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

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

et al. 2010). Despite this long history of biostratigraphic research and key evo-
lutionary 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 extinc-
tion (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, Gymni-
tidae, Ptychitidae, Isculitidae, Cladiscitidae, Arcestidae, Sphingitidae and Joanniti-
dae) 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 Tri-
assic 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 stand-
ing 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 mac-
roevolutionary 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 Fora-
minifera (Gould 1988; Norris 1991), increasing complexity of life forms from eu-
karyotic 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 pat-
terns 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
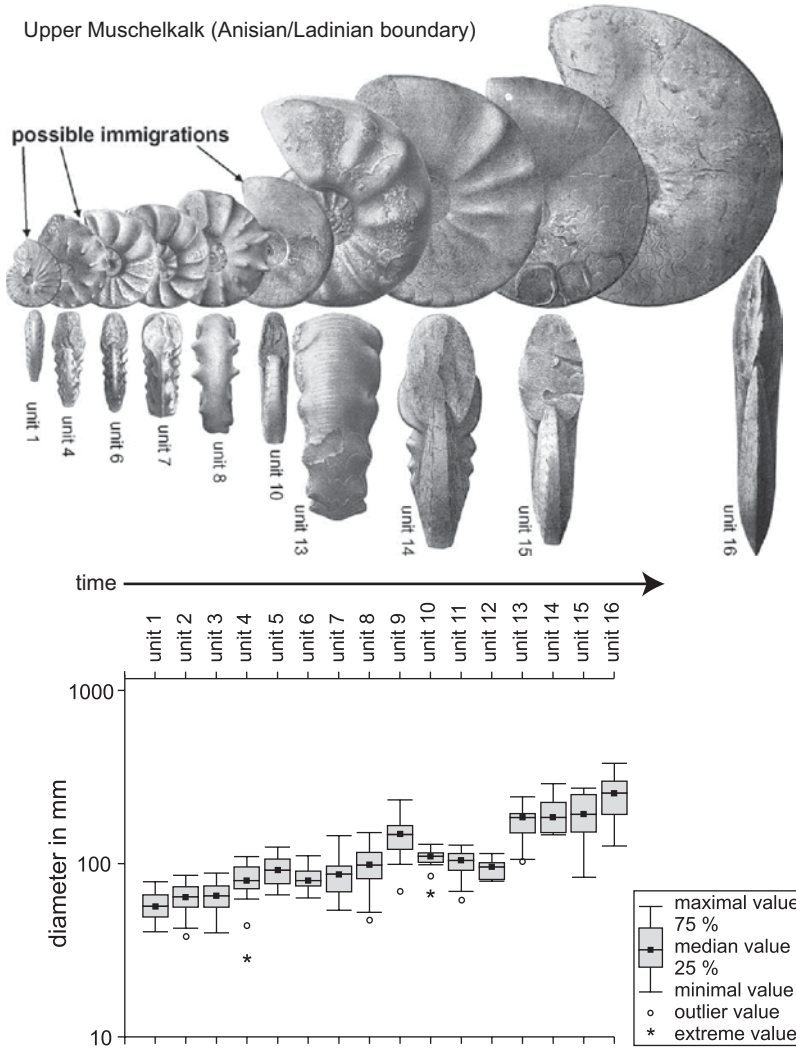
Fig. 2.1 Stratophenetic evolutionary trend of size increase of ammonoids during the deposition of the *Upper Muschelkalk* (Middle Triassic) of the Germanic Basin (modified after Klug et al. 2005)

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).
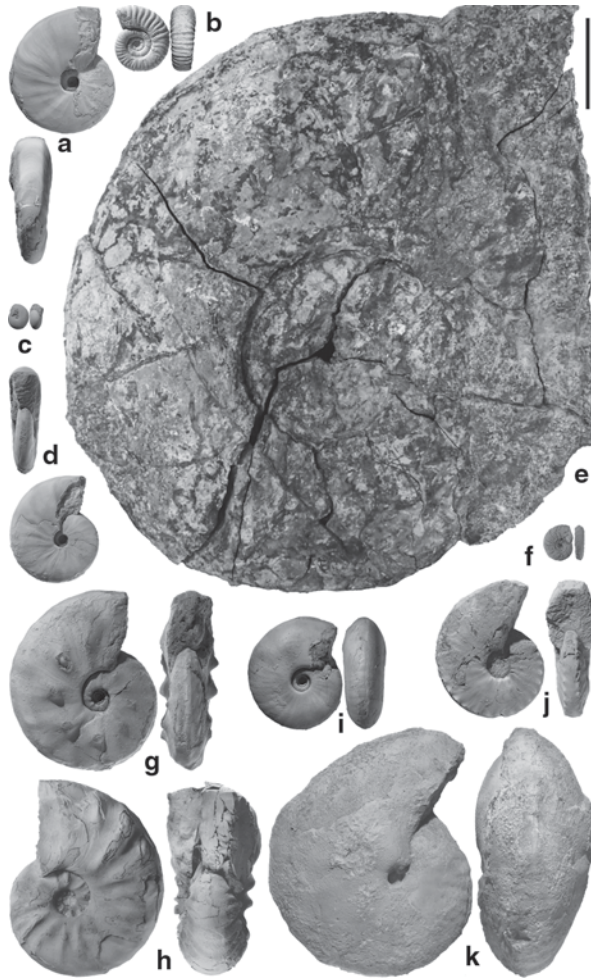
Fig. 2.2 The vast range of shell size in Triassic ammonoids. **a** *Billingsites cordeyi* (Anisian; after Monnet and Bucher 2005, pl. 7 Fig. 3). **b** *Paracrochordiceras americanum* (Anisian; after Bucher 2002, pl. 1 Figs. 1,2). **c** *Paranannites dubius* (Smithian; after Brayard and Bucher 2008, pl. 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
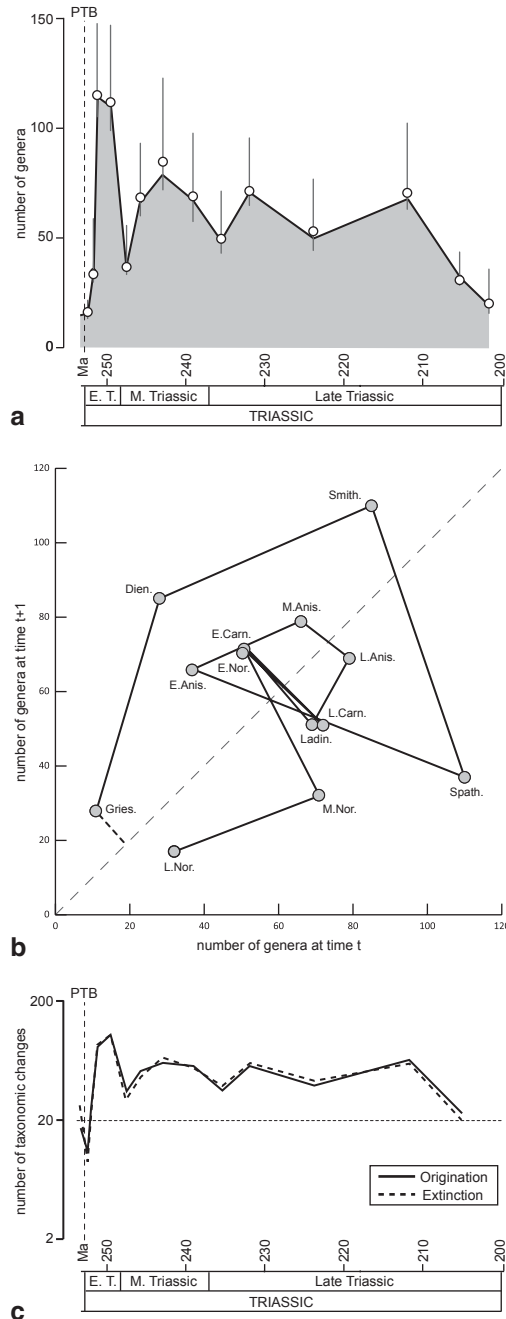
Fig. 2.3 Trends of taxonomic diversity of Triassic ammonoids (modified after Brayard et al. 2009). **a** Generic richness of Triassic ammonoids: black bold line: total generic richness (observed + inferred occurrences); large circles with vertical bars: mean Chao2 estimate of the overall generic richness 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 re-stricted 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 mark-edly delay the explosive recovery of ceratitid ammonoids, although it was the most important one within the entire Triassic. Other significant extinction events for am-monoids 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 fruit-fully focused upon taxonomic diversity (see above). However, there are multiple facets/metrics of biodiversity (e.g., genetic, morphological, ecological, phyloge-netic, 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 explo-sive 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 extinc-tion 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).
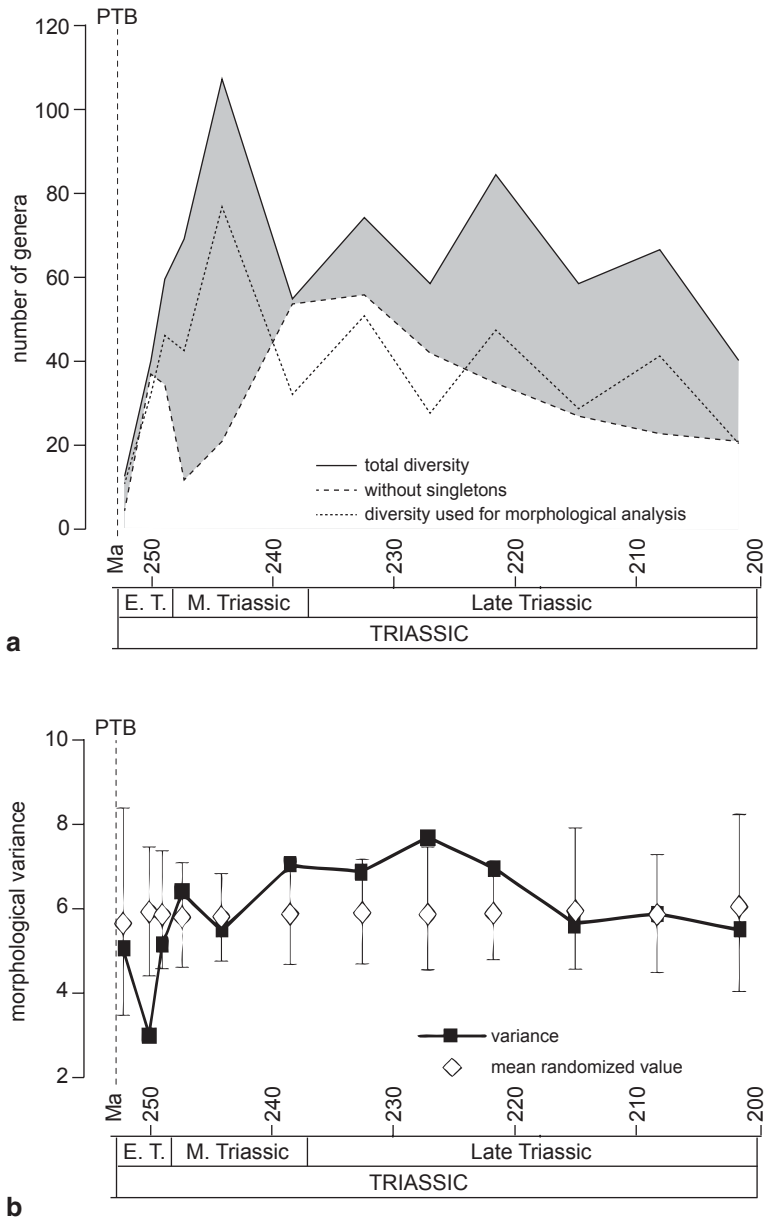
Fig. 2.5 Morphological disparity of Triassic ammonoids (modified after McGowan 2004). **a** Taxonomic diversity at the genus rank (total diversity and without singletons) and sampled diversity for analyzing morphological disparity (but compare with the more recent diversity curve of Brayard et al. 2009; Fig. 2.3). **b** Observed morphological disparity, as well as mean value and 90 % confidence interval for randomized samples
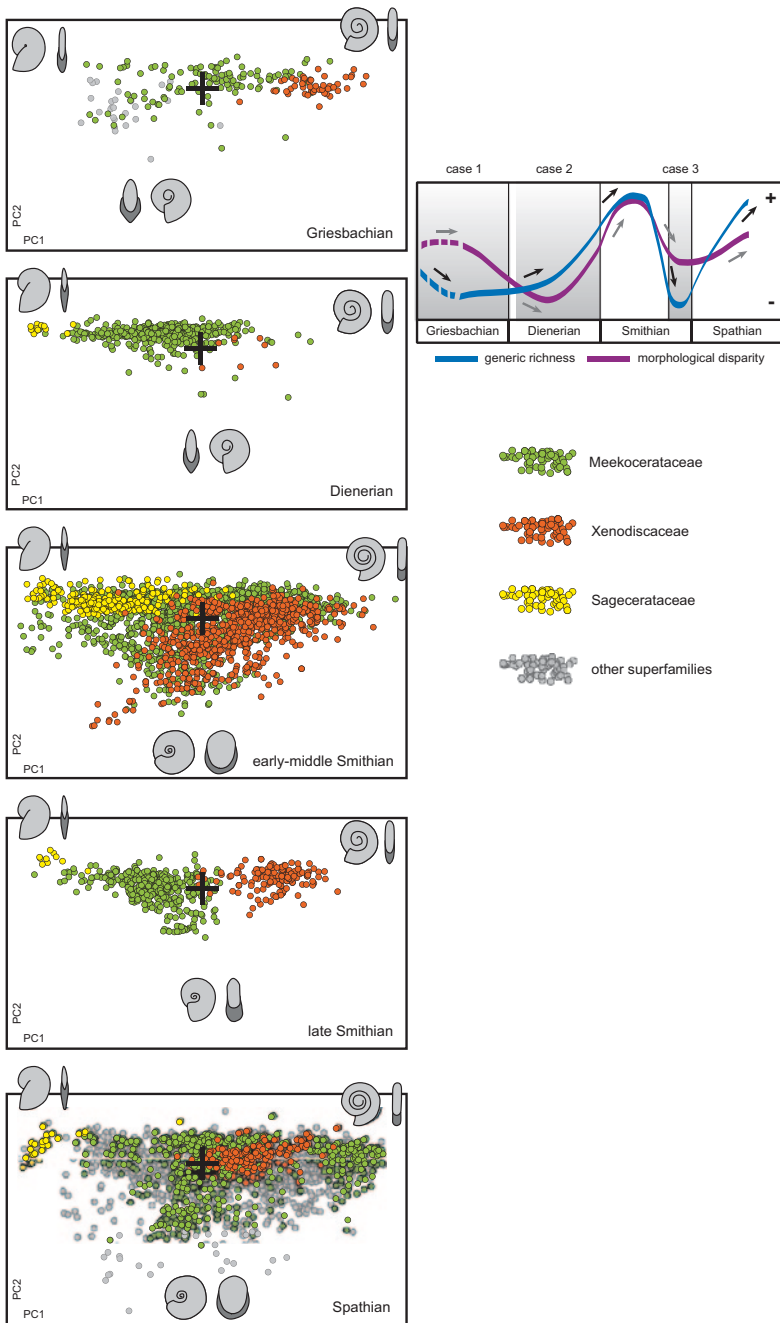
Fig. 2.6 Trends in morphological disparity of Early Triassic ammonoids (modified after Brosse et al. 2013). Superimposition of generic richness and disparity curves and evolution of the morphospace occupation, with the three main superfamilies highlighted, for each of the five studied time bins

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).
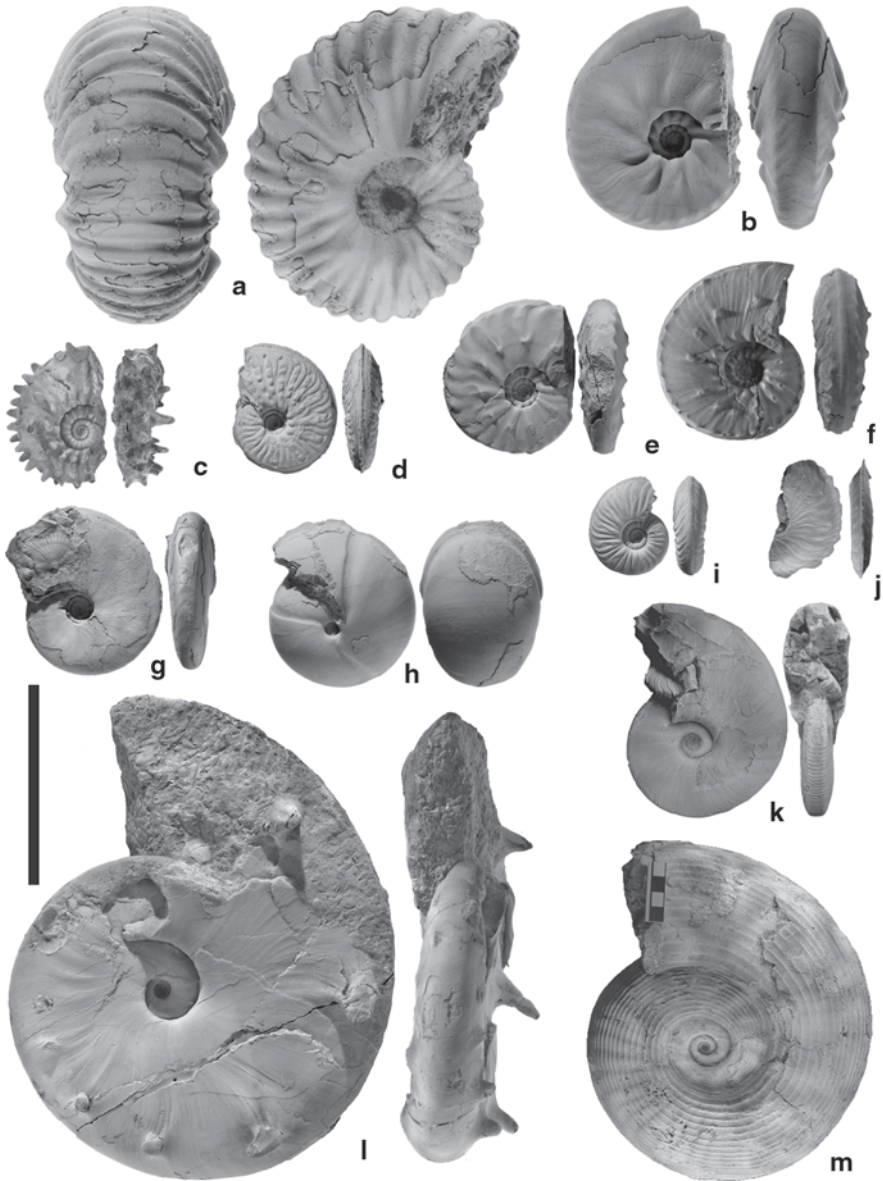
Fig. 2.7 Ornamentation of Triassic ammonoids. If not stated otherwise, the images are from Monnet and Bucher (2005). **a** *Acrochordiceras carolinae* (Anisian; after Monnet et al. 2010). **b** *Dixieceras* lawsoni (Anisian). **c** *Brackites spinosus* (Anisian). **d** *Eutomoceras dunni* (Anisian). **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
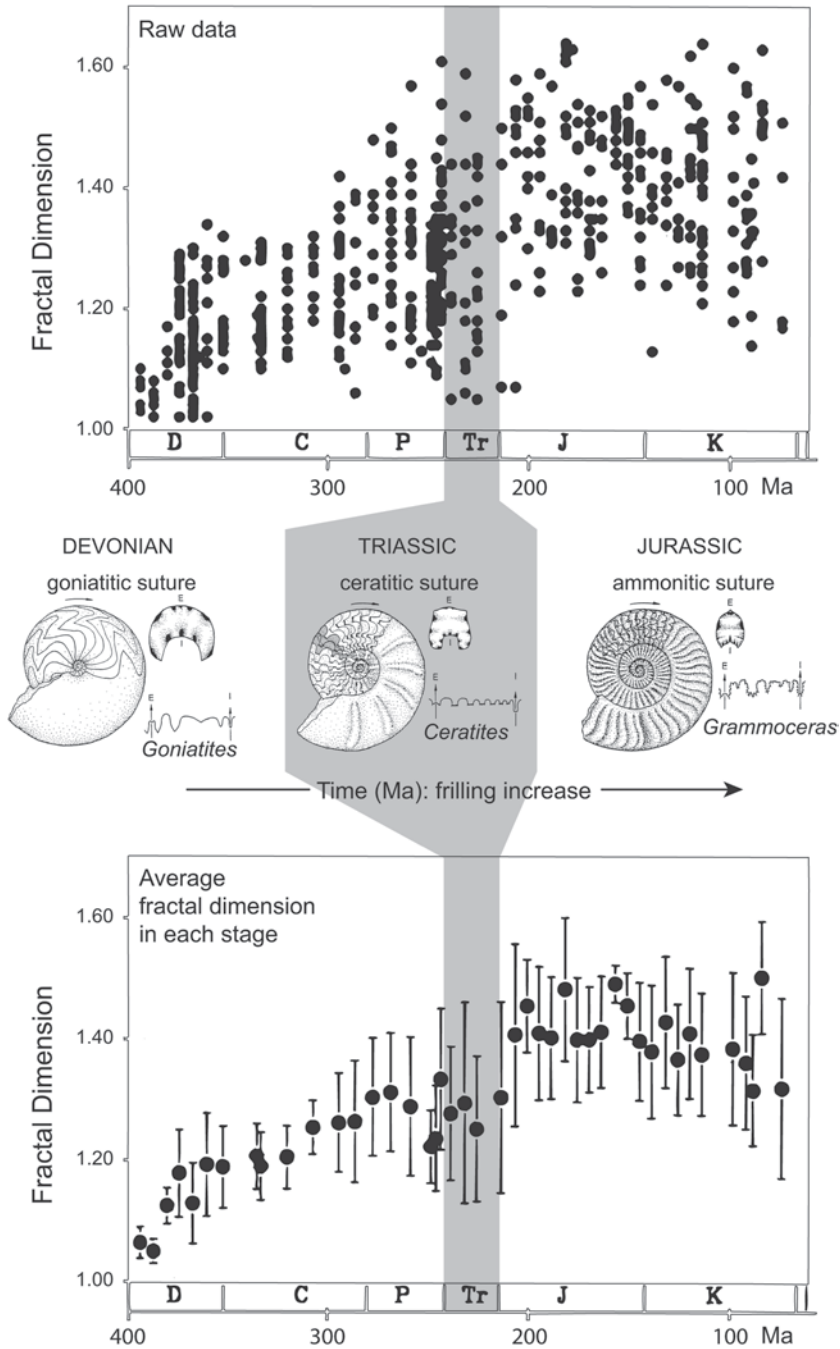
Fig. 2.8 Evolutionary trend in the fractal dimension of ammonoid suture throughout their entire history (modified after Boyajian and Lutz 1992) and illustration of the three major suture patterns (goniatitic, ceratitic, and ammonitic)
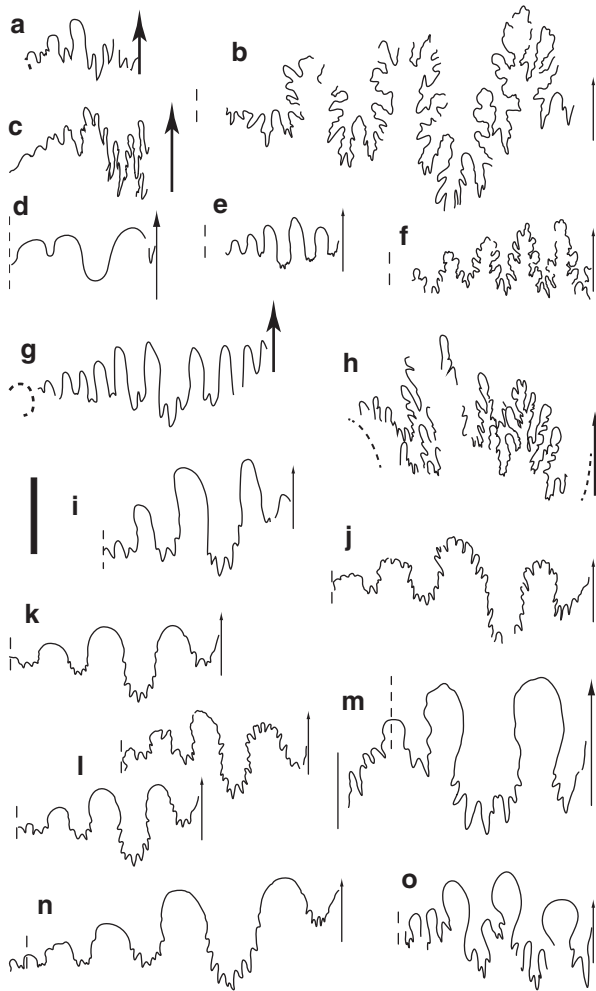
Fig. 2.9 The vast range of suture shapes in Triassic ammonoids. If not stated otherwise, the images are from Monnet and Bucher (2005). **a** *Xiaoqiaoceras involutus* (Smithian; after Brayard and Bucher 2008). **b** *Discoptychites megalodiscus* (Anisian). **c** *Lanceolites bicarinatus* (Smithian; after 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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