Chapter 20
Parasites of Ammonoids

Kenneth De Baets, Helmut Keupp and Christian Klug

20.1 Introduction

Parasites in many groups of extant cephalopods are still poorly investigated (Pascual et al. 2007) and even more so in fossil species, in spite of evidence that parasitism can provide important information on the ecology (i.e., diet, mode of life), phylogeny, and the evolutionary history of their hosts. There is currently no documented record of parasite body fossils from externally shelled cephalopods, which is probably related to the paucity of soft-tissue preservation in externally shelled forms like ammonoids, the small size of parasites (at least at some life stages), the residence of endoparasites within the host for the large part of their life cycle, and the rarity of preservable (hard) tissues in many parasites (Conway-Morris 1981, 1990; Littlewood and Donovan 2003; De Baets et al. 2011). The main evidence for parasitism in fossil cephalopods like ammonoids is indirect and in the form of shell pathologies (Hengsbach 1991a, 1996; Keupp 2000, 2012).

Shell "*malformations*" in ammonoids, coined "*paleopathies*" by Hengsbach (1996), have been known since the nineteeth century. The recognition that parasites might be responsible for at least some paleopathies came comparatively late

---

K. De Baets (✉)
GeoZentrum Nordbayern, Fachgruppe PaläoUmwelt, Friedrich-Alexander University
Erlangen-Nuremberg, Loewenichstraße 28, 91054 Erlangen, Germany
e-mail: kenneth.debaets@fau.de

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

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

C. Klug et al. (eds.), *Ammonoid Paleobiology: From Anatomy to Ecology*,
Topics in Geobiology 43, DOI 10.1007/978-94-017-9630-9_20

in paleopathological research on ammonoids (compare Hengsbach 1991a). Engel (1894) was the first to suspect parasites and other pathogens ("Schmarotzer") to be responsible for some of these pathologies. Hölder (1956) introduced a classification of pathologies based on their morphological expressions into '*forma*' types, each of which encompasses a disease and/ or healing pattern. He was also the first to attribute ammonoid gigantism to bacterial infection following reports from pathological gigantism in gastropods. Rieber (1963) was the first to explain asymmetrical growth of suture lines and shells by parasitism. Wetzel (1964) dedicated an entire article to parasitism in the ammonoid shell, which was later reinterpreted as bioerosion by fungi that might have occurred post-mortem (Keupp 2012). Significant contributions to the study of ammonoid parasites were published by Hengsbach (1979a, 1986a, 1986b, 1991a, 1996) and Keupp (1976, 1977, 1979, 1986, 1995, 2000, 2012). Additional contributions were made by various authors (e.g., House 1960; Schindewolf 1962, 1963; Rieber 1963; Bayer 1970; Hölder 1970; Morton 1983; Landman and Waage 1986; Rein 1989; Manger et al. 1999; Kröger 2000; Seltzer 2001, 2009; Larson 2007; De Baets et al. 2011, 2013b; Mironenko 2012; Rakociński 2012).

Proving a parasitic origin of these shell structures is not straightforward (Hengsbach 1991a, 1996). Among extant *Nautilus*, only parasitic copepods have been reported in natural environments (e.g., Ho 1980), which are of little help to the interpretation of these structures since they are not known to influence shell growth. A variety of parasites have been described from extant coleoids (Hochberg 1983, 1989, 1990; Castellanos-Martínez and Gestal 2013; Keupp and Hoffmann 2014), the closest relatives of ammonoids (Kröger et al. 2011), but comparatively little research has been carried out on pathological reactions on their shells (Keupp 2012). Initially, we will briefly discuss the definition of parasitism and their recognition in both extant and extinct cephalopods. Then, we demonstrate the importance of comparative work on pathologies in other shelled mollusks, particularly bivalves and gastropods, to identify causes and host reactions to parasites. We also discuss how pathologies caused by parasitic infestations can be recognized.

20.2 Definitions

Parasitism is usually defined as a symbiotic relationship whereby one individual, the parasite, derives benefits (e.g., energy, matter, nutrition, protection) at the expense of another, the host, by means of close or long-term association (Conway-Morris 1990; Rohde 2005); parasitism often tends to result in demonstrable negative effects on the host (Kinne 1980). An organism can be parasitic for its whole life (holoparasitism) or only part of its life cycle (meroparasitism). The (metabolic) dependence of the parasite may be facultative or obligate. Ectoparasites live externally on the host body, while endoparasites live inside cells (intracellular), between cells (intercellular) or within alimentary tracts, cavities, kidneys, and other open spaces inside the host (extracellular; Kinne 1980). Most species of parasites are obligate parasites which means that they need a host for survival at least during certain stages of their life cycle. Parasites can have a simple or direct life cycle with a single host, or a complex or indirect one with various additional intermediate hosts (Rohde 2005). Intermediate hosts harbor immature, developing stages, while definitive or final hosts harbor the sexually mature stage of a parasite. Paratenic hosts harbor larval forms that do not develop within the host (Rohde 2005) and are therefore not crucial to the development of a particular species of parasite; but these hosts can serve an important role in maintaining the life cycle of that parasite (Combes 2001). The ecological definition of parasitism sometimes grades into other symbioses (Zapalski 2011) and different long-term interactions between organisms including epizoism (Hengsbach 1991a) or (*in-vivo*) bioerosion (Wisshak and Tapanila 2008) which can also harm or influence the growth of their hosts (Keupp 2012). In some cases, *in vivo* epizoism can be detrimental to both the epizoa and their hosts (e.g., Meischner 1968, Hengsbach 1991a, Larson 2007; Keupp 2012; Keupp and Hoffmann 2014). In the fossil record, parasitism can mostly only be recognized by negative effects on its host and by comparisons with extant parasite-host associations.

20.3 Parasites of Extant Cephalopods

Measured by the number of times it evolved independently in several lineages and how many parasitic species are presently in existence, parasitism is one of the most successful modes of life displayed by living organisms (Poulin and Morand 2000). Although research has advanced significantly in the last decades, parasites of many groups of extant cephalopods are still poorly known (Hochberg 1983, 1989, 1990; Pascual et al. 1996; 2007; Gonzalez et al. 2003; Castellanos-Martinez and Gestal 2013). Adult specimens of commercially exploited species which have been the most investigated, are all known to harbor multiple groups of parasites (Pascual et al. 2007). Morphological determination of the systematic affinity of these parasites is not always straight forward, because of their high degree of specialization compared with their free-living relatives, high degree of reduced/ simplified morphology related with their parasitic lifestyle, and sometimes complex life cycles consisting of morphologically distinct ontogenetic stages (Brooks and McLennan 1993). An anecdotal example for cephalopods is the original description of the hectocotylus or modified arm of some male cephalopods as a parasitic helminth (Della Chiaje 1825; Cuvier 1829, 1830). The heterogeneous distribution and differing prevalence of parasites (and host reactions) within the infected tissues, within certain individuals and/ or regions, might also hamper their discovery when species have been poorly investigated or sampled. Molecular techniques have become useful complementary taxonomic tools to parasite diagnosis and specific identification in many groups including cephalopods (Pascual et al. 2007), but are of course unavailable in long extinct fossil forms.

The only parasites known from the extant externally shelled cephalopods (*Nautilus* and *Allonautilus*) in the wild (natural environments) are copepods living on the gills (Willey 1897; Haven 1972; Ho 1980; Hochberg 1983, 1990; Carlson 1987; Ward 1987). A possible exception might be a bacterial infection and a nematode infestation reported by Barord et al. (2012) in a captive *Nautilus* soon after it was captured from the wild. Many different kinds of parasites have been reported from extant coleoids, which are now generally accepted to be more closely related to ammonoids than to nautilids (e.g., Jacobs and Landman 1993; Kröger et al. 2011). Parasites have been recovered from almost all tissues and organs of these cephalopods (Hochberg 1983, 1989, 1990). They are most commonly located on gills, in digestive tracts, the excretory organs, mantle cavities, gonads, and in the musculature (Hochberg 1989, 1990; Pascual et al. 2007; Castellanos-Martinez and Gestal 2013). Pathogens of extant coleoids (Hanlon and Forsythe 1990; Hochberg 1983, 1989, 1990; Castellanos-Martinez and Gestal 2013) include bacteria, fungi, Sarcomastigophora, Apixcomplexa, Ciliophora, Dicyemida, parasitic flatworms (Monogenea, Trematoda, Cestoda), Acanthocephala, Nematoda, Annelida (Hirudinae, Polychaeta), and various crustacean Arthropoda (Copepoda, Isopoda, Branchiura, Malacostraca). Parasites can actively penetrate the host's body or be passively obtained through feeding or respiration. Many cephalopod species serve as primary hosts for protozoans, dicyemids, helminths, and crustaceans, but more commonly serve as secondary, third or reservoir (paratenic) hosts for intermediate (larval) stages of helminths such as digeneans, cestodes, and nematodes (Hochberg 1983, 1989, 1990). Cephalopods thus play a vital role in the transfer of parasites through the food web of marine ecosystems to final hosts such as elasmobranchs, fishes, and marine mammals (Hochberg 1983, 1989, 1990; Pascual et al. 2007). Crustaceans are macroparasites that mainly inhabit the mantle cavity and gills of cephalopods (Castellanos-Martinez and Gestal 2013), although they can also be found on external surfaces of the body such as on the arms or the head (Hochberg 1990).

Many parasites are acquired through contact with hosts in their habitat or through feeding, so that they might even give information about the feeding grounds or ecology of extinct cephalopods. Parasites cannot only provide information on cephalopod predator-prey interactions, but also on their distribution in the water column. Benthic and coastal cephalopods usually have different parasites then pelagic and oceanic species (compare Hochberg 1983; Pascual et al. 1996; Gonzalez et al. 2003).

20.4 Parasites of Fossil Cephalopods

Despite the ubiquity of the parasitic life style, its independent appearance in several unrelated lineages, and hypothesized ancient origins, relatively few clues can be derived from the fossil record. This is related with the fact that parasites (at least in some stages) are commonly small (+/− microscopic), frequently lack hard parts, often live within the (soft parts of the) host for the longest portion of their lifecycle (endoparasites), and/or might be isolated from their host post-mortem (Conway-Morris 1981; De Baets et al. 2011). These phenomena weigh against the preservation and recognition of fossil parasitoses, and as a consequence, the detection of parasitic biota is rare and mostly restricted to localities with exceptional preservation such as Konservat-Lagerstätten (Littlewood and Donovan 2003; Boucot and Poinar 2010). Additionally, even when preserved and detected, the quality of preservation will hamper precise identification of such fossil parasites. Soft part preservation is also rare in ammonoids (e.g., Klug et al. 2012; Klug and Lehmann 2015) and therefore, no direct evidence for parasitism in the form of body fossils has yet been found.

Ammonoid workers (like many other palaeontologists), therefore, have to rely on host shell pathologies which are characteristic of parasitism. Similar pathologies can however be caused by different agents that are difficult to assign to a particular extant parasite lineage and in some cases might belong to extinct lineages of parasites. Just as with trace fossils, different parasites can create similar pathologies when infesting similar tissues or behaving in the same way. The same parasite can induce different pathologies depending on their abundance, behavior, as well as the state of and position within the host.

20.5 Identifying Parasitism as A Cause for Ammonoid Pathologies

Identifying a parasitic cause for pathologies is not straight forward, but some general guide lines can be given (compare also Hengsbach 1991a, 1996; Keupp 2000, 2012; De Baets et al. 2011):

1. Preservation of parasite remains: The perfect evidence for parasitism in ammonoids would be the remains of the parasites preserved with the ammonoids showing these pathologies. Unfortunately, such cases have not been documented. The closest thing so far are blister pearls, which are interpreted to have enclosed the dead parasite remains and partially reproduced its shape as well as size. Examples include organic tubes preserved in some Housean pits in the Devonian (De Baets et al. 2011) and elliptical (now recrystallized) egg-shape inclusions in Jurassic ammonoid blister pearls (Keupp 1986, 2000, 2012). It should also be noted that traces of small soft-bodied parasites are known to vanish during pearl formation (Lauckner 1983).
2. Comparison with pathologies in extant externally shelled mollusks (Fig. 20.1): Interpretation of parasitism should be biologically plausible (Hengsbach 1991a), so that similar, characteristic pathologies in extant shelled mollusks could indicate that a related parasite or a parasite behaving in the same way might have caused these injuries in ammonoids. One must remain cautious if alternative interpretations for these phenomena also exist. Gigantism could be related to parasitic castration (which is often caused by parasitic flatworms in extant gastropods and bivalves), but can also be explained by different pathologies, a natural rarity of larger individuals, and/ or considerable intraspecific variation in adult size, which is not unusual in extant cephalopods. Therefore, gigantic size of individuals on its own is insufficient to prove a parasitic infestation (Klug et al. 2014; De Baets et al. 2015).

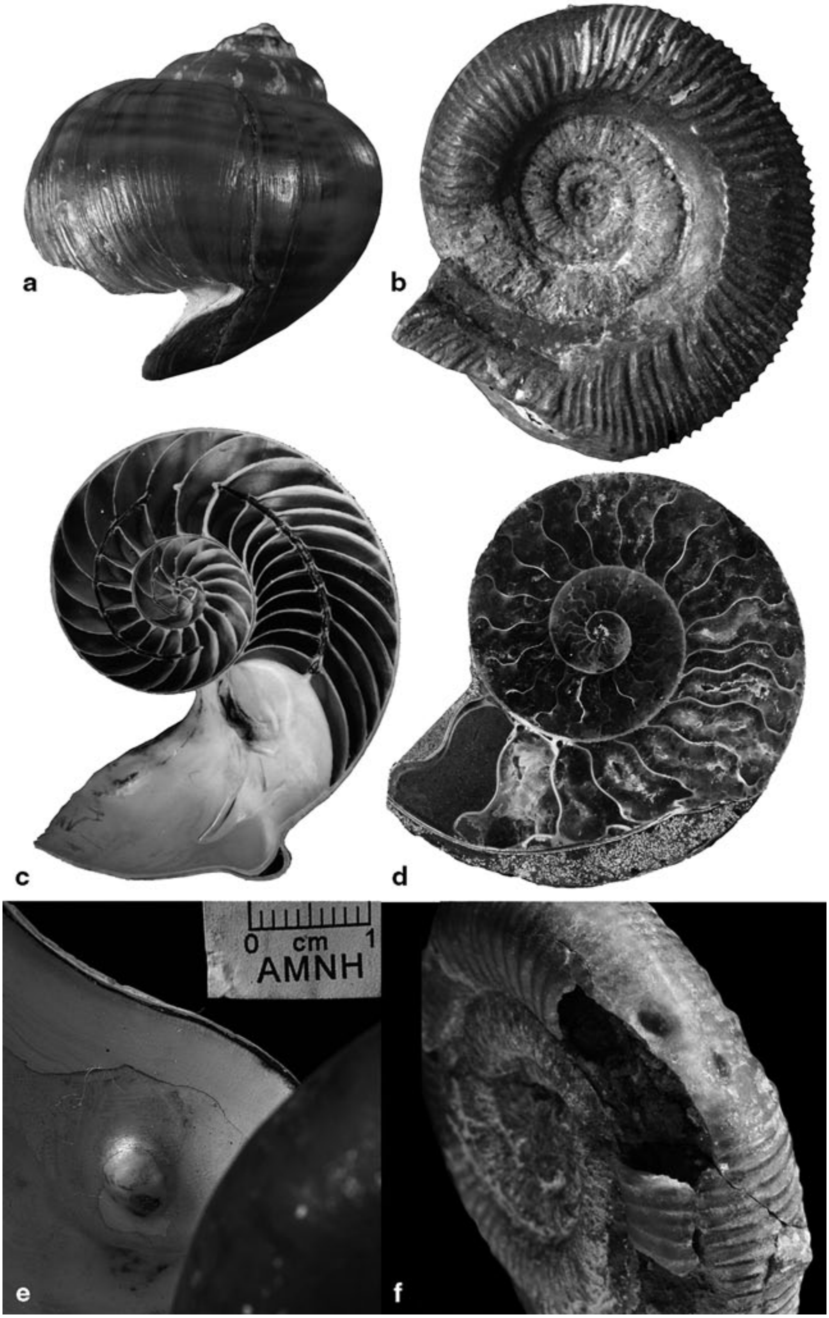

Fig. 20.1 Comparisons of similar pathologies in extant shelled mollusks and ammonoids (modified from Keupp 2012 unless otherwise stated). **a**, **b** progressive development of a deep slit-shaped recess in the apertural margin attributed to parasitic infestation in *Pila* sp. (**a**) Recent, Egypt and *forma umbilicata* in *Dactylioceras anguinum* (**b**) Early Toarcian (Jurassic), Altdorf near Nürnberg (Germany), SHK PA-1694a, dm 39 mm. **c**, **d** development of shell lamellae related with a local

3. Misinterpretation of normal shell features as pathologies: Parasitism should be excluded if features misidentified as pathologies are part of the normal growth or anatomy (e.g., soft-tissue). In some cases, muscle attachment scars might be confused with certain pathologies (*forma umbilicata* of Kröger 2000; Fig. 20.1b), but are restricted to internal moulds and always orientated towards the back of the body chamber (Keupp 2012).
4. Lack of external injury: Parasitic or other endogenous causes are often put forward in absence of external injuries or epizoa. In rare cases, parasitic infestations or infections might have happened preferentially after soft-tissue was exposed due to injury causing short-term swellings such as *forma inflata* (compare Keupp 1976, 2000, 2012), although the injury and the pathology are not directly related. Lack of proof as an argument for endogenous cause on its own cannot be accepted (Zapalski 2011), as one never knows if such an absence is caused by a true absence or only that it is impossible to identify it (soft parts not preserved).
5. Characteristics of the structures: The position, distribution, size, and morphology of these structures might also reveal a parasitic origin, particularly, when similar structures are known from extant shelled molluscs. Even when similar structures are absent in extant shelled molluscs, the position of these pathologies deep in the soft-tissue and/or far away from the aperture which could only be reached and/or inhabited by parasitic organisms feeding on tissues or benefitting from the host in different ways, can still corroborate their parasitic nature.
    a. Asymmetric development: Deviations from bilateral symmetry or symmetropathies (Hengsbach 1991b) have been attributed to parasitism including asymmetry of the suture line or shell sculpture and whorl section. In several taxa, the position of the lateral lobe as well as siphon are tightly constrained and asymmetry of suture line can even be species-specific and not of pathological origin (Keupp 2012). A progressive development of asymmetry of whorl section or suture line could potentially relate to the asymmetrical swellings which could be caused by local infections and parasitic infestations (Hengsbach 1991a, 1996). However, a gradual development of asymmetry of the suture line might also be related with non-pathological asymmetrical growth of soft-tissues during ontogeny, particularly towards maturity (e.g., Yacobucci and Manship 2011). The low prevalence and irregular appearance, variation in its development between individuals, sudden to temporary development in post-embryonic stages, and lack of traces of external injuries or epizoa are therefore of key importance to corroborate a parasitic origin of these phenomena (Hengsbach 1991a, 1996; Keupp 2000, 2012).

---

detachment of the mantle in a captive *Nautilus pompilius*, Recent (1990–1993), aquarium of the Jura-Museum Eichstätt, SHK PN-12, dm 110 mm (**c**) and a specimen of *Cleoniceras besairiei*, Albian (Cretaceous), Ambatolafia (Madagascar), PA-33582–1, dm 85 mm (**d**). **e, f** blister pearl in *Nautilus macromphalus*, Recent, New Caledonia, AMNH, max dm of pearl: 6 mm (**e**) and casts of two blister pearls on an internal mold of *Dactylioceras anguinum* **f** Toarcian (Jurassic), Altdorf near Nürnberg (Germany), SHK PA-643, dm 59 mm. The formation of blister pearls is typically induced by irritants (organic material, parasites, sediment grains, epizoa, etc.), which get lodged between the mantle and the shell

b. Prevalence of pathologies within population: The prevalence of parasites (and associated pathologies) in their host populations can be quite variable (from about 1% to over 70% or higher, but usually significantly below 100%) and hard to predict. Typically, not all specimens of a species within a population are infested and even less might develop deformities indicative of parasitism. According to some authors, the number of pathological specimens attributable to parasitism should be consistently low (1–10%: compare Keupp 2012). Higher prevalence (70% or more) might be related with a specialist among parasites (e.g., Hengsbach 1991a, 1996; but compare Keupp 2000, 2012 for a different viewpoint). In certain cases, one kind of parasitosis might be particularly common in some regions, while in other areas, they might be rare or absent (even in large samples of the same taxon with similar preservation). Some authors have interpreted a high prevalence of a pathology as a sign that a certain area supported a high population of parasites (Morton 1983; Keupp 2000, 2012), but this could also be related with higher infection rates (in response to different feeding or living habits in separate regions), different immune responses or to ammonoids being accidental hosts (which do not normally harbor the parasite) in these environments. If the phenomenon occurs in 100% of the representatives of a taxon and if its appearance is consistent from one individual to another (same side affected, same degree of development), parasitism is unlikely and genetic causes can be suspected. It can be difficult to classify a feature as pathology if all specimens have it (Keupp 2012) and most postnatal causes with the exception of obligate symbiosis can be ruled out (Hengsbach 1996). However, symbiosis is hard to verify in the fossil record (Zapalski 2011).

6. Appearance after hatching and later in ontogeny: In most cases, species are infested directly or by taking in infested food after hatching, which means that the pathologies should at the earliest develop after hatching or probably much later, when the ammonoid came in contact with the parasite or their larvae (intermediate stages). Structures being present at or before birth might be related with teratological causes (e.g., congenital disorders). The blister pearls in certain species of Paleozoic ammonoids occur early in ontogeny (but always clearly after the embryonic shell) and more importantly, appear at different points in the ontogeny of different individuals within the same species. In the case of parasitism, such variability and no correlation with growth of the organism (e.g., ontogenetic stages, septal spacing) is expected (Hengsbach 1996; De Baets et al. 2013b).
7. Host specificity: Not all ammonoid taxa at a locality show identical pathologies; parasites are often quite host-specific and might cause different reactions in separate taxa, so that the pathologies might often be restricted to a single species, clade or lineage. Sometimes, ecology might play a bigger role than phylogeny, so that certain parasitic infestations can be present in one or multiple (not necessarily closely related) taxa with a particular ecology (food source, mode of life, habitat).
8. Gradual development of irregular, ontogenetically long-lasting pathologies: Rieber (1963) interpreted a pathological ammonoid individual with a progressive displacement of the keel and the siphuncle after at least three normal whorls

as the results of parasite infestation, which has been generally accepted as a plausible explanation. This probably reflects a struggle between the host and the infesting parasite(s). After the death of the parasites, the malformation might remain this way or gradually disappear depending on the damage as well as the need and available mechanisms to return to normal morphology (Hengsbach 1991a, 1996). In cases of swellings, the pathologies might disappear as suddenly as they have developed.

These guidelines can be used to evaluate the plausibility and certainty of several pathologies attributed to parasites in ammonoids. Due to the difficulties in identifying the potential parasitic culprits; we will discuss possible cases of parasitism in ammonoids grouped by the morphological expression of pathologies or paleopathies.

Several structures and pathologies have been related with parasitism in shelled cephalopods with various degrees of certainty (Hengsbach 1991a, 1996; Keupp 2000, 2012; De Baets et al. 2011; Fig. 20.2). These pathologies range from (blister) pearls, symmetropathies (asymmetry of shell tube and suture line), temporal increase in shell volume and ornamentation, anomalies in shell secretion to various other pathologies. Parasitic flatworms have most commonly been implicated in several pathologies, including pathological gigantism (Manger et al. 1999), blister pearls (Keupp 1986; De Baets et al. 2011, Fig. 20.1f), and certain perturbations in shell growth (e.g., *forma umbilicata*: Keupp 2000, 2012; Fig. 20.1b) in analogy with prevalence of these parasites in extant cephalopods and cause of similar pathologies in extant shelled molluscs (Fig. 20.1). These hypotheses are not unlikely as parasitic flatworms have probably been around since the Ordovician based on the extrapolation of extant parasite-host relationships (Littlewood 2006), but so far, direct fossil evidence is lacking prior to the Permian (Dentzien-Dias et al. 2013). Earlier records of parasitic flatworms are still debated (Upeniece 2001); no remains have been found directly associated with ammonoids. It seems likely that other parasites were also present including forms that were unable to leave any trace (e.g., parasitic crustaceans and bacterial infections: compare Hölder 1956) and some traces might even relate to now extinct groups of parasites (Boucot and Poinar 2010).

20.5.1 Disturbances in Apertural Shell Growth

Keupp (1979) described a pathology, where the shell formation is delayed near the umbilicus leading to the progressive development of a deep slit-shaped recess (and ribbing vertices similar to *forma verticata*) in the apertural margin of some specimens of Jurassic *Dactylioceras* (Fig. 20.1b). In the absence of external injuries, he attributed this to parasitism based on the protected position of the paleopathies and comparisons to other specimens in the local population. Superficially similar structures ("Rippenscheitelungen") can also be formed in association with external injuries, traditionally described as *forma verticata* and *forma semiverticata* (compare Hengsbach 1991a, 1996; Keupp 2000, 2012; Zatoń 2010). Kröger (2000) introduced the term *forma umbilicata* for these pathologies in absence of external injuries. Their parasitic origin is corroborated by a similar phe-

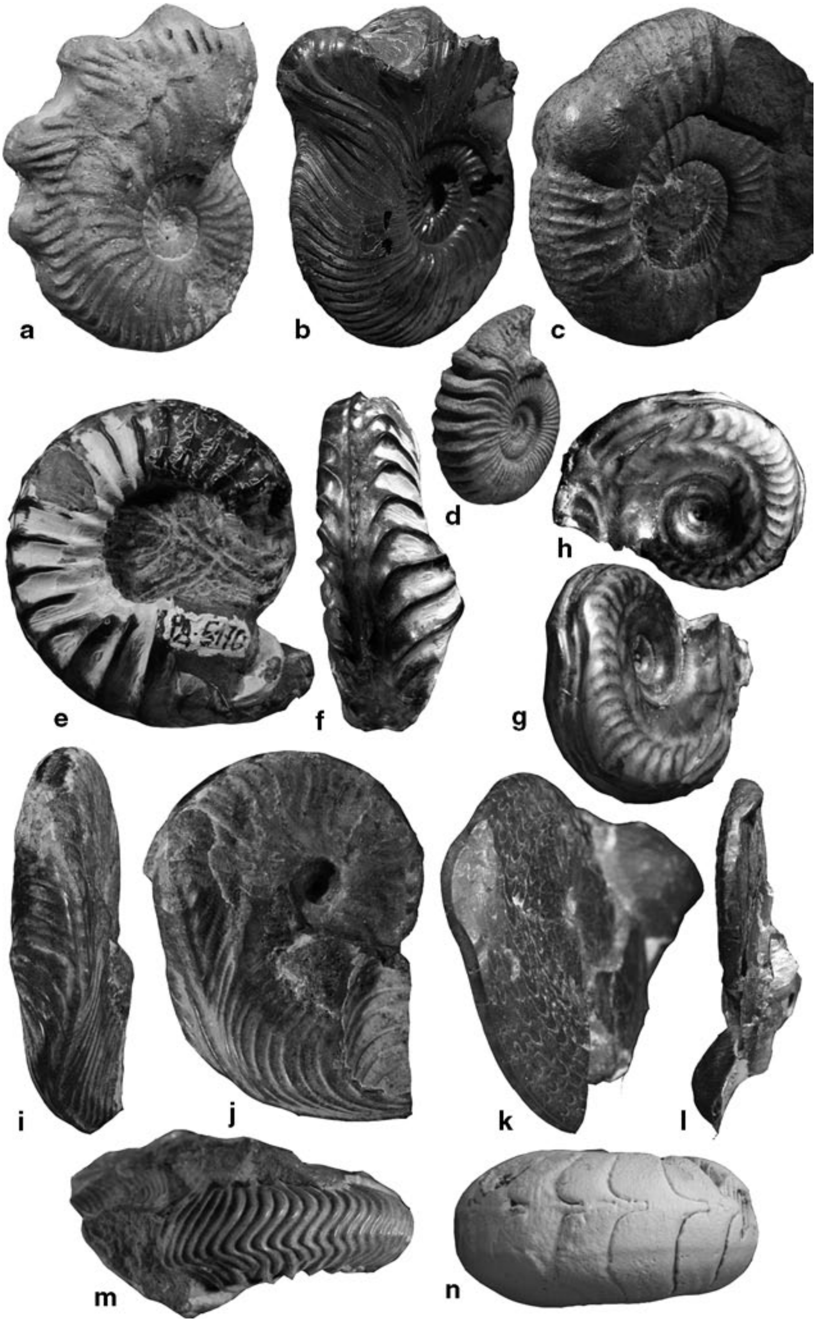

Fig. 20.2 Examples of different pathologies attributed to parasitic infestations with various degrees of certainty from the Devonian to Cretaceous (modified from Keupp 2012; unless stated otherwise): **a** *Amoeboceras alternans* with progressive enlargement of the ventral ornamentation (*forma augata* Kröger 2000), Oxfordian (Jurassic), Kucha near Hersbruck (Germany), SHK PA-785, dm 12 mm. **b** *Quenstedtoceras leachi* with a conspicuous, temporary bulbous swelling of the ventral shell and

nomenon in the freshwater gastropod *Pila* (Keupp 2000, 2012; Fig. 20.1a), where the infestation with intermediate stages of trematode flatworms in the mantle tissue of the apertural margin leads to the formation of similar abnormal slit-shaped openings in the aperture, which becomes progressively broader with the increasingly infested tissue. These structures should not be confused with muscle scars ("*Muskelleisten*": compare Keupp 2012) which are restricted to internal moulds from the back of the body chamber to the phragmocone (as opposed to the front of the body chamber on both the shell and internal mould).

These pathologies have also been reported from rare specimens of *Epivirgatites* from the Tithonian and *Quenstedtoceras* from the Callovian of Russia (Keupp 2012, pp. 223–224). These specimens demonstrate that the infestations are not always restricted to the umbilical margin and can vary even within the same taxon which probably depends on the position of the parasite; some specimens were able to subsequently close the recess with smooth or irregular shell material (Keupp 2012). So far, the structures are only confidently known from these three genera of Jurassic Ammonitida (Keupp 2012). These pathologies are best known from the Early Toarcian of Altdorf near Nürnberg (Germany), where they are restricted to dactylioceratids (Fig. 20.1b) and absent from all other ammonoid taxa (Harpoceratidae, Hildoceratidae, Phylloceratidae, Lytoceratidae). This might indicate that these parasites are host specific. These structures are rare in dactylioceratids in other regions, which might suggest that the ecology (mode of life, predator-prey relationships) of these taxa in this region also increased their infection risk. The prevalence is quite high in the Toarcian of Altdorf where up to 5 % of *Dactylioceras* display these structures which Keupp (2012) attributed to a high regional population of these parasites.

20.5.2 Pathological Gigantism

Parasites are well known to alter the behavior, growth, and morphology of their hosts (Miura et al. 2006). Gigantism is one of the most striking modifications in

---

ornamentation (*forma augata* Kröger 2000), Callovian (Jurassic), Dubki near Saratov (Russia), SHK PA-20114, dm 58 mm. **c** *Orthosphinctes* with conspicuous, temporary bulbous swelling of the shell without ornamentation behind the aperture (*forma inflata* Keupp 1976), Kimmeridgian (Jurassic), Hartmannshof (Germany), SHK PA-1871, dm 60 mm. **d** *Dactylioceras athleticum* with a progressive development of shovel-like ribs (*forma augata* Kröger 2000), Kimmeridgian (Jurassic), Hartmannshof (Germany), SHK PA-1871, dm 60 mm. **e, f** *Pleuroceras spinatum* with a unilateral thickening of the body chamber resulting in a significant *left-right* asymmetry of the whorl section, SHK PA-5170, Pliensbachian (Jurassic), Unterstürmig (Germany), dm 41 mm. **g, h** *Hildoceras bifrons* showing multiple oscillations of the keel around its normal ventral position (*forma undaticarinata*), SHK PA-6245, Toarcian (Jurassic), Grand Causses (France), dm 23 mm. **i, j** *Cleviceras elegans* with Morton's syndrome (sensu Landman and Waage 1986), SHK PA-543, Toarcian (Jurassic), Altdorf near Nürnberg (Germany), dm 55 mm. **k, l** *Pseudosageceras multilobatum* with Morton's syndrome (sensu Landman and Waage 1986), SHK PA-9204, Early Triassic, Vikinghøgda south of Sassendalen (Spitzbergen), dm 34 mm. **m** *Amoeboceras sp.* with a progressive asymmetric shift of the keel (*forma juxtacarinata* Hölder 1956; similar to the case described by Rieber 1973), SHK PA-786, Oxfordian (Jurassic), Scarborough (United Kingdom), dm 20 mm (previously unpublished). **n** *Latanarcestes noeggerathi* with an exentrical position of the external lobe (*forma juxtalobata* Hölder 1956), Emsian (Devonian), Tafilalt (Morocco), dm 27 mm morphology and growth, which can be induced by parasitic organisms and can significantly alter the size-structure, use of resources, and intraspecific competitive interactions of the host population. It is one of the common paleopathies to be linked with parasitic infestations in ammonoids (Hölder 1956; Hengsbach 1991a, 1996; Manger et al. 1999; Keupp 2000, 2012). Hölder (1956) was the first to suspect that parasite-caused gigantism might have occurred in ammonoids based on studies of the present-day terrestrial snail *Zebrina* by Boettger (1953a, 1953b), who documented parasite-caused delay in sexual maturation, corresponding castration, and retardation in growth.

Pathological gigantism should only be used to refer to rare specimens of a certain taxon which have abnormally large sizes (Tasnadi-Kubacska 1962) that were triggered by pathogens, hormonal disorders or other endogenic causes. Hengsbach (1996) introduced the term *forma gigantea* to refer to pathological gigantism in ammonoids (which effects only a small fraction of ammonoid populations). Other causes for size differences such as continuous and discontinuous (e.g., sexual dimorphism) intraspecific variability in adult size or ecological causes should be ruled out (De Baets et al. 2015; Keupp and Hoffmann 2015). So far, pathological gigantism caused by parasitic castration has only been suggested by Manger et al. (1999) to explain rare exceptionally larger individuals of some Carboniferous ammonoid and nautiloid taxa. Manger et al. (1999) suggest that infestation of the gonads by trematode larvae and castration might have been responsible. Several gastropod species exhibit growth to abnormally large sizes following infection by trematodes or other parasites (Sousa 1983; Sorensen and Minchella 2001), which can be caused by enhanced growth, sexual retardation, or even castration. Castration in extant bivalves and gastropods is most commonly caused by parasitic flatworms (Lafferty et al. 2009; but see Boettger 1953a, b for an example with a bacterial cause). However, not all infestations or even castrations result in abnormally larger sizes or noticeable effects on (shell) growth in molluscs. Some specimens can become mature before castration or continue to grow after castration. Additionally, gigantism has only been documented in short-lived and primarily fresh water and terrestrial gastropods, while studies on long-lived marine gastropod species have found that trematodes have either no effect on growth or even stunt growth (Sousa 1983; Sorensen and Minchella 2001; Miura et al. 2006). Castration and pathological gigantism have so far not been reported from extant cephalopods, which are commonly infested by parasitic flatworms and other parasites, highlighting the need for independent evidence for parasitic infestation of these specimens other than size.

However, there is no direct proof in the form of shell reactions or preserved parasite remains (compare Hengsbach 1996; De Baets et al. 2011; Klug et al. 2014 for a review) to corroborate the views of pathological gigantism caused by parasitism in ammonoids. Indications used to support this interpretation comprise the large size of these cephalopod fossils (two to four times as big as "normal" specimens from the same layers), the scarcity of specimens of this size belonging to members of a species that are common, and the absence of indications for adulthood. Ivanov (1971, 1975) introduced the term *"megaconch"* to refer to rare abnormally large specimens of Jurassic ammonoid species which show no signs of maturation, although he did not specifically discuss parasitism as a cause for this phenomenon and these criteria might be hard to interpret in incomplete specimens. Rare larger specimens in semelparous accumulations might reflect the general paucity of larger individuals as well as multiple spawning seasons and areas in cephalopods (Rocha et al. 2001). Castrated ammonoids are usually interpreted to not have reached maturity and/or grew beyond their normal size (Hölder 1956; Manger et al. 1999). The absence of signs of adulthood could also be explained by various other factors, including incomplete preservation of the body chamber of the specimens, a common taphonomic and collection bias in larger specimens, and the lack of no clear signs of maturity in the shell or continuous growth until death which is not uncommon in some taxa of ammonoids (compare Davis et al. 1996; Bucher et al. 1996). Furthermore, some commonly caused adult modifications such as septal crowding might be useless in some cases as they can also be induced by environmental stress (Kraft et al. 2008). Although it is difficult to impossible to prove the absence of pathogens or the normal levels of hormones in these giants, we suggest that the most likely explanation for many cases of supposedly pathologic gigantism might just be highly variable adult sizes (not uncommon in extant cephalopods and can sometimes be discontinuous: compare De Baets et al. 2015) and/or reproductive strategies, where only a few individuals achieved maturity out of a thousand eggs. More evidence is necessary to ascribe giant size of rare specimens of a species to pathologies and even more to attribute this to parasitism, although it is biologically plausible (Klug et al. 2015).

20.5.3 Pearl Formation

The formation of blister and free pearls in bivalves has often been linked with parasitic flatworms (Conway-Morris 1981; Combes 2001; Littlewood and Donovan 2003; Boucot and Poinar 2010). Nevertheless, various other parasitic organisms such as fungi, unicellular organisms, nematodes or arthropods (and their eggs) as well as various other irritants including inorganic material which get stuck between mantle and shell can induce pearl formation (Götting 1974, 1979; Lauckner 1983). Nevertheless, the morphology of some parasite-induced structures in extant bivalves are believed to be very specific to parasitic flatworms such as pits in shells and igloo-shaped shell secretions or to polychaete worms such as borings and can be traced back in the fossil record (Liljedahl 1985, Ruiz and Lindberg 1989; Ituarte et al. 2001, 2005; Huntley 2007; De Baets et al. 2011). Blister pearls (Fig. 20.1f) in ammonoids have therefore often been linked with parasitic infestations (House 1960; Keupp 1986; Hengsbach 1996; Davis and Mapes 1999; De Baets et al. 2011, 2013b). Furthermore, the fact that blister pearls (cephalopods, bivalves, and gastropods) and free pearls (bivalves, gastropods) are known from a wide variety of fossil and extant taxa (Binder 2002; Boucot and Poinar 2010 and references therein) suggest that every shelled mollusc is capable of forming such structures (Landman et al. 2001). In the fossil record, these pearls can be preserved as pits on internal moulds (steinkerns).

House (1960) was the first to describe more or less regularly distributed pits on internal moulds of Early to Middle Devonian ammonoids (Fig. 20.3, 20.4, 20.5). Many authors (Chlupáč and Turek 1983; Becker and House 1994; Klug 2002a,

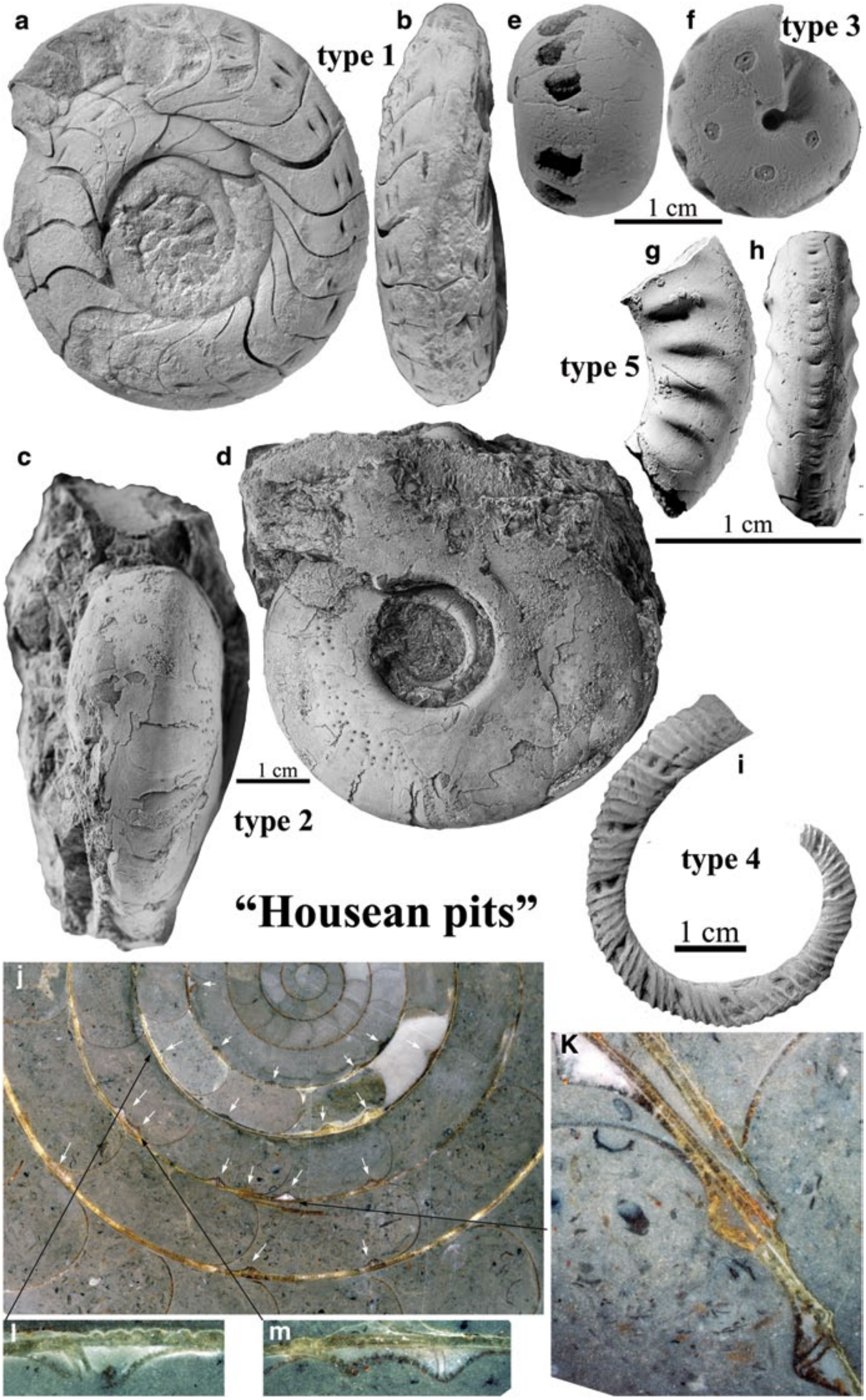

Fig. 20.3 Types of Housean pits and morphological details. Images from De Baets et al. (2011). **a**, **b** lateral and ventral views of *Sellanarcestes* cf. *ebbighauseni*, PIMUZ 28582, Sellanarcestes wenkenbachi Zone, Emsian, Jebel Ouaoufilal, Tafilalt, Morocco. **c**, **d** ventral and lateral view of *Crispoceras tureki* Klug, 2002, PIMUZ 28591, Pinacites jugleri Zone, Eifelian, Jebel Ouaou-

2002b, 2007; Bockwinkel et al. 2009; Ebbighausen et al. 2011) published specimens showing these pits, but without discussing them in detail. House (1960) and others concluded that these pits represent the moulds of pearls that must have formed during the ammonoid's life on the inside of the shell within the body chamber, i.e., the part of the shell that contained the soft parts and lacked chambers. These pits/pearls are commonly arranged spirally, radially or chaotically on the flanks and venter of these ammonoids and are oval to circular in outline, occurring in varying numbers. House (1960) lacked sufficient information to decide whether these pits represent traces of a parasite or particles that entered between mantle and shell, causing an irritation and the formation of a pearl-like structure. Davis and Mapes (1999) named these features "*Housean pits*" in honor of House and favoured a parasitic origin. Hengsbach (1991a, 1996) included these pathological shell concretions together with more isolated blister pearls (e.g., Keupp 1986) in a paleopathology he dubbed *forma concreta*.

De Baets et al. (2011) reviewed the morphology and distribution of these structures and distinguished five types of pits on Devonian ammonoids (Fig. 20.4):

- Type 1: fairly large oval pits, which are lengthened in a longitudinal direction, predominately ordered in large spiral rows and often paired. They are common in *Anarcestes* and *Sellanarcestes*.
- Type 2: multiple, small pits, arranged in more or less radial rows or more chaotically. They were initially thought to be restricted to the late Early Devonian to Middle Devonian (Late Emsian to Givetian: *Anarcestes*, *Afromaenioceras*, *Crispoceras*, *Sobolewia* and *Subanarcestes*), but were recently also reported from the Late Devonian (*Felisporadoceras*: Rakociński 2012).
- Type 3: rare circular pits with a central deepening, which have so far only been reported from five specimens of *Sobolewia* from the Givetian of Algeria. Although similar pits might also be present in Aulatornoceratinae (Jürgen Bockwinkel, personal communication 2013)
- Type 4 (Opitzian pits): flat, large, radially arranged, paired pits which have so far only been reported from *Ivoites* from the early Emsian Hunsrück Slate (De Baets et al. 2013b) and absent from the same taxon at other localities (De Baets et al. 2013a)
- Type 5: kidney-shaped pits in the middle of the venter, which are found in certain taxa of Early Emsian ammonoids (*Chebbites*, *Gracilites*, *Lenzites*). These pits usually coincide with the most posterior points of the hyponomic sinus of their growth lines (compare Becker and House 1994; Klug 2001; Korn and Klug 2002; Klug et al. 2008)

---

filal, Tafilalt, Morocco. **e**, **f** *Sobolewia nuciformis* (Whidborne 1889), three specimens kept under the same number (MNHN–R.08459), Givetian, Redjel Iamrad, Algeria, Jacques Follot coll., **g**, **h** *Chebbites reisdorfi* Klug, 2001, PIMUZ 7484. **i** *Ivoites opitzi*, Lehmann col., early Emsian, Bundenbach, Germany. **j-k** Longitudinal section through PIMUZ 28583 of *Sellanarcestes* spp., *wenkenbachi* Zone, Emsian, Oufrane (S of Tata), Morocco. **j** median section displaying many "Housean pits" (*arrows*), most with internal tube; overview. **k** three closely spaced pits, two with internal tubes, note the continuous ammonoid shell layer covering pits and septum. **l** corroded pit with tube, note the continuation of the innermost ammonoid shell layer. **m** two fused pits, the right pit shows the delicate internal tube, mural part of septum on the left

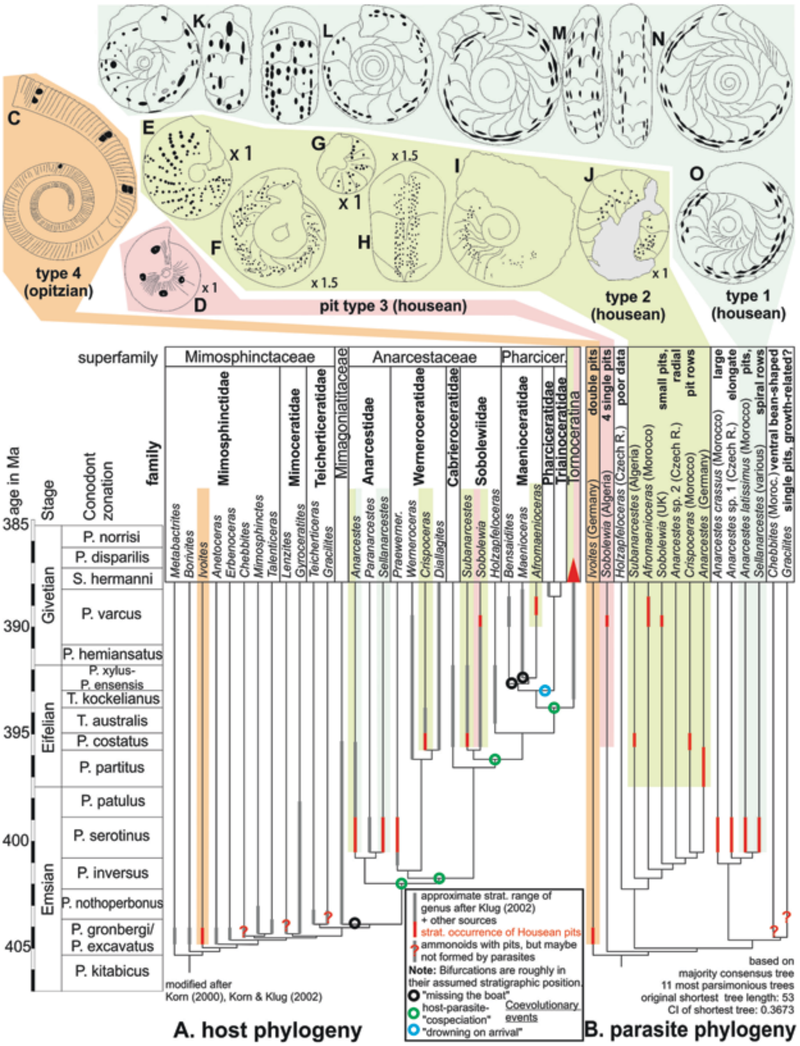

Fig. 20.4 Morphology and Distribution of Opitzian (type 4), Housean (type 1–3) and other pits (type 5) known from Devonian ammonoids updated from De Baets et al. (2011) to include Late Devonian records discussed in the text: *red arrow* list the extended range of type 2 (*green*: Rakocinski 2012) and type 3 (*pink*) pits in Tornoceratina. Note the coevolution of Devonian ammonoids and their parasites as reflected in the arrangement and shape of the blister pearls. **a** Host phylogeny. **b** Parasite phylogeny. The ammonoid phylogeny is based on a majority consensus tree consisting of the11 most parsimonious trees original shortest tree length (compare Korn 2001; Korn and Klug 2002; De Baets et al. 2011). **c** *Ivoites opitzi* (early Emsian, middle Kaub Formation, Hunsrück, Germany: from De Baets et al. 2013b). **d** *Sobolewia nuciformis* (Givetian, Redjel Iamrad, Algeria). **e** *Subanarcestes* sp. (Eifelian, Erg El Djemel, Algeria; after House 1960). F. *Afromaenioceras sulcatostriatum* (Givetian, Jebel Ouaoufilal, Morocco). G. *Sobolewia* aff. *nuciformis* (Givetian, Cornwall). H. *Anarcestes* sp. (late Emsian, Koněprusy, Czech Republic). I. *Crispoceras tureki* (Eifelian, Jebel Ouaoufilal, Morocco). J. *Anarcestes* sp. (Eifelian, Wissenbacher Schiefer, Germany). K. *Anarcestes* sp. (late Emsian, Jebel Mech Agrou, Morocco). L. *Anarcestes latissimus* (late Emsian, Hassi Moudaras, Morocco). M. *Sellanarcestes* cf. *ebbighauseni* (late Emsian, Jebel Ouaoufilal, Morocco). N. *Sellanarcestes ebbighauseni* (late Emsian, northern Jebel Amessoui, Morocco). O. *Sellanarcestes neglectus* (late Emsian, southern Jebel Mech Agrou, Morocco)

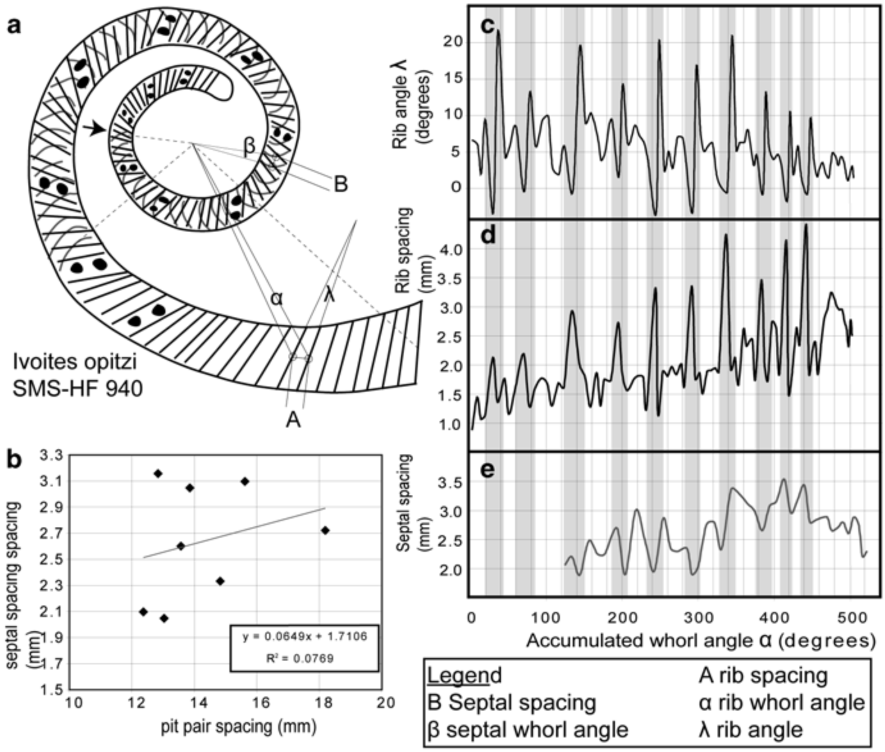

Fig. 20.5 Specimen of *Ivoites opitzi* from the Hunsrück Slate showing the morphology of Opitzian pits and their local influence on rib angle and spacing. Note, the lack of a general correlation of pit pair spacing with growth rhythms or septal spacing (modified from De Baets et al. 2013b). **a** Schematic drawing of the retrodeformed specimen with position of pits, ribs, and septa and analysed parameters. The *arrow* marks the starting point of the analyses (0 on the graphs), which proceed counter-clockwise. **b** Correlation between pit pair and septal spacing. **c** Plot of rib angle λ versus accumulated whorl angle Σ α. Note the drop in the angle between the rib before and following the pit pair and the subsequent rise between the rib and the second rib after the pit pair. **d** Plot of rib spacing A versus accumulated whorl angle Σ α. Note the rise in rib spacing A coinciding with the position of the pit pair. **e** Plot of septal spacing A versus accumulated whorl angle Σ α. Note a drop in septal spacing which more or less follows on each pit pair. The septal spacing has been translated for a rib angle corresponding to the body chamber length of about 115° (cf. Bucher et al. 1996)

De Baets et al. (2011) demonstrated that the Housean pits were the casts of blister pearls at least for type 1 pits which were overgrowing organic tubes, because they found these structures in specimens where the associated shell and the blister pearls were preserved (Fig. 20.3). The tubes are interpreted to be the remains of parasitic organisms which lodged themselves between mantle and shell due to their position far away from the aperture (other symbiotic relationships or long-term guests such as epizoa are therefore unlikely) and which were overgrown by shell material (probably after the death of the parasite). No borings in the shell or inorganic particles were found inside of the pearls. Tubes are also present in type 3 pits suggesting a similar parasitic cause for these blister pearls. Type 2 is tentatively interpreted as being of parasitic origin as well due to their similarities in morphology and distribution with type 1 and type 3 pits. Type 1–3 are typical Housean pits because they form at the back of the body chamber. Type 4 pits are an exception because they are formed at the front of the body chamber and locally affect shell growth at the aperture (Fig. 20.4, 20.5). Similarities with the other pit types and the fact that not all specimens of a species have them suggest a similar origin, but specimens with pristine shell preservation are necessary to directly test the hypotheses that they are casts of blister pearls and have a parasitic origin. A parasitic origin is also corroborated by a lack of correlation with growth rhythms (long-term rib and septal spacing), although they did temporarily and locally affect rib spacing and angle (De Baets et al. 2013b; Fig. 20.5). This apertural location might reflect an evolutionary change in site specificity of the parasite that formed pit types 1–3 or a different type of parasite (De Baets et al. 2011). De Baets et al. (2013b) therefore introduced the name "*Opitzian pits*" for these type 4 pits after Opitz (1932), who first figured a specimen showing these paired pits. A pathological origin is also corroborated by the fact that Housean and Opitzian pits are not known from all specimens of a species and the ratio even varies between regions (Fig. 20.6) as well as signs of healing of damaged mantle tissue (e.g., spiral traces: Fig. 20.3) in some specimens (De Baets et al. 2011, 2013b). Type 5 pits probably do not have a parasitic origin as they are clearly linked with growth and occur in all specimens of these taxa, so that they probably should not be called "*Housean pits*" at all. It is tempting to attribute Housean (Type 1–3) and Opitzian (Type 4) blister pearls to parasitic flatworms as they are known to cause shell concretions (mostly after death of the parasite: compare Lauckner 1983) in living bivalves, but so far no identical structures are known from extant cephalopods and the identity of these Devonian parasites remains a mystery. Other structures like igloo-shaped concretions can be formed when both the bivalve and parasite are alive (Ituarte et al. 2001, 2005).

The types of pearls correspond well with large groups of ammonoids suggesting a certain degree of parasite-host coevolution (De Baets et al. 2011; Fig. 20.4). The pits become rarer during the Givetian (Fig. 20.6) which might also explain why they have initially been overlooked in the Late Devonian (House 1960; De Baets et al. 2011). Rakociński (2012) subsequently described type 2 pearls in *Felisporadoceras* from the Famennian of Poland extending their range into the latest Devonian. They might also be present in other Late Devonian taxa (e.g., Frasnian aulatornoceratids: Jürgen Bockwinkel, personal communication 2013). Superficially similar pits in *Cymaclymenia* figured by Schindewolf (1934) are probably borings (House 1960). Housean pits seem to have disappeared at the end of the Devonian which might indicate the extinction of this particular lineage of parasites or that ammonoids found countermeasures against them or that the parasites stopped inducing the formation of pearls. It is unclear if the absence in derived ammonoids reflect changes in the complexity of food webs, because pearls might suggest the presence of complex parasite life cycles and food webs involving bivalves as well as jawed vertebrates (compare De Baets et al. 2011). Clusters of blister pearls (or their possible casts) have also been reported from Silurian nautiloids (Stridsberg and Turek 1997; Manda

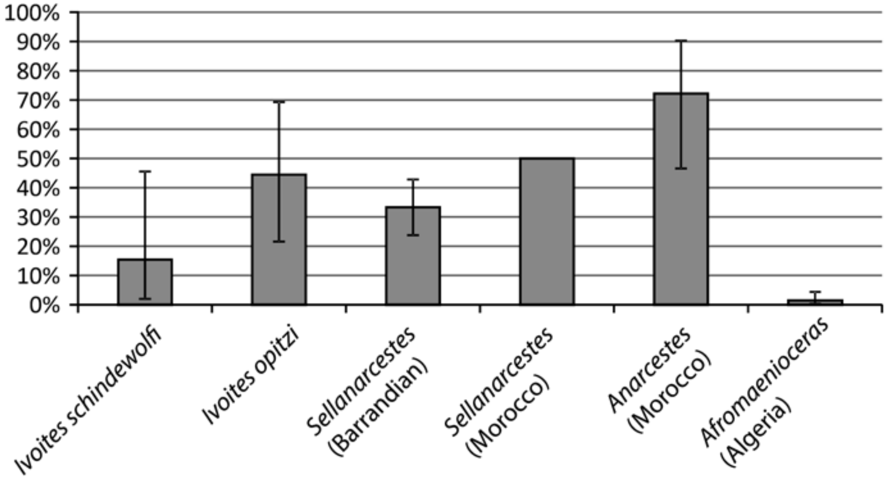

Fig. 20.6 Prevalence of Opitzian and Housean Pits in Early to Middle Devonian ammonoids. *Ivoites opitzi* and *I. schindewolfi* derive from the early Emsian, *Sellanarcestes* from the late Emsian; *Anarcestes* from the late Emsian to early Eifelian; *Afromaenioceras* from the Givetian. Data compiled from Chlupáč and Turek (1983) and De Baets et al. (2011). Note the large variability between taxa and within *Sellanarcestes* depending on the region (left: Barrandian, Czech Republic, right: Anti-Atlas, Morocco) as well as the low prevalence of Housean pits in Givetian *Afromaenioceras*. The 95 % binomial confidence intervals (following Raup 1991 and De Baets et al. 2012) were calculated using the binom.confint function of the Binom Package in R (using the exact approach)

and Turek 2009; Turek and Manda 2010) and Late Jurassic ammonoids (Mironenko 2012), although they are never long-lasting and not regularly arranged in rows as with Devonian Housean or Opitzian pits (De Baets et al. 2011). It is unclear what causes their repeated and rather regular appearance in the Devonian, however, it might be linked to an episodic release of new parasitic stages as these rhythms are not related with the growth rhythm of the ammonoid itself (e.g., apertural growth or septal spacing: De Baets et al. 2011, 2013b). Furthermore, the parasite might target certain tissues or organs which possibly contribute to their regular position or paired arrangement (compare De Baets et al. 2011).

Isolated blister pearls and their casts have been reported from the Devonian (*Cheiloceras*: Keupp 2012), Triassic (*Ceratites*: Kirchner 1927), and Jurassic (Keupp 1986, 2000, 2012; Mironenko 2012), but not all might be of parasitic origin. Blister pearls are also reported from extant *Nautilus* (Landman et al. 2001; Fig. 20.1e) and fossil nautiloids (Kieslinger 1926; Manda and Turek 2009), although their causes are not well investigated. They are mostly located in a lateral (Fig. 20.1e) or dorsal position on the shell (compare Kieslinger 1926). On internal moulds, casts of blister pearls could be confused with borings or dissolved epicoles which grew postmortem on the inner part of the shell (e.g., Miller 1938; House 1960; Keupp 2012). A boring in the shell would, however, result in a positive structure in the internal mould rather than in a negative structure (De Baets et al. 2013b). The best evidence

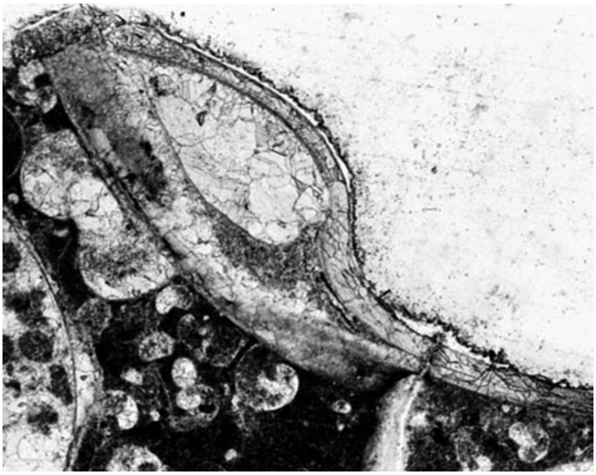

Fig. 20.7 Cross section through a blister pearl from a *Dactylioceras anguinum*, Toarcian (Jurassic), Altdorf near Nürnberg (Germany), PA-1696 (modified from Keupp 2012). Note, the egg shaped cavity (dm 3 mm) within the blister pearl, now filled with cement, interpreted to be the original shape of overgrown parasite (compare Keupp 1986, 2012)

for pearls derives from specimens where the shell, the blister and potentially even the irritant are preserved together. Inorganic material and fossilized parasite hard parts can be preserved in the nucleus of these pearls, while soft-bodied remains of parasites can be erased during the pearl formation process (Lauckner 1983).

Keupp (1986) was the first to describe blister pearls in ammonoids and to discuss their parasitic nature for at least some blister pearls in the Jurassic. He described similar indentations along with the adhering shell and egg-like concretions in two specimens of *Dactylioceras anguinum* from the Toarcian of Germany (Fig. 20.1, 20.7). The strange elliptical concretions are attributed to an overgrown parasite (Keupp 2012), potentially parasitic flatworms (Keupp 1986). These particular types of blister pearls were recently also reported from the Tithonian of Russia (*Kachpurites*: Mironenko 2012) which extended their range from the Early into the Late Jurassic.

20.5.4 Volume and Ornamentation-Enlarging Pathologies

Temporary increases in the volume of the shell and ornamentation have been linked with parasitism by Keupp (1976) who described all these phenomena as *forma inflata*. Subsequent authors have consistently attributed these temporary swellings to mantle tissue infections and infestations caused by parasites (Keupp 1976, 2000, 2012; Hengsbach 1979b, 1991a, 1996; Kröger 2000). Nevertheless, this needs to be further corroborated by studies on extant bivalves or other shelled molluscs. Since the work of Kröger (2000) two main types have been defined: shell volume-enlarging pathologies (*forma inflata* Keupp 1976; Fig. 20.2c) and ornamentation-enlarging pathologies (*forma augata* Kröger 2000; Fig. 20.2a, b, d).

Keupp (1976, 2000) described a pathological specimen of *Amoeboceras* (Fig. 20.1a) in which the crenulated keel temporally and progressively developed several large protuberances (superficially similar to the keel in *Creniceras*), which he attributed to a short-term infestation of the ventral apertural mantle tissue by parasites. Keupp (1984, 1997, 2000) described a similar phenomenon in *Dactylioceras* (Fig. 20.1d); in the material described therein, the ribs suddenly and progressively developed into large shovel-like bands on the venter which subsequently return back to normal ribs.

Such malformations which progressively develop and return to normal, have only been reported from single specimens of taxa from the Early and Late Jurassic which have been related to the parasitic infestation of the ventral mantle epithelium (Keupp 1976; Hengsbach 1996). The appearance of this anomaly seems to be dependent on the type of ornamentation and its development program (e.g., transformation of the crenulated keel to large protuberances in *Amoeboceras* or the enlargement of ventral ribs to successive shovel-like bands in *Dactylioceras*; compare Keupp 2000). The increase in development of ornamentation might give rare specimens a polygonal outline (Keupp 2012), although this should not be confused with other types of pathologies resulting in a polygonal shape possibly linked to endogenic causes (*forma polygonia* Hüne and Hüne 2006) or taxa where a polygonal whorl is normal and all specimens have it (e.g., triangular *Soliclymenia* from the Late Devonian: Korn et al. 2005b or the tetrangular *Entogonites* from the Carboniferous: Korn et al. 2005a). Fernandez-Lopez (1987, pl. 1, Fig. 1) figured a specimen of *Bajocisphinctes* with a similar pathology which can be attributed to the struggle between ammonoid and parasite (Hengsbach 1996). Keupp (2012) described phenomena resulting from the single swelling of ornamentation from the Late Triassic (*Arcestes*), Early Jurassic (*Pleuroceras*), Middle Jurassic (*Quenstedtoceras*; Fig. 20.2b), and Late Jurassic (*Orthospinctes*). The normal ornamentation surrounding these structures suggests that the mantle tissue at the apertural margin was probably not infected. These phenomena were originally described as *forma inflata*, but Kröger (2000) introduced the *forma augata* to refer to this ornamentation-enlarging phenomena, particularly in case of multiple swellings. Further examples of *forma augata* in Quenstedtoceratinae were also figured by Keupp (1985), Seltzen (2001, 2009) and Larson (2007).

The *forma inflata* should be restricted to conspicuous, temporary bulbous swellings of the shell behind the aperture which are typically associated with the regeneration of external injuries (Kröger 2000; Keupp 1995, (2006, 2012; Fig. 20.2c). The swellings are mostly smooth indicating that the mantle tissue at the aperture was not involved in their formation, although in rare cases, damages to the apertural mantle tissue might have resulted in phenomena similar to *forma augata* during further growth. Such temporary swellings were first figured by Lehmann (1975) which he related to the mantle protruding considerably outside of the shell after some injuries behind the aperture. Keupp (2012) pointed out that Lehmann's explanation would be rather unlikely because of the consistency of the mantle musculature as well as the offset between the injuries and the bulbous swellings. According to Keupp (1976, 1995, 2000, 2006, 2012), the temporarily exposed mantle tissue (as consequence of an injury) was more prone to infection and infestation by parasites, thus resulting in the temporary swelling. The *forma inflata* is known from a wide variety of taxa (Lehmann 1975; Keupp 1976, 1995, 2000, 2006, 2012; Hengsbach 1996; Kröger 2000) from the Early to Late Jurassic (e.g., *Dactylioceras*, *Pleuroceras*, *Rehmannia*, *Divisosphinctes*, *Orthosphinctes*: Fig. 20.2c) and the Late Cretaceous (e.g., "*Jeletzkytes*", now synonymized with *Hoploscaphites* by Landman et al. 2010).

Keupp (1995, 2012) also described additional volume increasing phenomena which might be linked to parasitism. They correspond with a gradual thickening of one side of the whorl resulting in significant left-right asymmetry of the whorl section which could be interpreted as volume enlargement of the soft-tissue along one side of the body in response to a parasitic infestation and/or tumor-like swelling (extant cephalopods are not believed to develop real tumors: Sparks 1972). So far, these unilaterial swellings have been reported from a *Pleuroceras* (Early Jurassic: Keupp 1995; Fig. 20.2e, f) and a "*Jeletzkytes*" (Late Cretaceous: Keupp 2012).

20.5.5 Symmetropathies

Hengsbach (1991b) introduced the term "symmetropathy" to refer to pathological asymmetry or deviations from the plane of bilateral symmetry. Several symmetropathies in both the phragmocone and conotheca in absence of external injuries or epizoa have been attributed to parasitism with various degrees of certainty (Hengsbach 1991a, 1996; Keupp 2000), including asymmetry in the position of the keel or the entire shell as well as asymmetry of the siphuncle and ventral lobe.

Rieber (1963) was the first to interpret a parasitic cause for a paleopathy he observed in *Cardioceras* with an asymmetrically situated keel (*forma juxtacarinata* Hölder 1956; compare Fig. 20.2m) and siphuncle (*forma juxtalobata*). The formation of the septa by the mantle is spatially and temporarily separated from the formation of shell material at the aperture, so that pathologies that affected both the phragmocone and the aperture are usually rare (Keupp 2012). Rieber (1963) interpreted this lateral displacement of the keel as being the result of an infestation of the ventral mantle by parasites. A parasitic infestation seems plausible as the *Cardioceras* specimen showed a lateral displacement of both medial elements after at least three normal whorls without indications for external injuries and with a progressively increasing degree of deviation of the keel (and the siphuncle) adaperturally. Several authors have discussed similar cases and followed Rieber (1963) in attributing similar deviations in symmetry of the ventral elements of the conotheca to parasitic infestations (Bayer 1970; Hölder 1970; Hengsbach 1991a, 1996; Keupp 2000, 2012).

Heller (1958) described a *Pleuroceras* with an asymmetrical keel that shows multiple oscillations and only normalizes towards the end of the body chamber. Heller (1958) dubbed this phenomenon *forma undaticarinata* (Fig. 20.2g, h). It can probably be best explained by a temporary parasite infestation of the ventral mantle epithelium. This is supported by the fact that it can be associated with a flattening and asymmetrical appearance of the keel crenulation, which is reminiscent

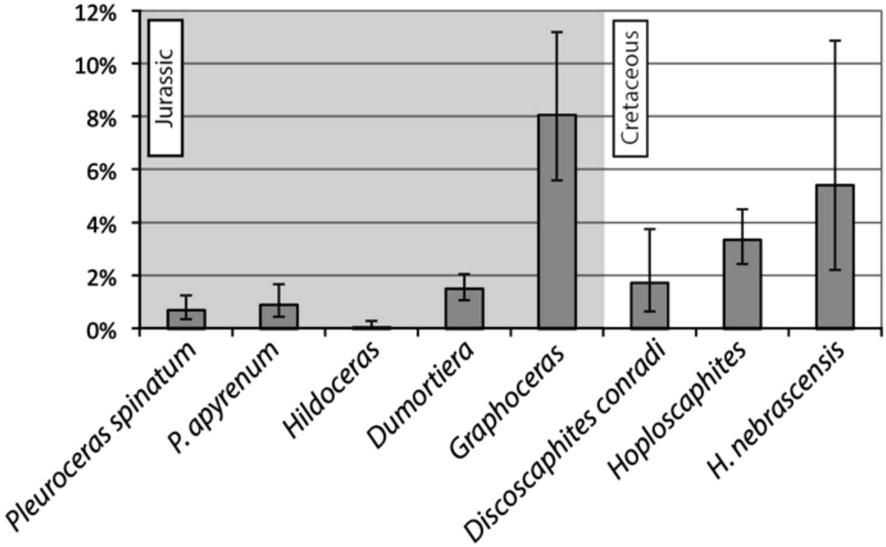

Fig. 20.8 Prevalence of Morton's syndrome and similar phenomena (*forma undaticarinata*) in Early Jurassic to Late Cretaceous ammonoids (in chronological order). Data compiled from Morton (1983), Landman and Waage (1986) and Keupp (2012). The 95% binomial confidence intervals (following Raup 1991 and De Baets et al. (2012) were calculated using the binom.confint function of the Binom Package in R (using the exact approach).

of pathologies dubbed *forma cicatricocarinata* (Heller 1964) caused by injuries to the ventral mantle epithelium as well as unilateral temporary disappearance of the groove surrounding the keel. This phenomenon is not only known from the Amaltheidae, but also from the Harpoceratidae and Hildoceratidae (Fig. 20.2g, h) as well as potentially other taxa with keeled or sharp venters (Keupp 2012). Rare quantitative analyses (Fig. 20.8) show a 10 times higher prevalence of this pathology in *Pleuroceras* than in *Hildoceras* (compare Keupp 2012). The keel can maximally deviate about 90° from the planispiral position and if it exceeds this value, it can result in one or multiple reestablishments of the keel and an associated chaotic, zigzag pattern of the ornamentation (*forma choatica* of Keupp 1977).

Landman and Waage (1986) introduced the term Morton's Syndrome to refer to forms of shell asymmetry in which the midline of the shell venter is deflected to the right or left of the plane of symmetry (Fig. 20.2i, j, k, l, 20.8). The name was based on the work of Morton (1983), who described a high proportion (8.1%) of both macro- and microconchs of *Graphoceras* from the Aalenian, whose whorls grew over to one side resulting in unilateral deformation of the whorl cross section and an excentrical position of the planispiral plane after initial normal growth. Morton (1983) attributed this displacement to parasitic infestation or disease, an opinion shared by Hengsbach (1991b, 1996) and Keupp (2000, 2012). It can result in a bowl-shaped morphology which could be described with the term *forma excentrica* (Hölder 1956) and can also be caused by *in vivo* encrustations of epizoa.

According to Keupp (2012), these pathologies can be associated with counteroscillations of the ornamentation or even the entire whorl (*forma undatacarinata* or *undaticoncha*, respectively) in rare cases. Keupp and Ilg (1992) introduced the term *forma undatispirata* to refer to temporal oscillations of whorls, while Hengsbach (1996) used the term *forma undaticoncha*, particularly when associated with oscillations of the ventral keel or groove. Landman and Waage (1986) described a deviation of the flattened external side from the median plane in *Discoscaphites* and *Hoploscaphites* (also known as *forma juxtasulcata* of Gezcy 1965) as Morton's syndrome (Fig. 20.8). Hölder (1970) used the prefix *juxta*- for cases in which there is a separation of medial elements that are normally coincident with one another (compare Hengsbach 1996). Comparable deviations have become known from a wide variety of taxa (reviewed by Keupp 2012) with mostly planulate to discocone conchs ranging from the Early to Middle Triassic (*Pseudosageceras*, *Columbites*, *Tropigastrites*), over to the Early to Middle Jurassic (Amaltheidae, Graphoceratidae such as *Graphoceras*, Hildoceratidae such as *Cleviceras, Dumortiera* or *Pleydellia*, Cardioceratidae such as *Quenstedtoceras*) to Cretaceous (*Deshayesites*: Doguzhaeva et al. 1990; *Saynoceras:* Ploch 2007). Similar pathologies might be present in the Devonian as well (compare Bockwinkel et al. 2013, Fig. 6D for a report of a specimen of *Pseudoprobeloceras pernai* with possible Morton's Syndrome), but the deviations from normal coiling of the inner whorls in this case might also be related with external injuries or epizoa (compare Klug and Korn 2001) which are now overgrown and not detectable anymore.

The proportion of these pathologies is variable between populations and localities (0.05– 8.1 %; Fig. 20.8). The high proportion of these structures in some populations (e.g., *Graphoceras* of the Isle of Skye: Morton 1983; *Hoploscaphites nebrascensis*: Landman and Waage 1986; Fig. 20.8) might point to a large parasite population at certain localities (e.g., Keupp 2012), although they might also be related with other factors such as a particular ecology (food, mode of life) or an oversensitivity of a population or that these ammonoids were false or facultative hosts at some sites.

In most ammonoid taxa, the midventral position of the siphuncle and of the ventral lobe of the suture line is constant, however, in some taxa the ventral placement can be quite variable or its lateral displacement is even species-specific (Keupp 2012; Fig. 20.9) and it can also change towards the end of ontogeny through the asymmetrical growth of organs (Yacobucci and Manship 2011). This phenomenon has been documented from the Devonian to the Cretaceous (Ziegler 1958; Kemper 1961; Hengsbach 1977a, 1977b, 1977c, 1978, 1979a, 1986a, 1986b; Landman and Waage 1986) with differing prevalences in separate taxa and populations. It also shows no clear boundary (smooth transition) between pathological and normal development of this asymmetry (Keupp 2012; Fig. 20.9). Hölder (1956) introduced the term *forma juxtalobata* (Fig. 20.2n) to refer to the pathological ventral displacement of the siphuncle and the ventral lobe of the suture to one side which should only affect a certain portion of the ammonoid population. According to Keupp (2012), only a small fraction of ammonoid specimens should be affected by parasites (~1 %) and show pathologies, while others like Hengsbach (1996) still attribute a significantly higher prevalence of these pathologies (up to 70 %) to specialized parasitic infection. In the absence of external injuries

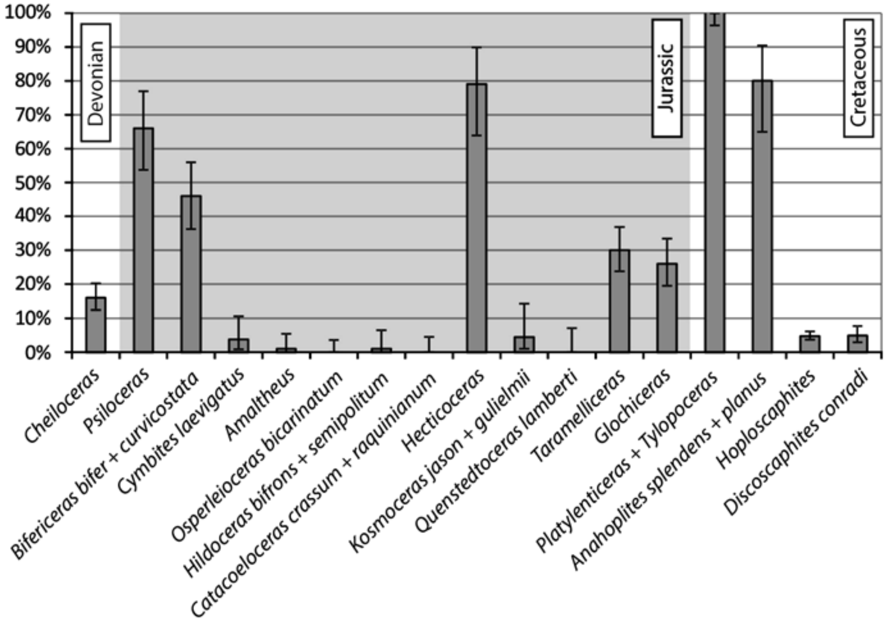

Fig. 20.9 Prevalence of asymmetry of the ventral lobe and siphuncle (not restricted to pathological cases: *forma juxtalobata*: see discussion in text) in Devonian to Cretaceous ammonoids (in chronological order). Data derive from Ziegler (1958), Hengsbach (1976, 1977a, 1977b, 1977c, 1978, 1979a, 1980, 1986a, 1986b) and Landman and Waage (1986); fide Keupp (2012). The 95 % binomial confidence intervals (following Raup 1991 and De Baets et al. 2012) were calculated using the binom.confint function of the Binom Package in R (using the exact approach).

or developmental disorders, the *forma juxtalobata* could potentially be related with various endogenic diseases such as those caused by parasitic infestations (Hengsbach 1991b, 1996; Keupp 2012). Hengsbach (1986a, 1986b, 1991a, 1996) argued that at least some sutural asymmetry-paleopathies in Jurassic taxa were caused by parasitism. He attributed them to an infestation of the septal mantle at or near the siphuncle of young ammonoids (potentially resulting in an asymmetrical swelling) which caused a displacement of the septal root and hence the ventral lobe. According to Keupp (2000, 2012), a pathological cause for the asymmetry of septa in several groups of Jurassic ammonoids with a high proportion of asymmetry (including the cases discussed by Hengsbach) are still speculative.

This is related to the fact that the direction and degree of asymmetry of the suture line seems to be constant (genetically fixed?) in some taxa to highly variable in other taxa (Keupp 2012). Furthermore, a parasitic (or a different pathological) cause appears rather unlikely in many cases as the asymmetry of the suture often lacks a gradual development and can show a continuum between a very low to very high prevalence within some genera (Keupp 2000, 2012; Fig. 20.9, 20.10). Hengsbach (1986a) reported a 26 % prevalence of asymmetry in *Glochiceras*, while Keupp (2012, p. 253), based on the material of Ziegler (1958), stated that the prevalence within this taxon differs between species from 0–100 % (compare Keupp 2012, p. 253; Fig. 20.10).

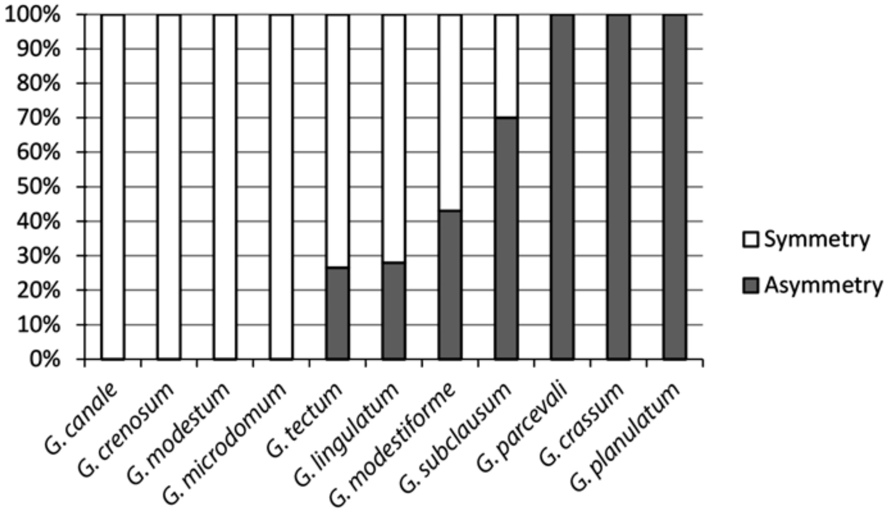

Fig. 20.10 Prevalence of asymmetry of the ventral lobe and siphuncle in *Glochiceras* as listed in Keupp (2012; compare Ziegler 1958)

Exceptions include the specimen described by Rieber (1963) and potential similar cases, where both the siphuncle and the keel progressively develop a lateral displacement after a certain amount of normal coiling as discussed above. Extant *Nautilus* is of little help to interpret the asymmetry of the ventral lobe because its siphuncle is located centrally, so that the parasitic cause remains unproven.

Parasitism remains attractive to explain asymmetry, even in the buccal mass, where Schweigert (2009) suggested parasites to be responsible for assymmetrically arranged deformations in anaptychi without an apparent orientation preference (e.g., Schweigert and Dietl 2001). Kruta and Landman (2008) investigated injuries and anomalies in *Nautilus* jaws which are probably mostly related to diet or mating behavior. They hypothesized that one type of anomaly might potentially be linked to parasitism, however, only parasitic copepods have been reported from *Nautilus* in the wild (see 3.6.3) which are not known to cause these pathologies.

20.5.6 Other Pathologies attributed to Parasitism

Some other pathologies without clear signs for external injuries or epizoa have also been attributed to parasitism or more generally to endogenic causes (see Hengsbach 1996; Keupp 2012 for a more general reviews). Shell lamellae (*forma aptycha* of Keupp 1977; *forma conclusa* of Rein 1989; Fig. 20.1d) have also been discussed to encapsulate foreign bodies (Lehmann 1990, p. 194) such as parasites (Rein 1989) or an injured or diseased area. Such secondary shell lamellae (Keupp 1977; Rein 1989; Lehmann 1990; Rein 1994; Keupp 1994, 1996, 1998, 2000, 2012) have been reported from several ammonoid taxa ranging from the Triassic (*Ceratites, Nevadites*) to the Jurassic (*Chondroceras*, *Dactylioceras*, *Elatmites*, *Kosmoceras*, *Pleuroceras, Sigaloceras, Virgatites*) and in to the Cretaceous (*Audouliceras*, *Pavlovia/Strajevskya*).

Similar lamellae have been reported from extant captive *Nautilus* (Keupp and Riedel 1995; Keupp 2012, p. 231–234; Fig. 20.1c), where the shell material is secreted by the mantle and a local detachment of the mantle and shell occurs (Keupp 2012). No parasitic cause is necessary to explain these structures and according to Keupp (2012), they are mostly related with external injuries. However, parasitic or other endogenic causes cannot be completely ruled out if no obvious injury can be found (compare Keupp 2012, p. 161).

The temporary loss or diminution of ornamentation (described by Lange 1941 as *forma cacoptycha*) might also be related to endogenic causes (Keupp 2012), including parasitism or metabolic-physiological disorders (Hengsbach 1996); however, similar phenomena are also known during regeneration of injuries. Hengsbach(1996) suggested that parasitism could have been involved in cicatrisations of the crenulated keel (*forma cicatricocarinata* of Heller 1964) and Keupp (2012) suggested that endogenic causes might be involved in keel-like raised cicatrices along the venter and flanks of some ammonoids (*forma pseudocarinata* of Fernandez-Lopez 1987), although more comparative studies and data are necessary to corroborate these hypotheses.

20.5.7 Negative Effects of Bioerosion and Epizoa

Parasitism should not be confused with other symbiotic or long-term associations such as epizoa and bioerosion which can also affect the growth of ammonoids (but do necessarily bring advantage to the bioeroding or encrusting agents). Epizoa (Fig. 20.11, 20.12) can form long-term associations and may cause damage or influence growth of ammonoids (e.g., Davis et al. 1999; Klug and Korn 2001; Checa et al. 2002; Larson 2007; Keupp 2012). They are, however, not necessarily parasites since many grew on shells of both living and dead ammonoids as sclerobionts or epicoles (Fig. 20.11, 20.12; Keupp and Hoffman 2015), colonizing their floating shell or their shell when it is already deposited on the seafloor forming a benthic island (Seilacher 1982; Paul and Simms 2012; De Baets et al. 2013b). We follow the terminology suggested by Davis et al. (1999) to refer to epizoa as organisms living on other organisms while both are alive, while we will use epicoles to refer to organisms that live on a hard substrate or shells also when the host is already dead and gone. *In vivo* encrusters of ammonoid shells are known from the Devonian (Klug and Korn 2001) to the Cretaceous (reviewed by Keupp 2012) and include algae, foraminifers, tabulate corals, bryozoans, brachiopods, annelids, lepadomorphs, gastropods, bivalves, and crinoids (see also Rakociński 2011). Various other organisms ranging from fungi to cystoids have also been documented to encrust ammonoid shells, but so far there is no evidence that this happened during their life. Some re-

Fig. 20.11 Epizoans and post-mortem epicoles from the Devonian: **a**, **b** cf. *Latanarcestes* sp. with tabulate coral epizoans, PIMUZ 31083, late Emsian, Hamar Laghdad (morocco), dm 22.5 mm. **c**, **d** body chamber of *Latanarcestes* sp., GPIT 1881–2, dm 11 mm with tabulate coral epizoans. **c**, dorsal view, note the last septum and the imprint zone, x 4. **d** detail of **c**, note the imprints of the overgrown corals. **e**, detail of a *Endosiphonites muensteri* with a crinoid epicole, GPIT 1850–10, late Famennian, Ouidane Chebbi (Morocco), dm 72 mm, x 1. **f** *Paranarcestes chalix*, elliptical coiling due to epizoans, GPIT 1871–206, late Emsian, Ouidane Chebbi (Morocco), dm 7.9 mm. **g** *Rherisites tuba* with tabulate coral epicoles, GPIT 1869–7, late Emsian, Jebel Mech Agrou, Tafilalt (Morocco), dm 52.2 mm. **h** *Cymaclymenia involvens* with auloporid coral epicole (? *Cladochonus*

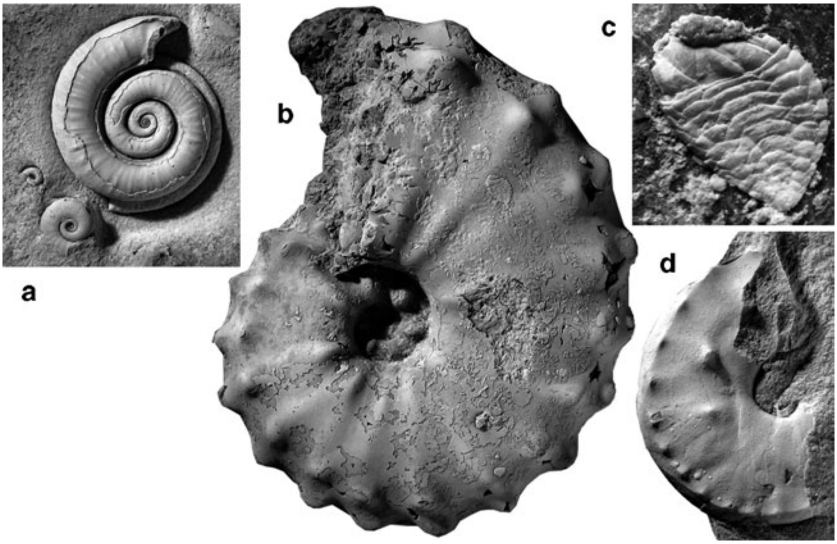

Fig. 20.12 Epizoans and post-mortem epicoles from the Mesozoic: **a** *Arnioceras miserabile*, with a serpulid epizoan, which forced the ammonite to alter its shell morphology, Early Sinemurian, Semicostatum Zone, Charmouth, Dorset (UK), dm 30 mm. **b**, **c** *Mammites nodosoides* with four specimens of the crustacean epicole *Stramentum* sp., Turonian, Goulmima (Morocco), dm 75 mm. **d** *Ceratites pulcher* with 15 juvenile brachiopod epicoles of *Discinisca discoides*, PIMUZ 31080, Anisian, Triassic, dm 37 mm

ports of epicoles might be actually conellae (inorganic growths) which have sometimes been confused and wrongly described (Keupp 2012) as barnacle-like epicoles (Maubeuge 1949, Gerasimov 1955) or limpet gastropods (Quenstedt 1884; Busse 1976). When correctly recognized, epizoa can provide important information on ammonoid growth (Bucher et al. 1996) and ecology (Seilacher 1960; Keupp et al. 1999) including shell orientation in the water column (Hauschke et al. 2011; Ritterbush et al. 2014). *In vivo* epizoism can be easily recognized when epizoa are attached on both sides or overgrown by the ammonoid shell (Paul and Simms 2012) which often influence the growth of the ammonoid resulting in changes in shell morphology such as asymmetry of the whorl section and deviations from normal coiling (Checa et al. 2002). When the final size is reached, *in vivo* epizoism can only be recognized by a preferential orientation of epizoa to currents (Seilacher 1960). Multiple generations of epizoa showing a clear size gradation and exceptional preservation of ammonoid remains (presence of buccal mass) might also point to the

---

sp.), GPIT 1850–22, late Famennian, Madene El Mrakib (Morocco), dm 60 mm. **i**, **j** lateral and dorsal view of *Chlupacites praeceps* with the cystoid epicole *Eucystis* sp., GPIT 1881–5, late Emsian, Tazoulait, Morocco, dm 46 mm. **k** *Sellanarcestes* cf. *tenuior* with the cystoid epicole *Eucystis* sp., late Emsian, Filon 12 (Morocco), dm 64 mm. **l** *Cymaclymenia* sp. with a coral epicole (Cleistoporidae gen. et sp. indet.), late Famennian, Lambidia (Morocco), dm 60 mm. Images **c** to **j** from Klug and Korn (2001) fact that organisms encrusted the ammonoid shell during its lifetime (Keupp et al. 1999). Multiple generations of epizoa would take a while to grow superseding the phase of post-mortem drift. After a long postmortem drift or slow burial, one would not expect the exceptional preservation with *in situ* buccal masses (compare Wani 2007; Keupp 2012) and renal concrements or uroliths.

The type of relationship between the epizoa and the ammonoids probably varied from taxon to taxon. In some cases, only the ammonoid might have had disadvantages as his mobility was constrained by increased drag, additional weight, and the influence on growth because of the epizoa. In some cases, *in vivo* infestation brought negative effects for both the epizoa and the host (compare Larson 2007; Keupp 2012), for which Meischner (1968) introduced the term "*perniciöse Epökie*". This was particularly the case for epizoa which could not change their relative position after fixation on the substrate or which grew longitudinally, because they soon ended up away from their preferred current orientation and were eventually overgrown by the ammonoid shell (Keupp 2012, p. 183). The epizoa in turn influenced ammonoid growth as well as shell shape and therefore the orientation and drag in the water column of the shells.

Whether or not carbonate boring fungi, found as trace fossils (Wetzel 1954; Schindewolf 1962, 1963; Wetzel 1964; Keupp 2012) and more rarely as body fossils (Weitschat 1986; Lehmann 1990) in ammonoid shells, already infested ammonoids during their life and can be treated as parasites is still debated (Keupp 2012). Algae and some parasites are also known to be actively involved in bioerosion of shelled mollusks (e.g., the foraminifer *Hyrrokin*: Beuck et al. 2008). These and other microborers could already have infested the ammonoid during their lifetime (Schindewolf 1962, 1963; Wetzel 1964), but often do so after death (Dullo 1981; Keupp 2012). The traces described by Schindewolf (1962) as *Mycelites* from ammonoid shells are definitively microborings, although this ichnogenus and its ichnospecies are no longer applied following the invention of the cast-embedding technique (Wisshak and Tapanila 2008). The study of microborings has greatly advanced and a lot of ichnotaxa have been erected that were formerly subsumed under terms like *Mycelites*. Most of the traces are reminiscent of *Orthogonum lineare* (Glaub 1994) which are produced by a heterotrophic organism based on its distribution down to aphotic depths and fungi have been tentatively assigned to be the most likely producer. Not all traces reported by Schindewolf are produced by heterotrophic organisms (Max Wisshak, personal communication 2012). However, the hypothesis of Schindewolf (1962, 1963) and Wetzel (1964) of a *syn vivo* infestation of the microborers is not inconceivable and has been reported from oysters, balanids, and serpulids (Max Wisshak, personal communication 2012). The periostracum might, however, serve as a barrier for many microendoliths, but not for all. Some microborings have been described, which even specifically penetrate or entirely dwell within the periostracum (e.g, in the deep-sea bivalve *Bathymodiolus*: Hook and Golubic 1988, 1992). Bioerosion already starts during the animal's lifetime in extant *Nautilus* (Seuss et al. 2015). So far, no direct evidence for a *syn vivo*-infestation of ammonoids (such as active countermeasures) have been documented, so it appears more reasonable to assume that in many cases, the boring traces were mostly formed postmortem unless demonstrated otherwise (Keupp 2012).

20.6 Conclusions and Future Perspectives

Pathologies in ammonoid shells show that they were frequently infested- and affected by parasites of various kinds. Among the most convincing manifestations of such parasitoses are blister pearls (Devonian-Jurassic: Keupp 1986; De Baets et al. 2011), asymmetry of the shell in absence of external injuries or epizoa (Triassic-Cretaceous: Rieber 1963; Morton 1983; Keupp 2012), and disturbances in shell growth (Jurassic: Keupp 1979; Kröger 2000) which is corroborated by comparative studies on extant and fossil shelled mollusks. Pathological gigantism (Carboniferous: Manger et al. 1999) and pathological enlargement of shell volume or ornamentation (Triassic-Cretaceous: Keupp 1976; Kröger 2000) could also be related with parasitism, although more evidence is necessary to further confirm these hypotheses. Only in some cases (e.g., Rieber 1963), asymmetry of the suture line (Devonian-Cretaceous: Keupp 2012), could potentially also be related with parasitoses. Parasitic infestations were more widespread than suspected from counting such paleopathies in the ammonoid shell because most soft-tissue parasites did not leave direct traces in the fossil record and only a fraction caused shell growth pathologies in their hosts. For the same reasons, the identity of the parasites causing these pathologies is so far mostly unknown. Parasitic flatworms were among the likely suspects which is based on extant parasite-host relationships, their high prevalence in extant coleoids, and studies of similar pathologies they cause in other externally shelled mollusks today. Various other extant and even extinct lineages of parasites with similar behavior might also have been responsible. Furthermore, many common cephalopod parasites like bacteria, helminths, as well as crustaceans living in gills of both Recent coleoids and *Nautilus* have a low fossilization potential. The high concentration or restriction of these anomalies to certain taxa or timeframes (Housean pits in Devonian Anarcestina, Pharciceratina and Tornoceratina: De Baets et al. 2011, "*forma umbilicata*" in Dactylioceratidae of the Early Toarcian: Keupp 1979, 2000, 2012; particular cases of "*forma augata*" in Quenstedtoceratidae of the Early Callovian: Seltzer 2001, 2009; Larson 2007; Keupp 2012) suggests parasitic culprits with a high degree of host specificity and makes them potentially an important tool for investigating coevolution in deep time (e.g., De Baets et al. 2011). It has been suggested that the presence of blister pearls in the earliest ammonoids might also indicate the presence of complex parasite life cycles and food webs already in the Devonian because extant parasitic flatworms inducing pearls are transmitted from intermediate host to final hosts by feeding (compare Fig. 20.13). Keupp (2000) suggested that the prevalence of possible trematode-induced pearls in Jurassic *Dactylioceras* might corroborate their planktic lifestyle as intermediate hosts today are mostly mollusks feeding on plankton. However, more studies on the distribution of pathologies are necessary to confirm such hypotheses, as they might not only give important information on the evolutionary history of their hosts but also on their mode of life and predator-prey relationships. Such hypotheses can only be adequately corroborated by finding exceptionally preserved parasites in ammonoid soft parts which is highly implausible, but not impossible (cf. Klug et al.

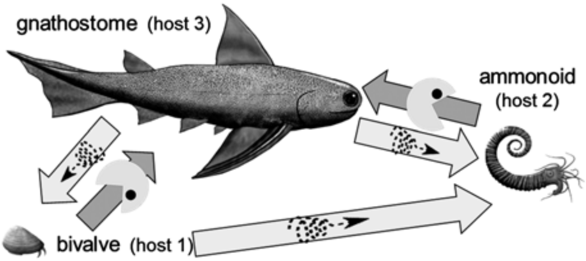

Fig. 20.13 Possible complexity of parasite life cycles and food webs in the Devonian. Infestation of bivalves and ammonoids is based on the presence of blister pearls, possibly induced by intermediate life stages parasitic flatworms or other parasites with similar behaviours (De Baets et al. 2011). Infestation of gnathostomes is indicated by the presence of parasitic attachment organs in gill region and abdomen of Late Devonian acanthodians and placoderms attributed to parasitic flatworms (Upeniece 2001, 2011)

2012). Further comparative work on pathologies in extant and fossil cephalopods and other molluscs with an accretionary shell, particularly bivalves and gastropods, can also be useful to identify their parasitic causes and the behavior of the culprit. The influence of *in vivo* epizoa and bioerosion during the lifetime of ammonoids also needs to be further investigated.

Acknowledgements Some of the materials and studies used for this contribution resulted from research which was carried out in the research projects with the numbers 200021–113956⁄ 1, 200020–25029, and 200020–132870 funded by the Swiss National Science Foundation SNF. We would like to thank: Matthias López Correa (Geozentrum Nordbayern, Erlangen), Barbara Seuß (Geozentrum Nordbayern, Erlangen) and Max Wisshak (Senckenberg am Meer, Wilhelmshaven) for discussions on bioerosion in extant molluscs; Carlo Romano (Palaontologisches Institut und Museum, Zürich) for helping with obtaining literature; Aleksandr Mironenko (Moscow) and Mikhail Rogov (Geological Institute of Russian Academy of Sciences, Moscow) for help with Russian literature. We thank the reviewers Arnaud Brayard (Université de Bourgogne, Dijon), Isabella Kruta (AMNH, New York) and Joshua Slattery (University of South Florida) for their constructive comments and suggestions. John Huntley (University of Missouri) proofread an earlier draft of the manuscript.

References

Barord GJ, Ju C, Basil JA (2012) First report of a successful treatment of a mucodegenerative disease in the chambered nautilus (*Nautilus pompilius*). J Zoo Wildl Med 43:636–639

Bayer U (1970) Anomalien bei Ammoniten des Aaleniums und Bajociums und ihre Beziehung zur Lebensweise. Neues Jahrb Geol Paläontol Abh 135:19–41

Becker RT, House MR (1994) International devonian goniatite zonation, Emsian to Givetian, with new records from Morocco. Cour Forschungsinst Senckenb 169:79–135

Beuck L, Correa M, Freiwald A (2008) Biogeographical distribution of *Hyrrokkin* (Rosalinidae, Foraminifera) and its host-specific morphological and textural trace variability. In: Wisshak M, Tapanila L (eds) Current developments in bioerosion. Springer, Berlin

Binder H (2002) Fossile Perlen aus dem Karpatium des Korneuburger Beckens (Österreich, Untermiozän). Beiträge zur Paläontologie 27:259–271

Bockwinkel J, Becker RT, Ebbighausen V (2009) Upper Givetian ammonoids from Dar Kaoua (Tafilalt, SE Anti-Atlas, Morocco). Berl Paläobiol Abh 10:61–128

Bockwinkel J, Becker RT, Ebbighausen† V (2013) Late Givetian ammonoids from Hassi Nebech (Tafilalt Basin, Anti-Atlas, southern Morocco). Foss Rec 16:5–65

Boettger CR (1953a) Größenwachstum und Geschlechtsreife bei Schnecken und pathologischer Riesenwuchs als Folge einer gestörten Wechselwirkung beider Faktoren. Zoologischer Anzeiger (Suppl 17):468–487

Boettger CR (1953b) Riesenwuchs der Landschnecke *Zebrina* (*Zebrina*) *detrita* (Müller) als Folge parasitärer Kastration. Archiv für Molluskenkunde 82:151–152

Boucot AJ, Poinar GO Jr (2010) Fossil behavior compendium. CRC Press, Boca Raton

Brooks DR, McLennan DA (1993) Parascript: parasites and the language of evolution. Smithsonian Institution Press, Washington

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

Busse E (1976). Eine Napfschnecke (Gastropoda, Cyclobranchia, Patellaceae) im Oberen Muschelkalk (Mittlere Ceratitenschichten/Ladin) Niederhessens. Geol Jahrb Hessen 104:5–7

Carlson BA (1987) Collection and aquarium maintenance of nautilus. In: Saunders WB, Landman NH (eds) Nautilus. Springer, Dordrecht

Castellanos-Martínez S, Gestal C (2013) Pathogens and immune response of cephalopods. J Exp Mar Biol Ecol 447:14–22

Checa AG, Okamoto T, Keupp H (2002) Abnormalities as natural experiments: a morphogenetic model for coiling regulation in planispiral ammonites. Paleobiology 28:127–138

Chlupáč I, Turek V (1983) Devonian goniatites from the Barrandian area. Rozpr Ustred Ust Geol 46:1–159

Combes C (2001) Parasitism: the ecology and evolution of intimate interactions. University of Chicago Press, Chicago

Conway Morris S (1981) Parasites and the fossil record. Parasitology 83:489–509

Conway Morris S (1990) Parasitism. In: Briggs DEG, Crowther PR (eds) Palaeobiology: a synthesis. Blackwell Science, Oxford

Cuvier G (1829) Le règne animal distribué d'après son organisation. Tome I. Imprimerie D'Hippolyte Tilliard, Paris

Cuvier G (1830) Considérations sur les mollusques, et en particulier sur les céphalopodes. Ann Sci Nat 19:241–259.

Davis RA, Mapes RH (1999) Pits in internal molds of cephalopods. Ber Geol BA 46:31

Davis RA, Landman NH, Dommergues J-L, 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, Klofak SM, Landman NH (1999) Epizoa on externally shelled cephalopods. In: Rozanov AY, Shevyrev AA (eds) Fossil cephalopods: recent advances in their study. Russian Academy of Sciences Paleontological Institute, Moscow

De Baets K, Klug C, Korn D (2011) Devonian pearls and ammonoid-endoparasite co-evolution. Acta Palaeontol Pol 56:159–180

De Baets K, Klug C, Korn D, Landman NH (2012) Early evolutionary trends in ammonoid embryonic development. Evolution 66:1788–1806

De Baets K, Goolaerts S, Jansen U, Rietbergen T, Klug C (2013a) The first record of Early Devonian ammonoids from Belgium and their stratigraphic significance. Geol Belg 16:148–156

De Baets K, Klug C, Korn D, Bartels C, Poschmann M (2013b) Emsian Ammonoidea and the age of the Hunsrück Slate (Rhenish Mountains, Western Germany). Palaeontogr A 299:1–113

De Baets K, Bert D, Hoffmann R, Monnet C ,Yacobucci MM, Klug C (2015) Ammonoid intraspecific variability. In: Klug C, Korn D, De Baets K, Kruta I, Mapes RH (eds) Ammonoid Paleobiology: From anatomy to ecology. Springer, Dordrecht

Della Chiaje S (1825) Memorie sulla storia e notomia degli animali senza vertebre del regno di Napoli, 2. Napoli. Stamperia Della Societá Tipografica 1–4:185–444

Dentzien-Dias PC, Poinar G Jr, de Figueiredo AEQ, Pacheco ACL, Horn BLD, Schultz CL (2013) Tapeworm Eggs in a 270 Million-Year-Old Shark Coprolite. PlosOne 8:1–4, DOI: 10.1371/journal.pone.0055007

Doguzhaeva LA, Michailova IA, Kabanov GK (1990) Irregular forms of *Deshayesites* (Ancyloceratina) from the Volga Region near Uljanowsk. Trans Paleontol Inst 243:120–127 [in Russian]

Dullo C (1981) Zur Erhaltung und Mikrostruktur der Ammonitenschalen aus Unterstürmig (Ofr.). Geol Nordost-Bayern 31:75–83

Ebbighausen V, Becker RT, Bockwinkel J (2011) Emsian and Eifelian ammonoids from Oufrane, eastern Dra Valley (Anti-Atlas, Morocco)—taxonomy, stratigraphy and correlation. Neues Jahrb Geol Paläontol Abh 259:313–379

Engel MS (1894) Über kranke Ammonitenformen im Schwäbischen Jura. Nova Acta Leopold 61:327–384

Fernández-López SR (1987) Necrocinesis y colonización posmortal en *Bajocisphinctes* (Ammonoidea) de la Cuenca Ibérica: implicaciones paleoecológicas y paleobatimétricas. Bol Real Soc Esp His Nat Secc Geol 82:151–184

Geczy B (1965) Pathologische jurassische Ammoniten aus dem Bakony-Gebirge. Ann Univ Sci Budap Rolando Eötvös Nominatae Sect Geol 9:31–37

Gerasimov PA (1955) Guide-fossils of Mesozoic of the central regions of the European part of USSR. Part II. Echinodermata, Crustaceans, Vermes, Bryozoans and corals from the Jurassic deposits. Gosgeolyekhizdat, Moscow [in Russian]

Glaub I (1994) Mikrobohrspuren in ausgewählten Ablagerungsräumen des europäischen Jura und der Unterkreide (Klassifikation und Palökologie). Cour Forsch Senckenberg 174:1–324

González AF, Pascual S, Gestal C, Abollo E, Guerra A (2003) What makes a cephalopod a suitable host for parasite? The case of Galician waters. Fish Res 60:177–183. doi:10.1016/s0165–7836(02)00059–0

Götting K-J (1974) Malakozoologie. Grundriss der Weichtierkunde. Fischer, Stuttgart

Götting K-J (1979) Durch Parasiten induzierte Perlbildung bei *Mytilus edulis* L. (Bivalvia). Malacologia 18:563–567

Hanlon RT, Forsythe JW (1990) Diseases caused by microorganisms In: Kinne O (ed) Diseases of Marine Animals. Vol. III. Biologische Anstalt Helgoland, Hamburg

Hauschke N, Schöllmann L, Keupp H (2011) Oriented attachment of a stalked cirripede on an orthoconic heteromorph ammonite—implications for the swimming position of the latter. Neues Jahrb Geol Paläontol Abh 262:199–212

Haven N (1972) The ecology and behavior of *Nautilus pompilius* in the Philippines. Veliger 15:75–81

Heller F (1958) Gehäusemißbildungen bei Amaltheiden. Ein neuer Fund aus dem fränkischen Jura. Geol Blätter für Nordost-Bayern und angrenzende Gebiete 8:66–71

Heller F (1964) Neue Fälle von Gehäuse-Mißbildungen bei Amaltheiden. Paläontol Z 38:136–141

Hengsbach R (1976) Über Sutur-Asymmetrie bei *Cymbites laevigatus* (Ammonoidea; Jura). Senckenb Lethaea 56:463–468

Hengsbach R (1977a) Cheiloceraten (Ammon., Devon) mit asymmetrischen Phragmocon. Sitzungsber Ges Natur Freunde Berlin (N F) 17:69–72

Hengsbach R (1977b) Über die Sutur-Asymmetrie einiger Psiloceraten. Sitzungsber Ges Natur Freunde Berlin (N F) 17:59–67

Hengsbach R (1977c) Zur Sutur-Asymmetrie bei *Platylenticeras.* Zool Beitr 23:459–468

Hengsbach R (1978) Zur Sutur-Asymmetrie bei *Anahoplites.* Senck leth 59:377–385

Hengsbach R (1979a) Zur kenntnis der Asymmetrie der Ammoniten-Lobenlinie. Zool Beitr 25:107–162

Hengsbach R (1979b) Weitere Anomalien an Amaltheen-Gehäusen (Ammonoidea; Lias). Senck leth 60:243–251

Hengsbach R (1980) Über die Sutur-Asymmetrie bei *Hecticoceras* (Ammonoidea; Jura). Senck leth 60:463–473

Hengsbach R (1986a) Zur Kenntnis der Asymmetrie der Sutur-Asymmetrie bei Ammoniten. Senck leth 67:119–149

Hengsbach R (1986b) Ontogenetisches Auftreten und Entwicklung der Sutur-Assymmetrie bei einigen Psilocerataceae (Ammonoidea; Jura). Senck leth 67:323–330

Hengsbach R (1990) Studien zur Paläopathologie der Invertebraten. 1: Die Paläoparasitologie, eine Arbeitsrichtung der Paläobiologie. Senck leth 70:439–461

Hengsbach R (1991a) Studien zur Paläopathologie der Invertebraten III: Parasitismus bei Ammoniten. Paläontol Z 65:127–139

Hengsbach R (1991b) Studien zur Paläopathologie der Invertebraten II: Die Symmetropathie—ein Beitrag zur Erforschung sogenannter Anomalien. Senck leth 71:339–366

Hengsbach R (1996) Ammonoid pathology. In: Landman NH, Tanabe K, Davis RA (eds) Ammonoid paleobiology. Plenum, New York

Ho JS (1980) Anchicaligus *nautili* (Willey), a caligid copepod parasitic on *Nautilus* in Palau, with discussion of *Caligulina* Heegaard, 1972. Publ Seto Mar Biol Lab 25:157–165

Hochberg FG (1983) The parasites of cephalopods: a review. Mem Natl Mus Vic 44:109–145

Hochberg FG (1989) Les parasites. In: Mangold K (ed) Traité de Zoologie, Tome V (Cephalopodes), Fascicule 4. Masson, Paris

Hochberg FG (1990) Diseases of mollusca: cephalopoda. In: Kinne O (ed) Diseases of marine animals, Vol. III. Biologische Anstalt Helgoland, Hamburg

Hölder H (1956) Über Anomalien an jurassischen Ammoniten. Paläontol Z 30:95–107

Hölder H (1970) Anomalien an Molluskenschalen, insbesondere Ammoniten, und deren Ursachen. Paläontol Z 44:182–195

Hook JE, Golubic S (1988) Mussel periostracum from deep-sea redox communities as a microbial habitat: the scalloping periostracum borer. Mar Ecol 9:347–364

Hook JE, Golubic S (1992) Mussel periostracum from deep-sea redox communities as a microbial habitat: 3. Secondary inhabitants. Mar Ecol 13:119–131

House MR (1960) Abnormal growths in some Devonian goniatites. Palaeontology 3:129–136

Hüne L, Hüne P (2006). Des phénomènes paléopathologiques chez une faune d'ammonites du Callovien superieur de Bénerville-sur-Mer (Calvados, France). L'ècho des falaises 10: 33–37

Huntley JW (2007) Towards establishing a modern baseline for paleopathology: trace-producing parasites in a bivalve host. J Shellfish Res 26:253–259

Ituarte CF, Cremonte F, Deferrari G (2001) Mantle-shell complex reactions elicited by digenean metacercariae in *Gaimardia trapesina* (Bivalvia: Gaimardiidae) from the Southwestern Atlantic Ocean and Magellan Strait. Dis Aquat Org 48:47–56

Ituarte C, Cremonte F, Zelaya DG (2005) Parasite-mediated shell alterations in Recent and Holocene sub-antarctic bivalves: the parasite as modeler of host reaction. Invertebr Biol 124:220–229. doi: 10.1111/j.1744–7410.2005.00021.x

Ivanov AN (1971) Problems of the periodization of ontogeny in ammonites. Yarosl Ped Inst Uch Zap Geol i Paleont 87:76–119 [in Russian]

Ivanov AN (1975) Late ontogeny in ammonites and its characteristics in micro-, macro- and megaconches. Yarosl Ped Inst. Sb Nauchn Trudy 142:5–57 [in Russian]

Jacobs DK, Landman NH (1993) *Nautilus*-a poor model for the function and behavior of ammonoids? Lethaia 26:101–111

Kemper E (1961) Die Ammonitengattung *Platylenticeras* (= *Garnieria*). Beihefte zum Geologischen Jahrbuch 47:1–195

Keupp H (1976) Neue Beispiele für den Regenerationsmechanismus bei verletzten und kranken Ammoniten. Paläontol Z 50:70–77

Keupp H (1977) Paläopathologische Normen bei Amaltheiden (Ammonoidea) des Fränkischen Lias. Jahrb Coburg Landes-Stiftung 1977:263–280

Keupp H (1979) Nabelkanten-präferenz der *forma verticata* Hölder 1956 bei Dactylioceraten (ammonoidea, Toarcien). Paläontol Z 53:214–219

Keupp H (1984) Pathologische Ammoniten, Kuriositäten oder paläobiologische Dokumente? (Teil 1). Fossilien 1984: 258–262

Keupp H (1986) Perlen (Schalenkonkretionen) bei Dactylioceraten aus dem fränkischen Lias. Natur und Mensch 1986:97–102

Keupp H (1994) Volumenvermindernde Gehäuse-Anomalien bei Jura-Ammoniten. Fossilien 1994:38–44

Keupp H (1995) Volumenvergrößernde Anomalien bei Jura-Ammoniten. Fossilien 1995:54–59

Keupp H (1996) Paläopathologische Analyse einer Ammoniten-Vergesellschaftung aus dem Ober-Jura Westsibiriens. Fossilien 1996:45–54

Keupp H (1997) Paläopathologische Analyse einer „Population“ von *Dactylioceras athleticum* (Simpson) aus dem Unter-Toarcium von Schlaifhausen/Oberfranken. Berl Geowiss Abh E 25:243–267

Keupp H (1998) Mundsaumverletzungen bei *Pleuroceras* (Ammonoidea). Fossilien 1998:37–42

Keupp H (2000) Ammoniten—Paläobiologische Erfolgsspiralen. Thorbecke, Stuttgart

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 80:112–123

Keupp H (2012) Atlas zur Paläopathologie der Cephalopoden. Berl Paläobiol Abh 12:1–390

Keupp H, Hoffmann R (2015) Ammonoid paleopathology. In: Klug C, Korn D, De Baets K, Kruta I, Mapes RH (eds) Ammonoid Paleobiology: From anatomy to ecology. Springer, Dordrecht

Keupp H, Ilg A (1992) Paläopathologie der Ammoniten fauna aus dem Obercallovium 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, 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

Kieslinger A (1926) Untersuchungen an triadischen Nautiloideen. Paläontol Z 7:101–122

Kinne O (1980) Diseases of marine animals: general aspects. In Kinne O (ed) Diseases of marine animals, volume I: general aspects, protozoa to gastropoda. Biologische Anstalt Helgoland, Hamburg

Kirchner H (1927) Perlbildung bei einem Ceratiten. Zentra Miner Geol Paläont Abt B Geol Paläont 4:148–150

Klug C (2001) Early Emsian ammonoids from the eastern Anti-Atlas (Morocco) and their succession. Paläontol Z 74:479–515

Klug C (2002a) Quantitative stratigraphy and taxonomy of late Emsian and Eifelian ammonoids of the eastern Anti-Atlas (Morocco). Cour Forschungsinst Senckenb 238:1–109

Klug C (2002b) Conch parameters and ecology of Emsian and Eifelian ammonoids from the Tafilalt (Morocco) and their relation to global events. Ber Geol BA 57:523–538

Klug C (2007) Sublethal injuries in Early Devonian cephalopod shells from Morocco. Acta Palaeontol Pol 52:749–759

Klug C, Korn D (2001) Epizoa and post-mortem epicoles on cephalopod shells—examples from the Devonian and Carboniferous of Morocco. Berl Geowiss Abh E 36:145–155

Klug C, Lehmann J (2015) Soft part anatomy of ammonoids: reconstructing the animal based on exceptionally preserved specimens and actualistic comparisons. In: Klug C, Korn D, De Baets K, Kruta I, Mapes RH (eds) Ammonoid Paleobiology: From anatomy to ecology. Springer, Dordrecht

Klug C, De Baets K, Kröger B, Bell MA, Korn D, Payne JL (2015) Normal giants? Temporal and latitudinal shifts of Palaeozoic marine invertebrate gigantism and global change. Lethaia 48:267–288. DOI: 10.1111/let.12104

Klug C, Kröger B, Korn D, Rucklin M, Schemm-Gregory M, De Baets K, Mapes RH (2008) Ecological change during the early Emsian (Devonian) in the Tafilalt (Morocco), the origin of the Ammonoidea, and the first African pyrgocystid edrioasteroids, machaerids and phyllocarids. Palaeontogr A 283:83–176

Klug C, Riegraf W, Lehmann J (2012) Soft–part preservation in heteromorph ammonites from the Cenomanian–Turonian Boundary Event (OAE 2) in north–west Germany. Palaeontology 55:1307–1331

Korn D, Klug C (2002) Ammoneae Devonicae. In: Riegraf W (ed) Fossilium Catalogus 1: Animalia, 138. Backhuys, Leiden

Korn D, Klug C, Mapes RH (2005a) The lazarus ammonoid family Goniatitidae, the tetrangularly coiled Entogonitidae, and Mississippian biogeography. J Paleontol 79:356–365

Korn D, Niedzwiedzki R, Posieczek JB (2005b) Age, distribution, and phylogeny of the peculiar late Devonian ammonoid *Soliclymenia.* Act Geol Pol 55:99–108

Kraft S, Korn D, Klug C (2008) Patterns of ontogenetic septal spacing in Carboniferous ammonoids. N Jahrb Geol Paläont Abh 250:31–44

Kröger B (2000) Schalenverletzungen an jurassischen Ammoniten—ihre paläobiologische und paläoökologische Aussagefähigkeit. Berl Geowiss Abh E 33:1–97

Kröger B, Vinther J, Fuchs D (2011) Cephalopod origin and evolution: a congruent picture emerging from fossils, development and molecules. Bioessays 33:602–613

Kruta I, Landman NH (2008) Injuries on *Nautilus* jaws: implications for the function of ammonite aptychi. Veliger 50:241–247

Lafferty KD, Kuris AM (2009) Parasitic castration: the evolution and ecology of body snatchers. Trends Parasitol 25:564–572

Lange W (1941) Die Ammonitenfauna der Psiloceras-Stufe Norddeutschlands. Palaeontogr A 93:1–186

Lauckner G (1983) Diseases of mollusca: Bivalvia. In: Kinne O (ed) Diseases of marine animals, vol II. Biologische Anstalt Helgoland, Hamburg

Landman NH, Waage KM (1986) Shell abnormalities in scaphitid ammonites. Lethaia 19:211–224

Landman NH, Mikkelsen PM, Bieler R Bronson B (2001) Pearls: a natural history. Abrams, New York.

Landman NH, Kennedy WJ, Cobban WA, Larson NL (2010) *Scaphites* of the “Nodosus Group” from the Upper Cretaceous (Campanian) of the Western Interior of North America. Bull Am Mus Nat Hist:1–242

Larson N (2007) Deformities in the Late Callovian (late Middle Jurassic) ammonite Fauna from Saratov, Russia. In: Landman NH, Davis RA, Mapes RH (eds) Cephalopods—Present and Past: new insights and fresh perspectives. Springer, Netherlands

Lehmann U (1975) Über Biologie und Gehäusebau bei *Dactylioceras* (Ammonoidea) aufgrund einer Fraktur-Analyse. Mitt Geol-Paläontol Inst Univ Hamburg 44:195–206

Lehmann U (1990) Ammonoideen: leben zwischen Skylla and Charybdis. Enke, Stuttgart

Liljedahl L (1985) Ecological aspects of a silicified bivalve Fauna from the Silurian of Gotland. Lethaia 18:53–66

Littlewood DTJ (2006) The evolution of parasitism in flatworms. In: Maule AG, Marks NJ (eds) Parasitic flatworms: molecular biology, biochemistry, immunology and physiology. CABI, Wallingford

Littlewood DTJ, Donovan SK (2003) Fossil parasites: a case of identity. Geol Today 19:136–142

Manda S, Turek V (2009) Minute Silurian oncocerid nautiloids with unusual colour patterns. Acta Palaeontol Pol 54:503–512

Manger WL, Meeks LK, Stephen DA (1999) Pathologic gigantism in middle Carboniferous cephalopods, Southern Midcontinent, United States. In: Olóriz F, Rodríguez-Tovar FJ (eds) Advancing research on living and fossil cephalopods. Springer, Dordrecht

Maubeuge PL (1949) Sur la nature des “conelles” (Quenstedt). Bull Soc Sci Nancy 1:1–3.

Meischner D (1968) Perniciöse Epökie von *Placunopsis* auf *Ceratites*. Lethaia 1:156–174

Miller AI (1938) Devonian ammonoids of America. GSA Spec Pap 14:1–294

Mironenko AA 2012. Traces of lifetime damage on the shells of Upper Jurassic (upper Volgian) *Kachpurites* (Craspeditidae, Ammonoidea). In: Leonova TB, Barskov IS, Mitta VV (eds) Modern problems of studying of cephalopod molluscs: morphology, taxonomy, evolution, ecology, biostratigraphy. Paleont Inst Russian Acad Sci, Moscow [in Russian]

Miura O, Kuris AM, Torchin ME, Hechinger RF, Chiba S (2006) Parasites alter host phenotype and may create a new ecological niche for snail hosts. Proc R Soc Lond B 273:1323–1328

Morton N (1983) Pathologically deformed *Graphoceras* (Ammonitina) from the Jurassic of Skye, Scotland. Palaeontology 26:443–453

Opitz R (1932) Bilder aus der Erdgeschichte des Nahe-Hunsrück-Landes Birkenfeld. Enke, Birkenfeld

Pascual S, Gestal C, Estévez JM, Rodríguez H, Soto M, Abollo E, Arias C (1996) Parasites in commercially-exploited cephalopods (Mollusca, Cephalopoda) in Spain: an updated perspective. Aquaculture 142:1–10

Pascual S, Gonzáez A, Guerra A (2007) Parasites and cephalopod fisheries uncertainty: towards a waterfall understanding. Rev Fish Biol Fish 17:139–144

Paul CRC, Simms MJ (2012) Epifauna on ammonites from the Lower Jurassic of the Severn basin, southern England, and their palaeoenvironmental and taphonomic significance. Proc Geol Assoc 123:508–519

Ploch I (2007) Intraspecific variability and problematic dimorphism in the Early Cretaceous (Valanginian) ammonite *Saynoceras verrucosu*m (d'Orbigny, 1841). Act Geologica Sin 81:877–882

Poulin R, Morand S (2000) The diversity of parasites. The Quart Rev Biol 75:277–293. doi:10.2307/2665190

Quenstedt FA (1884) Petrefaktenkunde Deutschlands, Erste Abtheilung, B, 1. Band Fues´s, Leipzig

Rakociński M. (2011) Sclerobionts on Upper Famennian cephalopods from the Holy cross mountains, Poland. Palaeobiol Palaeoenviron 91:63–73, doi 10.1007/s12549–010-0045-x

Rakociński M (2012) The youngest Devonian record of "Housean pits" in ammonoids. Geol Q 56:387–390

Raup DM (1991) The future of analytical paleobiology. Short Course Paleontol 4:207–216

Rein S (1989) Über das Regenerationsvermögen der germanischen Ceratiten (Ammonoidea) des Oberen Muschelkalks (Mitteltrias). Veröff Naturhistorischen Mus Schleus 4:47–54

Rein S (1994) Sekundärschalenbildungen (*forma conclusa*) bei germanischen Ceratiten. Fossilien 1994:372–376

Rieber H (1963) Ein *Cardioceras* (Ammonoidea) mit asymmetrischer Lage von Phragmokon und Kiel. Neues Jahrb Geol Paläontol Mh 1963:289–294

Ritterbush KA, Hoffmann R, Lukeneder A, De Baets K (2014) Pelagic palaeoecology: the importance of recent constraints on ammonoid palaeobiology and life history. J Zool 292:229–241

Rocha F, Guerra A, Gonzalez AF (2001) A review of reproductive strategies in cephalopods. Biol Rev 76:291–304

Rohde K (2005) Definitions, and adaptations to a parasitic way of life. In: Rohde K (ed) Marine parasitology. CSIRO, Oxon

Ruiz GM, Lindberg DR (1989) A fossil record for trematodes: extent and potential uses. Lethaia 22:431–438

Schindewolf OH (1934) Über Epöken auf Cephalopoden-Gehäusen. Paläontol Z 16:15–31

Schindewolf OH (1962) Parasitäre Thallophyten in Ammoniten-Schalen. Paläontol Z 36:206–215

Schindewolf OH (1963) Pilze in oberjurassischen Ammoniten-Schalen. N Jahrb Geol Paläont Abh 118:177–181

Schweigert G (2009) First three-dimensionally preserved in situ record of an aptychophoran ammonite jaw apparatus in the Jurassic and discussion of the function of aptychi. Berl Paläobiol Abh 10:321–330

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 (1960) Epizoans as a key to ammonoid ecology. J Paleont 34:189–193

Seilacher A (1982) Ammonite shells as habitats—floats or benthic islands? (Abstract). In: Einsele G, Seilacher A (eds) Cyclic and event stratification. Springer, Berlin

Seltzer VB (2001) About anomal shells from the callovian ammonites. Transactions of the scientific research geological institute of the N. G. Chernyshevskii Saratov State Univ 8:29–45

Seltzer VB (2009) Anomalous phragmocones of the Late Callovian Cardioceratidae (Ammonoidea) In: Leonova TB, Barskov IS, Mitta VV (eds) Contributions to current cephalopod research: morphology, systematics, evolution, ecology and biostratigraphy. PIN RAS, Moscow

Seuss B, Wisshak M, Mapes RH, Landman NH (2015) Syn-Vivo Bioerosion of *Nautilus* by Endo- and Epilithic Foraminiferans (New Caledonia and Vanuatu). *PLoS ONE* 10:e0125558

Stridsberg S, Turek V (1997) A revision of the Silurian nautiloid genus *Ophioceras* Barrande. GFF 119:21–36

Sousa WP (1983) Host life history and the effect of parasitic castration on growth: a field study of *Cerithidea californica* Haldeman (Gastropoda: Prosobranchia) and its trematode parasites. J Exp Mar Biol Ecol 73:273–296

Sorensen RE, Minchella DJ (2001) Snail-trematode life history interactions: past trends and future directions. Parasitology 123(7):S3–S18

Sparks AK (1972) Invertebrate Pathology: Non-communicable Diseases. Academic Press, New York

Tasnádi-Kubacska A (1962) Paläopathologie: Pathologie der Vorzeitlichen Tiere: Vol. 1. Fischer, Jena

Turek V, Manda S (2010) Variability of colour pattern and shell abnormalities in Silurian nautiloid *Peismoceras* Hyatt, 1884. J Natl Mus (Prague), Nat Hist Ser 179:171–178

Upeniece I (2001) The unique fossil assemblage from the Lode quarry (Upper Devonian, Latvia). Foss Rec 4:101–119

Upeniece I (2011) Palaeoecology and juvenile Individuals of the Devonian placoderm and acanthodian fishes from Lode Site, Latvia. University of Latvia, Riga

Wani R (2007) How to recognize in situ fossil cephalopods: evidence from experiments with modern *Nautilus*. Lethaia 40:305–311

Ward PD (1987) The natural history of *Nautilus*. Allen and Unwin, Winchester

Weitschat W (1986) Phosphatisierte Ammonoideen aus der Mittleren Trias von Central-Spitzbergen. Mitt Geol-Paläont Inst Univ Hamburg 61:249–279

Wetzel W (1954) Untersuchung eines großen Jurafindlings von besonderem sedimentologischen und paläobiologischen Interesse. Palaeontogr A 105:133–165

Wetzel W (1964) Schalen-Parasitismus bei Ammoniten (aufgrund schleswig-holsteinischer Funde). Meyniana 14:66–69

Willey A (1897) Zoological observations in the South Pacific. Q J Microscopical Sci (N. S.) 39:219–231

Wisshak M, Tapanila L (2008) Current developments in Bioerosion. In: Freiwald A (ed) Erlangen earth conference series. Springer, Heidelberg

Yacobucci MM, Manship LL (2011) Ammonoid septal formation and suture asymmetry explored with a geographic information systems approach. Palaeontol Electron 14(1):3A:17p

Zapalski MK (2011) Is absence of proof a proof of absence? Comments on commensalism. Palaeogeogr Palaeoclimatol Palaeoecol 302:484–488

Zatoń M (2010) Sublethal injuries in middle Jurassic ammonite shells from Poland. Geobios 43:365–375.

Ziegler B (1958) Monographie der Ammonitengattung *Glochiceras* im epikontintalen Weißjura Mitteleuropas. Palaeontogr A 110:93–164