, partially because of evolutionary patterns of the associated organisms, their geographic distribution, and the different environments with different paleoecological parameters through time.

20.4.2 Implosion

Modern nautilus shells are imploded under high water pressure during live and/or after death. Some experiments have demonstrated that depths of 750–800 m are

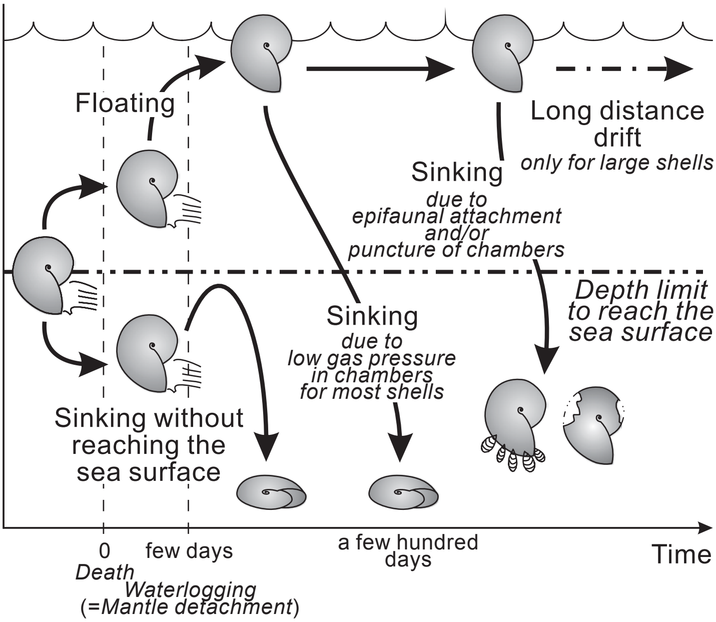

Fig. 20.7 Schematic diagram of post mortem floatation and drift in ammonoid shells (updated with recent experimental results, based on Maeda and Seilacher (1996). Waterlogging starts when the mantle tissue is detached from the shells, at least in modern nautili (Wani et al. 2005). The theoretical calculations of the buoyancy and gravity of empty shells (Chamberlain et al. 1981) suggest that most ammonoid shells, especially < 50 mm in shell diameter, do not reach the sea surface after a short period of ascent. Even if the shells reach the sea surface, the smaller shells (especially < 120 mm in shell diameter) passively sink more quickly due to the low air pressure inside the phragmocone (< 0.9 atm.; Wani et al. 2005). These theoretical and experimental studies strongly suggest smaller ammonoid shells (especially < 50 mm in shell diameter) sank rapidly close to their habitats, and only large shells had the potential to drift post mortem over long distances

enough to cause implosion in modern nautili (Denton and Gilpin-Brown 1966; Denton 1973; Saunders and Wehman 1977; Kanie et al. 1980; Westermann and Ward 1980; Ward and Martin 1980; Kanie and Hattori 1983; Saunders 1984; Chamberlain and Chamberlain 1985; Hewitt and Westermann 1987, 1988; Dunstan et al. 2011). However, sea water floods the empty shell until the cameral gas pressure equals ambient water pressure, and therefore, the phragmocone does not implode, even at great water depths (Boston and Mapes 1991). Thus, implosion by hydrostatic pressure may be a subordinate factor in ammonoid taphonomy (Maeda and Seilacher 1996).

20.4.3 Post Mortem Surfacing

To be preserved as fossils, ammonoid shells must finally have sunk to the seafloor (Maeda and Seilacher 1996). In life, ammonoids probably maintained neutral buoyancy in seawater, like modern nautili (e.g., Jacobs and Chamberlain 1996; Westermann 1996). When the soft parts were removed from the shells after death (by predation or passively dropping out due to putrefaction), the neutral buoyancy was lost, and then, the empty shells supposedly gained positive buoyancy and surfaced. The shells that floated on the sea surface have the potential to drift with ocean currents, if the shells can float for a long period. By this post mortem surfacing and floating, empty shells of modern nautilus are known to sometimes appear in areas far outside of their habitat area (e.g., Toriyama et al. 1965; Reyment 1973, 2008; House 1987). In this context, the fundamental question is the frequency of the occurrence of such a long-distance drift (Chamberlain et al. 1981).

For the purpose of understanding the possibility of surfacing or sinking of empty shells in ammonoids and modern nautili, Chamberlain et al. (1981) calculated the buoyancy and mass of empty shells using estimates of influx rates in ammonoid siphuncles, and therefore concluded that most shells, especially those larger than 50 mm in diameter, do not reach the sea surface after a short period of ascent (Fig. 20.7). Even if the shells reach the sea surface, the smaller shells (especially at less than 120 mm in diameter) passively sink more quickly due to the low air pressure inside the phragmocone (<0.9 atm.; Wani et al. 2005). This is confirmed by field experiments with empty shells of modern nautilus, and this mechanism is more significant for small shells, because of the lower total gas pressure in their phragmocones compared to larger shells, and the smaller limit of seawater volume that still allows flotation. These theoretical and experimental studies strongly suggest that smaller empty ammonoid shells (especially at less than 50 mm in diameter) sank rapidly close to their habitats, even if they floated initially, and only large empty shells had some potential to post mortem drift over long distances (Fig. 20.7). This is consistent with field observations of ammonoid shells that had been drifted over a long distance as inferred from infestations of pelagic limpets (mostly >200 mm in diameter; Kase et al. 1994, 1998).

Some exceptions, however, have been previously reported and discussed. Maeda and Seilacher (1996) examined the taphonomic attributes (frequent punctures in phragmocones) of some phylloceratid ammonoids from the Upper Cretaceous of Hokkaido, Japan, and therefore assumed their biostratinomic history as once surfacing, floating for a while, during which the shells were broken, and then sank toward the seafloor, even at smaller shell sizes (<50 mm in diameter). As for phylloceratid ammonoids from the Middle Jurassic of the Iberian Chain, Spain, Fernández-Lópes and Meléndez (1996) interpreted that their occurrences were controlled by post-mortem floatation and drift by water currents, related to relative sea-level changes. This interpretation is based on the detailed study of taphonomic attributes of the specimen (polyspecific assemblages, dominated by adult individuals).

Furthermore, Maeda et al. (2003) examined taphonomic attributes (preservational features, size distribution, burial orientation, faunal composition) of Lower Permian cephalopod assemblages from Central Texas, USA, and concluded that these shells (<20 mm in diameter) floated and drifted for some distance, and then beached in a muddy beach facies. This is a rare report that the ammonoid shells were beached and then preserved as fossils, which is probably related to the observation that most beached shells did not become fossilized, because such shells were commonly destroyed by subsequent reworking and weathering (Maeda et al. 2003). Based on these detailed examinations, Maeda et al. (2003) suggested that the highly fragmented shells with only the inner whorls of the phragmocone preserved were damaged either in their biotope, perhaps through predation, or during post-mortem transport, and these shells were able to retain sufficient positive buoyancy to float to the muddy shoreline in spite of massive damage.

The waterlogged and therefore submerged shells might have regained positive buoyancy and floated to the sea surface (Mapes et al. 2010b). Based on direct observations of submerged empty shells of modern nautili in the shallow sea (1–3 m deep), Mapes et al. (2010b) concluded that some submerged nautilus shells can either be transported shoreward along the seafloor or float back to the surface after they have been submerged, although the mechanism that allows shells to regain positive buoyancy is not yet understood. Regaining positive buoyancy after submersion might have occurred in ammonoid shells, but the unknown mechanism to regain positive buoyancy appears to be restricted to the shallow sea, because the higher water pressure in deeper marine settings leads to waterlog with a larger amount of seawater seeping into the phragmocone than in those shells that maintained neutral or slightly negative buoyancy.

20.4.4 Transport on the Seafloor

After ammonoid dead (or empty) shells have sunk down on the seafloor, tthey were more or less transported on the seafloor by bottom water currents. Sometimes, ammonoid shells left trace marks on the bedding planes of such transport on the seafloor (landing, roll, and drag marks; Rothpletz 1909; Seilacher 1963; Barthel et al. 1990). Sunken shells with completely waterlogged phragmocone probably have a light density (~ 1.212 g/cm^3; calculated by Maeda and Seilacher 1996), so that the shells would flow hydrodynamically similar to lightweight materials, such as plant remains and pieces of pumice, and consequently accumulated together with these lightweight materials (Maeda 1987; Maeda and Seilacher 1996). Such occurrences are commonly recognized within calcareous concretions (Maeda 1987; Maeda and Seilacher 1996; Zatoń and Marynowski 2006; Olivero 2007), which is a strong support for this consideration.

Ammonoid shells with a light density can be transported and accumulated by bottom water currents around large ammonoid shells, which is known as "*shelter ed preservation*" (Maeda 1991). Generally, small shells (< 12 mm in diameter; called "*refugees*"), which are accumulated together with plant remains, lack their jaws and show signs of preburial damage caused by transport (Maeda and Seilacher 1996). These transported "*refugees*" can be preserved within body chambers of large ammonoid shells (~ 300–500 mm in diameter; called "*shelter*"), and their original shell geometry is well preserved together with the intact protoconch (Maeda 1991). Sheltered preservation probably enhances the preservational potential of small (e.g., immature) ammonoid shells than other modes of occurrences (directly embedded within host rocks and preserved within calcareous concretions), suggesting that the immature portion of the original thanatocoenosis is well preserved in sheltered preservation (Maeda 1991).

The transportation characteristics of modern nautilus shells by bottom water currents were experimentally determined by Wani and Ikeda (2006), who revealed that the shells are reorientated and transported by slow currents (~0.20 m/s and 0.25–0.37 m/s, respectively). Considering the difference of coefficients of drag in various ammonoid shell types, the velocities of water currents needed for reorienting and transporting ammonoid shells can be estimated as in Fig. 20.8. Therefore, the shells of most ammonoids (especially leiostraca, serpenticones, and cadicones) probably have the coefficients of drag similar to those of modern nautili and therefore had reorientation and threshold velocities similar to modern nautili, suggesting that ammonoid shells were highly sensitive to bottom water currents (Wani and Ikeda 2006).

Seilacher (1968) experimentally demonstrated that the draft-through currents produced by water turbulence outside the shells lying on the seafloor can pile up sediments into the phragmocones after the siphuncular tube is lost and there is a puncture somewhere in an inner whorl (Fig. 20.9). Such phragmocones partially filled with sediments by draft-through currents have been preserved and reported both in settings with clastic and with carbonate rocks (e.g., from clastic rocks in Japan and Russia, Tanabe et al 1984; Maeda 1987; Maeda et al. 2010; from carnonate rocks in Germany, Seilacher 1971; Seilacher et al. 1976).

20.4.5 Deformation After Sedimentation in Soft Sediments

The diplomoceratid heteromorph ammonoid *Polyptychoceras* is known to becommonly preserved with an oblique posture against the bedding plane in the Upper Cretaceous of Hokkaido, Japan, which is unique and a peculiar mode of preservation in these diplomoceratid ammonoids (e.g., Maeda and Seilacher 1996, Fig. 20.6; Okamoto and Asami 2002, Fig. 20.11). Based on the detailed observation of fossiliferous concretions, hydrostatic calculations, and laboratory experiments with plastic models, Okamoto and Asami (2002) concluded that initially, waterlogged and horizontally sunk *Polyptychoceras* shells had rotated within soft sediments when the shells were covered with sediments, which probably behaved like a viscous fluid, because of the distant positions of the centers of buoyancy and gravity in the horizontally lying hetermorph shells. Okamoto and Asami (2002) named this post-burial non-biological movement "*Zombie model*" and suggested that this mechanism is applicable to several other heteromorph ammonoids buried in soft muddy sediments.

Mapes and McComas (2010) examined the collapsed and/or telescoped septa within undistorted shells of fossil coiled nautiloids from Late Carboniferous in Ohio and concluded that it is due to the soft mud flowing into the phragmocone during

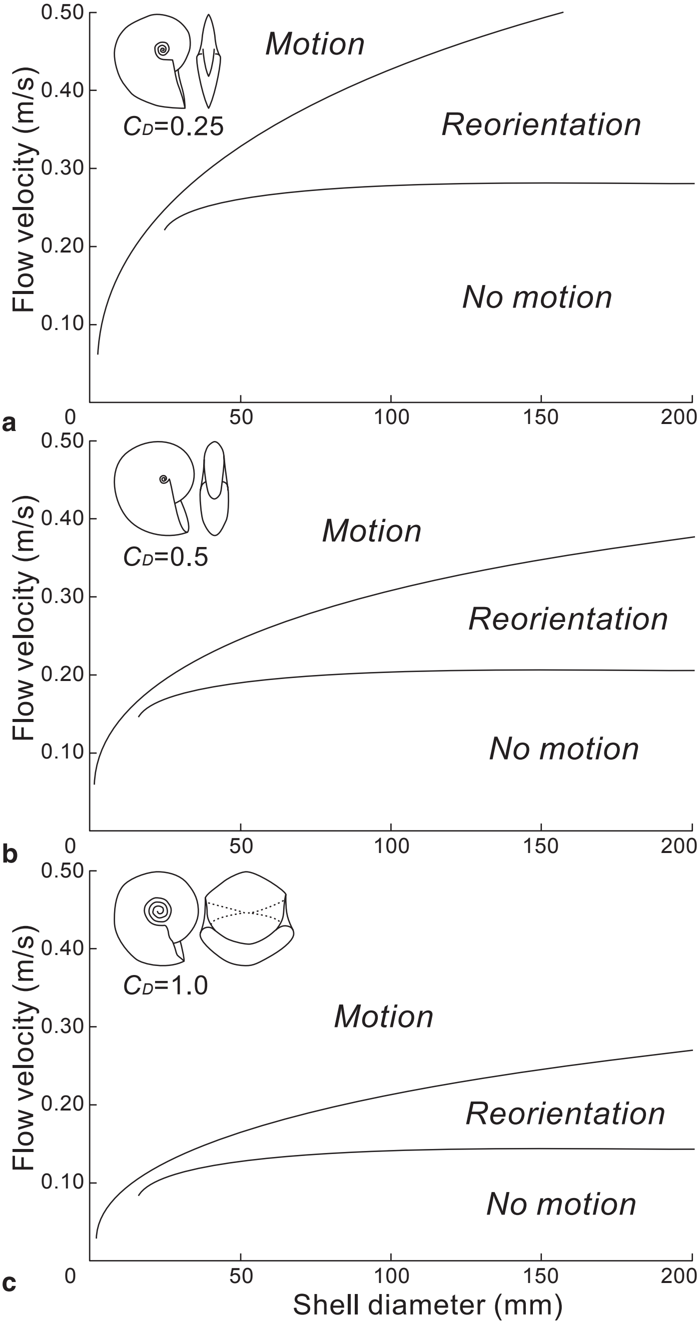

Fig. 20.8 Estimated reorientation and threshold velocity for ammonoid shells, based on flume experiments with modern nautilus shells (modified from Wani and Ikeda 2006). **a** Oxycones (coefficient of drag =0.25). **b** Leiostraca and serpenticones (coefficient of drag =0.5). **c** Cadicones (coefficient of drag =1.0). C_D coefficient of drag of ammonoids

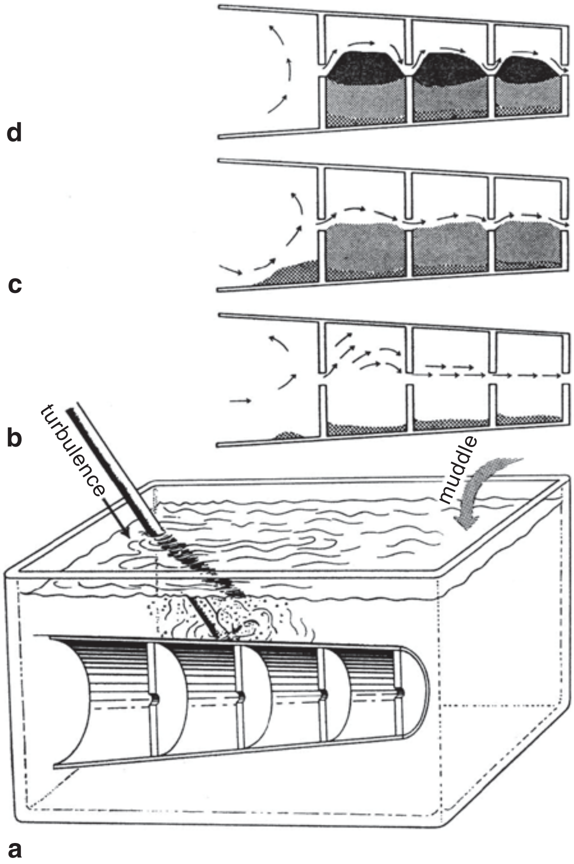

Fig. 20.9 Laboratory experiment with plastic models simulating chambered cephalopod shell in turbulent tank (modified from Seilacher 1968). **a** set up of experiment; **b–c** even sedimentation up to the level of septal passages; and **d** sediment piles up in the *middle*, while draft-through currents keep septal passages open, producing an initial zigzag channel

septal collapse and then quickly resolidified providing internal conch support that prevented the collapse of the conch. This study suggests that a similar taphonomic history within soft sediments can also be expected in ammonoids.

20.4.6 Shell Fragmentation

Ammonoid shells became possibly fragmented and broken by various mechanisms during their taphonomic history (especially biostratinomic and early diagenetic processes; e.g., implosion by water pressure, collision during post mortem floating as well as further transport with sediment on the seafloor, sediment loading after burial within sediments). Wani (2004) performed experiments mimicking some fragmentation patterns by transport with sediment on the seafloor, sediment loading after burial within sediments, and collision during floating, and considered the breaking patterns by other mechanisms (predation and implosion by water pressure) documented in the literatures (for predation, Haven 1972; Tucker and Mapes 1978; Saunders 1984; Arnold 1985; Ward 1987; Saunders et al. 1987, 1991; Tanabe et al. 1988; for implosion by water pressure, Denton and Gilpin-Brown 1966; Denton 1973; Saunders and Wehman 1977; Kanie et al. 1980; Westermann and Ward 1980; Ward and Martin 1980; Kanie and Hattori 1983; Saunders 1984; Chamberlain and Chamberlain 1985; Hewitt and Westermann 1987, 1988). Based on these considerations, Wani (2004) concluded that the fragmentation patterns produced by various mechanisms are distinct and therefore can be differentiated, which would allow the identification of distinct mechanisms responsible for specific fragmentation patterns both in modern nautili and ammonoids.

Ammonoid shells, of course, are possibly fragmented and broken during the diagenetic process (compaction and soft deformation within sediments; see Seilacher et al. 1976; Maeda and Seilacher 1996). However, experimental approaches with modern analogues are limited to mimic these diagenetic processes, because they generally take a long time. Such time interval is difficult to reproduce by experimental methods. To recognize and interpret what happened during the diagenetic processes, the 'traditional' method, such as the detailed observation of taphonomic attributes, is definitely one of the most appropriate approaches.

20.4.7 Transportation and Preservation of Jaws: Autochthonous or Allochthonous?

Although autochthonous or *in situ* preservation of nektic or nektobenthic ammonoids in the strict sense is improbable, occurrence of chitinous jaws (beaks or mandibles) within the body chamber has been vaguely thought to indicate some state close to an autochthonous preservation, regardless of the detailed taphonomic attributes (Lehmann 1981; Nixon 1996; Maeda and Seilacher 1996; Tanabe and Landman 2002; Klug and Jerjen 2012; and references therein). However, there are two scenarios for such jaw occurrence within the body chamber: (1) true autochthonous preservation, or (2) jaws were secondarily deposited within the empty body chamber by water currents (i.e., allochthonous preservation). Based on the laboratory experiments with modern nautili, Wani (2007b) revealed (1) The upper jaws of modern nautili start to move at a water velocity of >0.2 m/s, when the shells are reoriented with the aperture downstream; jaws are therefore unlikely to be secondarily deposited near the shell aperture by bottom currents; and (2) the lower jaws, moved at a velocity of >0.1 m/s, can be deposited around the shell aperture by weak currents (0.1–0.2 m/s in velocity), but never enter the inside of body chamber (Fig. 20.10). In addition, the field experiments revealed that neither jaw is likely to be separately and selectively displaced from the inside of the body chamber through scavenging of the soft parts by burrowing infaunal animals (Wani 2007b). These experimental

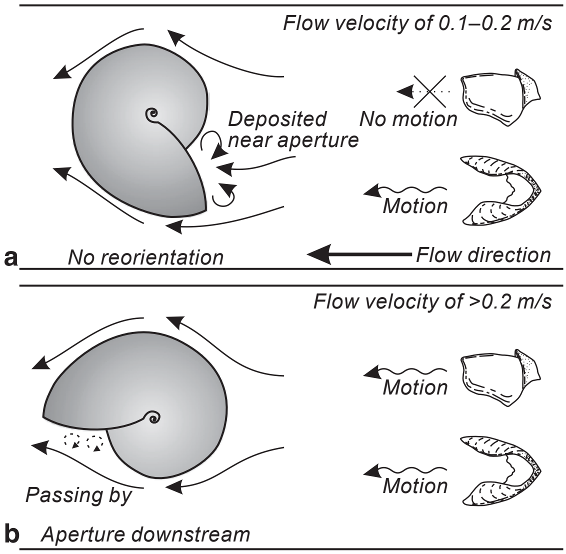

Fig. 20.10 Schematic plan views of flume at flow velocity of 0.1–0.2 m/s (**a**) and >0.2 m/s (**b**), showing transportation of upper and lower jaws and orientation of shells (modified from Wani 2007b). In modern nautili, only lower jaw has potential to be deposited near shell aperture by weak bottom current (0.1–0.2 m/s in velocity)

results suggest an upper jaw preserved inside the body chamber, together with a lower jaw, is a reliable indicator of an autochthonous preservation of the jaws; a sole lower jaw preserved around the shell aperture is likely to be secondarily deposited in allochthonous preservation.

These prerequisites identified for modern nautili (Wani 2007b) could be applied to some ammonoids as a preliminary tool to recognize their autochthonous preservation, because morphology of shells and jaws in modern nautili and ammonoids (especially Cretaceous Lytoceratina and Phylloceratina) are similar (Saunders et al. 1978; Lehmann 1981; Nixon 1996; Jacobs and Chamberlain 1996; Tanabe and Fukuda 1999; Tanabe et al. 2013). However, the detailed morphological differences between modern nautili and ammonoids affect the application of the prerequisites to ammonoids. This is because ammonoid jaws are classified into five types (see Chap. 10 in Volume I): (1) normal type (Goniatitina and Ceratitina), (2) anaptychus type (some Early Jurassic Ammonitina), (3) aptychus type (Ammonitina and Ancyloceratina), (4) rhynchaptychus type (Lytoceratina and Phylloceratina), and (5) intermediate type (Cretaceous Desmoceratoidea). The difference in shell shape is also a controlling factor for secondarily deposited jaws. The reorientation flow velocity is different according to shell streamlines (Fig. 20.8; Wani and Ikeda 2006): slower in depressed (i.e., high whorl expansion rate) shells (~0.13 m/s) and faster in compressed (i.e., low whorl expansion rate) ones (~0.27 m/s). These different reorientation flow velocities (Fig. 20.8; Wani and Ikeda 2006) suggest that both jaws moved with the water flow after depressed shells reoriented with the aperture downstream, and therefore deposition of both jaws around the shell aperture was rare, and therefore that jaws within the body chamber of depressed shells are more reliable as evidence of autochthonous preservation than those in compressed shells (Wani 2007b).

20.5 Diagenetic Processes: Compaction and Dissolution

After ammonoid shells were buried within sediments (i.e., after biostratinomic processes), shells (outside and/or inside the shells) were cemented by secondary precipitated minerals, were compacted and flattened, and/or were dissolved during the following diagenetic processes. These diagenetic processes are related to the degree of sediment infilling into phragmocones and early diagenetic cementation (e.g., bacterial pyrite coating in dysaerobic condition, precipitation of carbonates) within phragmocone. Without such early diagenetic cementation increasing shell toughness, ammonoid shells were commonly compacted by sediment loading and therefore flattened. Therefore, early diagenetic cementation processes played an important role to three-dimensionally preserve ammonoid shells (Seilacher et al. 1976; Maeda and Seilacher 1996; Zatoń and Marynowski 2006; Stephen et al. 2012).

The unique shell structure of ammonoids (i.e., septate phragmocone with a penetrating siphuncle) yields, in case, phragmocones partly filled by sediments. This resulted in the difference of shell toughness against sediment compaction, so that various preservational styles of compaction and subsequent dissolution are developed. The phragmocones partially filled with sediments and subsequent diagenetic processes sometimes display the half-ammonoid preservation that the upper half of the horizontally lying shell is dissolved, retaining only the lower side (Fig. 20.11; Maeda 1987; Maeda and Seilacher 1996). The uniformity of half-ammonoid preservation belonging to various taxa and occurring in various horizons suggests that the partial sedimentary infilling of the phragmocone by draft-through currents and then diagenetic compaction as well as shell dissolution happened after complete burial (Fig. 20.11; Maeda 1987; Maeda and Seilacher 1996). The partial infilling of the phragmocone is prescribed by the position of septal neck, causing the uniform half-ammonoid preservation in which only the lower half of the horizontally lying shells are preserved (Maeda 1987). In related to the difference in sedimentation rates, these partial infilling of phragmocones and subsequent partly dissolved shells display various modes of preservation, which are reviewed as follows in different environments (Chap. 20.7–20.8).

Another interesting mode of preservation related to biased dissolution is the ventral-tire preservation: venter and outer flanks of the last or last second whorl are only preserved and inner flanks and umbilical margins are dissolved, just looking like a "*tire*" (Maeda 1987; Maeda and Seilacher 1996). The preserved ventral portions correspond to the imprint zone of the outer whorl, suggesting the preserved ventral portions were originally covered with the dorsal shell of the outer whorl, so that only the ventral portions were not exposed directly to the external environment, resulting in no or less dissolution of shell during diagenesis (Maeda 1987; Maeda and Seilacher 1996).

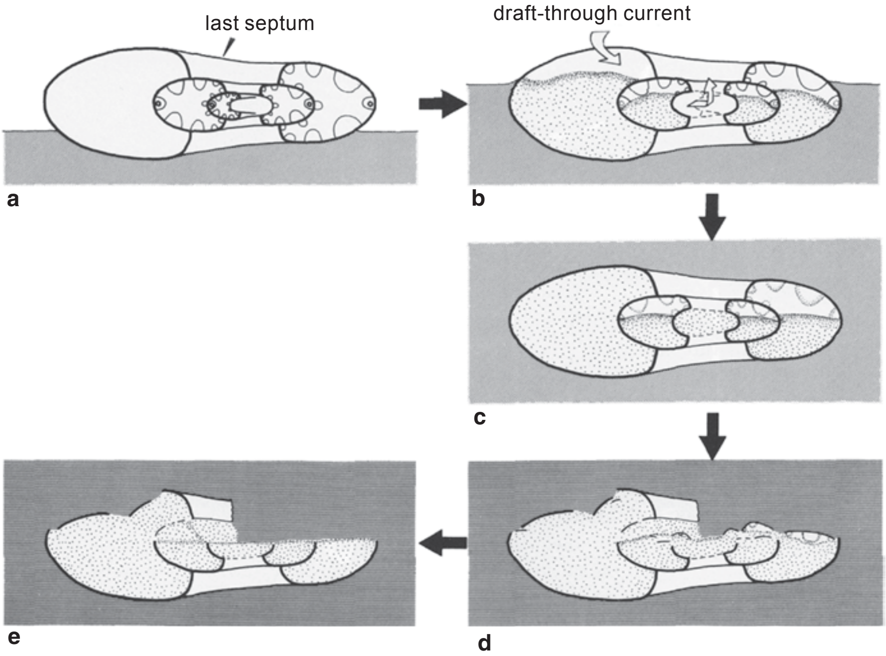

Fig. 20.11 Presumable taphonomic history of half-ammonoid preservation (modified from Maeda 1987). **a** A dead ammonoid shell settled horizontally down on the seafloor. **b** Draft-through current transported soft sediments into the phragmocone through septal necks, and piled them in the lower part of the phragmocone. **c** Dissolution of fully naked septa, without any kind of sediment sealing, began and the dissolution of the upper half might follow this. **d** The dissolution of septa triggered collapse of the upper half of phragmocone that remained empty, by compaction. **e** Crushed shell-materials had been dissolved away

20.6 Exceptional Preservation

Ammonoids consist of several materials with different chemical and physical properties: shells of calcium carbonate (outer shell walls and septa), chitinous, calcitic and aragonitic jaws, organic components of soft parts. These different physical properties are intimately linked with special diagenetic processes. IAmmonoids with complete soft tissue remains have not yet been known in the available fossil record. Soft parts of aquatic animals are generally decomposed and decayed during the early phase of taphonomic history. Only in the special case of limited decomposition and decay in anaerobic or dysaerobic condition together with rapid burial within sediments, soft parts of ammonoids were supposed to be fossilized (e.g., Seilacher et al. 1985). This is because organic components are rapidly broken down by microbes in aerobic condition (Allison 1990a). Only from the sediments of anaerobic or dysaerobic conditions together with rapid cementation during the early diagenesis, the remains of ammonoid soft parts are actually known (Lehman

1971; Seilacher et al. 1976; Hagdorn and Mundlos 1983; Weitschat 1986; Mapes 1987; Doguzhaeva and Mutvei 1991, 1996; Rein 1993, 1995, 2005; Etter 1996; Summesberger et al. 1999; Tanabe et al. 2000; Wippich and Lehmann 2004; Klug 2004; Klug et al. 2004, 2007a, 2007b, 2012; Ifrim and Stinnesbeck 2007; Landman et al. 2010; Paul 2011; Klug and Jerjen 2012, among others), although the biological nature of some structures reported as gills and ink sacs is still unclear because of the lack of detailed anatomical features.

Originally aragonitic ammonoid shells (Kulicki 1996) are commonly substituted for calcite during diagenetic processes, because calcite is mineralogically more stable than aragonite in general (Tucker 1990). At some localities all over the world of various ages, however, the unaltered aragonitic ammonoid shells that retain original shell geochemistry are preserved, so that their isotopic analyses have been done (e.g., several genera from the Triassic–Cretaceous: Lukeneder et al. 2010; the Cretaceous in Western Interior Seaway, USA: Tourtelot and Rye 1969; Whittaker et al. 1987; Fatherree et al. 1998; He et al. 2005; Cochran et al. 2003, 2010; Landman et al. 2012; Late Cretaceous in northwestern Hokkaido, Japan: Moriya et al. 2003).

Differential survival of aragonitic shells versus chitinous and calcitic jaws is also common (e.g., Tanabe 1983; Maeda and Seilacher 1996; Tanabe and Fukuda 1999; Tanabe and Landman 2002). In the Jurassic Solnfohen Plattenkalk of Germany, jaws are completely preserved within body chambers, although the shells are flattened like periostracal impressions on the bedding planes (Seilacher et al. 1976). Mapes (1987) reported the frequent occurrences of cephalopod jaws from the Mississippian–Permian of North America. Radulae and microstructure of the jaw surfaces are sometimes preserved within such preserved jaws (e.g., Lehmann 1971, 1979; Doguzhaeva and Mutvei 1992; Tanabe and Mapes 1995; Doguzhaeva and Mikhailova 2002; Kruta et al. 2011; Klug and Jerjen 2012; Tanabe et al. 2012), probably because of the condition with less dissolution prohibited by surrounding jaws, like sheltered preservation reviewed above.

Similar special preservations of soft parts (e.g., siphuncular tubes, organic membranes, digestive tract, eyes) within relatively more isolated environments (e.g., septate phragmocones) have been reported. Tanabe et al. (2000) reported exceptionally well-preserved soft-part remains within the siphuncular tubes of Permian prolecanitid ammonoids (see also Chap. 13 in Volume I). Ifrim and Stinnesbeck (2007) illustrated the goethitic stains preserved in Early Turonian ammonoids from the ‘Plattenkalk’ of Vallecillo, northeastern Mexico, which they interpreted as diagenetically pyritized stomach contents. Klug et al. (2012) illustrated the cephalic cartilage, such as eye capsules, the digestive tract, and the siphuncular tube of heteromorphic ammonoids from the laminated marlstones in northwestern Germany, which represents the Late Cenomanian Oceanic Anoxic Event (OAE2). In phragmocones of Paleozoic and Mesozoic ammonoids, furthermore, organic membranes that cover the surfaces of septa and the outer surfaces of septal necks and the siphuncular tubes are commonly recognized (Weitschat and Bandel 1991; Hewitt et al. 1991; Lominadze et al. 1993; Landman et al. 1993, 2006; Tanabe and Landman 1996; Checa and Garcia-Ruiz 1996; Tanabe et al. 2005; Polizzotto et al. 2007).

These preservations of organic membranes are probably related to more isolated environments within septate phragmocones.

20.7 Preservation of Ammonoids in Clastic Rocks

Ammonoids are commonly preserved in clastic rocks, directly from host sediments and from concretions embedded in clastic rocks. Ammonoids are generally better preserved in concretions than in the host clastic sediments (e.g., Kennedy and Cobban 1976; Maeda 1987; Dagys and Weitschat 1993; Zatoń and Marynowski 2006), probably because of the earlier cementation of the concretions than those of host rocks.

In ammonoid shells preserved both in host clastic sediments and in concretions, the sedimentation into phragmocones by draft-through currents (Fig. 20.9) has been commonly recognized (e.g., Tanabe et al 1984; Maeda 1987; Maeda et al 2010). The phragmocones partially filled with sediments and subsequent diagenetic processes sometimes display the half-ammonoid preservation in clastic rocks (Maeda 1987; Maeda and Seilacher 1996; Maeda et al. 2010). Recently, Maeda et al. (2010) examined large Campanian pachydiscid shells (50–800 mm in shell diameter) from the Naiba area in south Sakhalin, Russia, in which the body and air chambers are somewhat compressed by compaction and are filled with sediments. These authors commonly recognized *Phycosiphon* burrows in both open body chambers and inside the phragmocones of these ammonoid shells. Based on these observations, Maeda et al. (2010) suggested that the inner whorls and siphuncular tubes degraded before the final burial and therefore sediment infilling to the inside of the phragmocones by draft-through currents followed. After the partial sedimentation within the phragmocones, the continuous supply of oxygen and nutrients by the draft-through currents supported the *Phycosiphon* producers in the inside of phragmocones, therefore displaying the unique relationship between the partially filled phragmocone of pachydiscid shells and the *Phycosiphon* producers within the phragmocones (Maeda et al. 2010).

The phragmocones partially filled with sediments can be directly observed as geopetal-void structure (for ammonoids preserved in clastic rocks; e.g., Hudson 1982; Wani 2001). The geopetal-void structure makes it possible to determine whether they are the right way up (i.e., in the attitude in which they were originally deposited) and to recognize parts of their taphonomic history during which they were lying on the seafloor and when early cementation of infilling sediments after the burial under the seafloor occurred. Wani (2001) recognized two upward directions within a single ammonoid shell from the Upper Cretaceous of Hokkaido, Japan, which cannot be formed by a single sedimentary event with draft-through currents, and concluded that the shells were reworked after the initial burial during which one of the upward directions was preserved. Furthermore, based on the comparison of fragmentation patterns with those of modern nautili that are experimentally produced (Wani 2001, 2004) and detailed observation of the shell fragments, Wani (2001) interpreted that (1) most shells were fragmented within sediments by

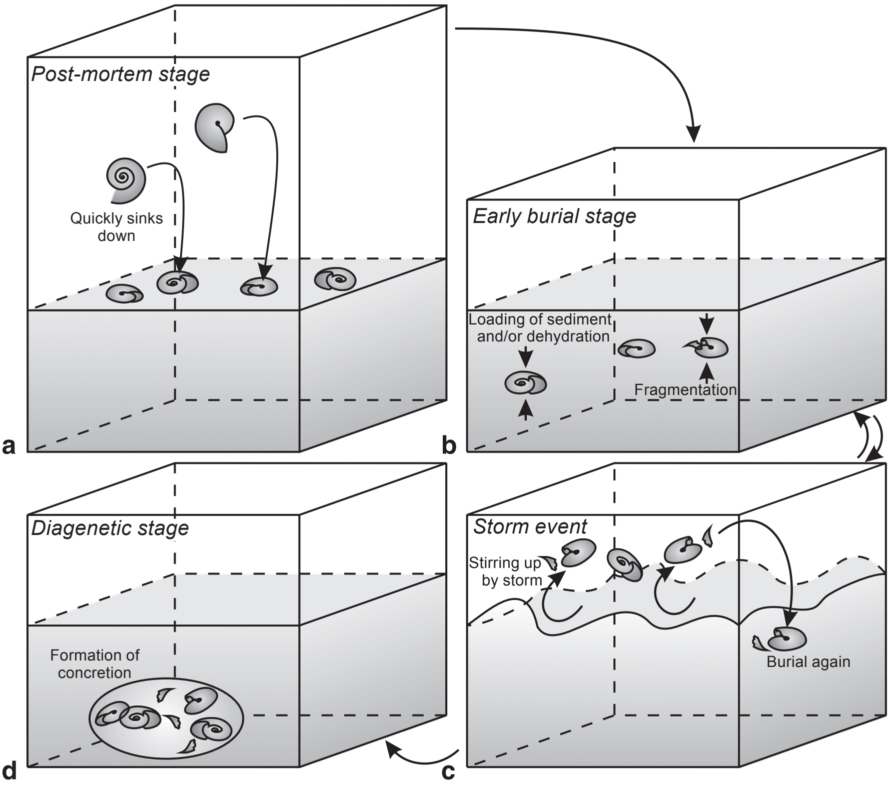

Fig. 20.12 Reconstructed taphonomic interpretation of ammonoids preserved in calcareous concretions embedded within clastic rocks (modified from Wani 2001). **a** After the death of the animals, the shells sank to the sediment-water interface in the post mortem stage. **b** In the early burial stage, loading and/or dehydration of sediment worked as a causal factor of fragmentation of some shells. **c** Ammonoid shells were lifted during storm events, and reburied. **d** Calcareous concretions formed in the early diagenetic stage

sediment loading, and then reworked (Fig. 20.12); (2) such reworking events are not rare in the Upper Cretaceous of Hokkaido (e.g., Wani 2003, 2006, 2007a), probably in relation to the storm-dominated shelf setting of a fore-arc basin with high sedimentation rates (e.g., 270–370 mm/10^3 years in the outer shelf environment of the Upper Cretaceous in northwestern Hokkaido; Okada and Matsumoto 1969; Takashima et al 2004). In particular, the taphonomic history of the late Campanian ammonoid *Metaplacenticeras subtilistriatum* reconstructed in Wani (2006) is closely linked to its streamlined, oxyconic shell with flat flanks and a smoothly tapering venter. Flume experiments by Wani and Ikeda (2006) suggest that such streamlined shells might have been transported together with pebbles by water currents (>0.25–0.5 m/s; Fritz and Moore 1988; Fig. 20.8a), and thereby, the shells possibly collided with pebbles and then fractured. In fact, the taphonomic attributes of *M. subtilistriatum* characteristically display the broken ventral portions (Wani 2006, Fig. 20.4), which are comparable to the experimentally reproduced fragmentation pattern by collision during transport by water current (Wani 2004, Fig. 20.3). These results suggest the effectuality to combine the detailed observations of taphonomic attributes of ammonoid shells and the experimental approaches with modern analogues,in order to reconstruct and recognize the taphonomic history of ammonoids in detail.

20.7.1 Preservation of Ammonoids in Claystones

Among the different kinds of preservation of ammonoids in various clastic deposits, those in claystones are especially highlighted herein, because they generally display characteristic preservational features, which are different from those in other clastic sediments reviewed above. In claystones, most of which are deposited in stagnant environments with low sedimentation rates (e.g., Seilacher 1982), the shells usually become strongly flattened. This is the case because the coarser-grained sediments are more resistant to compaction resulting from the supporting effect of the grains and the lower pore-water volume (Briggs 1990). Such flattened ammonoid shells are well known and reported from numerous localities where they are preserved within claystones or shales, except where ammonoid shells are preserved in concretions (e.g., the Posidonienschiefer at Holzmaden in West Germany: De Baets et al. 2013; the Oxford Clay in Southern and Midland England: Page 1991, Tang 2002; the Late Bajocian and Bathonian in South–Central Poland: Zatoń and Marynowski 2006; the Late Cretaceous Mancos Shale of Utah: Stephen et al. 2012).

The flattened ammonoid shells mainly from the Posidonienschiefer at Holzmaden in West Germany (Toarcian, Early Jurassic) and also from other localities have been hitherto examined in numerous articles and the sedimentary environments as well as the taphonomic histories have been reconstructed (Seilacher et al. 1976; Kauffman 1978; Seilacher 1982; Wild 1990; Hudson and Martill 1991; Etter and Tang 2002). According to Seilacher et al. (1976), shell dissolution, compaction, and cementation processes during early diagenesis have been classified into several types (Fig. 20.13), which resulted from the heterochronous interplay of shell strength, compactional flattening, aragonite dissolution, mud stiffening, and concretionary cementation. In a stagnant environment with relatively low turbulence, only the body chambers became sediment filled, while most of the phragmocones remained empty (Seilacher et al. 1976; Maeda and Seilacher 1996), which resulted in more complete flattening of the phragmocones than of the body chamber (Fig. 20.13i). The cementation process during early diagenesis also played an important role, because fossil evidences suggest that the shell aragonite dissolved during the time period between body chamber and phragmocone collapse (i.e., two-phase collapse; Seilacher et al. 1976).

Ammonoid shells preserved in claystones are known to commonly co-occur with and/or to be preserved in pyrite (FeS_2) or siderite ($FeCO_3$), the latter of which sometimes forms siderite concretions (Seilacher et al. 1976; Saunders and Richardson 1979; Hudson 1982; Curtis et al. 2000; Doguzhaeva et al. 2007; Young et al. 2010). Associated with anaerobic decay of organic carbon (Allison 1990b), siderite

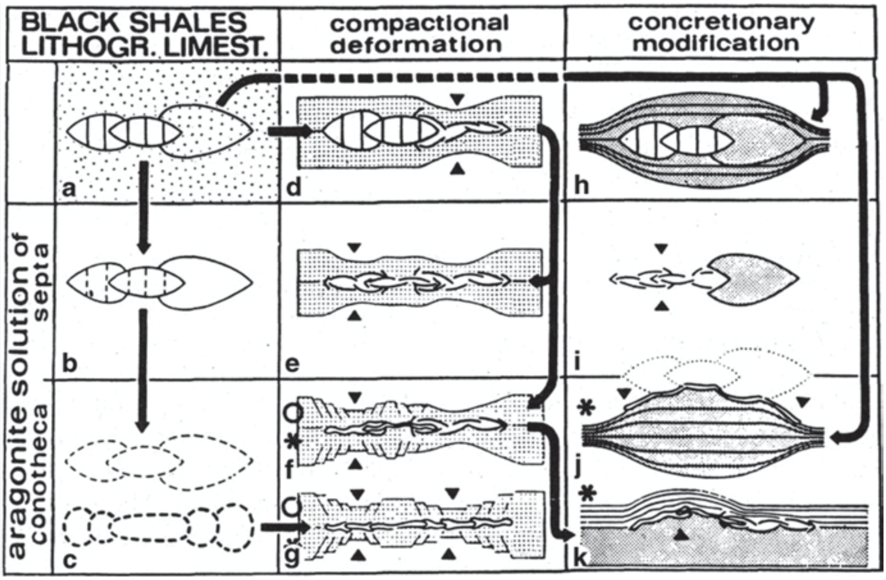

Fig. 20.13 Case histories of ammonoid preservation in the Posidonienschiefer and the Solnhofen Plattenkalk (Jurassic of Germany; modified from Seilacher et al. 1976). **a** Unaltered shell, which is preserved by early cementation. **b** Hypothetical hollow phragmocone stage. **c** Periostracum foil, undeformed. **d** Body chamber collapsed with telescope fracture. In the absence of early cementation, oxyconic shells suffered the first collapse in body chamber. **e** Beer mat preservation after second collapse phase. Telescope fractures on both shell flanks indicate a two-phase collapse. **f** Partial leaf preservation. Because aragonite dissolved between the two collapsing events, oxyconic shells from Holzmaden show rigid fractures on body chambers and soft compaction on phragmocones. **g** Entire leaf preservation. Evolute shells show rigid fractures on body chambers and soft compaction on phragmocones, with their outline always remaining a smooth spiral in spite of no keel to catch the fragments. **h** Nucleus concretion, which may contain the stage d. Undeformed shells are preserved only by early cementation of the surrounding sediments. **i** Body chamber concretion. Body chambers filled by sediment and empty phragmocones result in more complete flattening of the phragmocones than of the body chamber. **j** Umbilicus concretion. Concretions formed below the lower umbilicus, so that only the central part of shells left an undeformed impression. **k** Phragmocone dome. Already flattened shells are pushed up by a cementation front ascending from an underlying bed

is produced under conditions without sulfuric acid ion (SO_4^{2-}). Sulfuric acid ion completely consumes below several meters below the seafloor in a modern, fine-grained, clastic, continental shelf (Borowski et al. 1999). Pyrite is produced by sulphate reduction under dysaerobic conditions with sulfuric acid ions (SO_4^{2-}) during early diagenesis where hydrogen sulphide (H_2S) generated by the decomposition of organic matter that has reacted with iron, so that this must have occurred before sediment compaction (Raiswell 1976; Hudson 1982; Berner 1984; Young et al. 2010). These early diagenetic cementation processes enhance the possibility to preserve ammonoid shells uncrushed and unflattened within the host claystones and sideritic concretions embedded in the claystones (e.g., Seilacher et al. 1976; Hudson 1982; Riegraf et al. 1984; Curtis et al. 2000; Schellenberg 2002; Tang 2002; Paul 2011).

In relation to these early diagenetic cementation processes, dysaerobic conditions generally prevent organic materials from decaying (e.g., soft parts, periostracum, siphuncular tubes; Seilacher et al. 1985). However, even from such claystones and concretions embedded within the claystones that were probably deposited under dysaerobic conditions, the remains of ammonoid soft parts are exceedingly rare (Lehmann 1971; Weitschat 1986; Doguzhaeva and Mutvei 1991, 1996; Etter 1996; Klug et al. 2007a, 2012; Paul 2011), although the soft parts of coleoids (tentacles, ink sac, eyes, mantle muscles, intestines, blood vessels, and gills) are sometimes preserved in claystones (from the Late Pennsylvanian of Mazon Creek: Schellenberg 2002; Doguzhaeva et al. 2007; from the Hettangian of Somerset: Klug and Fuchs 2010; from the Toarcian of Holzmaden: Riegraf 1982, 1983; Reitner and Urlichs 1983; Riegraf and Hauff 1983; Riegraf et al. 1984, 1998; Etter and Tang 2002; from the Callovian of Ardèche, France: Fischer and Riou 1982; from the Callovian to Oxfordian Oxford Clay Formation: Donovan 1983; Martill 1987; Allison 1988; Donovan and Crane 1992; Kear et al. 1995; Tang 2002; from the Permian Arcturus Formation, Nevada: Landman et al. 2006a; Fuchs 2006a). This discrepancy between ammonoids and coleoids suggests that ammonoid musculature was perhaps so weak that it had a much lower fossilization potential than that in strong swimmers such as coleoids (Maeda and Seilacher 1996). On the other hand, chitinous jaws of ammonoids, which generally have a higher fossilization potential than soft parts, are sometimes preserved within claystones or concretions embedded within the claystones at various localities (from the Mazon Creek of Pennsylvanian, Saunders and Richardson 1979; from the Mississippian–Permian of North America, Mapes 1987; from a black platy shale of the Fayetteville Formation of Late Mississippian, Tanabe and Mapes 1995; from the Posidonienschiefer of Toarcian, Etter and Tang 2002; Klug et al. 2007a).

Early diagenetic cementation processes possibly played an important role to preserve ammonoid shells (e.g., Fig. 20.13h; Zatoń and Marynowski 2006; Stephen et al. 2012). In some cases, the preservational styles are similar to those in the clastic rocks with coarser grain size reviewed above. The Late Bajocian and Bathonian in South–Central Poland are composed mainly of dark-grey claystones with siderite and carbonate concretions, in which ammonoid shells (especially small, juvenile ones) were accumulated together with plant remains by bottom currents on the seafloor (Zatoń and Marynowski 2006). Zatoń and Marynowski (2006) suggest that the early diagenesis forming the siderite and calcareous concretions occurred under a sediment cover of tens of cm to even a few meters. This resulted in well-preserved ammonoid assemblages probably reflecting the composition of the original biological assemblage well. Stephen et al. (2012) examined dense concentrations of juvenile ammonoids in the Late Cretaceous Mancos Shale of Utah, and hypothesized the cause as the semelparous reproductive strategy of ammonoids, environmentally driven mass mortality, and a peculiar taphonomic phenomenon (condensed intervals, post mortem hydrodynamic transportation, etc.). Tanabe et al. (1993, 1995) examined the concentrated occurrence of embryonic ammonoids in carbonate concretions from offshore shales of the Late Pennsylvanian in Kansas, the Late Mississipian in Texas, and the Middle Carboniferous (Namurian) in England and west Ireland.

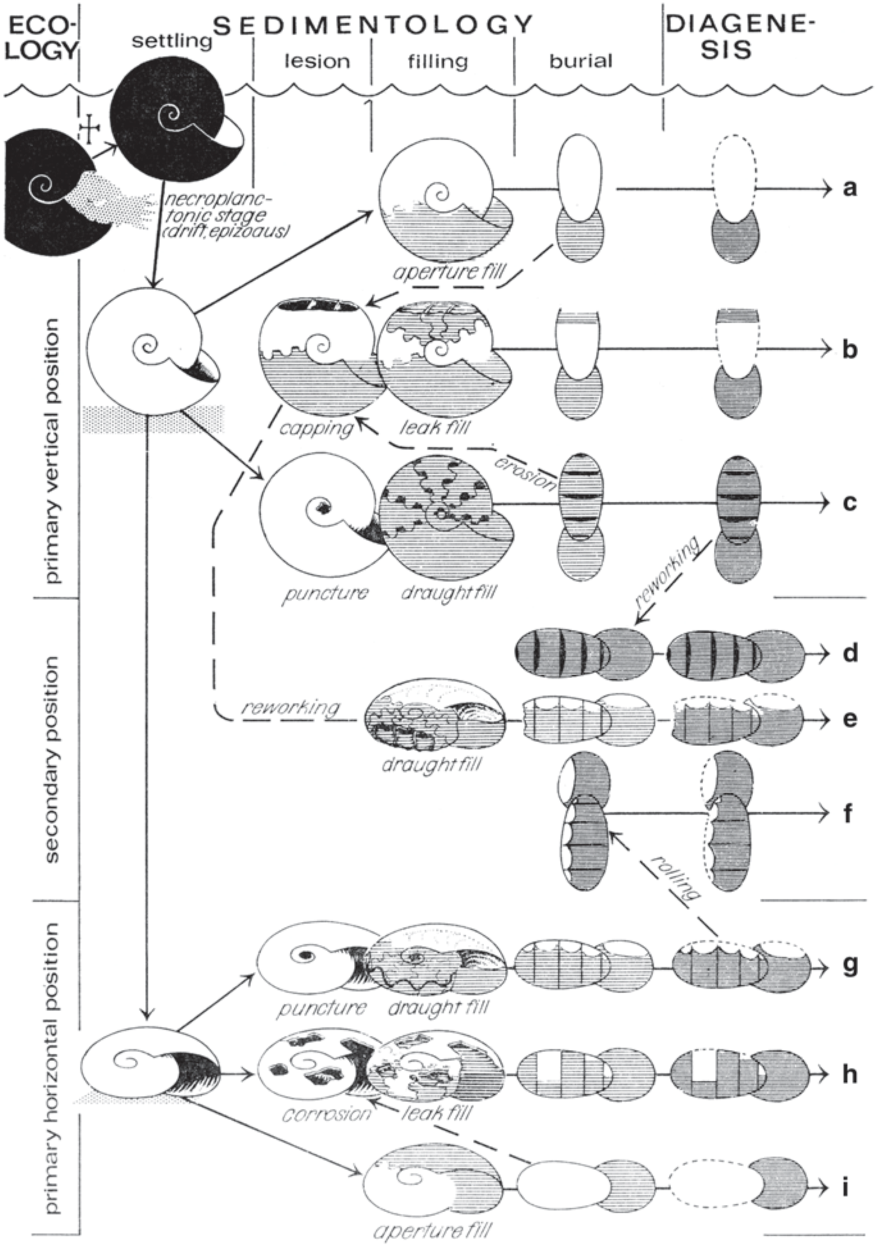

Fig. 20.14 Case histories of ceratite preservation in the Muschelkalk (Triassic of Germany; modified from Seilacher 1971). **a** Due to rapid burial of the upright shell, the phragmocone remains unfilled and disappeared during shell dissolution. **b** Upright shells become re-exposed and capped by erosion so that sediment could fill into some of the chambers. **c** A puncture allows the phragmocone to draft fill before it becomes completely buried, retaining the upright position and lobe voids recording the filling mechanism. **d** Reworking has brought ore-fossilized specimens of case

Ammonoid shells have been rarely reported from shales deposited in brackish water or mud beach environments, although their shells have been reconstructed to have floated and drifted over some distance prior to beaching in muddy beach facies (in the Early Permian from Central Texas, USA; Maeda et al. 2003). Such ammonoid shells transported and beached into muddy beach facies are possibly preserved and recognized within claystones in a few rare cases.

20.8 Preservation of Ammonoids in Carbonates

The supposed taphonomic history of ammonoid shells in carbonates is basically similar to those in clastic rocks: e.g., partial sediment infill of the phragmocones by draft-through currents, early diagenesis forming concretions that generally contain well preserved shells. The exception is in the exposure time of shells near the seafloor in relation to low rates of background sedimentation and lower levels of water turbulence in many carbonate environments (generally <100 mm/10^3 years in ancient carbonate settings; Wright and Burchette 1996), which probably had an important role to differentiate the preservational styles between carbonates and clastic rocks (e.g., Fernández-López et al. 2000; Olóriz et al. 2002; Preto et al. 2005; Fernández-López 2007, 2008, 2011).

Seilacher (1971) examined the taphonomic attributes of the ceratite shells from the Upper Muschelkalk of Germany (Middle Triassic) and classified them into several categories, which resulted from different combinations of shell attitude and fill mechanisms, and sometimes from the resedimentation of pre-buried and pre-fossilized shells (Fig. 20.14). Partial sedimentation in phragmocones by draft-through currents and therefore geopetal-void structures are observed (Fig. 20.14; for other carbonate environments, see, e.g., Wendt 1973; Neumann et al. 1976; Curtis et al. 2000; Martire and Torta 2000; Olóriz et al. 2002; Preto et al. 2005; Hornung et al. 2007; Fernández-López 2008). However, because of low rates of background sedimentation and lower levels of water turbulence, prefossilized shells were able to become partially exposed during the later sedimentation events. During the exposure, the upper unfilled parts of the shells were dissolved away (Fig. 20.14).

Similar partly dissolved shells after partial infilling of the phragmocones are commonly developed in various carbonate environments (Seilacher 1963; Wendt 1973; Neumann et al. 1976; Hagdorn and Mundlos 1983; Martín-Algarra and Sánchez-Navas 1995; Curtis et al. 2000; Martire and Torta 2000; Fernández-López 2000, 2008, 2011; Fernández-López et al. 2002; Olóriz et al. 2002, 2004; Fernández-López and

c into horizontal position, but they preserve the lobe voids from their primary upright position. **e** The shells of case (b), reworked before their sedimentary filling had become hardened, can be distinguished from case g by cappings inconsistent with their present position. **f** Reworking of pre-fossilized shells of case (g) from horizontal into upright position. **g** Like case (c), but without lobe voids; instead, draft filling often leaves a sinus-shaped fill channel above the mid-line of the phragmocone and/or sickle marks on the infill of the body chamber. **h** Like case (b), but leaks situated on flank. **i** Like case (a), but after the shell had been tipped into horizontal position. Light hatching, filled with soft sediments. Dark hatching, fill sediment diagenetically hardened

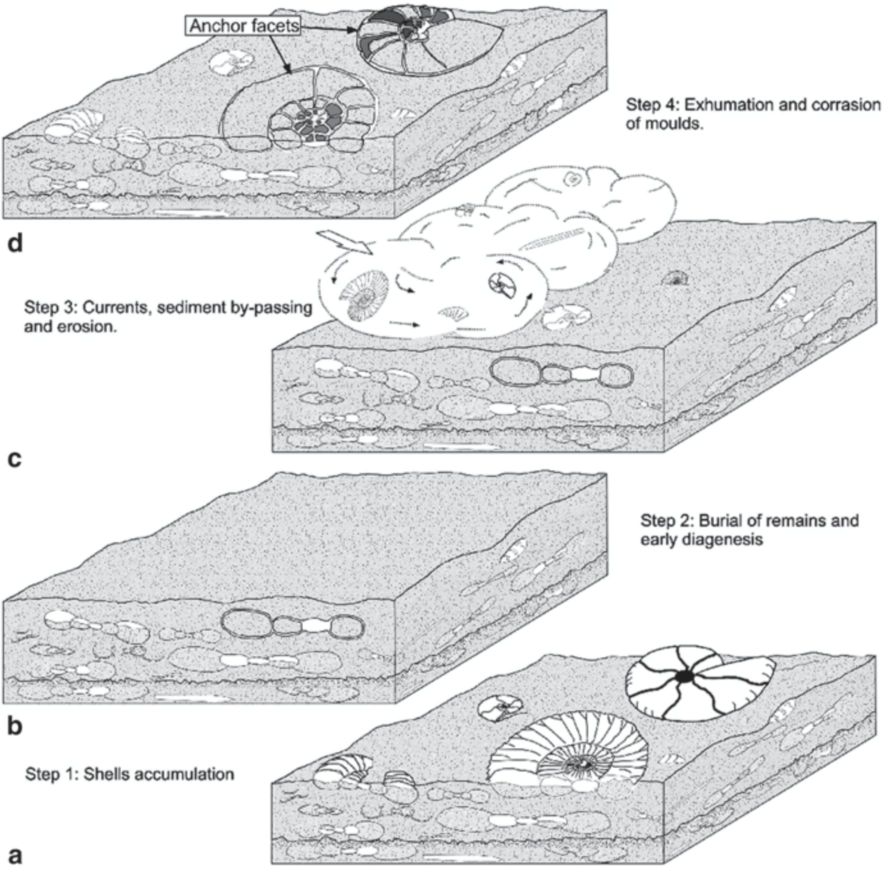

Fig. 20.15 Steps leading to the formation of the anchor facets, which are abraded internal moulds of ammonoid shells, showing a kind of truncational facets (in the Middle Jurassic of southeastern Spain; modified from Reolid et al. 2010). Anchor facets are produced when shells are strongly fixed to the grounds so that the exposed surface is worn (**d**), after shell accumulation (**a**), burial of remains and early diagenesis (**b**), and currents, sediment by-passing and erosion (**c**)

Meléndez 2004; Preto et al. 2005; Hornung et al. 2007; Reolid et al. 2010; Fig. 20.15). Due to the partial filling of the phragmocones and selective cementation of the fill sediment (i.e., pressure-shadow concretion), the sediments surrounding the shells replicated the suture lines on the internal mold, resulting in the replica acting as a stencil projecting the "*relief*" of the original suture lines into deeper levels during the later diagenetic stage, where they intersect with less undulating cross sections of the respective septa as double suture lines (Seilacher 1988). After the partial dissolution of ammonoid shells on the seafloor, shells are known to get sometimes reworked in various carbonate settings (Seilacher 1963, 1968, 1971; Martire and Torta 2000; Fernández-López et al. 2000; Fernández-López 2000, 2007, 2008, 2011, Reolid et al. 2010).

Within the fine-grained carbonates (e.g., marls), flattened ammonoid shells and steinkerns with their aragonitic shells dissolved are commonly developed similar as those in claystones (e.g., from the Muschelkalk of Germany, Seilacher 1971; from the Basque-Cantabrian Basin, northern Spain, Lopez-Horgue et al. 2009; from the Cretaceous Chalk in England, Wright and Kennedy 1981, 1984; from the Solnfohen Plattenkalk of Germany, Seilacher et al. 1976; Barthel et al. 1990; Etter 2002; Fig. 20.13; from the Provincial Formation of Villa Clara Province, Cuba, Barrágan et al. 2011). From such flattened shells and also from concretions or steinkerns embedded in host carbonates, which probably related to the early cementation process (Fig. 20.14), original organic structures (e.g., periostracum, and siphuncular tubes) have been found occasionally (Seilacher et al. 1976; Hagdorn and Mundlos 1983; Mapes 1987; Wang and Westermann 1993; Rein 1993, 1995, 2005; Tanabe et al. 2000; Klug 2004; Klug et al. 2004, 2007a, 2007b). However, the remains of ammonoid soft parts are exceedingly rare also from carbonates, although, in contrast, soft parts of coleoids have been more frequently reported from the Solnhofen Plattenkalk (Tithonian; Bandel and Leich 1986; Mehl 1990; Engeser and Reitner 1992; Briggs et al. 1993; Frickhinger 1994, 1999; Donovan 1995; Briggs and Wilby 1996; Engeser and Keupp 1997, 1999; Donovan et al. 2002), from La Voulte-sur-Rhône, France (Callovian; Fischer and Riou 1982; Fröhlich et al. 1992; Wilby et al. 1995, 1996; Etter 2002; Haas 2002; Charbonnier et al. 2007; Charbonnier 2009), from the Nusplinger Plattenkalk (Kimmeridgian; Schweigert 1998; Schweigert and Dietl 1999, 2001; Klug et al. 2005), and from the Late Cretaceous Plattenkalks of Lebanon (Cenomanian; Fuchs 2006b; Fuchs and Larson 2011a, 2011b).

20.9 Conclusions and Future Researches

In this chapter, present knowledge about ammonoid taphonomy (necrosis, biostratinomy, and diagenesis) is reviewed, especially focusing on the recent literatures published after 1996. For further recognition of necrosis and fossils diagenesis of organic components, new data using pyrolysis-gas chromatography-mass spectrometry (Py-GC-MS) were shown. Fossil ammonoids display no moieties diagnostic of the chitin biopolymer, although it was detected in modern cephalopods, possibly as it is prone to degradation by chitinophosphatic bacteria as well as by oxidation and hydrolysis (for a detailed discussion, see Gupta et al. 2008). Reconstruction of ammonoid biostratinomy has improved based on experimental techniques with modern analogues (modern nautilus shells, plastic models). The similarities between taphonomic attributes expected from these techniques and actual preservation styles suggest the efficiency of experimental approaches to reconstruct and recognize ammonoid biostratinomy. Diagenetic processes are related to the degree of sediment infilling into septate phragmocones and early diagenetic cementation. The unique shell structure of ammonoids (i.e., septate phragmocone with a penetrating siphuncle) yields phragmocones partly filled by sediments. This resulted in the difference of shell toughness during diagenetic processes, so that various preservational styles of compaction and subsequent dissolution are developed. Relatively isolated environments within septate phragmocones and body chambers also played an important role to preserve tiny little ammonoid shells, organic components of soft parts, and chitinous and calcareous jaw elements that are generally rarely fossilized due to their brittle physical properties. The remnants of ammonoid soft parts (e.g., siphuncular tissues, muscles) and organic hard tissues such as jaw apparatuses, radulae, and cameral membranes are sometimes preserved within their septate phragmocones and body chambers. These preservational characteristics suggest the uniqueness of ectocochleate cephalopod taphonomy.

In future studies of ammonoid taphonomy, one of interesting fields is seeking exceptional preservation of ammonoid soft parts. If we find them, or if we can correctly recognize why soft part preservation of ammonoids is extremely rare, relative to other cephalopods (e.g., coleoids), our knowledge about ammonoid paleobiology (e.g., anatomy of soft parts and its phylogenetic implications) and paleoecology(e.g., feeding habits, mode of life, unique taphonomic history) will definitely increase. The anatomy of soft parts in modern nautili (e.g., Sasaki et al. 2010) would provide a comparable model to recognize the similarity and/or dissimilarity to those in ammonoids.

Furthermore, the attachment scars of ammonoid soft tissues have potentially preserved inside their body chamber, which would have a chance to fossilize due to more isolated environments within ammonoid shells. It is very important to recognize in detail whether or not muscular system and therefore muscle attachments are similar to those in modern nautili, because it is a key factor how to prevent seawater from waterlogged by ambient water pressure (Wani et al. 2005; see Chap. 20.4.3). How to maintain the neutral buoyancy in ammonoids is crucial not only to reconstruct their post mortem biostratinomic history but also to recognize ammonoid paleobiology and paleoecology.

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