

Chapter 21

Ammonoid Paleopathology

René Hoffmann and Helmut Keupp

21.1 Introduction

21.1.1 Definition of (Paleo-)Pathological Phenomena

“*Normality is fiction*” (Hölder 1956) and is best understood as arithmetic average. Deviations from the “*normal*” phenotype of a given population that are caused by endogene or exogene growth anomalies are called pathologies. Paleopathologies, as a rule, are constrained to growth anomalies of mineralized hardparts that passed down in the fossil record. In case of ammonoids these hardparts are the conch and subordinate jaw elements, especially the calcareous aptychi, often found isolated from their host.

21.1.2 Historical Aspects

During early scientific time, pathological ammonoids were regarded as monstrous curiosities till the end of the nineteenth century, e.g., d’Orbigny 1842–1851; Fraas 1863; Quenstedt 1885–1888. Modern scientific treatment appeared at the beginning of the twentieth century with the publication of Engel (1894) who conducted research regarding the causes of such phenomena. Finally, the summarizing paleopathological descriptions of Moodie (1926) and Tasnadi-Kubacska (1962) focused

R. Hoffmann (✉)

Department of Earth Sciences, Institute of Geology, Mineralogy, and Geophysics,
Ruhr-Universität Bochum, 44780 Bochum, Germany
e-mail: rene.hoffmann@rub.de

H. Keupp

Institute of Geological Sciences, Branch Palaeontology, Freie Universität Berlin,
12249 Berlin, Germany
e-mail: keupp@zedat.fu-berlin.de

on vertebrate paleontology and introduced the field of paleopathology as an independent paleobiological discipline (Hengsbach 1991).

Engel (1894) mentioned four factors causing paleopathological phenomena: (1) “*Krüppel ab ovo*” (cripple within the egg), (2) “*Bastarde bzw. senile Formen*” (bastards respectively senile forms), (3) “*kranke Formen*” (ill forms), (4) “*verletzte Formen*” (injured forms). Today, according to Lehmann (1976), anomalies are understood as conch modifications that only affect single or few specimens of a species and can be attributed to diseases, injuries or other interactions between organisms, e.g., parasites, epizoa (Keupp 2012). Disease that affect the whole population (=“*Überindividuelle krankhafte Erscheinungen*” of Schwegler 1939), and higher taxonomic units e.g., heteromorph ammonoids, specific modification of the aperture, or ontogenetic changes in ornamentation patterns, that were described by former authors as “*ill*”, “*abnormal*” or “*degenerated*” (Quenstedt 1858; Engel 1894; Pompeckj 1894; Tornquist 1896; Schindewolf 1929), do not represent pathological phenomena.

For paleontologists, confirmation or identification of conch anomalies that are caused by genetic dysfunctions (Engel 1894: “*ab ovo*” or crossing) is difficult because the mutagenic character hinders a differentiation between intraspecific variability or speciation (development of new species). In many cases traumatic events during an early/juvenile ontogenetic stage that caused phenotypical modifications also in later ontogenetic stages were misinterpreted as being caused by genetic dysfunctions. Such cases are the source of taxonomic confusion and phylogenetic misconceptions in paleontology (e.g. Maubeuge 1957). Based on singular pathological cases, several new species have been raised; Keupp (2012) lists 40 such cases. Two cases will be explored in more detail in the following: (1) fastigate ceratitids from the German Muschelkalk, and (2) ring-ribbed pleuroceratitids from the middle Lower Jurassic.

The species “*Ammonites fastigatus*” was established by Credner (1875) based on a single ceratitid ammonite from the German Muschelkalk, whose strong ventral ribs extended over the otherwise smooth ventral side (=ring ribs; Fig. 21.1). Afterwards, additional specimens of fastigate ceratitids from different species were found (e.g., Eck 1879; Zimmermann 1883; Blankenhorn 1887; Philippi 1901; Riedel 1916; Bülow 1918; Böttcher 1938; Müller 1954, 1970a, b, c; Busse 1954; Wenger 1957; Weyer 1964; Mayer 1966, 1974, 1978, 1981; Rummel 1973; Rein 1989, 1991; Claus 1992). In most cases, the preservation as internal moulds prevents the recognition of the causing injury of the juvenile ceratitid aperture. Only the more or less pronounced asymmetry of the ornamentation perturbation itself indicates a traumatic event (Keupp 1985). The misinterpretation of these anomalies as genetic dysfunction led to new “*fastigo-species*” (Rothe 1949, 1955; Wunsch 1957; Mundlos 1963). Müller (1976) interprets fastigate ceratitids as “*prologism*”, i.e. single specimen genetically implement ornamentation patterns that become regular later during the Jurassic. Considering the fact that ceratitids represent a blind ending group of ammonoids that is not phylogenetically connected to the younger groups of Jurassic and Cretaceous ammonoids, demonstrates the unreliability of that hy-

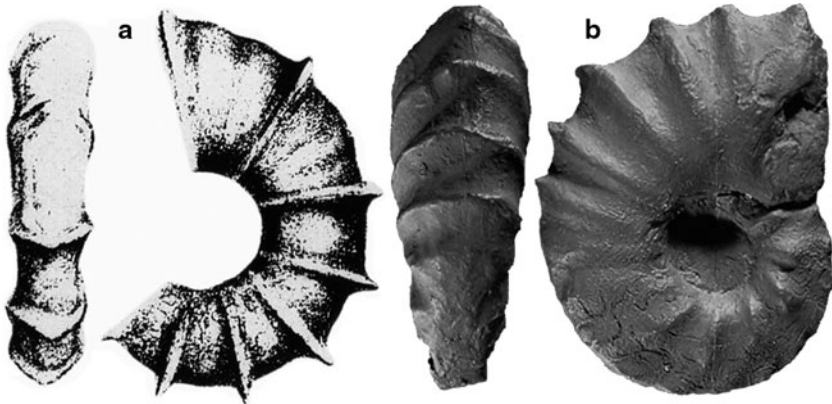


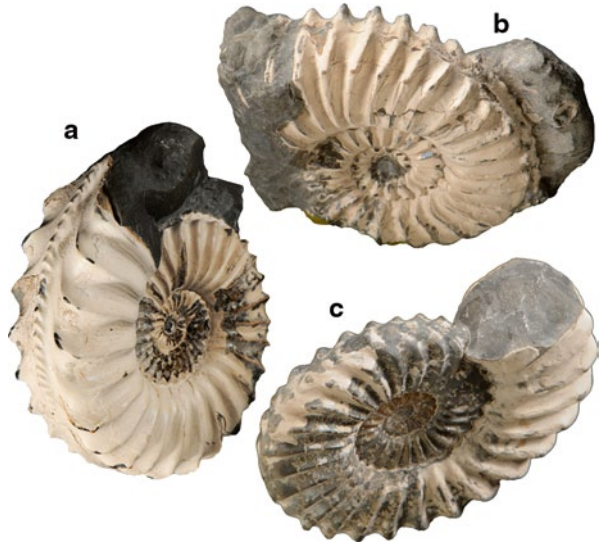
Fig. 21.1 **a** Reproduction of “*Ceratites fastigatus*” from Credner (1875). **b** fastigate *Ceratites nodosus* (Schlotheim) from Oberstetten/Mainfranken, already described by Eck (1897), Philippi (1901) and Wenger (1957) (original housed at Staatliches Museum für Naturkunde Stuttgart, Nr. 21076)

pothosis. Hence, fastigate ceratitids are the result of traumatic events that caused a so-called “*compensations ornamentale*” (Guex 1967).

Two Lower Jurassic pleuroceratitids with ring-ribs were described in a similar way. The lack of the typical “*Zopfkiel*” was caused by an injury of the shell-secreting, ventral mantle epithelium during an earlier ontogenetic stage, but was misinterpreted as genetic dysfunction by Kolb (1955). The resulting phenotype resembles some Aegoceratidae, the phylogenetically ascending keel-less group from which the Amaltheidae arise. Kolb (1955) therefore argued that this phenomenon might represent atavism. Maubeuge (1957) re-examined the same two specimens. He draws the same conclusion as he did before for similar cases (Maubeuge 1949a), that these ring-ribbed pleuroceratitids represent independent valid taxa, which he transferred to the genus *Androgynoceras* and *Oistoceras*, respectively. Both genera are restricted to the Lower Pliensbachian.

The morphological variability of anomalies causing ring-ribs is reflected in the assignment to two different aegoceratid genera. Strength of expression of that anomaly depends on the intensity of the injury and degree of regeneration of the injured epithelia; both allow for differing growth rates of the ventral part of the conch (Fig. 21.2). Hölder (1956) introduced for these anomalous ring-ribbed ammonites the forma *aegra circumdata* (forma *aegra* will be abbreviated as f. a. onwards) as one of his “standardized anomalies” (see below). That was based on his observations of ring-ribbed *Schlotheimia* that was earlier described by Martin (1858) as “*Ammonites circumdatus*”

Fig. 21.2 Three specimens of *Pleuroceras spinatum* (Bruguière) from the Upper Pliensbachian of Buttenheim/Germany (leg. J. Schobert): **a** normal conch morphology, **b** pathological specimen (f. a. circumdata), that after a traumatic loss of its keel resembles *Androgynoceras*, **c** after loss of its keel during early ontogeny this ring-ribbed *Pleuroceras* resembles *Oistoceras*



21.1.3 Taxonomic Handling: Symptom versus Syndrome

Hölder (1956) introduced an open nomenclature below the species level for characteristic, so-called “*standardized*” anomalies that occur in different ammonoid taxa and cause similar phenomena (= forma aegra). In many cases different causes, partly endogenic or exogenic underlie the descriptive-phenomenologically defined types of forma aegra. Therefore in most cases an etiology of the phenomenon cannot be clarified. A summarizing table of all hitherto known 42 types of forma aegra defined for ammonoids was presented by Keupp (2012) and is reproduced here (Tab. 21.1).

Two different ways of treatment has been established in order to handle cases where several anomalous phenomena (=symptoms) due to larger perturbances of the shell geometry occur. One option is to describe the sequence of anomalous morphologies by application of the correct f. a. types (e.g., Keupp 1976, 1984). On the other hand, several anomalies can be combined and described as a complex medical syndrome under its own name (e.g., “*Morton’s syndrome*” by Landman and Waage 1986). As a rule, only the reaction of the organism, here the ammonoids, to the disturbing factor should be considered to characterize a pathological phenomenon. However, in some cases also the potential trigger of growth disturbances like the configuration of shell injuries have been determined in a nomenclatorial manner (e.g., characteristic bite marks; f. a. seccata Hölder 1956, f. a. mordata Hengsbach 1996). Accordingly, Kröger (2000) suggested in dependence to Ward (1987) three different types of characteristic injuries of the peristome. These are “*typus stupidus*”, “*typus acutus*” and “*typus parvus*”.

Table 21.1 Alphabetic list of “standardized anomalies” (=forma aegra) modified after Keupp (2012)

Forma aegra	Author	Primarily thought causality	Description of the phenomenon	Remarks
abrupta	(Stahl 1824) Hölder 1956	Injury	Abrupt sculptural perturbation along a distinct line	Collective term describing f. <i>verticata</i> Hölder 1956 and f. <i>substructa</i> Hölder 1973
augata	Kröger 2000	Parasitism	Temporarily enlargement of single sculptural elements	Ex forma <i>inflata</i> Keupp 1976
altermospinata	Keupp 1977	Asymmetry of the peristome	Alternating nodes (or ribs) on the flanks	The phenomenon affected also parabolic nodes.
aptycha	Keupp 1977	Mostly injuries	Internal, horizontal sheets of the body chamber reducing its inner space	= forma <i>conclusa</i> Rein 1989
bovicornuta	Keupp 1977	Injury of the peristome	Anomalous orientation (mostly forwards) of marginal spines	Special phenomenon connected with the “compensations ornamentale” Guex, 1967
cacoptycha	Lange 1941	Endogenic cause	Temporarily loss or reduction of sculptural elements	Similar phenomena can be observed also during regeneration of sublethal injuries
calcar	(Zieten 1830) Hölder 1956	Predominantly injuries of the peristome	Coalescence of two primarily marginal nodes to a single median element (incl. Parable nodes)	cf. Keupp 1993; special case of “compensations ornamentale” Guex 1967
chaotica	Keupp 1977	Endo- and exogenic causes	Iterative zigzag-like dislocation of the keel from extern median to the flanks	Compare with “chaotische Skulptur” (chaotic sculpture) Hölder 1970
cicatricocarinata	Heller 1964	Injury of the peristome, partly with endogenic causes	Irregular scars and grooves instead of a median keel	
circumdata	(Martin 1858) Hölder 1956	Predominantly injuries of the peristome	Anomalous continuation of lateral ribs over the otherwise smooth or covered with other elements ventral side.	Special case of “compensations ornamentale” (Guex 1967) = forma <i>fastigata</i> (Credner 1875) Rein 1989

Table 21.1 (continued)

Forma aegra	Author	Primarily thought causality	Description of the phenomenon	Remarks
complicata	Keupp and Riedel 1995	Endogenic perturbation	Folding of the shell at the peristome	
conclusa	Rein 1989; junior syn. of f. aptycha Keupp 1977	Predominantly injuries	Calcareous sheets within the body chamber	
concreta	Hengsbach 1996	Parasitism	Internal shell concretion (blister? pearls)	see Keupp 1987
disseptata	Hölder 1956	Endogenic perturbation	Single incomplete or lack of septa	
duplicarinata	Keupp 1976	Injury of the peristome	Temporary development of a double keel due to laterally dislocated new insertions of a regenerative keel	Special case of “compensations ornamentale” (Guex 1967)
excentrica	Hölder 1956	Endogen and exogen	Anomalous trochospiral conch	Phenomen of the “Morton-syndrom”, epizoa: Merkt 1966, Keupp 1984
fastigata	(Credner 1875) Rein 1989	Injury of the peristome often misinterpreted as genetic dysfunction (e.g., Müller 1976)	Lateral ribs cross the otherwise smooth venter (term predominantly used for ceratitids)	Special case of “compensatio ornamentale” (Guex 1967)=forma circumdata (Martin 1858) Hölder 1956
fenestra	Keupp 2006	Injury	Window-like shell breakage caused a perturbation of shell sculpture in all directions	
gigantea	Hengsbach 1996	Parasitism	Pathological gigantism	=“megaconchs”: Ivanov 1975
inflata	Keupp 1976	Parasitism	Anomalous enlarged sculptural elements and blister-like shell outgrowth (protuberance)	According to Kröger 2000 only blister-like structures. anomalous enlarged sculptural elements represent forma aegra augata Kröger 2000

Table 21.1 (continued)

Forma aegra	Author	Primarily thought causality	Description of the phenomenon	Remarks
intracarinata	Keupp 2000b	Endogenic	Spiral-furrows visible on the internal mould caused by anomalous strengthened muscle attachments	
heterumbilicata	Keupp 2007c	Injury of the peristome	Enlargement of the umbilical width caused by the regenerative backwards dislocation of the umbilical edge on one side of the conch	
juxtacarinata	Hölder 1956	Injury or endogenic	Dislocation of the median keel to the lateral side of the shell	Analogue for ammonoids with a ventral furrow: forma juxtasulcata Geczy 1965
juxtalobata	Hölder 1956	Endogenic	Asymmetric phragmocone with dislocation of the external lobe and siphuncle to the side	For a few taxa this phenomenon has been recognized as being species specific and not pathologic
juxtasulcata	Geczy 1965	Injury or endogenic	Dislocation of the median furrow to the lateral side of the shell	Analogue to the forma juxtacarinata Hölder 1956 reported for ammonoids with a median keel
mediosulcata	Hengsbach 1986a	No pathology, within the range of intraspecific variability	Formation of ventral ridges for muscle attachment	Bayer 1977a, b; Dagys and Keupp 1998
mordata	Hengsbach 1996	Lethal injury	Bite marks of vertebrates	Without any traces of regeneration
pexa	Hölder 1973	Injury of the peristome	Thickening of growth lines as a late effect of a forma aegra verticata	Special phenomenon that belongs to the forma verticata Hölder 1956
polygonia	Hüne and Hüne 2006	Endogenic causes	Polygonal cross section of the whorl	Compare with Keupp and Richier 2010
pseudocarinata	Fernandez-López 1987	Injury of the peristome	Forma aegra verticata (ribbing vertex) developed as keel-like ridge	Special phenomenon that belongs to the forma verticata Hölder 1956

Table 21.1 (continued)

Forma aegra	Author	Primarily thought causality	Description of the phenomenon	Remarks
refecta	Rein 1994a	Injury of the peristome	Regenerated shell which underpinne the breaking edge is bulged outwards above the normale shell niveau	Junior synonym of forma substructa Hölder 1973
seccata	Hölder 1956	Lethal attack of crustaceans	Fragmentation of the shell by the activity of crustaceans	See: Roll 1935; Hölder 1955
semiverticata	Hölder 1977	Injury of the peristome	Forma aegra verticata (Rippenscheitel) on only one side due to the positioning parallel to the umbilical edge	Special phenomenon that belongs to the forma aegra verticata Hölder 1956, similar phenomena can be triggered by parasitism (Keupp 1979 2000b); Kröger 2000: f. umbilicata
septiaedeformata	Rein 1990	Endogenic: dislocation of the rear soft body within the body chamber	Septal inclination followed a disseptie	Rein 1993; 2000
substructa	Hölder 1973	Injury of the peristome	Regeneration of a shell injury by underpinning the breakage edge with new shell material	Junior synonym: forma refecta Rein 1994a
superstructa	Keupp 1998	Injury of the peristome	Regeneration due to overlapping of regenerating shell material	
syncosta	Hengsbach 1976	“Genetic”	Two former independent ribs growth together in amaltheids to a ventrolateral spine; however this represents part of the normal Bauplan of spine bearing taxa	See Hengsbach 1996; according to Keupp and Ilg 1992 a phenomenon of forma aegra substructa Hölder 1973 after an injury of the peristome (see also Kröger 2000)
umbilicata	Kröger 2000	Parasitism	Flattening and delay of shell secretion along the umbilical edge, similar to forma aegra semiverticata Hölder 1977	See: “Nabelkanten-Anomalie” (umbilical edge anomaly by Keupp 1979

Table 21.1 (continued)

Forma aegra	Author	Primarily thought causality	Description of the phenomenon	Remarks
undaticarinata	Heller 1958	Endogenic, ? Parasitism	Iterative swinging and partly buckling of the median keel	Similar phenomena can be triggered during the aftermath of the regeneration of injuries see: Keupp 1985
undaticarinata-undaticoncha	Hengsbach 1996	Parasitism	Temporarily swinging of the whorl in combination with the swinging of ventral keel or—furrow	See: “Mortons’s syndrome” Landman and Waage 1986; Morton 1983; junior synonym of forma aegra undaticarinata Keupp and Ilg 1992: cf. Kröger 2000
undaticarinata	Keupp and Ilg 1992	Epizoans and endogenic	Temporary swinging of the whorls	Junior synonym: forma aegra undaticoncha Hengsbach 1996
verticata	Hölder 1956	Injury of the peristome	Crest-like splitting of growth lines and ribs (ribbing vertex) caused by the regeneration of injured punctation of shell secreting epithelia	See: Keupp 1992a: different morphologies: f. pexa Hölder 1973, semiverticata Hölder 1977; abrupta Hölder 1956 (pars), pseudocarinata Fernandez-López 1987

21.2 Exogenic Reasons

For practical reasons, pathological phenomena caused by exogenic factors and recognizable on the shell (injuries, epibiosis) are differentiated from endogenic disturbances (illness, parasitoses). For the first case, intensity of anomalies is constantly decreasing during regeneration. Contrary, intensity of anomalies is constantly increasing for the latter case of intrinsic growth irregularities.

21.2.1 Injuries

The majority of conch injuries were caused by predator-prey interactions. While injuries of lethal attacks are hard to distinguish from post-mortem shell damages (Roll 1935; Mayr 1967; Keller 1977; Lehmann 1990; Radwanski 1996; Keupp 2008, 2012; Wani et al. 2012), the post-traumatic reaction of shell growth document the syn-vivo character of sublethal injuries. Mainly the interplay of four factors controls the phenotype of anomalies caused by injuries:

- Position at the conch (peristome, rear part of the body chamber, phragmocone)
- Configuration of the injury which depends on the predator
- Intensity of injury (shell only or additionally the shell-secreting mantle epithelium)
- Genetically-fixed Bauplan (whorl parameter, sculpture, etc.) of a certain ammonoid.

Injuries which did not affect the shell secreting epithelium, caused only short-term anomalies during the post-traumatic phase (Fig. 21.3). Oblique anomalies of the

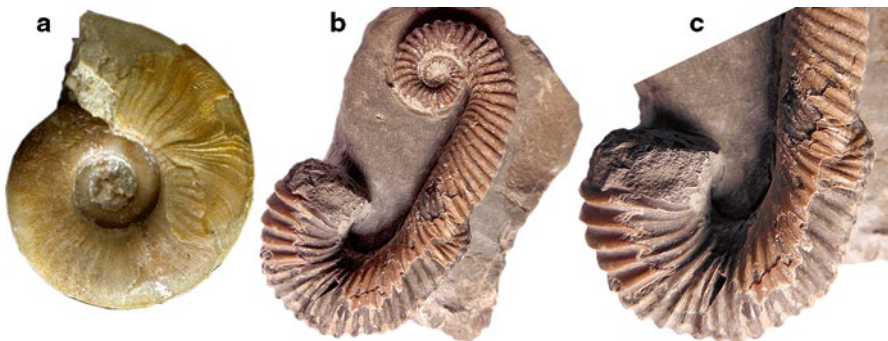
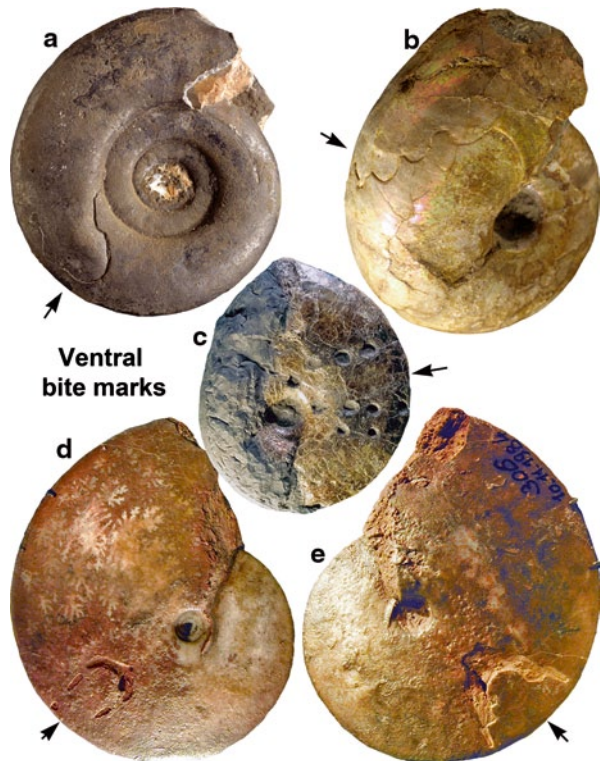


Fig. 21.3 Simple, regenerated injuries of the former peristome only affecting the shell not the shell secreting epithelium (f. a. *substructa* Hölder 1973): **a** clymeniid from the Upper Devonian of the south Urals (from Keupp 2012), **b, c** *Labecereras bryani* (Whitehouse), Upper Aptian of Walsh River, Australia. Injuries often depend on the construction and configuration of their producer. Vertebrates, due to their isolated teeth, can cause partly characteristic bite marks (Fig. 21.4; Kauffman and Kesling 1960; Mapes and Hansen 1984; Sims et al. 1987; Hansen and Mapes 1990; Keupp 1985; 1991, 2000b, Kauffman 1990; Martill 1990; Hewitt and Westermann 1990; Mapes et al. 1995; Tsujita and Westermann 1998; King 2009; Richter 2009a, b), and partly non-specific u-shaped exposures along the peristome (Keupp 2012)

Fig. 21.4 Vertebrate bite marks, regenerated (a, b) and lethal (c, d, e): a u-shaped exposure caused by a fish (*Gymnites* sp., Anisian of Epidaurus, Greece), d, e pycnodontid bite mark on both sides (*Oxycerites*, Upper Bajocian, Sengenthal, southern Germany), b *Desmoceras latidorsatum* Michelin from the Lower Albian of Ambatolafia, Madagascar with typical bite mark of a semionotid fish, c *Placenticerias* sp. from the Upper Cretaceous of South Dakota with presumed bite marks of a mosasaur (original: Ruhrland-Museum, Essen, Germany, coll. no. RE 551 763 333 A 3073)



sculpture of the regenerated shell are caused due to the underpinning of the break edge by the peristomal epithelium and depend on the size of the injury. In adoral direction obliqueness of the sculpture decreases and merges into the normal sculptural pattern. Regenerated shell portions of window-like injuries of the body chamber behind the peristome show a distorted sculpture if the position of the puncture allows for a generation of the injury by the retracted peristomal epithelium. Shell areas of regenerated punctures are smooth without growth lines when these were repaired by the mantle epithelium of the rear part of the body chamber.

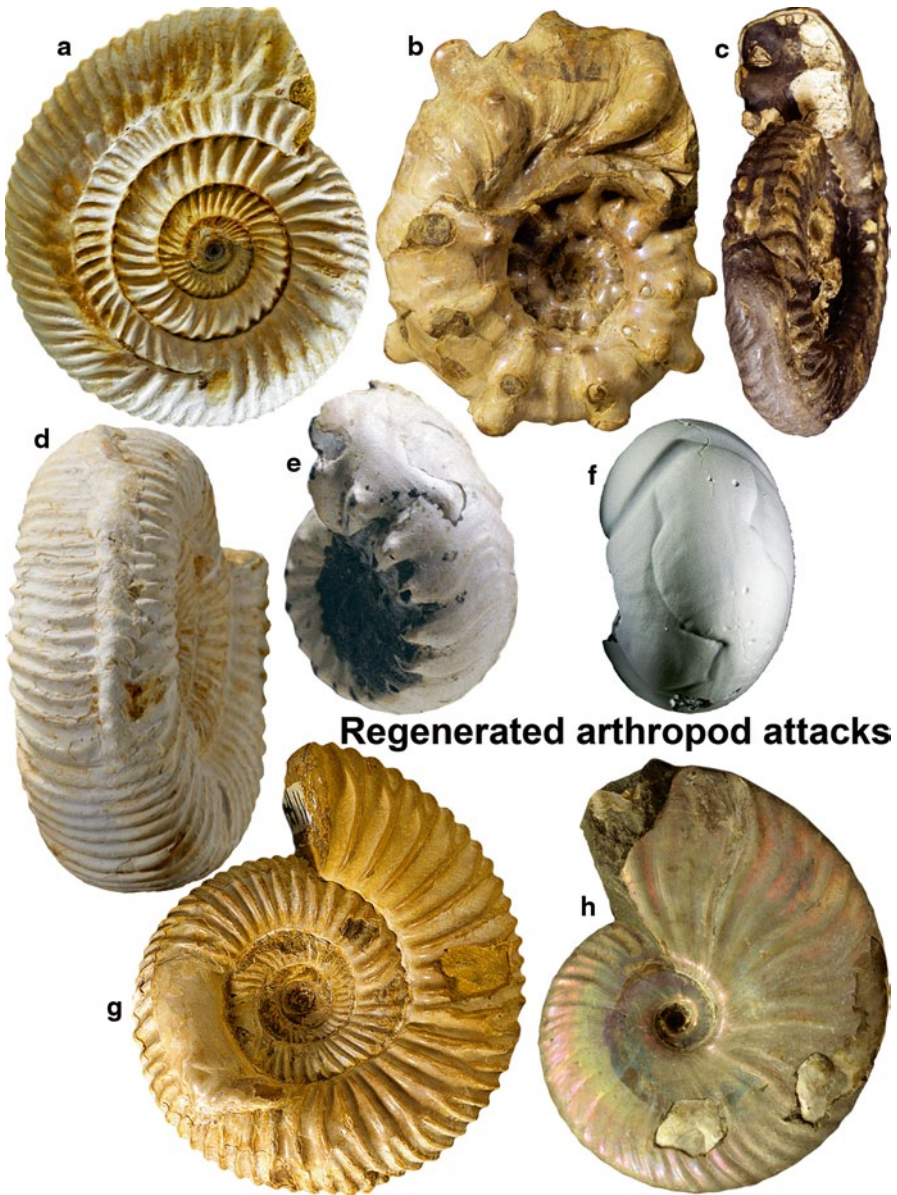
Injuries along the phragmocone were predominantly lethal, especially for breviodomic ammonoids (Kröger 2000). For nautilids, some cases of small injuries of the phragmocone were reported which did not cause a lethal fluting of the shell but could be successfully sealed from the outside. One prerequisite is the position of the injury within the zone influenced by the soft body (Stumbur 1960; Kröger and Keupp 2004; Tsujino and Shigeta 2012).

21.2.2 *Characteristic Phenomena and their Producers*

Arthropoda: Benthic crustacea (malacostraca) which radiated during the Mesozoic played an important role as predators. With their specialized limbs they could produce characteristic injuries. On the one hand, they could cause point-like injuries with their claws at the peristome which usually also perforated the peristomal epithelium. On the other hand, they could cut the body chamber starting at the peristome and produce far-reaching back “*band cuts*” (Kröger 2000). Usually broad band cuts are reported for Lower Paleozoic ammonoids; their producers are to be sought among the chelicerates (Keupp 2012). The stomatopods with their specialized angled pair of maxillipeds, which can be thrown with high active force against the hard parts of potential prey, evolved during the Upper Paleozoic. They crush preferred molluscan shells and produce characteristic window-like holes in the shells (Baluk and Radwanski 1996; Radwanski 1996; Keupp 2006). Thylacocephalan arthropods that ranged from Early Cambrian to Late Cretaceous had similar raptorial limbs as recent stomatopods. (Schram et al. 2003). They are too are hypothesised to prey as ambush predators, throwing the limbs with high active force stabbing the prey (Fig. 21.5).

Nautilids/ coleoids: One basic character of cephalopods is the chitinous, parrot-like jaw apparatus, which allows nautilids and coleoids a predatory lifestyle. Only certain ammonoids, due to their microphageous and partly planktotrophic diet, modified the jaw apparatus (Keupp 2000b; Kruta et al. 2011; Tanabe 2011). With the advent of the aptychus some ammonoid jaws were no longer able to cause significant bite marks. The most frequently occurring nautilid and coleoid bite marks during the early Paleozoic are typical trigonal in their configuration (Fig. 21.6).

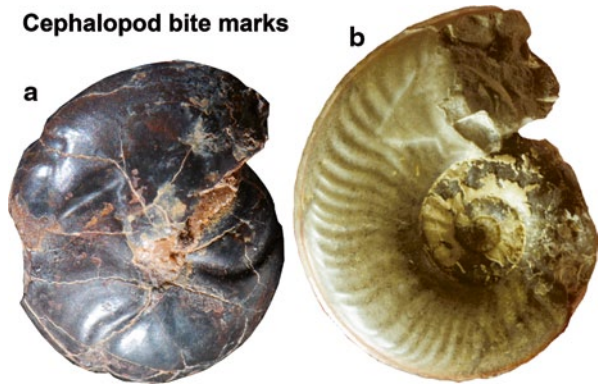
If in addition to the conch, the shell secreting mantle is injured, long-term post-traumatic conch anomalies with decreasing intensity during the process of regeneration of the epithelium are the results. However, in many cases a complete regeneration of the shell-forming function was not possible, so that anomalous phenomena were built permanently. The mechanism of the “*compensations ornamentale*” (Guex 1967) causes significant deformation of conch features after a partial failure of the peristomal epithelium. The intact, not included in the injury parts of the epithelium were dragged under strain at the site of injury, in order to take over the shell-forming function. Single parts of the ammonoid peristomal epithelium seem to be strictly genetically programmed in favour of a realisation of a narrow part of the sculpture pattern. Therefore, this regeneration mechanism results in a shift and distortion of certain sculptural elements during the post-traumatic shell formation. In the case the ventral epithelium of the keel-bearing ammonite migrates towards the flank, the keel was not built at the median position, but dislocated by the amount of dislocation of the epithelium. Usually the keel was not only dislocated but deformed as well (= f. a. juxtacarinata Hölder 1956; Fig. 21.7). Another characteristic phenomenon of “*compensations ornamentale*” is the f. a. calcar (Zieten; see Hölder 1956). The latter two rows of marginal nodes merge to a single row of median cusps by shortening of the ventral epithelium. Accordingly, Zieten (1830) has described a



Regenerated arthropod attacks

Fig. 21.5 Regenerated arthropod attacks: **a, b** ribbing vertex (f. *a. verticata* Hölder 1956) *Divisosphinctes* sp., Upper-Oxfordian of Sakaraha, SW-Madagascar (**a**), and *Douvilleiceras inaequinodosum* Parona and Bonarelli from the Lower Albian of the Mahajanga Basin, Madagascar. **c, d** “Band-cuts” *Clionites acutocostatum* (Klipstein), Ladinian of Nifukokko, Timor (**c**) and “*Kranaosphinctes*” sp. from the Oxfordian of Sakaraha, Madagascar (**d**). **e** tongue-shaped anomaly of dwarf and juvenile amaltheids caused by paginurid crustaceans (Keupp and Schobert 2011). **f** broad “Band-cuts” are characteristic injuries of Devonian ammonoids: cheiloceratid ammonoid, Upper Devonian, Tafilalt, Morocco. **g, h** stomatopod attacks left window-like punctures on the shell of Mesozoic ammonoids (Keupp 2006): “*Divisosphinctes*” sp. from the Upper Oxfordian of Sakaraha, Madagascar (**g**), *Cleonicerias besairiei* Collignon from the Lower Albian of Ambatolafia, Madagascar

Fig. 21.6 Regenerated cephalopod bite marks with trigonal outline. **a** cheiloceratic from the Upper Devonian of the Tafilalt, Morocco (\varnothing 8 mm). **b** *Pelekodites* sp. from the Bajocian of Gerzen, Germany (\varnothing 2.5 cm)



Distichoceras from the Callovian as a separate species “*Ammonites calcar*”. Such cases are not only found in ammonoid taxa with marginal rows of nodes (e.g. ceratitids, kosmoceratids, mammitids, scaphitids), but is analogous and transferable to parabolic nodes (Fig. 21.8; Keupp 1993, 2012). Prerequisite for the functioning of the “*compensatio ornamentale*” is a targeted and differentiated mobility of the mantle edge. A differentiated dislocation of epithelia in ammonoids may have been favored by the complex attachment of the soft body in the shell. Thus, at least three independent paired retractor systems have been recognized, which are ventral, ventrolateral and dorsolateral in position (Doghuzhaeva and Mutvei 1991, 1996; Richter 2002). The unpaired dorsal tissue attachment, which also occurs in endo-cochleate cephalopods, probably served as an attachment of the septal shell sac to the septa.

It seems that nautiloids, by their comparatively simple attachment to the conch by means of the annular ring and a pair of large ventro-lateral muscles (Keferstein

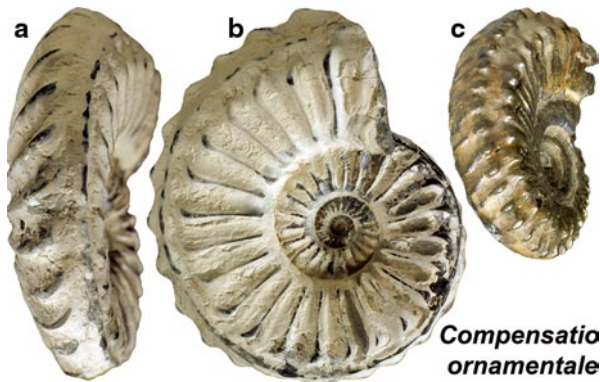


Fig. 21.7 Examples for “*compensations ornamentale*”: **a, b** *Pleuroceras spinatum* f. *a. juxtacarinata* Hölder 1956 from the Upper Pliensbachian of Unterstürmig, southern Germany, **c** *Kosmoceras* sp. f. *a. juxtasulcata* Geczy 1965 from the Callovian of Rijasan, Russia

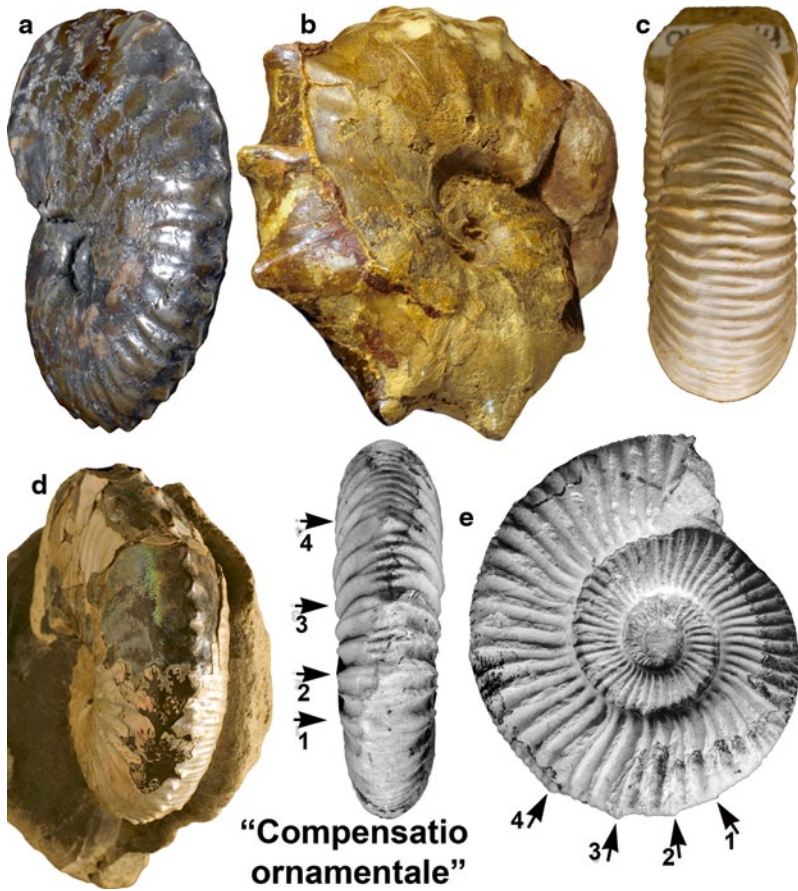


Fig. 21.8 Examples for “*compensatio ornamentale*”: **a, b, d** f.a. calcar (Zieten 1830), *Distichoceras bicostatum* (Stahl) from the Callovian of Thanheim, Württemberg (**a**), *Mammites* sp. from the Lower Turonian of Asfla, Morocco (**d**), *Discoscaphites* sp. from the Pierre Shale (Upper Cretaceous), Fox Hills, South Dakota (**c**) analogue to the shortening of the ventral epithelium in a perisphinctid causes clasp-like ventrally furcating ribs due to the lack of marginal nodes (Upper Oxfordian, Sakaraha, southwest Madagascar), **e** analogue phenomena of parabolic nodes of a perisphinctid (Lower Kimmeridgian, Hartmannsdorf, southern Germany) do also belong to the f. a. calcar

1861; Mutvei 1957), were not capable of the necessary mantle mobility. Herewith, the mechanism of the “*compensations ornamentale*” is regarded as species-specific in ammonoids.

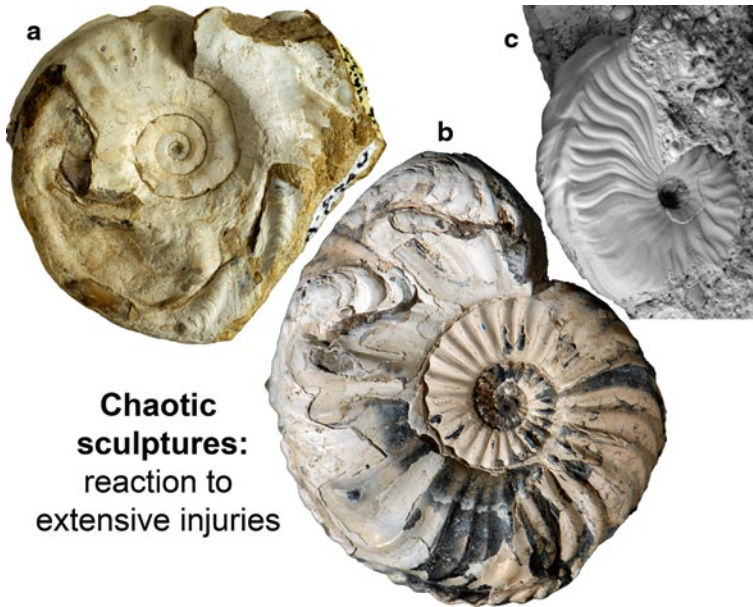


Fig. 21.9 Chaotic sculptures triggered by large-scaled injuries **a** *Eleganticeras elegantulum* (Young and Bird), Lower Toarcian, “Ahrensburger Geschiebegruppe” (i.e. well-established glacial erratic boulder association) versus endogenic dysfunction. **b** *Pleuroceras solare* Phillips, Upper Pliensbachian of Buttenheim, southern Germany. **c** *Cleiviceras exaratum* (Young and Bird), Lower Toarcian of Altdorf, southern Germany)

21.2.3 Chaotic Sculptures

A continuous shell growth obviously was not possible after a disruption of the lateral shell-secreting epithelium, due to a large scale injury or endogenic reasons that exceeds the maximal tolerable dislocation. The result is a “chaotic” sculptural phenomenon characterized by a repeated redeployment of shell formation. The specific mode of regeneration is particularly evident in keel-bearing ammonites. A saw-tooth-like course of the keel was achieved by the iterative attachment of parts of the shell partly in order to bring the keel back to an approximately normal position but sliding back to the maximum tolerable juxtaposition. A case study of 286 pleuroceratids from the middle Lower Jurassic of southern Germany bearing an anomalous keel position demonstrated two different scenarios. First, a lateral dislocation of the keel by 20% of the whorl height usually results in a permanent keel-dislocation; contrary dislocations of about 25–50% of the whorl height cause usually a chaotic course of the keel (Fig. 21.9, 21.10 Keupp 2012).

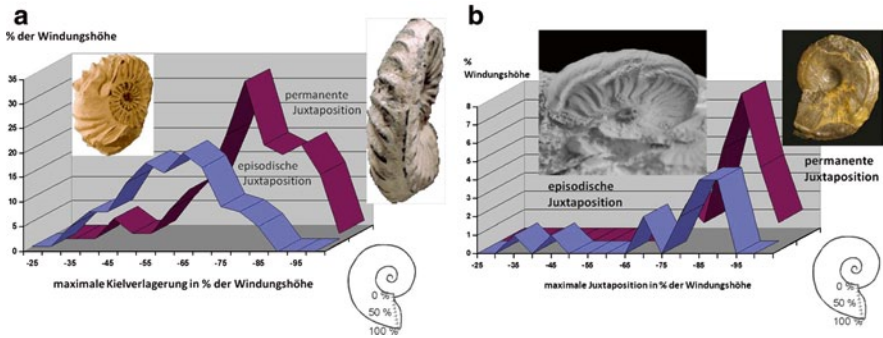


Fig. 21.10 Tolerance of permanent dislocation of the keel varies between taxonomic groups. **a** *Pleuroceras spinatum* (Bruguière), Lower Jurassic of Unterstürmig, Germany ($n = 286$) tolerates permanent dislocation of the keel (= f. a. juxtacarinata Hölder 1956) up to 20 % of the corresponding whorl height, above that dislocation will cause chaotic sculptures. **b** Contrary, the limit of tolerance in hildoceratids from the Lower Toarcian of Altdorf, Germany ($n = 35$) is only 90–95 % of the whorl height (after Keupp 2012)

21.2.4 Internal Growth-Disturbations

Damage of the aperture/peristome sometimes lead to secondary phenomena. These secondary phenomena could only be recognized in the internal mould within the body chamber. Thus, the retraction of the peristomal epithelium could occasionally cause a detachment of mantle segments from the inner surface of the conch. That detachment triggered the formation of one or more mineralized internal sheets/lamellae showing nacre ultrastructure (Fig. 21.11). Keupp (1977) introduced for

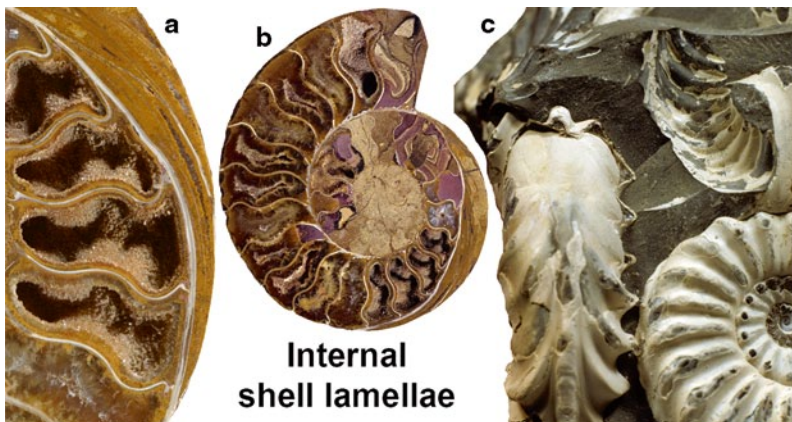


Fig. 21.11 Internal shell lamellae (f. a. aptycha Keupp 1977) significantly restrict the body chamber: **c** *Pleuroceras spinatum* Brug. from the Upper Pliensbachian of Unterstürmig, southern Germany, **a, b** median section showing the phragmocone of *Cleoniceras besairiei* Coll. (Lower Albian of Ambatolafia, Madagascar) with a multiple insertion of internal lamellae and fitting of septa afterwards



Fig. 21.12 Recent *Nautilus pompilius* Linné from the aquarium of the Jura-Museums Eichstätt, with anomalous shell bulge bridged by multiple internal shell lamellae. The lacking continuation of body chamber growth causes an extreme shortening of the body chamber due to continuous septal formation

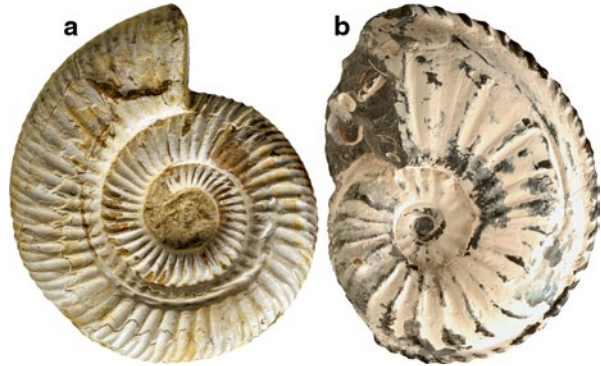
such phenomena the f. a. type *aptycha*. For the same phenomenon observed for Middle Triassic (Muschelkalk) *Ceratites*, Rein (1989) suggested the f. a. *conclusa* (Lehmann 1990; Keupp 1994). The principle mechanism of formation of internal shell lamellae was observed in modern *Nautilus*, which were aquarium-reared at unnatural water chemistry by Keupp and Riedel (1995). Under these artificial conditions the peristome grew outwards in a bead-like form. The resulting gap between soft body and shell is like an open shell injury bridged by underpinning with a regenerative shell. A multiphased, repeatedly initiated underpinning of the shell-bulge prevents growth progress (Fig. 21.12) and causes a continuously shortening of the body chamber due to the progression of septal formation.

Injuries of shell area related to tissue attachment site usually cause, similar to intrinsic disruption, internal problems, especially for the attachment of the large retractor-muscles. These problems generated ridge-like structure at the inner shell surface (f. a. *intracarinata* Keupp 2000a; Fig. 21.13).

21.2.5 *Aptychi*

There is a long controversial discussion about the function of the double-valved, calcareous *aptychi* interpreted as lower jaw, lid, or a combination of both (e.g., Schindewolf 1958; Lehmann 1972, 1990; Morton 1981; Lehmann and Kulicki 1990; Seilacher 1993; Keupp and Veit 1996; Keupp 2003; Schweigert 2009; Kruta et al. 2011; Tanabe 2011; Keupp and Mitta 2013). Regenerated injuries causing

Fig. 21.13 Anomalous internal ridges serving as attachment sites of the large retractor muscle; **a** dorsolateral muscle of *Divisosphinctes* (Oxfordian, Sakaraha, SW-Madagascar), **b** ventrolateral muscle of *Amaltheus gibbosus* (Pliensbachian, Buttenheim, Germany)



partly long-term growth anomalies like growth line vertices or longitudinal bulges are also recorded for aptychi (Schindewolf 1958; Keupp et al. 1999; Engeser and Keupp 2002, see Fig. 21.14). Usually these anomalies start along the aboral margin of the aptychus pointing towards the inner body. Due to the exposed position for potential predators (usually crustaceans) of the rear edge of the aptychus when in the locked-position, injuries of the aptychus were used by Keupp et al. (1999) and Keupp (2012) as an argument for a potential lid-function of that structure. Contrary, Schweigert and Dietl (2001) and Schweigert (2009) assume a specialized jaw function for the aptychi. These authors interpret growth anomalies as a possible consequence of parasites. Damage of the lower jaw by the hard parts of their potential

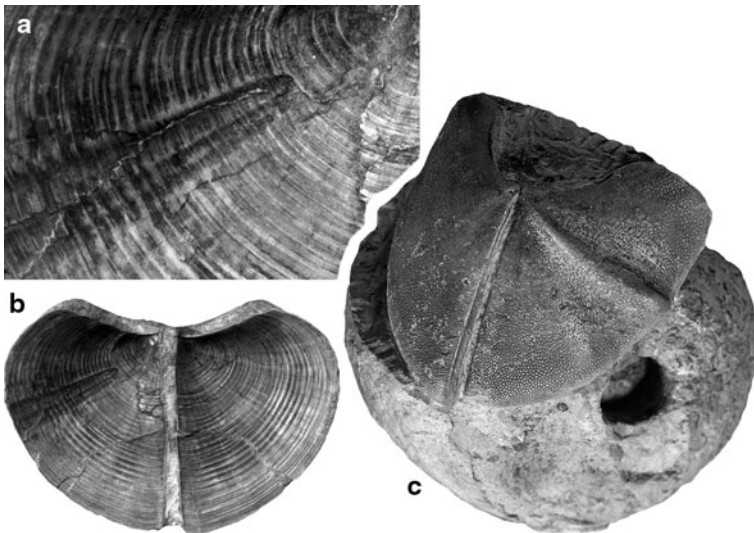


Fig. 21.14 Growth anomalies of *Laevaptychus latus* from the Kimmeridgian presumably caused by injuries of the aboral edge: **a**, **b** growth line vertices, aptychus from Nusplingen. **c** longitudinal bulges, aptychus in living position, from Kirchheim, Ries, southern Germany

prey, as described by Kruta and Landman (2007) for modern nautilids, is unlikely for aptychi-bearing ammonoids (Aptychophora—see Engeser and Keupp 2002) due to the mostly microphageous diet (Keupp 2000b; Kruta et al. 2011; Tanabe 2011).

21.2.6 *Paleobiological Aspects of Sublethal Injuries*

The analysis of shell injuries allows for new insights in aut- and synecological aspects. One autecologic aspect, i.e., group-specific variable tolerance to compensate for growth asymmetries, was exemplified for the permanent dislocation of the median keel in succession of the “*compensations ornamentale*” (see above). In general, it seems likely that ammonoids that lived as demersal in low-energy water had a higher tolerance of shell asymmetries compared to taxa that lived close to the surface water in a high energetic milieu. Injuries are also useful to identify construal limits of survival. Two examples below illustrate that issue

21.2.6.1 *Efficiency of the Hydrostatic Apparatus*

The amount of liquid, that was retained within the nautilid phragmocone in order to balance weight changes, is negligibly small (Ward 1979) with a maximum of 7 g (=about 2% of the total chamber volume). Therefore, shell loss of more than 5 g (=4% of the total shell mass) exceeds the limits of compensation (Ward 1986) and is lethal for *Nautilus* due to buoying upwards to the surface waters.

Kröger (2000, 2002a) calculated for Jurassic ammonoids the sudden shell loss of large-scaled (up to 20% of the total shell mass) but re-generated, i.e. survived, shell breakages (Fig. 21.15). Thereby, he recognized that ammonites could survive shell loss (decreasing weight) being five times higher compared to modern *Nautilus*. Accordingly, Kröger (2000, 2002a) concluded that ammonoids had flooded a larger part of their phragmocone.

21.2.6.2 *Mobility of the Soft Body in the Body Chamber*

Kröger (2002b) demonstrated for meso- and longidomic ammonites (cf. Westermann 1996), that shell injuries extending from the aperture to approximately half the length of the body chamber could be survived and repaired. Similar cases were reported by Keupp (2012, p. 109) for brevidomic taxa. The regenerated shell, in particular of those species with long body chambers (dactylioceratids, perisphinctids), shows growth lines and sculptural elements. They prove that the peristomal epithelium could withdraw up to the aboral edge of injury. The required flexibility of the ammonoid soft body, was facilitated due to the differentiated retractor muscle system consisting of the paired dorsolateral, ventrolateral, and attachment sites, as already pointed out for “*compensations ornamentale*”. The ability of the potential

Fig. 21.15 Regenerated shell area of “*Lithacoceras*” *torquatiforme* Collignon from the Upper Oxfordian of Sakaraha, SW-Madagascar (67 mm in diameter, coll. Keupp, PA-10675), equates a relative weight proportion of 20 % of the complete shell (Kröger 2000), demonstrating that ammonoids could at least compensate fivetimes the amount of shell loss compared to modern *Nautilus*



retraction of the soft body reveals the ammonoid body chamber fundamentally had a volume that significantly exceeds that of the soft body.

Comparative quantitative analysis of the abundance of injuries and types of injuries observed for ammonoid taphocoenosis also provides interesting insight into synecological aspects, in particular predator-prey relationships. Using this detour may help to elucidate different life habits of ammonoids with different shell morphologies. Accordingly, Keupp and Ilg (1992) interpret decreasing abundances of regenerated injuries caused by benthic crustaceans, observed for an ammonite fauna from the Upper Callovian of Normandie, as indicator for different frequencies of demersal contacts. Therefore, Keupp and Ilg (1992) assumed a demersal lifestyle for the coarse ribbed peltoceratids (rate of injuries ca. 14%), a habitat in the middle of the water column for cosmoceratids and *Quenstedtoceras* (rate of injuries 3–4%), and for hecticoceratids a habitat close to the sea surface (rate of injuries 1%). A similar interpretation can be drawn from the analysis of Upper Oxfordian ammonoids from Madagascar (Fig. 21.13). The strongly ornamented perisphinctids show the highest rate of injuries (13%). About 1/3 of these injuries were caused by benthic crustaceans. Contrary, less sculptured lytoceratids (*Protetragonites*) and phylloceratids show significant lower rates of injuries (1.25–2.21%) are presumed fish attacks.

The analysis of a total number of 1190 weakly ornamented (“*leiostracans*” and 328 strongly ornamented (“*trachyostracans*”) ammonoids from the Upper Triassic of SW-Timor (Keupp 2012, Fig. 7) shows significant differences between the rates of injuries of smooth shelled species (2–6%) and sculptured species (8–17%). These differences confirmed that the phylogenetic megatrend within the ammonoids towards sculptured species, were a defensive strategy (Ward 1981), particularly

Taxon	Individuals	Nr. of sublethal injuries	Portion of crab attacks (f. a. verticata)	Rate of injuries (%)
1 <i>Taramelliceras</i> cf. <i>externnodosum</i>	440	5	3	1.14
2 <i>Protetragonites fraasi</i>	400	5	0	1.25
3 Phylloceratidae div. sp.	1356	30	0	2.21
4 <i>Aspidoceras</i> sp.	864	31	11 (=35%)	3.6
5 <i>Epaspidoceras jeanneti</i>	215	5	1	2.3
6 Perispinctidae div. sp.	2593	337	113 (=33.5%)	13

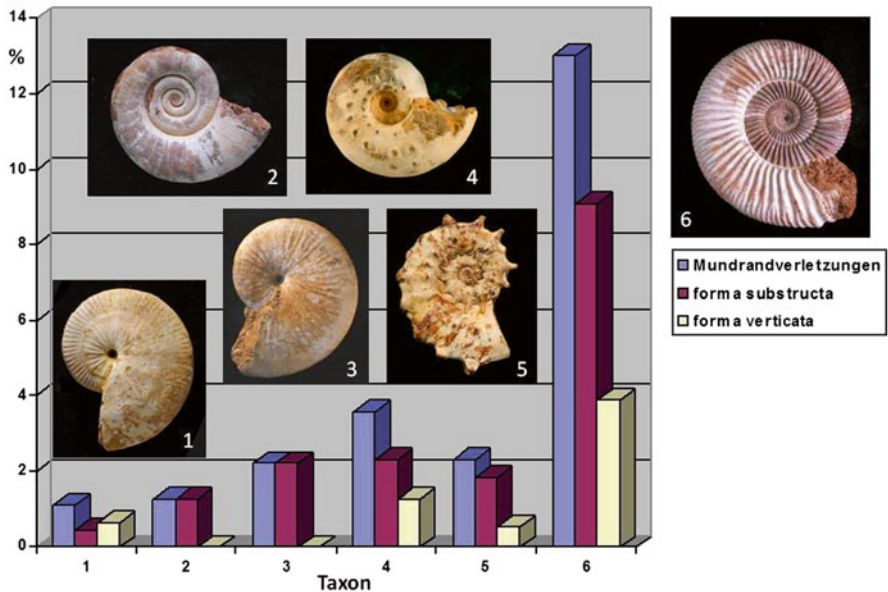


Fig. 21.16 Different rates of injuries within taphocoenoses ($n = 5868$) from the *Upper-Oxfordian* of Sakaraha, Madagascar

since the earliest Mesozoic, in order to counteract the increasing predation pressure in the benthic regime (Vermeij 1977, 1982, 1983, 1987). The increasing predatory pressure was predominantly due to the radiation of malacostracan crustaceans since the beginning of the Triassic (Walker and Brett 2002).

Kröger (2002c), on the basis of another quantitative analysis of 1500 specimens of Jurassic ammonites with sublethal injuries, postulated a connection between characteristic shell features (shell form, body chamber length and sculpture) and susceptibility for injuries. His results show that the antipredatory traits were in adaptational conflict with traits demanded for high manoeuvrability and streamlining.

21.2.7 *Epizoans and Reactions of Shell Growth*

The external shells of ammonoids were a welcome hard substrate for a plethora of different colonizers. Two categories can be distinguished within the group of epizoans: On the one hand, sessile suspension feeder, attached with their body to the shell and being partly pseudoplanctonic as free-rider on a mobile raft that ensures a varied diet. On the other hand, mobile benthic-organisms, occupying the shell and use it as a temporarily feeding ground, consuming organic particles on the shell surface or incorporated in the shell. While the first group usually colonize the shell surface during the lifetime of the ammonoid animal (=“*true epoecy*” *sensu* Linck 1956), but also colonize empty shells floating in the water column or lying on the ground as substrate islands (=“*false epoecy*” *sensu* Linck 1956). Contrary, the second group of grazing animals attack the shells usually post-mortem (Schindewolf 1962; Wetzel 1964; Kase et al. 1998; Seilacher 1998; Keupp and Richter 2010). Following Davis et al. (1999) we summarize, as an umbrella term, the colonization of the shell surface by filter feeding organisms, independently whether the emplacement took place during the lifetime of the host or after its death, as Epicoles. The subset of epicoles, that colonize the shell surface during the lifetime of the host are called Epizoa (=Epoecy).

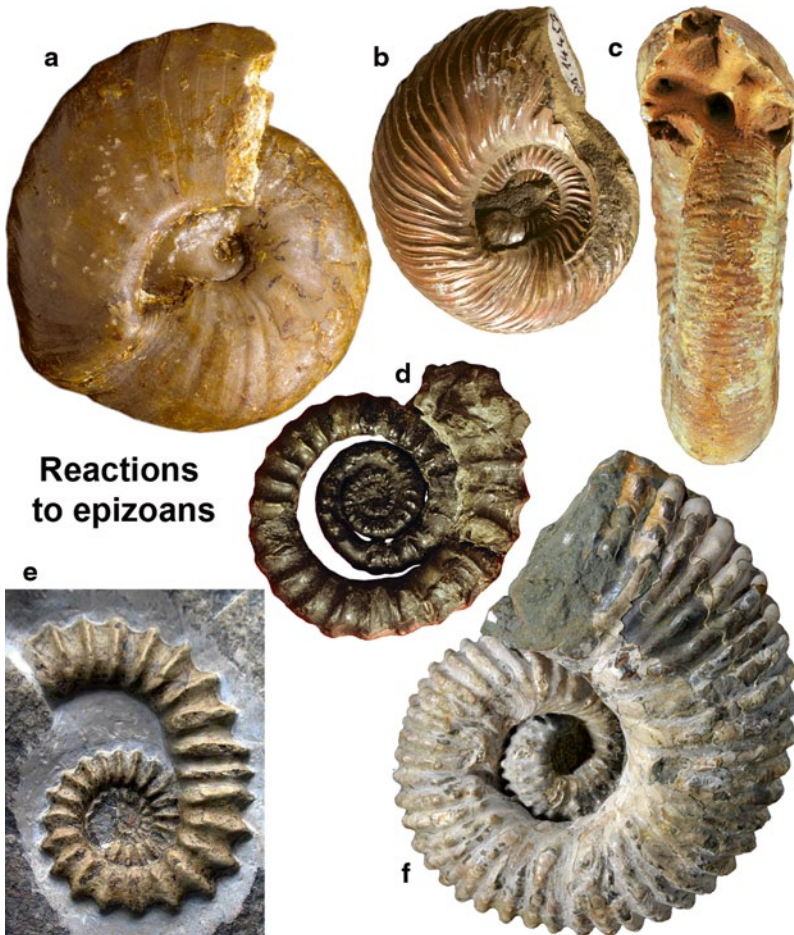
In particular *syn vivo* epizoa are of interest in connection with paleopathological studies, since the affected ammonoids usually show characteristic reactions documented in their shell growth.

Evidence of *syn-vivo* colonization can be drawn in two ways:

1. By means of morphological reactions of the host during shell growth (cf. Lange 1932; Merkt 1966; Hölder 1970; Keupp 1984, 1992b, 1996; Davis et al. 1999; Klug and Korn 2001).
2. With the help of shell-morphological reactions of the epizoans.

A prerequisite to document noticeable reactions in shell growth of ammonoids is the colonization of a juvenile, actively growing shell. Significantly reactions are the overgrowth of free riders, which were settled in the overlapping area of the whorls. The process of overgrowth causes a whorl-bend (Philippi 1897; Illovaisky 1917; Sornay 1955; Hölder 1970; Keupp 1984/1985, 1992b, 1996, 1997, 2000b, 2012; Klug and Korn 2002; Checa et al. 2002). Such morphologies can mimic the shape of heteromorphy ammonoids due to the loss of the epizoa by taphonomy (Quenstedt 1858, 1886/1887; Hyatt 1889; Vadász 1908; Lange 1932; Schindewolf 1934; Tasnadi-Kubacska 1962; Mitta et al. 1999; Keupp 1992b, 2000b, 2012; Keupp and Schweigert 2009; Wannemacher 2010; Frerichs 2011). On the other side, laterally attached epizoa caused counter-steering in growth direction in order to maintain balance. A trend towards a trochospiral shell was activated in some cases (Merkt 1966; Keupp 1984), but predominantly caused an oscillation of the whorls around the median plane ((Fig. 21.17) Keupp and Ilg 1992; Checa et al. 2002).

The morphological reactions of the epizoans are mainly related with their positioning at the ammonoid shell and their response to the spiral growth of the



Reactions to epizoans

Fig. 21.17 Reactions in shell growth due to epizoans: **a** *Owenites koeneni* (Hyatt and Smith), Upper Skythian, Crittenden Springs, Nevada with a bending whorl. **b** *Quenstedtoceras* sp. colonized with oysters, Upper Callovian, Dubki near Saratov, Russia. **d** Apparently gyrocone shell caused by diagenetically triggered *Serpula*-epoecy on *Gagaticeras neglectum* (Simpson), Sinemurian of Whitby, United Kingdom. **e** Eccentric growth in order to balance for laterally attached epizoan: perispinctid from the Upper Bajocian of Sengenthal, southern Germany. **e** Apparently ancylocone shell of a *Pleuroceras spinatum* (Bruguière), Upper Pliensbachian of Aubächle near Blumberg, southern Germany. **f** *Douvilleiceras albense* Spath (Lower Albian of Mahajanga, Madagascar) showing oscillating whorls due to infestation with a soft bodied epizoan (Keupp 2012)

ammonoid shell (Seilacher 1954, 1960; Meischner 1968, 2002; Baird et al. 1989; Keupp et al. 1999; Hauschke et al. 2011; Keupp et al. 2012). For example epizoan orientate during their settlement as larvae streamlined in terms of their own suspension feeding activities. During growth of the ammonoid shell, bivalves, brachiopods and other organisms attached to the shell, rotate away from their preferred position (=“*perniciöse Epökie*” *sensu* Meischner 1968).

Especially serpulids (Annelida) could offset the rotations from their preferred position by synchronizing the growth of their living tubes with the growth of the ammonoid shell (Lange 1932; Schindewolf 1934; Keupp et al. 2012; Fig. 21.14).

21.2.8 *Paleobiological Aspects of Anomalies Caused by Epizoans*

The interpretation of close organismic interactions between the now extinct ammonoids and their epizoa, whose modern representatives allow us to draw some conclusions about their needs, open up a broad range of interesting paleobiological aspects, for example:

- habit and life style of ammonoids (position of the peristome, predominant swimming direction)
- age
- efficiency of the hydrostatic apparatus

The nature of organismic interactions between host and epizoans whether symbiosis, commensalism, or parasitism, usually remains speculative (Zapalski 2011). In most cases the alliance between host and epizoan was to the detriment of both (=“*perniciöse Epökie*”: Meischner 1968). The interaction between *Serpula varicosta* Quenstedt and various evolute ammonoids is largely restricted to the Lower Jurassic (Lange 1932; Schindewolf 1934; Merkt 1966; Müller 1982; Jäger 1991; Hungerbühler 1992; Keupp 1992b, 2000b, 2012), and indicates a possible adaptive relationship due to a single strategy. This strategy implies that the larvae of *Serpula* infested the umbilical area of juvenile ammonoids. During growth the shortest route was chosen to bring their living tube to the flow-exposed, ventral site of the shell. In order to keep its position the tubeworm could compensate further growth of the ammonite shell by lengthwise growth of its tube in the same direction. Older portions of the *Serpula* tube become overgrown by the spiral shell of the ammonite and incorporated between two whorls forming a double helix of same growth direction (Fig. 21.18 right).

Accumulations of colonized ammonoid shells were mainly reported from the margins of marine basins, due to the distribution of suspension feeders that attached their shells to the substrate (here the ammonoid shell), in coastal, high-energetic shallow marine settings (e.g., ceratitids of the German Muschelkalks: Philippi 1897; Linck 1956; Wenger 1957; Mayer 1975; Hagdorn and Simon 1985; Rein 1996; Suchopar 1997; Knoch 1989; Meischner 1968, 2002; *Quenstedtoceras* from the Callovian of Saratov, Russia: Seltzer 2001; Larson 2007; Keupp 2012; or aspidoceratids from the Kimmeridgian of Brunn, southern Germany, Bavaria: Keupp et al. 1999, 2012; Seilacher and Keupp 2000 and others). The colonization of the ventral center of mass by various epizoa (Seilacher 1960; Keupp et al. 1999, 2011; Seilacher and Keupp 2000) shows two things: the position of the peristome during the life time of the ammonoids and that the affected individuals had an “*epidemersal*” life style (Westermann 2013), otherwise the downward hanging epizoa



Fig. 21.18 *Left*: Concentration of epizoa attached to the centre of mass of a *Physodoceras* sp. (cirripeds: *Pollicipes*) and serpulid tube growing synchronous with the spiral shell of an ammonoid, both indicating syn-vivo infestation and an upward orientation of the aperture; Upper Kimmeridgian, platy limestones of Brunn, southern Germany, Bavaria. *Right*: Concordant growth direction of the ammonoid shell and serpulid tubes attached to the shell of *Schlotheimia angulosa* Lange (Hettangian of Holzen, Germany) suggests a possible adaptation of the worm to its favoured substrate (Keupp 2000b)

(cirripeds, serpulids, bivalves) would be stifled. Studies of the Upper Kimmeridgian *Physodoceras* from the platy limestones of Brunn (southern Germany) show that epizoans (such as cirripeds, serpulids, and bivalves) tend to be concentrated on the ventral center of mass indicating the peristome had an orientation of about 70–80° upwards (Fig. 21.15; Keupp et al. 1999). This is consistent with calculated values by Trueman (1941) derived from the ratio of phragmocone to body chamber length and demonstrates their basic orientation in the water column. Also the settling of *Stramentum* (cirripeds) at the centre of mass of the orthocone *Sciponoceras* (Upper Cretaceous) points toward a horizontal orientation of this heteromorph ammonoid with an upwardly directed peristome (Fig. 21.19; Hauschke et al. 2011). Another argument comes from mathematical modelling of some *Pavlovia* shells from the Tithonian of Russia. The whorls of these specimens bend and oscillate due to attached oysters and serpulids. The models show that the deformation of the shell served to keep a constant position of the peristome during shell growth/ ontogeny (Fig. 21.21; Checa et al. 2002).

Cirripeds always orient their feeding apparatus against the water current (Seilacher and Keupp 2000). The ammonoid shells infested with cirripeds clearly show a preferred orientation towards the peristome (Keupp et al. 1999; Hauschke et al. 2011). This proves that ammonoids preferred a frontal water current hitting the peristome first. Accordingly, Seilacher and Keupp (2000) assumed a predominantly forward migration pattern for all Mesozoic ammonoids. It reveals that, in accordance with the loss of the ventral sinus, since the beginning of the Triassic the jet propelling mechanisms plays no important role for movement.

There are several attempts to reconstruct the potential period of growth and age of ammonoids based on the growth rate of epizoans. Although such calculations are

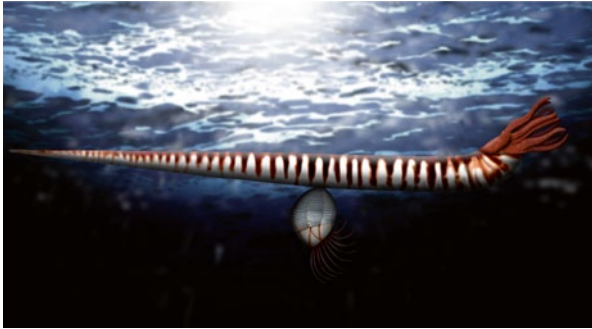


Fig. 21.19 Position of *Stramentum pulchellum* (Sowerby), a cirriped, at the ventral centre of mass of a *Sciiponoceras* sp. shell from the Upper Cenomanian of Lengerich, NW-Germany indicates a horizontal swimming position with upwardly directed peristome (from: Hauschke et al. 2011)

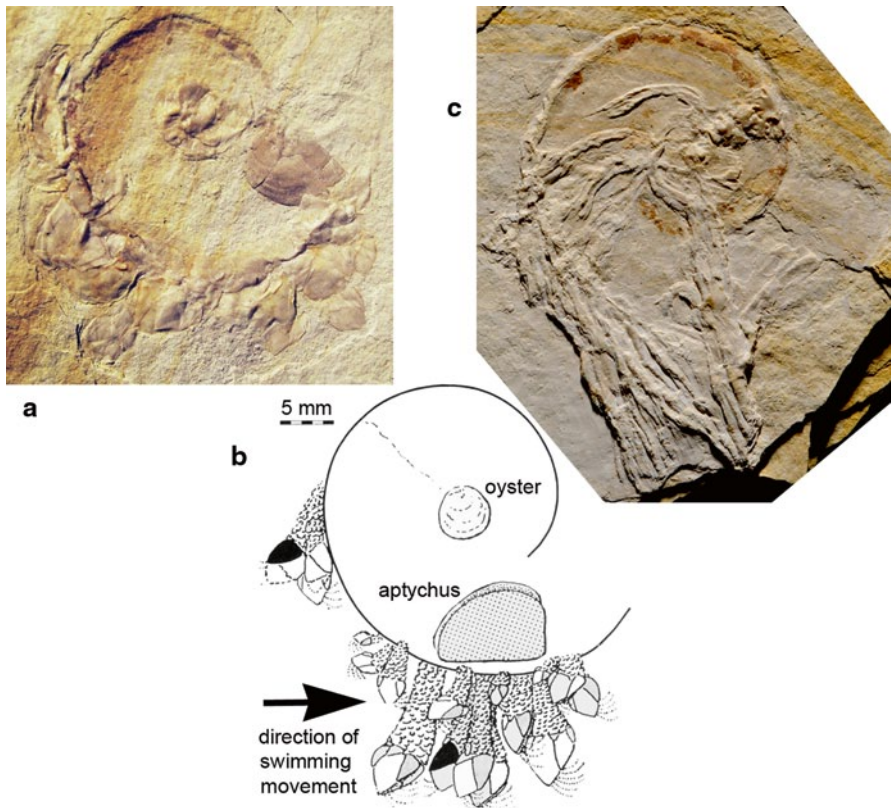


Fig. 21.20 Concentration of Epizoa on a *Physodoceras* sp. shell from the Upper Kimmeridgian of Brunn, southern Germany (Bavaria), platy limestone, marking the centre of mass and points to a 70–80° upward orientation of the peristome. The forward orientation of the filter apparatus of these suspension feeders like *Pollicipes* sp. (cirripeds in **a** and **b**) and serpulids (**c**) indicate a predominantly forward migration pattern of these ammonoids

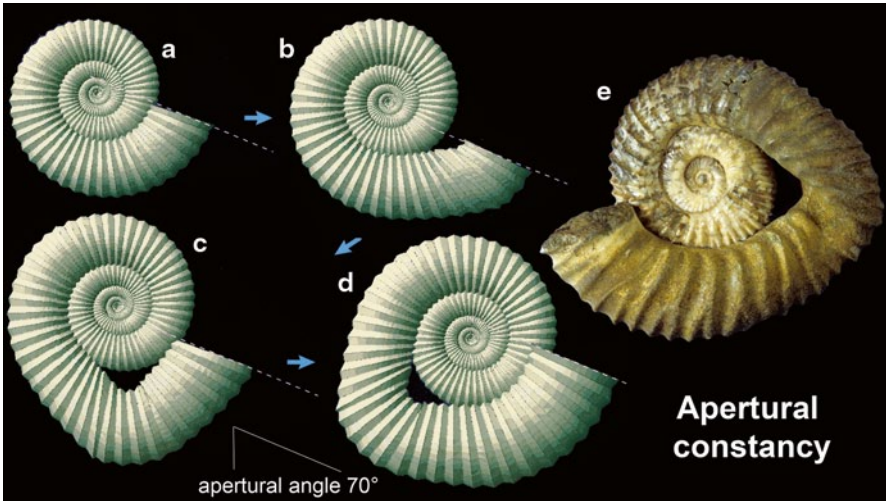


Fig. 21.21 Mathematical simulation made by T. Okamoto of bending whorls caused by epizoans for *Pavlovia cf. iatrensis* Illovaisky from the Tithonian of the polar Ural; it shows that during the phase of anomalous shell growth the peristome was orientated constantly in its normal position (from Keupp 2000b)

subject to many uncertainties, Schindewolf (1934); Seilacher (1960); Merkt (1966), and Meischner (1968, 2002), independently come to the same conclusion, that an average-sized ammonite had several years of growth followed by at least 3 more years as adults. The life expectancy of ammonoids thus corresponds approximately with that what is known for the modern *Nautilus* (Landman and Cochran 1987) reaching sometimes an age of about 20 years (Dunstan et al. 2011).

While modern nautilids tolerate only small amounts of epizoa (3–16% of the shell surface or 1% of the shell weight; Zann 1985; Landman et al. 1987), ammonite shells nearly completely covered with epizoa seem to keep their epi-demersal life-style (Keupp et al. 1999). It proves that ammonoids, as compared to modern *Nautilus*, possessed a much more effective hydrostatic apparatus. Kröger (2000), based on a number of large sublethal injuries, calculated that Jurassic ammonoids could handle significantly larger amounts of liquid within the phragmocone (see above) and could tolerate more than five times the shell losses compared with the extant *Nautilus*.

21.3 Endogenic Reasons

Anomalies that are not caused by injuries or epizoans are best summarized as endogenic or intrinsic. External causes for this type of pathologies cannot be recognized. Intrinsic pathologies are characterized by an usually increasing intensity of the anomaly.

Most endogenous ammonoid shell anomalies, attributed to dysfunctions of the soft body due to parasite infestation or at least the possibility of a parasitic infestation, is discussed (e.g., Rieber 1963; Keupp 1976, 1979, 1984/1985, 1995, 1997; Hengsbach 1990, 1991, 1996; Kröger 2000; Larson 2007; De Baets et al. 2011, 2015).

21.3.1 Gigantism and Dwarfism

Extraordinarily large ammonoid species repeatedly occur during transgressive phases of Earth history (Wiedmann 1973; Johnson 1984; Stephens 1988; Klug 1999). For example, some Upper Devonian mantioceratids and Permian metalegoceratids achieve shell diameters up to 60 cm, while some Upper Cretaceous parapuzosiids reached up to 3 m in shell diameter (Krüger 1984; Stephens 1988). Other cases of genetically controlled size differentiation within a certain ammonoid species can be seen in pronounced sexual dimorphism (Callomon 1963; Makowski 1963; Lehmann 1990; Keupp 2000b).

For pathological cases of gigantism, that affected only single specimens of otherwise growth-restricted species, Ivanov (1975) introduced the name megaconch. They can be seen as a pathological deregulation of the species specific growth limitation. Therefore, the shells of these megaconchs generally show no signs of growth limitation like septal crowding or deterministic differentiation of the aperture.

Manger et al. (1999) list a larger number of Upper Paleozoic species, the phenomenon of pathological gigantism. They also reported that affected individuals exceed the shell diameter by two to four times as compared to their normal counterparts with whom these are associated in the same beds (Stephen 1997). As a potential reason for pathological gigantism Manger et al. (1999) discussed a possible infestation of the gonads with trematod larvae. Analogous to modern cases of gigantism in terrestrial, tropical gastropods, trematod larvae prevent the advent of sexual maturity, and with it the hormone-controlled growth stop (Hölder 1956, 1960; Bucher et al. 1996; Davis et al. 1996).

The term dwarfism for dwarfish ammonites was coined by Tasch (1953). Ager (1963) distinguishes between genetically-fixed dwarfism and ecologically-related growth limitations (“stunting”). The former, partly representing phylogenetic end members of a neotenic development, e.g., *Cymbites laevigatus* (Sowerby) from the Pliensbachian (Donavan 1957), *Trochleiceras magneti* Collignon from the Albian, or partly representing a pronounced sexual dimorphism (e.g., *Oecoptychius* from the Callovian; Schweigert and Dietze 1999) are not related with pathological phenomena.

The so-called “*Miniconchs*”, which Matyja (1986) described for Callovian *Quenstedtoceras*, possibly documents a hormonally controlled early onset of sexual maturity in the sense of “*Microgerontie*” (Schmidt 1926). Miniconchs usually grow no larger than 1/3 of the normal sized microconchs and 1/8 of macroconchs. Keupp (2012) discussed a possible dwarfism for *Pleuroceras apyrenum* (Buckman), since no sexual dimorphism was detected for pleuroceratids (Fig. 21.22).

Fig. 21.22 Possible “Miniconch” of *Pleuroceras apyrenum* compared with normal-sized specimen (middle Lower Jurassic, Buttenheim, Germany). The small specimen shows characteristic features of an adult shell like final flattening of the ribs, and the depression of the ventral crenulated keel



21.3.2 *Disturbance of the Septal Apparatus*

The chamber formation in ammonoids was performed by the rear of the mantle sack. Septal formation was, most likely, temporally, spatially, and functionally independent of the growth processes at the peristome (Keupp and Riedel 1995). A regular and episodic phenomenon was observed on pre-adult shells, which ensured the regulation of weight equilibration of the growing and weight gaining animal. Ammonoid septal formation, however, was subject of a high flexibility in their species-specific but also individual configuration (Keupp 1995). Thus, orientation and symmetry of the septa within the conotheca (conch), as well as the relative distance from each other, vary considerably from specimen to specimen (Bayer 1977b).

The reactive flexibility to spontaneous changes in the geometry of the tube-shaped outer shell, which represents the frame in which the septum was formed, was considerable but independent from phylogenetic and ontogenetic controlled complexity. Perhaps, the punctual attachment of the organically preformed septa within the tube promoted that flexibility (Seilacher 1975). Sculptured ammonoids with a corrugated-metal-like shell for example were able to adapt their septa to constricted intercostals and widened costal sections of the conotheca. In addition, ammonoids were also able to cope with extreme changes of the whorl cross-section, due to pathological processes and proceed with the septal formation. This applies to both reduced and expanded cross-sections through anomalous internal shell lamellae (f. a. *aptycha* Keupp 1977) or bubble-like outgrowths (f. a. *inflata* Keupp 1976) (Fig. 21.23; Keupp 1994, 1995, 2000b, 2012). The extreme adaptability during the formation of the septal apparatus ensures its hydrostatic function and can be assumed as an essential survival strategy.

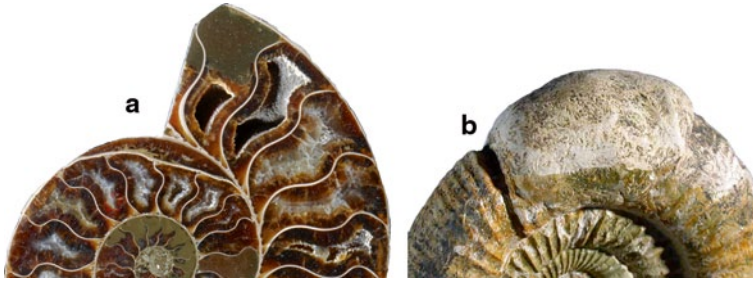


Fig. 21.23 Two examples showing the high flexibility of septal formation after anomalous changes of the whorl cross section. **a** *Cleoniceras besairiei* Collignon (Lower Albian, Mahajanga Basin, Madagascar), despite the reduction of the whorl height by 35 % caused by the f. a. *aptycha* it could form new septa. **b** *Orthosphinctes* sp. (Lower Kimmeridgian of Neumarkt, southern Germany) shows complexly folded suture lines also within its bubble-like extension of the whorl cross-section (f. a. *inflata* Keupp 1976)

First evidences of dysfunctions of the septal apparatus of fossil cephalopods with an external shell caused by pathologies go back to Kieslinger (1926). He described incompletely preserved septa for Mesozoic nautilids. However, the nature of the phenomenon described by Kieslinger remains controversial. It either could represent primary incompletely formed septa or was due to partial diagenetic dissolution (Hölder 1956).

For ammonoids a number of different phenomena of anomalous septal formation can be distinguished based on numerous findings:

21.3.2.1 Anomalous Septal Spacing and Orientation

In most cephalopods a growth stop is correlated with the onset of sexual maturity. Septal crowding indicates the final growth phase for pre-adult to adult ammonoids. Pre-adult septal crowding were partly triggered by rhythmic deceleration of growth due to specific and regular modifications of the sculpture (e.g., *Horrioceras*, Callovian; Bayer 1977b; Keupp 2012), and partly due to pathological growth anomalies during the regeneration of injuries or due to intrinsic or ecological reasons (Eichler and Ristedt 1966). Septal spacing can be reduced to almost zero in extreme cases, which results in the impression that the septa are in direct contact or bifurcate (Fig. 21.24 Right; Blind and Jordan 1979).

The opposite of septal crowding is the anomalous enlargement of septal spacing, which gives the impression of a septal loss (=f. a. *dissepta* Hölder 1956). Although most of these cases are better attributed to selective diagenetic secondary dissolution of the septa (Hölder 1956; Keupp 2012), individual cases in goniatites and ceratites seem to be primary in nature (Becker et al. 2000; Müller 1978; Rein 1990, 1997). One-sided enlargements of septal spacing can also be caused by anomalous inclination of individual septa (Fig. 21.25).

- Perturbance of the septal morphology

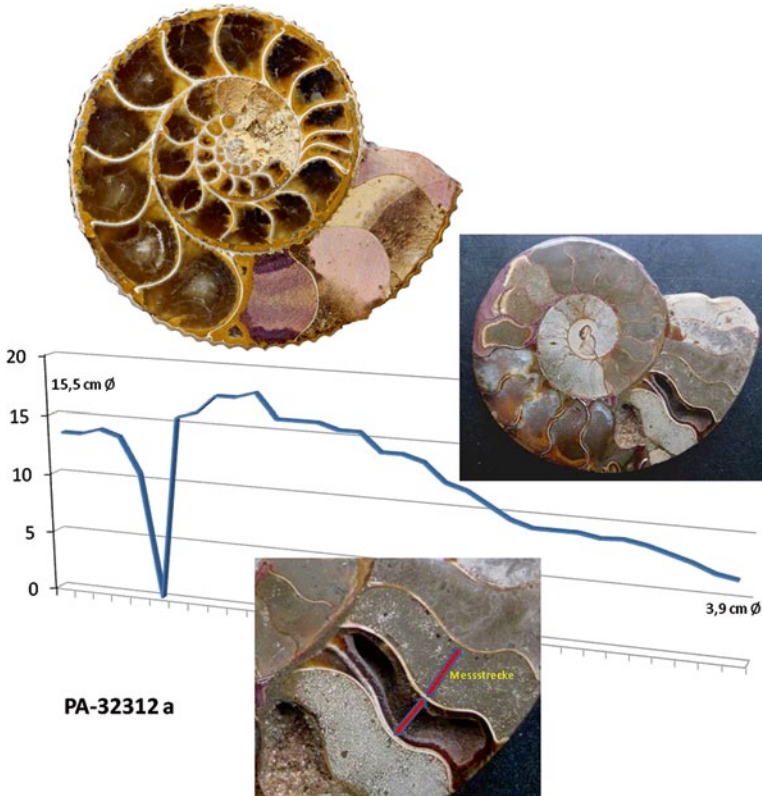


Fig. 21.24 *Left*: Median section through the phragmocone of a perisphinctid (Upper Oxfordian, SW-Madagascar, coll. Keupp, coll. no. PA-32896) with anomalous, pre-adult (endogenic) septal crowding, *Right*: *Cleoniceras besairiei* Collignon (Lower Albian, Mahajanga Basin, Madagascar) with apparently bifurcated septum caused by extreme pre-adult septal crowding

The general flexibility of the septal formation enabled many individuals, even if the whorl cross section was modified, e.g., deformation of the outline, increasing or decreasing volumes (Keupp 1994, 1995), to form their septa morphologically modified. This could cause asymmetric septal surfaces (=“adaptive septal-malformation” Keupp 2012; Fig. 21.26).

21.3.2.2 Disturbance of Suture Line Symmetry

A symmetropathy of the body chamber usually does not cause a corresponding asymmetry of the phragmocone due to the independent formation mechanisms and functions of the conotheca and phragmotheca (Nicolesco 1921, p. 49). Thus, only a few individual observations of a coupled asymmetry of conotheca and phragmotheca exist (e.g., Fraas 1863, pl. 1: 1.3; Rieber 1963).

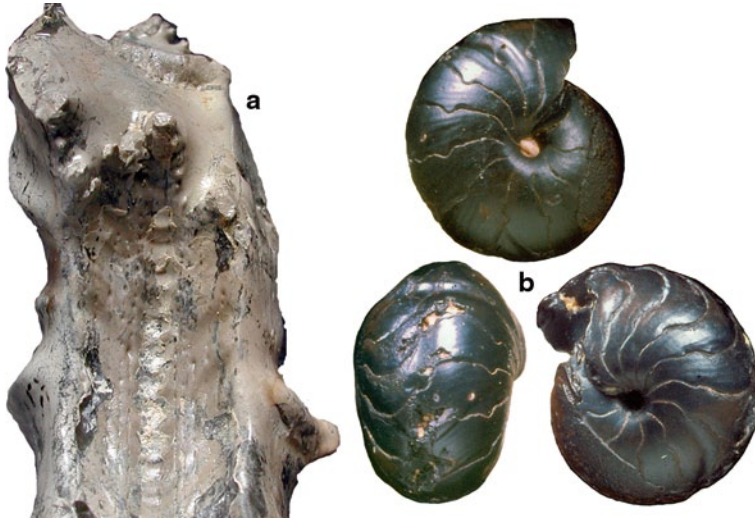


Fig. 21.25 Anomalous inclination of septa shown for *Pleuroceras salebrosum* (Hyatt) from the Upper Pliensbachian of Buttenheim, southern Germany (a) and for *Cheiloceras undulosum* (Münster) from the Upper Devonian of Fezzou/Morocco (b)

If one side of the rear soft body is deformed, and causes an asymmetric position within the shell, the described flexibility during the septal attachment would allow a modification of the septal formation. Thereby the original inclination is reflected by the asymmetric suture line. That process often results in different degrees of complexity of the suture line on both sides (Schindewolf 1961; Hengsbach 1976; Keupp 2012).

A frequently encountered phenomenon since the Paleozoic is the offset of the siphuncle from its ventral, median position (Fig. 21.27). Accordingly, the external lobe was displaced towards the right or left flank. At the same time the bilateral symmetry of the conotheca was retained. Other parts of the suture line, including the internal lobe are usually not affected by the asymmetry (Hölder 1956; Wiedmann 1972; Hengsbach 1986a). However, an analogue asymmetry was observed for the attachment site of the ventro-lateral retractor musculature (Landman and Waage 1986). New calculations of the effect of an offset siphuncle of *Badouxia columbiae* (Frebald) from the Sinemurian (Lower Jurassic) by Longridge et al. (2009) have shown that the effect of the eccentric position of the siphuncle is negligible for the position and the balance of the ammonoid shell within the water column due to its small mass as compared to the soft body of the animal. The asymmetric position of the siphuncle simply forced expansion of the septal suture line and septal folds on the non-siphuncle side of the shell but no significant counterbalance was in effect.

Within the ammonoids, we can distinguish three different groups in terms of the preferred constancy of the position of the external lobe:

Fig. 21.26 Adaptive septal malformation caused by pernicious epeocy deforming the conch tube (conotheca). *Quenstedtoceras* sp., Upper Callovian of Dubki near Saratov, Russia



- A species-specific constant eccentric position of siphuncle and external lobe for example characterizes the Lower Cretaceous platylenticeratids (particularly in the Boreal Realm, Kemper 1961) and *Anahoplites* (Hölder 1956; Hengsbach 1978).
- In some taxa [e.g., cheiloceratids and armatids (Upper Devonian), psiloceratids (Blind 1963) and schlotheimiids (Hettangian), arnioceratids (Sinemurian), Cymbites (Pliensbachian), *Hecticoceras* (Callovian), glochiceratids (Ziegler 1958), *Physodoceras* (Upper Jurassic), different hoplitid taxa, as well as numerous scaphitids (Upper Cretaceous)], the onset of an unstable positioning of the external lobe after the ammonitella stage results in frequent deviation from symmetry of larger portions of the population (Lange 1929, 1941; Hölder 1956;

Fig. 21.27 *Latanarcestes noeggerathi* (Buch), Lower Devonian, Tafilalt, southern Morocco with eccentric position of the siphuncle and the external lobe (= forma aegra juxtalobata Hölder 1956; from Keupp 2012)



Schindewolf 1961; Hengsbach 1976, 1977a, 1977b, 1980, 1986a, b). The degree of asymmetry varies between negligible and significant without a preferred direction (left or right).

- For *Hoploscaphites nicoletti* from the Upper Cretaceous, Landman and Waage (1986) have shown that asymmetries predominantly occur during the final growth phase of macroconchs. About 86% of the affected specimens indicate a deviation to the right.
- Most Mesozoic ammonoid taxa are characterized by a constant ventral, median position of the siphuncle and the external lobe. Deviations are pathological and affect single specimens of a population.
- Hölder (1956) introduced the f. a. juxtalobata based on his observations of *Harpoceras* (Toarcian) and *Taramelliceras* (Upper Jurassic) for such cases.

21.3.2.3 Suture-Inversion

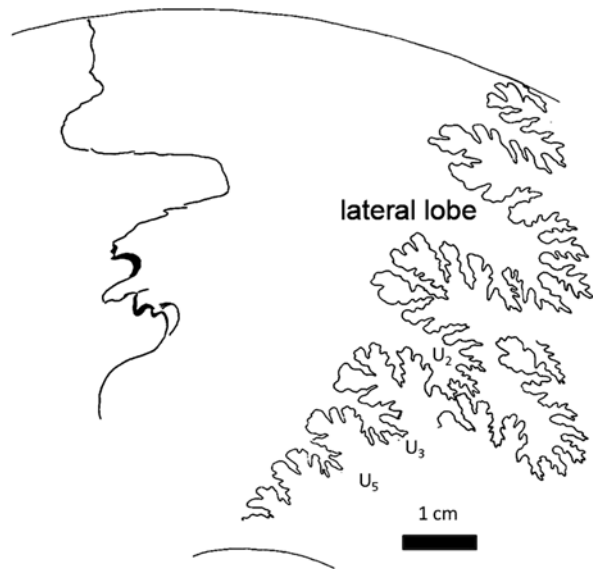
To date the question to what extent the different orientation of the septal concavity between nautiloids and ammonoids refers to different pressure regimes during the septal formation, is controversial. Ward (1987) demonstrates for the modern *Nautilus* that low/negative pressure exists after the preforming organic phragma of the septum was mineralized. That negative pressure creates an aboral oriented tension to the corresponding concave septum. The last chamber is still filled with liquid during the septal formation process and initial mineralization processes. Therefore, a uniformly directed pressure to all sides exists and the septum itself is formed without facing directed stress. Several authors postulated for ammonoids with gener-

ally convex, arched (towards the peristome) septa (Westermann 1975; Bayer 1977a, 1977b; Checa and Garcia-Ruiz 1996), a septal formation under high pressure or stressed conditions. In this case, stress was caused by muscular tension (Seilacher 1975; Seilacher and LaBarbera 1995). Bayer (1978) assumes that high pressure conditions within the ammonoid chambers are necessary for the morphogenesis of the septa that are punctually attached to the conotheca (“*Pneu-Model*”). According to this concept the configuration of the suture line, with its rounded saddle endings and pointed lobe endings, represent the expression of that tension. Any reversal of the suture line morphology, i.e., the formation of pointed saddles and rounded lobes, was therefore excluded categorically by Bayer (1978). However, Ward and Westermann (1976) and Henderson et al. (2002) report such a suture line inversion for the two heteromorph ammonoid genera *Glyptoxoceras* and *Baculites*. For the former the suture line inversion, including pointed saddles and rounded lobe endings, only occur temporarily during the juvenile stage (septata 2–6). During subsequent growth stages, the suture line returned to normal. For *Baculites* from the Santonian of the Western Interior, the overall morphology of the suture line and septal spacing was similar to its conspecifics. However, a continuous modification with pointed saddles and rounded lobe endings was reported. The authors conclude, from these extremely rare cases of suture line inversion, that the configuration and formation of the ammonoid septa was carried out under uniform hydrostatic pressure and therefore comparable to the modern *Nautilus*. The reason for the suture line inversion reported for *Baculites* is seen by these authors as a genetic defect. Thus, the rear visceral mass including the surrounding mantle has been shaped independently. On the other hand, particularly for *Baculites*, the difference between pointed lobe- and rounded saddle endings are less significant. Following the “*pneu-model*”, the tension and the postulated high pressure in the last chamber would already have been small. The assumption that straight shells had flooded a large part of their phragmocone with liquid in order to ensure a more or less horizontal swimming position (Hauschke et al. 2011) supports the idea of a more or less uniform pressure load on the forming septum. Therefore, the restricted observation of suture line inversions just for heteromorph ammonoids supports the “*pneu model*” of septal formation of normal planispirally coiled ammonoid shells.

21.3.2.4 Anomalous Simplification of Sutures

In this context the description of a *Brasilia* from the Middle Jurassic of Dorset with a pathological simplification of the suture by Rieber (1979) is interesting to be mentioned (Fig. 21.28). The specimen shows an inclined septum with one side unusually distant from the preceding septum. Its configuration shows simplified saddles and lobes. The non-subdivided lateral lobe appears broadly rounded and the rudimentary umbilical saddles have rather pointed protuberances. Rieber (1979) interprets the anomaly due to the asymmetric detachment of the rear subepithelial musculature and thus a shift of the “*Muralleiste*” (=mural ridge, *sensu* Blind 1975).

Fig. 21.28 Anomalous simplified and inverted suture line of *Brasilica decipiens* (Buckman) from the Middle Jurassic of Horn Park near Beaminster, diameter 17.7 cm. Drawing after Rieber (1979, Fig. 2; from Keupp 2012)



The mural ridge as forming organ for the septal wall no longer takes the usual course. An alternative interpretation can be drawn from the fact that the suture line is not only simplified but also inverted. This can be explained by a detachment of the aboral body portion that causes an anomalous low pressure and subsequently a collapse of the final, exceedingly large, chamber.

21.3.2.5 Pneumosepta

The term “*pneumosepta-syndrom*” was coined by Keupp and Mitta (2004) based on a *Quenstedtoceras* (Upper Callovian). The anomalous forward projected septum shows that during its formation there was a high pressure, which had already deformed the organic pre-septum. The reason for that septal projection is a breakaway of the siphuncle from its ventral position and could be visualized using computed tomography images. Thus, the foramen (point of passage of the siphuncle through the septum) was displaced dorsally due to the anomalous bulged septum. Another case of a “*pneumoseptum*” was reported by Keupp (2012) for *Douvilleiceras* (Lower Albian).

Occurrence of pneumosepta within planispiral ammonoids again support the “*pneu-model*” for chamber formation (Bayer 1978). The examples (Fig. 21.29) have shown that at least for individual cases the chamber formation and suture line configuration can also take place under adorally directed tension. Thus, it becomes conceivable that ammonoids, contrary to the modern *Nautilus*, form their chambers regularly under slightly higher pressure conditions.

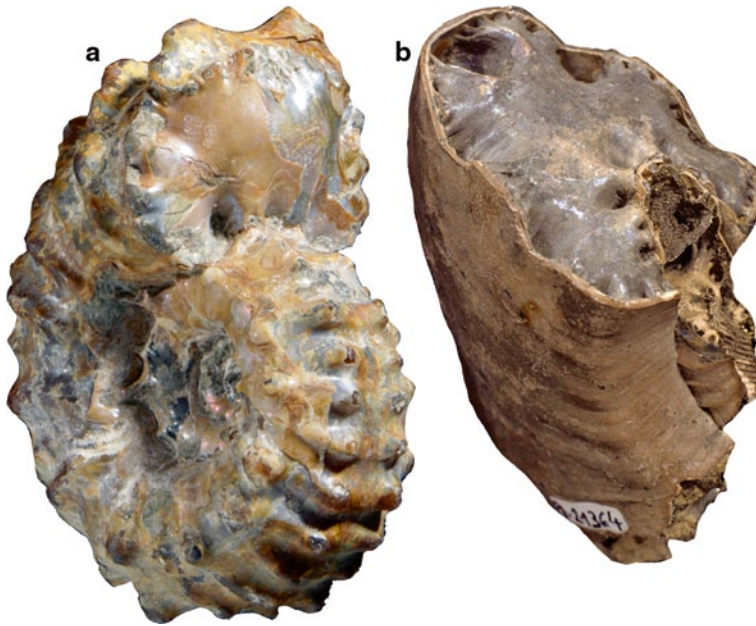


Fig. 21.29 Anomalous bulged septa indicate high pressure conditions within the chambers during the septal formation process (“pneumosepta-syndrom”). **a** *Quenstedtoceras* sp. from the Upper Callovian of Dubki near Saratov, Russia (from Keupp and Mitta 2004), **b** *Douvilleiceras mammillatum* (Schlotheim) from the Lower Albian, Mahajanga Basin, Madagascar (from Keupp 2012)

21.4 Anomalies Caused by Physiological Disturbations

Only a few descriptions about physiological malfunctions in succession of diseases (e.g., virulent tumors) are available for extant cephalopods (e.g., *Octopus* see Hanlon and Forsythe 1990; Rungger et al. 1971). In fact, these are fairly common in other molluscs (e.g., bivalves see Sparks 1972). In contrast, multiple disruptions of shell formation, especially the increased incorporation of black lines due to ecological stress especially of aquarium reared nautilids, were described (Carlson 1987). Adult nautilids develop a marginal thickening of their peristome and a black band of conchiolin which is of individual thickness in their natural habitat (Ward 1987). Almost all captive nautiloids show a typical response to stressed conditions in their shell, namely the reduced growth of the conotheca. The slowdown which simulates a complete growth stop for short episodes causes the occurrence of a sequence of pre-adult black bands. These pre-adult black bands will be incorporated into the shell during the next growth phase. The result is a shell with a high proportion of black polymeric proteins incorporated within the strong growth lines (Saunders and Landman 1987). Potentially, the stretch zones that were reported by Landman and Waage (1986) for ammonoids represent similar phenomena. Growth stress during the morphological transformation of the final, hook-shaped living chamber of

Fig. 21.30 *Kranaosphinctes rabei* Collignon with a stretch zone *sensu* Landman and Waage (1986) in connection with the development of parabolic ribs (Upper Oxfordian, Sakaraha, SW-Madagascar)



Upper Cretaceous scaphitids causes an anomalous sculpture at the rear living chamber according to Landman and Waage (1986). That sculpture consists of an anomalous ventral depression and is reduced to densely packed growth lines.

Comparable temporary growth retardations can also be found in perisphinctids in connection with the formation of parabolic ribs (Fig. 21.30). Stretch zones are not to be confused with the final weakening of the sculpture, e.g., on the adult body chamber, which were described as so-called “senile-sculptures” in *Pleuroceras* from the Lower Jurassic (Frentzen 1937). Pre-adult stretch zones, without changes of the shell, rather indicate a physiological or ecological stress.

“*Kümmervuchs*” (stunting *sensu* Ager 1963) has been postulated for various assemblages. Stunted populations of a certain species or species associations are due to certain environmental parameters. Therefore, these stunted forms represent ecophenotypes and thus, they are not pathological. However, it is difficult to distinguish between ecologically-induced stunting and true pathologies. Stunted ammonoid fauna, in which all representatives are smaller compared to other localities have usually been described as “*dwarf fauna*” (e.g., Sturani 1971). Stunted fauna can be caused by specific environmental situations. These parameters, including food availability, oxygen depletion, hazardous substances, or geographical restriction of the habitat, could have negatively influenced the growth of ammonoids (Tasch 1953; Vogel 1959; Hallam 1965; Clausen 1968; Wendt 1971; Krystyn et al. 1971; Wagenplast 1972; Mignot 1993; Mignot et al. 1993; Besnosov and Mitta 1996; Marchand et al. 2002). Another example comes from the Upper Triassic of Southern Tyrol with its peculiar miniaturized mollusc and brachiopod fauna. Richthofen (1860) and Laube (1869) discussed unfavourable life conditions within the Cassianian Basin, while Fürsich and Wendt (1977) interpreted them as remains of a sea-weed meadow. However, due to the presence of primary small ammonoids (e.g., *Lobites*), preservation of numerous juvenile forms (Fuchs 1871) and due to taphonomic phenomena, a stunting fauna was in some cases partly faked. Only the fully chambered inner whorls and juvenile specimens were recorded within the marly facies (Urlichs 2001, 2004). Comparative studies of septal spacing between the Cassian fauna and the contemporaneous Hallstatt limestones showed that no septal crowding occurred in trachyceratids,

proarcestids, lecantitids, and megaphyllitids from the Cassianian Basin, i.e. a true stunting was not verifiable for these taxa. For *Lobites* it seems apparent that the amount of very small “stunted” form is rather artificial and related to the intense collecting of the larger specimens (Urlichs 1994).

21.5 Conclusions

The presented pathological phenomena in ammonoids, which are related with shell anomalies and disturbances in the growth of aptychi, are caused partly exogenously (injuries, epibiosis), and partly endogenously (“diseases”, parasitism). It turns out that repeatedly occurring morphologically similar “standardized” anomalies are often overinterpreted and led to incorrect taxonomic and phylogenetic evaluations. For these “standardized” anomalies Hölder (1956) introduced in open nomenclature the term *forma aegra* which currently is in common usage. The etiology of anomalies and the reaction of affected ammonoids open a broad range of paleobiological interpretations. This applies equally to aut- and syncological aspects. As examples of autecological aspects we discussed: the hydrostatic efficiency of the phragmocone, the mobility of the soft body in the living chamber, life- and feeding habits, and the lifespan of the ammonites. Syncological aspects were developed on the basis of possible coevolutionary processes of parasites and epizoa, and especially of predator-prey relationships.

References

- Ager DV (1963) Principles of paleontology. McGraw Hill, New York
- Baird GC, Brett CE, Frey R (1989) “Hitchhiking” epizoans on orthoconic cephalopods: preliminary review of the evidence and its implications. *Senck leth* 69:39–465
- Baluk W, Radwanski A (1996) Stomatopod predation upon gastropods from the Korytnica Basin, and from other classical Miocene localities in Europe. *Acta Geol Pol* 46:279–304
- Bayer U (1977a) Cephalopoden-Septen, Teil I: Konstruktionsmorphologie des Ammoniten-Septens. *N Jb Geol Paläont Abh* 154:290–366
- Bayer U (1977b) Cephalopoden-Septen, Teil II: Regelmechanismen im Gehäuse- und Septenbau der Ammoniten. *N Jb Geol Paläont Abh* 155:162–215
- Bayer U (1978) The impossibility of inverted suture lines in ammonites. *Lethaia* 11:307–313
- Becker RT, House MR (1994) International Devonian goniatitic zonation, Emsian to Givetian, with new records from Morocco. *Courier Forschungsinst Senck (Willi Ziegler Festschrift II)* 169:79–135
- Besnosov NV, Mitta VV (1996) “Dwarf” ammonites from the Calloviense Zone of the Great Balkhan (Callovian, Western Turkmenistan), their ecological and taphonomic environments. *Paleontol J* 30(4):389–395
- Blankenhorn M (1887) Über Ceratiten des oberen deutschen Muschelkalks. *Verh Naturhist Ver preuß Rheinl Sitz Ber* 44:28
- Blind W (1963) Die Ammoniten des Lias alpha aus Schwaben, vom Fonsjoch und Breitenberg (Alpen) und ihre Entwicklung. *Palaeontogr A* 121:38–131

- Blind W (1975) Über die Entstehung und Funktion der Lobenlinie bei Ammonoideen. *Paläontol Z* 49:254–267
- Blind W, Jordan R (1979) “Septen-Gabelung” an einer *Dorsetensia romani* (Oppel) aus dem nordwestdeutschen Dogger. *Paläontol Z* 53 (3/4):137–141
- Böttcher J (1938) Versteinerungen des Oberen Muschelkalkes bei Ohrdorf als aufschlussreiche Dokumente für die Geschichte des deutschen Muschelkalkmeeres. *Beitr Geol Thüringen* 5: 99–105
- Bucher H, Landman NH, Klofak SM, Guex J (1996) Mode and rate of growth in ammonoids. In: Landman NH, Tanabe K, Davis RA (eds) *Ammonoid paleobiology*. Plenum, New York
- Bülow Ev (1918) Über einige abnorme Formen bei den Ammoniten. *Z dtsh geol Ges, Monatsber* 69:132–139
- Busse E (1954) Profil der Unteren und Mittleren Ceratitenschichten vom Eisenberg bei Hessisch-Lichtenau und Walburg. *Notizblatt hess LA Bodenforsch* 80(3):118–137
- Callomon JH (1963) Sexual dimorphism in Jurassic ammonites. *Trans Leicester Liter Philos Soc* 57:21–56
- Carlson BA (1987) Collection and aquarium maintenance of *Nautilus*. In: Saunders, WB, Landman NH (eds) *Nautilus, the biology and paleobiology of a living fossil*. Plenum, New York
- Checa A, García-Ruiz JM (1996) Morphogenesis of the septum in ammonites. In: Landman NH, Tanabe K, Davis RA (eds) *Ammonoid paleobiology*. Plenum, New York
- Checa AG, Okamoto T, Keupp H (2002) Abnormalities as natural experiments: a morphogenetic model for coiling regulation in planspiral ammonites. *Paleobiology* 28:127–138
- Claus W (1992) Der Obere Muschelkalk des Coburger Landes. *Fossilien* 1992(2):122–127
- Clausen CD (1968) Oberdevonische Cephalopoden aus dem Rheinischen Schiefergebirge, I Orthocerida, Bactritida. *Palaeontogr A* 128: 1–86
- Credner GR (1875) *Ceratites fastigatus* und *Salenia texana*. *Z Ges Naturwiss* 46:105–116
- Dagys AS, Keupp H (1998) Internal ventral keels in Triassic ceratid ammonoids: description and functional interpretation as muscle scars. *Z dtsh geol Ges* 149(1):81–89
- Davis RA, Landman NH, Dommergues JL, Marchand D, Bucher H (1996) Mature modifications and dimorphism in ammonoid cephalopods. In: Landman NH, Tanabe K, Davis RA (eds) *Ammonoid paleobiology*. Plenum, New York
- Davis RA, Mapes RH, Klofak SM (1999) Epizoa on externally shelled cephalopods. In: Rozanov AY, Shevryev AA (eds) *Fossil cephalopods: recent advances in their study*. Palaeontological Institute, Moscow
- De Baets K, Klug C, Korn D (2011) Devonian pearls and ammonoid-endoparasitic co-evolution. *Acta Paleontol Pol* 56:159–180
- De Baets K, Keupp H, Klug C (2015) Parasites of Ammonoids. In: Klug C, Korn D, De Baets K, Kruta I, Mapes RH (eds) *Ammonoid paleobiology: from anatomy to ecology*. Springer, Dordrecht
- Doguzhaeva LA, Mutvei R (1991) Organization of the soft body in *Aconeceras* (Ammonitina), interpreted on the basis of shell morphology and muscle-scars. *Paleontogr A* 218:17–33
- Doguzhaeva LA, Mutvei H (1996) Attachment of the body to the shell in ammonoids. In: Landman NH, Tanabe K, Davis RA (eds) *Ammonoid paleobiology*. Plenum, New York
- Donavan DT (1957) Note on the species *Cymbites laevigatus* (J. de C. Sowerby) and on the genus *Cymbites* Neumayr. *Geol Mag* 94(5):413–420
- Dunstan A, Bradshaw CJA, Marshall J (2011) *Nautilus* at risk-estimating population size and demography of *Nautilus pompilius*. *Plos ONE* 6(2):1–9 (e16716)
- Eck H (1879) Ueber einige Trias-Versteinerungen. *Z dtsh Geol Ges* 31:254–281
- Eichler R, Ristedt H (1966) Isotopic evidence on the early life history of *Nautilus pompilius* (Linné). *Science* 153:734–736
- Engel T (1894) Ueber kranke Ammonitenformen im schwäbischen Jura. *Nova Acta Kgl Leop Carol dtsh Akad Naturf* 61(5):326–384
- Engeser T, Keupp H (2002) Phylogeny of the aptychi-possessing Neoammonoidea (Aptychophora nov., Cephalopoda). *Lethaia* 34:79–96

- Fernández-López S (1987) Necrocinesis y colonización postmortal en Bajosphinctes (Ammonoidea) de la Cuenca Ibérica. Implicaciones paleoecológicas y paleobatimétricas. *Bol R Soc Española Hist Nat (Geol)* 82(1–4):151–184
- Fraas O (1863) Abnormitäten bei Ammoniten. *Jahresverh Ver vaterländ Naturkunde Wrttbg* 19:111–113
- Frentzen K (1937) Ontogenie, Phylogenie und Systematik der Amaltheen des Lias Delta Südwestdeutschlands. *Abh Heidelberger Akad Wiss mathem naturwiss Kl* 23:1–136
- Frerichs U (2011) Epöken: Über Siedler und “Piraten”. *Fossilien* 2011(5):295–298
- Fuchs T (1871) Über lokale Anreicherung kleiner Organismen und insbesondere über die Fauna von St. Cassian. *Verh k k geol Reichsanstalt* 1871:204–206
- Fürsich F, Wendt J (1977): Biostratigraphy and palaeoecology of the Cassian Formation (Triassic) of the Southern Alps. *Palaeogeogr Palaeoclim Palaeoecol* 22:257–323
- Geczy B (1965) Pathologische jurassische Ammoniten aus dem Bakony-Gebirge. *Ann Univ Sci Budapest Sec Geol* 9:31–37
- Guex J (1967) Contribution à l'étude des blessures chez les ammonites. *Bull Lab Géol Univ Lausanne* 165:1–16
- Hagdorn H, Simon T (1985) Geologie und Landschaft des Hohenloher Landes. Thorbecke, Sigmaringen
- Hallam A (1965) Environmental causes of stunting in living and fossil marine benthonic invertebrates. *Paleontology* 8:132–155
- Hanlon RT, Forsythe JW (1990) Diseases of Mollusca: Cephalopoda. 1.1 Diseases caused by microorganisms. In: Kinne O (ed) *Diseases of marine animals*, 3. Biologische Anstalt Helgoland, Hamburg
- Hansen MC, Mapes RH (1990) A predator-prey relationship between sharks and cephalopods in the Late Paleozoic. In: Boucot A (ed) *Evolutionary paleobiology of behaviour and coevolution*. Elsevier, Amsterdam
- Hauschke N, Schöllmann N, Keupp H (2011) Oriented attachment of a stalked cirripede on an orthoconic heteromorph ammonite—implications for the swimming position of the latter. *N Jahrb Geol Paläont Abh* 262(2):199–212
- Heller F (1958) Gehäusemißbildungen bei Amaltheiden. *Geol BI NO-Bayern* 8:66–71
- Heller F (1964) Neue Fälle von Gehäusemißbildungen bei Amaltheiden. *Paläontol Z* 38(3/4):136–141
- Henderson RA, Kennedy WJ, Cobban WA (2002) Perspectives of ammonite paleobiology from shell abnormalities in the genus *Baculites*. *Lethaia* 35:215–230
- Hengsbach R (1976) Über Sutura-Asymmetrie bei *Cymbites laevigatus* (Ammonoidea; Jura). *Senck leth* 56(6):463–468
- Hengsbach R (1977a) Cheiloceraten (Ammon., Devon) mit asymmetrischem Phragmocon. *Sitzungsberichte Ges Naturf Freunde Berlin (NF)* 17:69–72
- Hengsbach R (1977b) Über die Sutura-Asymmetrie einiger Psiloceraten. *Sitzungsber Ges Naturf Freunde Berlin (NF)* 17:59–67
- Hengsbach R (1978) Zur Sutura-Asymmetrie bei *Anahoplites* (Ammonoidea, Kreide). *Senck leth* 59:377–385
- Hengsbach R (1980) Über die Sutura-Asymmetrie bei *Hecticoceras* (Ammonoidea; Jura). *Senck leth* 60(4/6):463–473
- Hengsbach R (1986a) Zur Kenntnis der Sutura-Asymmetrie bei Ammoniten. *Senck leth* 67(1/4):119–149
- Hengsbach R (1986b) Ontogenetisches Auftreten und Entwicklung der Sutura-Asymmetrie bei einigen Psilocerataceae (Ammonoidea; Jura). *Senck leth* 67(1/4):323–330
- Hengsbach R (1990) Studien zur Paläopathologie I: Die Paläoparasitologie, eine Arbeitsrichtung der Paläobiologie. *Senck leth* 70(4/6):439–461
- Hengsbach R (1991) Die Symmetriopathie, ein Beitrag zur Erforschung sogenannter Anomalien. *Senck leth* 71(3/4):339–366
- Hengsbach R (1996) Ammonoid pathology. In: Landman NH, Tanabe K, Davis RA (eds) *Ammonoid paleobiology*. Plenum, New York

- Hewitt RA, Westermann GEG (1990) Mosasaur tooth marks on the ammonite *Placenticerias* from the Upper Cretaceous of Alberta, Canada. *Can J Earth Sci* 27:469–472
- Hölder H (1955) Die Ammonitengattung *Taramelliceras* im südwestdeutschen Unter- und Mittelalm. *Paleontogr A* 106:37–153
- Hölder H (1956) Über Anomalien an jurassischen Ammoniten. *Paläontol Z* 30:95–107
- Hölder H (1960) Zur Frage des Wachstumsendes bei Ammoniten. *Paläontol Z* 34:61–68
- Hölder H (1970) Anomalien an Molluskenschalen, insbesondere Ammoniten, und deren Ursachen. *Paläontol Z* 44:182–195
- Hölder H (1973) *Miscellanea cephalopodica*. *Münster Forsch Geol Paläont* 29:39–76
- Hölder H (1977) Zwei ungewöhnliche Erscheinungsformen anomaler Jura-Ammoniten der forma *aegra verticata*. *Paläontol Z* 51(3/4):254–257
- Hüne L, Hüne P (2006) Des phénomènes paléopathologiques chez une faune d'Ammonites du Callovien supérieur de Bénerville-sur-Mer (Calvados, France). *L'Echo des falaises* 2006(7):33–37
- Hungerbühler A (1992) *Fossilien*. Kosmos, Stuttgart
- Hyatt A (1889) *Genesis of the Arietidae*. *Smithson Contr Knowledge* 26, Art. II+XI: 673+238 pp.
- Ilovaisky D (1917) *Les ammonites du Jurassique supérieur du pays de Liapine*. *Ouvrage Sect Géol Soc Imper Am Sci Nat* 1(1–2):1–180
- Ivanov AN (1975) Late ontogeny in ammonites and its characteristics in micro-, macro- and megacochs. *Yarosl Pedagog Inst Sb Nauchn Tr* 142:5–57
- Jäger M (1991) Nicht alltäglich: Ein Ammonit mit zwei Spiralen. *Fossilien* 1991(6):351–353
- Johnson JG (1984) Temperature and biotic crisis in the marine realm. *Geology* 12(12):741
- Kase T, Johnston PA, Seilacher A, Boyce J (1998) Alleged mosasaur bite marks on Late Cretaceous ammonites are limpet (patellogastropod) home scars. *Geology* 26(10):947–950
- Kauffman EG (1990) Mosasaur predation on ammonites during the Cretaceous—a evolutionary history. In: Boucot A (ed) *Evolutionary paleobiology of behavior and coevolution*. Elsevier, Amsterdam
- Kauffman EG, Kesling RV (1960) An Upper Cretaceous ammonite bitten by a mosasaur. *Contr Michigan Univ Mus Paleont* 15:193–248
- Keferstein W (1861) *Kopftragende Weichthiere (Malacozoa cephalophora)*. In: *Bronn's Klassen und Ordnungen der Weichthiere*, Bd. 3. C.F. Winter'sche Verlagshandlung, Leipzig
- Keller T (1977) *Fraßreste im süddeutschen Posidonienschiefer*. *Jahresh Ges Naturkde Württ* 132:117–134
- Kemper E (1961) Die Ammonitengattung *Platylenticeras* (= *Garnieria*). *Beih Geol Jb* 47:1–195
- Keupp H (1976) Neue Beispiele für den Regenerationsmechanismus bei verletzten und kranken Ammoniten. *Paläontol Z* 50(1/2):70–77
- Keupp H (1977) Paläopathologische Normen bei Amaltheiden (Ammonoidea) des Fränkischen Lias. *Jb Coburger Landesstiftung* 1977:263–280
- Keupp H (1979) Nabelkanten-Präferenz der forma *verticata* Hölder 1956 bei *Dactylioceraten* (Ammonoidea, Toarciens). *Paläontol Z* 53:214–219
- Keupp H (1984/85) *Pathologische Ammoniten, Kuriositäten oder paläobiologische Dokumente*, Teil 1 und 2. *Fossilien* 1984/6:258–262, 267–275; 1985/1: 23–35
- Keupp H (1985) Das "Fastigatus"-Problem bei Ceratiten des Germanischen Muschelkalks. In: Hagdorn H (ed) *Geologie und Paläontologie im Hohenloher Land*. Symposium 100. Geburtstag von Georg Wagner. Künzelsau
- Keupp H (1987) *Perlen (Schalenkonkretionen) bei Dactylioceraten aus dem fränkischen Lias*. *Jahresmitt Naturhist Ges Nürnberg* 1986:97–102
- Keupp H (1991) *Bißmarken oder postmortale Implosionsstrukturen?* *Fossilien* 1991(5):275–280
- Keupp H (1992a) *Rippenscheitel bei Ammoniten-Gehäusen*. *Fossilien* 1992(5):283–290
- Keupp H (1992b) *Wachstumsstörungen bei Pleuroceras und anderen Ammonoidea durch Epökie*. *Berl geowiss Abh E* 3:113–119
- Keupp H (1993) *Fälle der forma aegra calcar (Zieten) bei mesozoischen Ammoniten*. *Fossilien* 1993(3):140–144

- Keupp H (1994) Volumenvermindernde Gehäuse-Anomalien bei Jura-Ammoniten. *Fossilien* 1994(1):38–44
- Keupp H (1995) Volumenvergrößernde Anomalien bei Jura-Ammoniten. *Fossilien* 1995/1:54–59
- Keupp H (1996) Paläopathologische Analyse einer Ammoniten-Vergesellschaftung aus dem Oberjura Westsibiriens. *Fossilien* 1996/1:45–54
- Keupp H (1997) Paläopathologische Analyse einer “Population” von *Dactyloceras athleticum* (Simpson) aus dem Unter-Toarcium von Schlaifhausen/Oberfranken. *Berl geowiss Abh E* 25:243–267
- Keupp H (1998) Mundsäumverletzungen bei *Pleuroceras* (Ammonoidea). *Fossilien* 1998(1):37–42
- Keupp H (2000a) Anomale Muskelleisten bei Ammoniten. *Berl Geowiss Abh E* 34:279–289
- Keupp H (2000b) Ammoniten- Paläobiologische Erfolgsspiralen. Thorbecke, Stuttgart
- Keupp H (2003) Aptychen: Kiefer, Deckel oder beides? *Fossilien* 2003(2):104–110
- Keupp H (2006) Sublethal punctures in body chambers of Mesozoic ammonites (forma aegra fenestra n.f.), a tool to interpret synecological relationships, particularly predator-prey interactions. *Paläontol Z* 80(2):112–123
- Keupp H (2007) Anomale Nabelweiten bei Ammoniten und Nautiliden. <http://www.leitfossil.de/Abonnenten/Lehrreiches>
- Keupp H (2008) Wer hat hier zugebissen? Ammoniten-Prädation. *Fossilien* 2008(2):109–112
- Keupp H (2012) Atlas zur Paläopathologie der Cephalopoden. *Berl Paläobiol Abh* 12:1–390
- Keupp H, Ilg A (1992) Paläopathologie der Ammonitenfauna aus dem Oberallovium der Normandie und ihre palökologische Interpretation. *Berl geowiss Abh E* 3:171–189
- Keupp H, Riedel F (1995) *Nautilus pompilius* in captivity: a case study of abnormal shell growth. *Berl geowiss Abh E* 16/2:663–681
- Keupp H, Veit R (1996) Ein *Phylloceras* mit Anaptychus. *Fossilien* 1996(6):343–351
- Keupp H, Mitta V (2004) Septenbildung bei *Quenstedtoceras* (Ammonoidea) von Saratov (Russland) unter anomalen Kammerdruckbedingungen. *Mitt Geol Paläont Inst Univ Hamburg* 88:51–62
- Keupp H, Schweigert G (2009) Scheinbare heteromorphe Ammoniten. *Fossilien* 2009(6):358–362
- Keupp H, Richter AE (2010) Napfschnecken-Fraßkuhlen als Ursache von blasenartigen Steinkernstrukturen bei meozoischen Ammoniten (*Kranaosphinctes*, *Eupachydiscus*) von Madagaskar. <http://www.leitfossil.de/Abonnenten/Lehrreiches>
- Keupp H, Schobert J (2011) Gehäuseanomalien bei Klein-Ammoniten von Buttenheim/Oberfranken. *Fossilien* 2011(3):164–174
- Keupp H, Mitta V (2013) Cephalopod jaws from the Middle Jurassic of the Unzha-Basin, Kostroma Region, Central Russia. *N Jahrb Geol Paläont Abh* 270(1):23–54
- Keupp H, Röper M, Seilacher A (1999) Paläobiologische Aspekte von syn vivo-besiedelten Ammonoideen im Plattenkalk des Ober-Kimmeridgiums von Brunn in Ostbayern. *Berl geowiss Abh E* 30:121–145
- Keupp H, Röper M, Rothgaenger M (2012) Serpuliden-Epökie auf Ammoniten aus dem Brunner Plattenkalk (Ober-Kimmeridgium) in Ostbayern. *Archaeopteryx* 29:1–12.
- Kieslinger A (1926) Untersuchungen an triadischen Nautiloideen. *Paläontol Z* 7:101–122
- King SD (2009) The ability of Mosasaur to produce unique puncture marks on ammonite shells. Master Thesis, Graduate College at Bowling Green State University, 144 pp.
- Klug C (1999) Devonian ammonoid biometry and global events. preliminary results. In: Histon K (ed) V Intern. Symp. Cephalopods—Present and Past. *Berl Geol BA* 46:60
- Klug C, Korn D (2001) Epizoa and post-mortem epicoles on cephalopod shells—Devonian and Carboniferous examples from Morocco. *Berl geowiss Abh E* 36:145–155
- Klug C, Korn D (2002) Occluded umbilicus in the Pinacitinae (Devonian) and its paleoecological implications. *Paleontology* 45:917–931
- Knoch U (1989) *Placunopsis* auf einem Ceratiten. *Fossilien* 1989(6):280
- Kolb A (1955) Über zwei abnorme Ammonitengehäuse der Gattung *Paltopleuroceras*. *Geol Bl NO-Bayern* 5:148–150
- Kröger B (2000) Schalenverletzungen an jurassischen Ammoniten – ihre paläobiologische und paläoökologische Aussagefähigkeit. *Berl Geowiss Abh E* 33:1–97

- Kröger B (2002a) On the efficiency to the buoyancy apparatus in ammonoids: evidences from sub-lethal shell injuries. *Lethaia* 35:61–70
- Kröger B (2002b) On the ability of withdrawing of some Jurassic ammonoids. *Berl Geol BA* 57:199–204
- Kröger B (2002c) Antipretatory traits of the ammonoid shell—interactions from Jurassic ammonoids with sublethal injuries. *Paläontol Z* 76:223–234
- Kröger B, Keupp H (2004) A paradox survival—report of a repaired syn vivo perforation in a nautiloid phragmocone. *Lethaia* 37:439–444
- Kröger FJ (1984) Professor Landois und die Riesenammoniten. *Fossilien* 1984(6):283–285
- Kruta I, Landman NH (2007) Injuries on *Nautilus* jaws: implications for the function of ammonite aptychi. *Veliger* 50(3):241–247
- Kruta I, Landman N, Rouget I, Cecca F, Tafforeau P (2011) The role of ammonites in the Mesozoic marine food web revealed by jaw preservation. *Science* 331:70–72
- Krystyn L, Schäfer G, Schlager W (1971) Über die Fossil-Lagerstätten in den triadischen Hallstätter Kalken der Ostalpen. *N Jb Geol Paläont Abh* 137:284–304
- Landman NH, Waage KM (1986) Shell abnormalities in scaphitid ammonites. *Lethaia* 19:211–224
- Landman NH, Cochran JK (1987) Growth and longevity of *Nautilus*. In: Saunders WB, Landman NH (eds) *Nautilus—the biology and paleobiology of a living fossil*. Plenum, New York
- Landman NH, Saunders WB, Winston JE, Harries PJ (1987) Incidence and kinds of epizoans on the shells of live *Nautilus*. In: Saunders WB, Landman NH (eds) *Nautilus—the biology and paleobiology of a living fossil*. Plenum, New York
- Lange W (1929) Zur Kenntnis des Oberdevons am Enkeberg und bei Balve (Sauerland). *Abh Preuß Geol LA, NF* 119:1–132
- Lange W (1932) Über Symbiosen von *Serpula* mit Ammoniten im unteren Lias Nordwestdeutschlands. *Z dtshch geol Ges* 84:229–234
- Lange W (1941) Die Ammonitenfauna der *Psiloceras*-Stufe Norddeutschlands. *Paleontogr A* 93:1–186
- Larson N (2007) Deformities in the Late Callovian (Late Middle Jurassic) ammonite fauna from Saratov, Russia. In: Landman NH, Tanabe K, Mapes RH (eds) *Cephalopods—present and past: new insights and fresh perspectives*. Springer, New York
- Laube GC (1869) Die Fauna der Schichten von St. Cassian. *Denkschr kaiserl Akad Wiss mathem naturwiss Kl* 30:1–106
- Lehmann U (1972) Aptychen als Kieferelemente der Ammoniten. *Paläontol Z* 46:34–48
- Lehmann U (1976) *Ammoniten, ihr Leben und ihre Umwelt*. Enke, Stuttgart
- Lehmann U (1990) *Ammonoideen, Leben zwischen Skylla und Charybdis*. Enke, Stuttgart
- Lehmann U, Kulicki C (1990) Double function of aptychi (Ammonoidea) as jaw elements and opercula. *Lethaia* 23:325–331
- Linck O (1956) Echte und unechte Besiedler (Epöken) des deutschen Muschelkalk-Meeress. *Aus der Heimat* 64:161–173
- Longridge LM, Smith PL, Rawlings G, Klaptocz V (2009) The impact of asymmetries in the elements of the phragmocone of Early Jurassic ammonites. *Paleontol Electron* 12(1):1A,15 pp. <http://paleo-electronica.org/2009>
- Makowski H (1963) Problem of sexual dimorphism in ammonites. *Paleontol Pol* 12:1–92
- Manger WL, Meeks LK, Stephen DA (1999) Pathological gigantism in Middle Carboniferous cephalopods, southern midcontinent, United States. In: Oloriz F, Rodriguez-Tovar (eds) *Advancing research on living and fossil cephalopods*. Kluwer, Plenum, New York
- Mapes RH, Hansen M (1984) Pennsylvanian shark-cephalopod predation: a case study. *Lethaia* 17:175–182
- Mapes RH, Sims MS, Boardman DR II (1995) Predation on the Pennsylvanian ammonoid *Gonioboceras* and its implications for allochthonous vs. autochthonous accumulations of goniatites and other ammonoids. *J Paleontol* 69:441–446
- Marchand D, Courville P, Bonnot A, Rossi J, Scoufflaire Q (2002) Very small ammonites (Micro-morphs) from Lower Oxfordian Marls (Mariae Zone). *Abh Geol BA* 57:467–478

- Martill DM (1990) Predation on *Kosmoceras* by semionotid fish in the Middle Jurassic Lower Oxford Clay of England. *Palaeontology* 33:739–742
- Martin J (1858) Notice paléontologique et stratigraphique du Lias inférieur de la Côte d'Or, de l'Yonne et de Luxembourg. *Bull Congr Sci France Auxerre* 1858:377
- Matyja BA (1986) Developmental polymorphism in Oxfordian ammonites. *Acta Geol Pol* 36:37–68
- Maubeuge PL (1949a) Sur quelques échantillons anormaux d'Ammonites jurassiques. *Arch Inst Grand-Ducal Luxembourg NS* 18:127–147
- Maubeuge PL (1949b) Sur la nature des "conelles" (Quenstedt). *Bull Soc Sci Nancy 1: Not Paléont AS*:1–3
- Maubeuge PL (1957) Deux ammonites nouvelles du Lias moyen de l'Allemagne septentrionale. *Bull Soc Sci Nancy* 1957:1–6
- Mayer G (1966) Ein *Ceratites* (*Ceratites?*) *sublaevigatus* Wenger *fastigatus* und zwei weitere Ceratiten mit *fastigatus*-Merkmalen. *Der Aufschluss* 17:295–298
- Mayer G (1974) Ein anomaler *Ceratites* (*Acanthoceratites*) *spinosus spinosus* Philippi aus dem mittleren Hauptmuschelkalk von Zuzenhausen (Kraichgau). *Der Aufschluss* 25:191–192
- Mayer G (1975) Ein bemerkenswerter Ceratit aus dem Oberen Muschelkalk von Schöningen/ Elm. *Der Aufschluss* 26:304–305
- Mayer G (1978) Ceratiten mit Skulpturanomalien aus dem süddeutschen und französischen Muschelkalk. *Der Aufschluss* 29:71–75
- Mayer G (1981) Zwei *fastigatus* Ceratiten aus dem mainfränkischen Muschelkalk. *Der Aufschluss* 32:345–347
- Mayr FX (1967) Paläobiologie und Stratonomie der Plattenkalke der Altmühlalb. *Erlanger Geol Abh* 67:1–40
- Meischner D (1968) Perniciöse Epökie von *Placunopsis* auf *Ceratites*. *Lethaia* 1(2):156–174
- Meischner D (2002) Aufwuchs von Muscheln auf Ceratiten – Ein Ärgernis? *Nat Museum* 132(1):23–29
- Merkt J (1966) Über Austern und Serpeln als Epöken auf Ammonitengehäusen. *N Jb Geol Paläont Abh* 125:467–479
- Mignot Y (1993) Un problem de paléobiologie chez les ammonoids (Cephalopoda): Croissance et miniaturisation en liaison avec les environnements. *Documents des Laboratoires de Géologie Lyon* 124:1–113
- Mignot Y, Elmi S, Domergues JL (1993) Croissance et miniaturisation de quelques *Hildoceras* (Cephalopoda) en liaison avec l'environnement contraignants de la Téthys Toarcienne. *Geobios Mém Spec* 15:305–312
- Mitta VV, Michailova IA, Sumin DL (1999) Unusual Volgian scaphitoid ammonites from Central Russia. *Paleontol J* 33(6):614–619
- Moodie RL (1926) La paléopathologie des mammifères du pléistocène. *Biol Médicale* 16(9):431–440
- Morton N (1981) Aptychi: the myth of the ammonite operculum. *Lethaia* 14:57–61
- Morton N (1983) Pathologically deformed *Graphoceras* (Ammonitina) from the Jurassic of Skye, Scotland. *Paleontology* 26(2):443–453
- Müller AH (1954) Zur Entwicklungsgeschichte der Ceratiten des Germanischen Muschelkalks, mit einigen Bemerkungen über Abnormitäten. *Geologie* 3:28–41
- Müller AH (1970a) Über die *Fastigatus*-Anomalie der Ceratiten (Ammonoidea, Cephalopoda) des Germanischen oberen Muschelkalkes. *Monatsber dtsh Akad Wiss* 12:303–321
- Müller AH (1970b) Weitere Aberrationen bei Ceratiten (Ammonoidea, Cephalopoda) aus dem germanischen oberen Muschelkalk und Bemerkungen zur Originalschale der Ceratiten. *Monatsber dtsh Akad Wiss* 12:219–231
- Müller AH (1970c) Neue Funde seltener Ceratiten aus dem germanischen Muschelkalk und Keuper. *Monatsber dtsh Akad Wiss* 12(8):632–642
- Müller AH (1976) Über einen besonderen Typ phylogenetisch deutbarer Aberrationen fossiler Tiere. *Biologische Rundschau* 14:190–204

- Müller AH (1978) Über Ceratiten mit fehlenden oder unvollständigen Kammerscheidewänden (Septen) und die Frage nach der Lebensweise der Ammonoidea (Cephalopoda). Freiburger Forschungsheft C 334:69–83
- Müller AH (1982) Zur Morphologie, Taxonomie und Ökologie fossiler und rezenter Serpulimorpha (Polychaeta). Biologische Rundschau 20:330–351
- Mundlos R (1963) Fundgrube Schöningen (Braunschweig). Der Aufschluß 14:76–80
- Mutvei H (1957) On the relation of the principal muscles to the shell in *Nautilus* and some fossil nautiloids. Arkiv Mineralogy and Geology. Stockholm 2:219–254
- Nicolesco CP (1921) Étude sur la Dissymétrie de certaines Ammonites. Paris
- Orbigny A de (1842–1851) Paléontologie Française, Terrain Jurassique, Tome 1: Cephalopodes. Masson, Paris
- Philippi E (1897) Ein interessantes Vorkommen von *Placunopsis ostracina* v.Schloth. sp. Z dt geol Ges 51:67–69
- Philippi E (1901) Die Ceratiten des oberen deutschen Muschelkalks. Paleontol Abh NF 4:347–458
- Pompeckj JF (1894) Über Ammonoideen mit anormaler Wohnkammer. Jh Ver vaterl Naturkunde Württ 49:220–290
- Quenstedt FA (1858) Der Jura. Schweizerbart, Tübingen
- Quenstedt FA (1885–1888) Die Ammoniten des Schwäbischen Jura, I–III. Schweizerbart, Stuttgart
- Radwanski A (1996) The predation upon, and the extinction of, the latest Maastrichtian populations of the ammonite species *Hoploscaphites constrictus* (J. Sowerby 1817) from the Middle Vistula Valley, Central Poland. Acta Geol Pol 46:117–135
- Rein S (1989) Über das Regenerationsvermögen der germanischen Ceratiten (Ammonoidea) des Oberen Muschelkalks (Mitteltrias). Veröff Naturhist Mus Schleus 4:47–54
- Rein S (1990) Über Ceratiten (Cephalopoda, Ammonoidea) mit “fehlenden” Septen. Veröff Naturhist Mus Schleus 5:22–25
- Rein S (1991) Die fastigaten Ceratiten in den Sammlungen des Erfurter Naturkundemuseums. Veröff Naturkundemuseum Erfurt 10:66–79
- Rein S (1993) Zur Biologie und Lebensweise der germanischen Ceratiten. In: Hagdorn H, Seilacher A (eds) Muschelkalk, Schöntaler Symposium 1991. Goldschneck, Korb
- Rein S (1994) Über eine interessante Gehäuseregenerierung der Ceratiten. Veröff Naturkundemuseums Erfurt 13:91–100
- Rein S (1996) Über Epöken und das Schwimmvermögen der Ceratiten. Veröff Naturhist Mus Schleus 11:65–75
- Rein S (1997) Biologie und Lebensweise von *Germanonutilus* Mojsisovics 1902: Teil I: Das Schwimmvermögen von *Germanonutilus*. Veröff Naturhist Mus Schleus 12:43–51
- Rein S (2000) Zur Lebensweise von *Ceratites* und *Germanonutilus* im Muschelkalkmeer. Veröff Naturhist Mus Schleus 15:25–40
- Richter AE (2009a) Ammoniten-Gehäuse mit Bissspuren. Berl paläobiol Abh 10:297–305
- Richter AE (2009b) Geologische Notizen: Ammonitengehäuse mit Bissspuren. Natur und Mensch, Jahresmitt der Naturhist Ges Nürnberg 2008:169–175
- Richter U (2002) Gewebeansatz-Strukturen auf pyritisierten Steinkernen von Ammonoideen. Geol Beitr Hannover 4:1–113
- Richthofen Fv (1860) Geognostische Beschreibung der Umgebung von Predazzo, Sanct Cassian und der Seiser Alpe in Süd-Tyrol. Gotha
- Rieber H (1963) Ein *Cardioceras* (Ammonoidea) mit asymmetrischer Lage von Phragmokon und Kiel. N Jahrb Geol Paläont Mh 1963:289–294
- Rieber H (1979) Eine abnorme, stark vereinfachte Lobenlinie bei *Brasilia decipiens* (Buckman). Paläontol Z 53:230–236
- Riedel A (1916) Beiträge zur Paläontologie und Stratigraphie der Ceratiten des deutschen oberen Muschelkalks. Jb Kgl preuß geol LA 37:1–116
- Roll A (1935) Über Fraßspuren an Ammoniten. Zbl Min Geol Paläont Abt B 1935:120–124
- Rothe HW (1949) Zum Problem des *Ceratites fastigatus* Credn. mit Beispielen von thüringischen Fundorten. Hallesches Jb mitteldt Erdgesch 1:27–32

- Rothe P (1955) Die Ceratiten und die Ceratitenschichten des Oberen Muschelkalks (Trias) im Thüringer Becken. *Beitr Geol Thüringen* 8:255–323
- Rummel O (1973) Fund eines dritten ringrippigen Ceratiten im Steinbruch Luxwinkel bei Schöninggen. *Der Aufschluss* 24:367–368
- Rungger D, Rastelli M, Braendle E, Malsberger RG (1971) A virus like particle associated with lesions in the muscles of *Octopus vulgaris*. *J Invertebr Pathol* 17:72–80
- Saunders WB, Landman NH (eds) (1987) *Nautilus*—The biology and paleobiology of a living fossil. Plenum, New York
- Schindewolf OH (1929) Vergleichende Studien zur Phylogenie, Morphogenie und Terminologie der Ammonoitenlinie. *Abh preuß geol LA, NF* 115:1–102
- Schindewolf OH (1934) Über Epöken auf Cephalopoden-Gehäusen. *Paläontol Z* 16(1/2):15–31
- Schindewolf OH (1958) Über Aptychen (Ammonoidea). *Paleontogr A* 111:1–46
- Schindewolf OH (1961) Die Ammoniten-Gattung *Cymbites* im deutschen Lias. *Paleontogr A* 117:193–232
- Schindewolf OH (1962) Parasitäre Thallophyten in Ammoniten-Schalen. *Paläontol Z H. Schmidt-Festband*: 206–215
- Schmidt H (1926) Neotenie und beschleunigte Entwicklung bei Ammonoiten. *Paläontol Z* 7:197–205
- Schram FR, Hof CJ, Steeman FA (2003) Thylacocephala (Arthropoda: Crustacea ?) from the Cretaceous of Lebanon and implications for Thylacocephalan systematics. *Palaeontology* 42:769–797
- Schwegler E (1939) Eine merkwürdige Krankheitserscheinung bei einem Belemniten aus dem Braunen Jura epsilon Schwabens und ihre Deutung. *Zentralbl Min Geol Paläont* 1939 Abt.B:74–80
- Schweigert G (2009) Doppelt gescheitelt: Aus der Schatzkiste eines Sammlers. *Fossilien* 2009(4):250–252
- Schweigert G, Dietze V (1999) *Oecoptychius* – des Rätsels Lösung. *Fossilien* 1999(1):51–58
- Schweigert G, Dietl G (2001) Die Kieferelemente von *Physodoceras* (Ammonitina, Aspidoceratidae) im Nusplinger Plattenkalk (Oberjura, Schwäbische Alb). *Berl geowiss Abh E* 36:131–143
- Seilacher A (1954) Ökologie der triassischen Muschel *Lima lineata* (Schloth.) und ihre Epöken. *N Jahrb Geol Paläont Mh* 1954:163–183
- Seilacher A (1960) Epizoans as a key to ammonoid ecology. *J Paleontol* 34(1):189–193
- Seilacher A (1975) Mechanische Simulation und funktionelle Evolution des Ammoniten-Septums. *Paläontol Z* 49:268–286
- Seilacher A (1993) Ammonite aptychi: how to transform a jaw into an operculum? *Am J Sci* 293(AS):20–32
- Seilacher A (1998) Mosasaur, limpets or diagenesis: How *Placentoceras* shells got punctured. *Mitt Mus Naturkd Berlin. Geowiss Reihe* 1:93–102
- Seilacher A, La Barbera M (1995) Ammonites as Cartesian divers. *Palaios* 10:493–506
- Seilacher A, Keupp H (2000) Wie sind Ammoniten geschwommen? *Fossilien* 2000(5):310–313
- Seltzer VB (2001) About anomalous shells from the Callovian ammonites. *Transact Sci Res Geol Inst Saratov State Univ, NS* 8:29–45
- Sims MS, Boston WB, Mapes RH (1987) Predation on an Upper Carboniferous ammonoid *Gonioloboceras*. *Geol Surv Am* 19(Abstracts with Program):57–58
- Sornay J (1955) Nautilie fossile à coquille anormale. *Muséum Nat Hist Bull, ser 2* 27:260–261
- Sparks AK (1972) *Invertebrate pathology*. Academic, New York
- Stahl KF (1824) Verzeichnis der Versteinerungen Württembergs. *Correspondenzbl kgl württemb landwirtsch Ver* 6:1–91
- Stephen DA (1997) Possible reproductive mass mortality and pathologic gigantism in Middle Carboniferous (Chesterian-Morrowan) cephalopod assemblages, southern Midcontinent. *Oklahoma Geol* 57(3):113
- Stephens GR (1988) Giant ammonites: a review. In: Wiedmann J, Kullmann J (eds) *Cephalopods—present and past*. Schweizerbart, Stuttgart
- Stumbur KA (1960) Life-time injuries in some nautiloid shells. *Paleontol J* 4:133–135

- Sturani C. (1971) Ammonites and stratigraphy of the “*Posidonia alpina*” beds of the Venetian Alps. *Memorie degli Institutid di Geologia e Mineralogia dell’Università di Padova* 28:1–190
- Suchopar J (1997) Die Ceratiten der semipartitus-Zone von Gänheim. *Fossilien* 1997(4):222–224
- Tanabe K (2011) The feeding habits of ammonites. *Science* 331:37–38
- Tasch P (1953) Causes and paleontological significance of dwarfed fossil marine invertebrates. *J Paleontol* 27:356–444
- Tasnadi-Kubacska A (1962) Paläopathologie, Pathologie der vorzeitlichen Tiere. Fischer, Jena
- Tornquist A (1896) Die degenerierten Perisphinctiden des Kimmeridge von le Havre. *Abh der Schweiz Paläont Ges* 23:1–43
- Trueman AE (1941) The ammonite body-chamber, with special reference to the buoyancy and mode of life of the living ammonite. *Quart J Geol Soc London* 94(4):339–383
- Tsujino Y, Shigeta Y (2012) Biological response to experimental damage of the phragmocone and siphuncle in *Nautilus pompilius* Linnaeus. *Lethaia* 45:443–449
- Tsujita CJ, Westermann GEG (1998) Ammonoid habitats and habits in the Western Interior Seaway: a case study from the Upper Cretaceous Bearpaw Formation of southern Alberta, Canada. *Paleogeogr Paleoclim Paleoecol* 144:135–160
- Urlichs M (1994) *Trachyceras* Laube 1869 (Ammonoidea) aus dem Unter-Karn (Obertrias) der Dolomiten (Italien). *Stuttg Beitr Natkde B* 217:1–55
- Urlichs M (2001) Die Zwergfauna aus der Obertrias von St. Kassian (Dolomiten). In: Weidert K (ed) *Klassische Fundstellen der Paläontologie*, Bd. IV. Goldschneck, Korb
- Urlichs M (2004) Kümmerwuchs bei *Lobites* Mojsisovics 1902 (Ammonoidea) aus dem Unter-Karnium der Dolomiten (Ober-Trias, Italien) mit Revision der unterkarnischen Arten. *Stuttg Beitr Natkde B* 344:1–37
- Vadász E (1908) Über eine oberliassische *Lytoceras*art mit aufgelöster Wohnkammer. *Z Ung geol Ges* 38:131–136
- Vermeij GJ (1977) Mesozoic marine revolutions. *Paleobiology* 3:245–258
- Vermeij GJ (1982) Gastropod shell form, breakage, and repair in relation to predation by the crab *Calappa*. *Malacologia* 23:1–12
- Vermeij GJ (1983) Traces and trends of predation with special reference to bivalve animals. *J Paleontol* 26:455–465
- Vermeij GJ (1987) *Evolution and escalation: an ecological history of life*. Princeton University Press, Princeton
- Vogel KP (1959) Zwergwuchs bei Polyptychiten (Ammonoidea). *Geol Jahrb* 76:469–540
- Wagenplast P (1972) Ökologische Untersuchungen der Fauna aus Bank- und Schwammfazies des Weißen Jura der Schwäbischen Alb. *Arbeiten aus dem Geologisch-Paläontologischen Institut an der Universität Stuttgart*. NF 67:1–99
- Walker, S.E. and Brett, C. (2002) Post-Paleozoic patterns in marine predation: was there a Mesozoic and Cenozoic marine predatory revolution? *Paleontol Soc Pap* 8:119–193
- Wani R, Jenkins RG, Mapes RH (2012) Preferential predatory peeling: ammonoid vs. nautiloid shells from the Upper Carboniferous of Texas, USA. *Geobios* 45(1):129–137
- Wannenmacher N (2010) Aus der Form geraten: Pathologische Lias-Ammoniten aus Schwaben. *Fossilien* 2010(4):225–228
- Ward PD (1979) Cameral liquid in *Nautilus* and ammonites. *Paleobiology* 5(1):40–49
- Ward PD (1981) Shell sculpture as an adaptation in ammonoids. *Paleobiology* 7:96–100
- Ward PD (1986) Rates and processes of compensatory buoyancy change in *Nautilus macromphalus*. *Veliger* 28 (4):356–368.
- Ward PD (1987) *The natural history of Nautilus*. Allen and Unwin, Boston
- Ward PD, Westermann GEG (1976) Sutural inversion in a heteromorphy ammonite and its implications for septal formation. *Lethaia* 9:357–361
- Wenger R (1957) Die germanischen Ceratiten. *Paleontogr A* 108:57–129
- Wendt J (1971) Genese und Fauna submariner sedimentärer Spaltenfüllungen im mediterranen Jura. *Paleontogr A* 136:121–192
- Westermann GEG (1975) Model for origin, function and fabrication of fluted cephalopod septa. *Paläontol Z* 49:235–253

- Westermann GEG (1996) Ammonoid life and habit. In: Landman NH, Tanabe K, Davis RS (eds) Ammonoid paleobiology. Plenum, New York
- Westermann GEG (2013) Hydrostatics, propulsion and life-habits of the Cretaceous ammonoid *Baculites*. *Revue de Paléobiologie* 32(1):249–265
- Wetzel W (1964) Schalen-Parasitismus bei Ammoniten (aufgrund schleswig-holsteinischer Funde). *Meyniana* 14:66–69
- Weyer D (1964) Ein ungewöhnlicher fastigater Ceratit aus dem germanischen Oberen Muschelkalk. *Geologie* 13(4):478–481
- Wiedmann J (1972) Ammoniten-Nuclei aus Schlammproben der nordalpinen Obertrias, ihre stammesgeschichtliche und stratigraphische Bedeutung. *Mitteilungen Ges Geol Bergbaustudent* 21:561–622
- Wiedmann J (1973) Evolution or revolution of ammonoids at Mesozoic system boundaries. *Biol Rev* 48(2):159–194
- Wunsch P (1957) Ein typischer *Ceratites fastigiotenuis* Rothe aus der Umgebung von Göttingen. *Geol Jb* 73:557–560
- Zapalski MK (2011) Is absence of proof a proof of absence? Comments on commensalism. *Palaeogeogr Palaeoclim Palaeoecol* 302:484–488
- Zann L (1985) The rhythmic activity of *Nautilus pompilius*, with notes on its ecology and behavior in Fiji. *Veliger* 27(1):19–28
- Ziegler B (1958) Monographie der Ammonitengattung *Glochiceras* im epikontinentalen Weißjura Mitteleuropas. *Paleontogr A* 110:93–164
- Zieten CHv (1830–1833) Die Versteinerungen Württembergs. Schweizerbart, Stuttgart
- Zimmermann E (1883) Über einen neuen Ceratiten aus dem Grenzdolomit Thüringens und über Glacialerscheinungen bei Klein-Pörthen zwischen Gera und Zeitz. *Z dtsh geol Ges* 35: 382–384