Chapter 1
Ancestry, Origin and Early Evolution of Ammonoids

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1.1 Introduction

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

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

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

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

1.2 Phylogenetic Position of the Ammonoids in the Cephalopod Tree

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

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

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

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

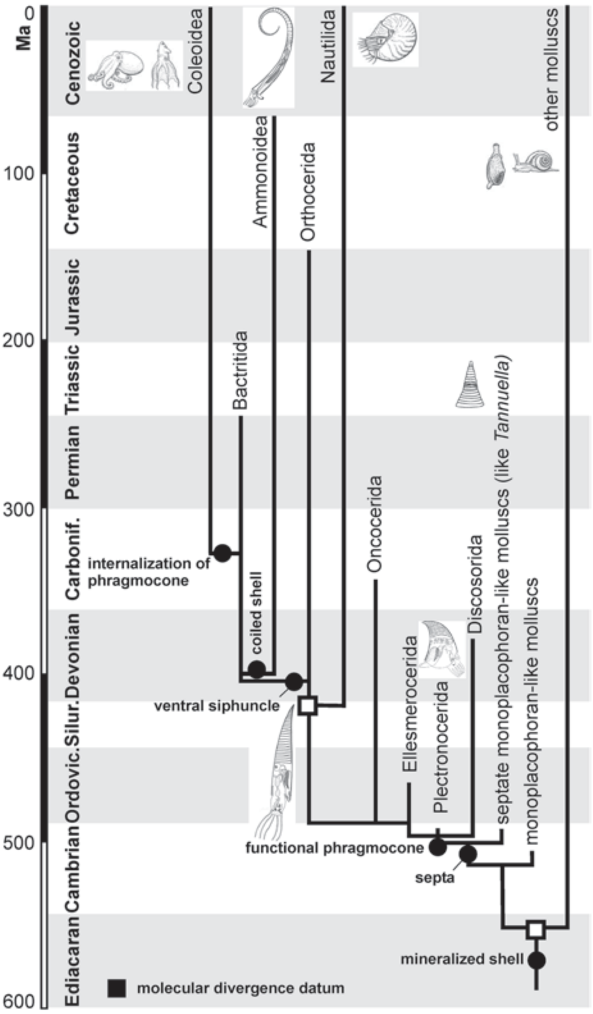

Fig. 1.1 Cephalopod phylogeny (modified after Kröger et al. 2011)

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

1.2.1 The Cephalopod Bauplan

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

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

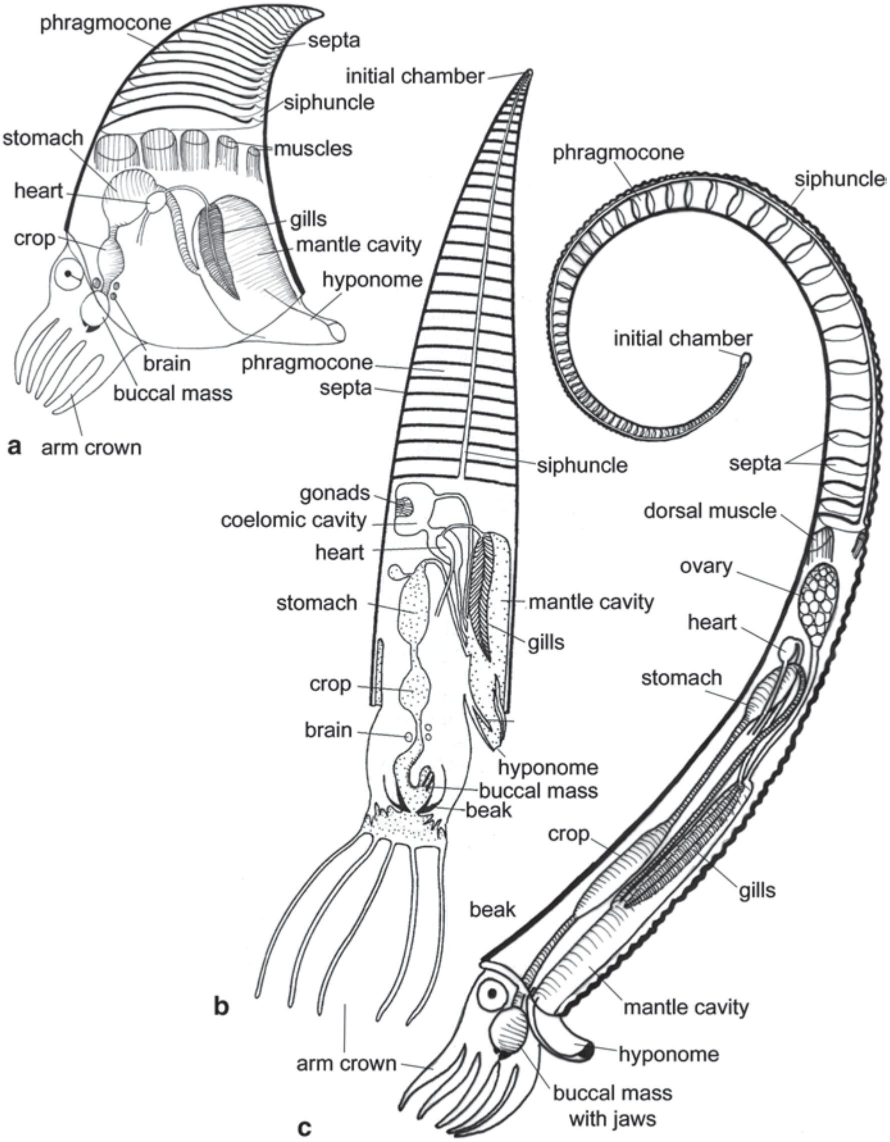

Fig. 1.2 Hypothesized Bauplan of **a** an ancestral cephalopod like *Plectronoceras* (based on Kröger 2007), **b** the HASC, modified after Engeser (1996) and **c** an ancestral ammonoid like *Metabactrites fuchsi* (De Baets et al. 2013b)

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

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

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

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

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

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

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

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

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

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

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

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

1.2.2 Position of the Bactritida and Ammonoidea

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

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

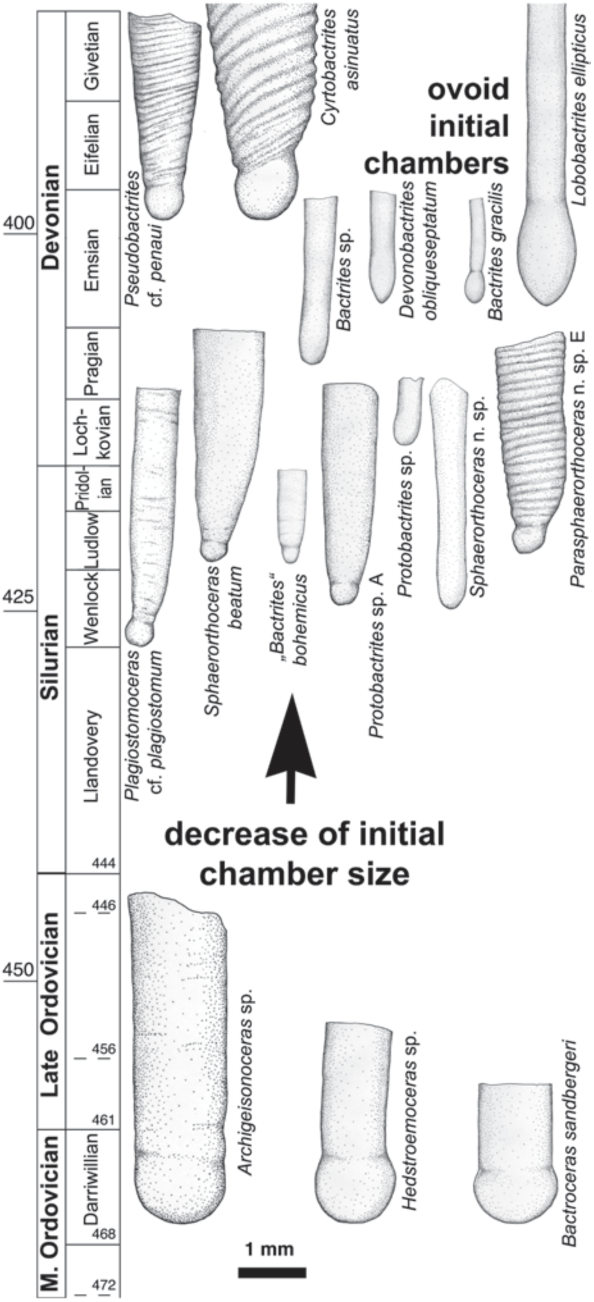

Fig. 1.3 Occurrences of embryonic shells of orthocerids and bactritids in the Paleozoic (modified after Kröger and Mapes 2007)

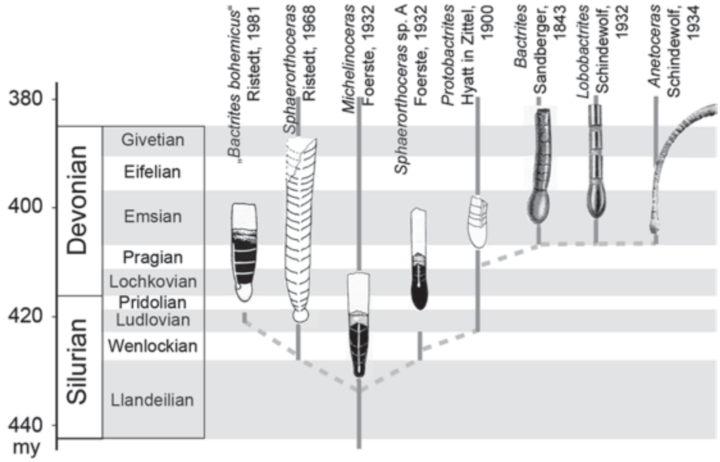

Fig. 1.4 Morphological changes of the embryonic shell around the origin of bactritids and ammonoids (modified after Kröger and Mapes 2007)

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

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

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

1.3 Origin of the Ammonoidea

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

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

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

1.3.1 Ammonoid Bauplan and the HASC

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

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

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

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

1.3.2 Early Evolution of Ammonoids

1.3.2.1 Morphological Changes

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

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

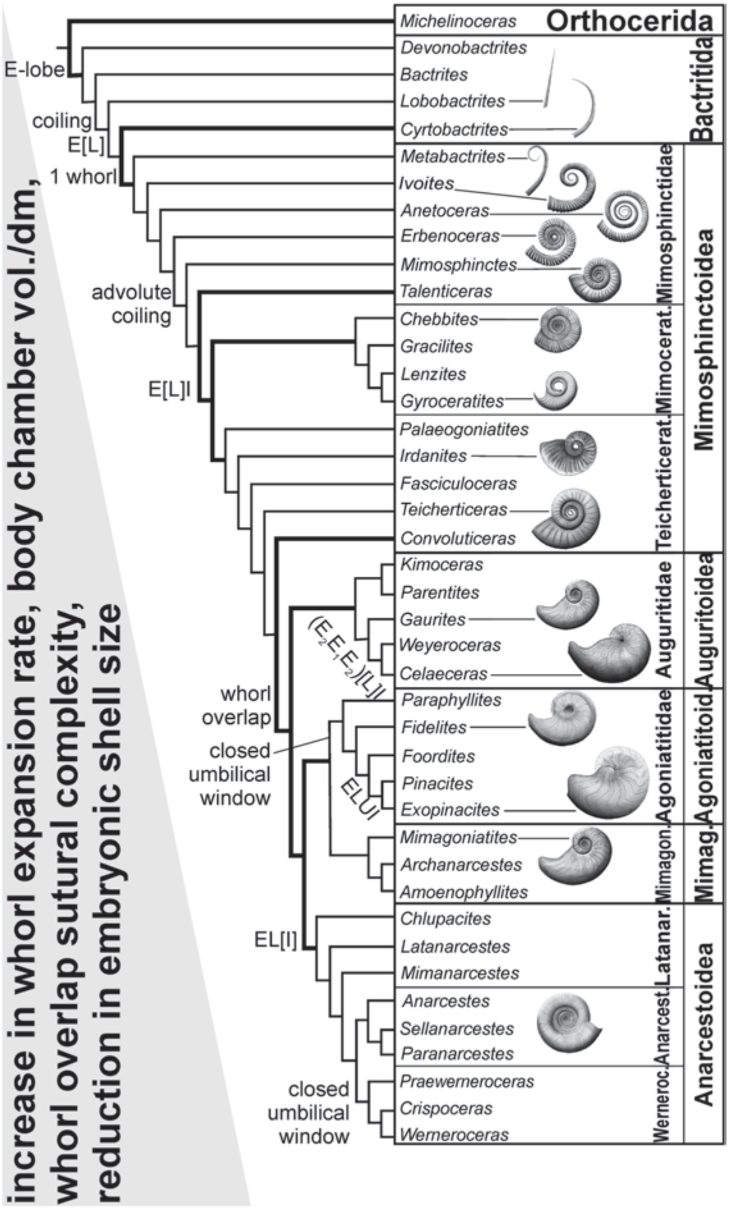

Fig. 1.5 Phylogeny of Emsian and Eifelian cephalopods, mainly based on Korn (2001) and Klug (2001b); compare Korn and Klug (2003)

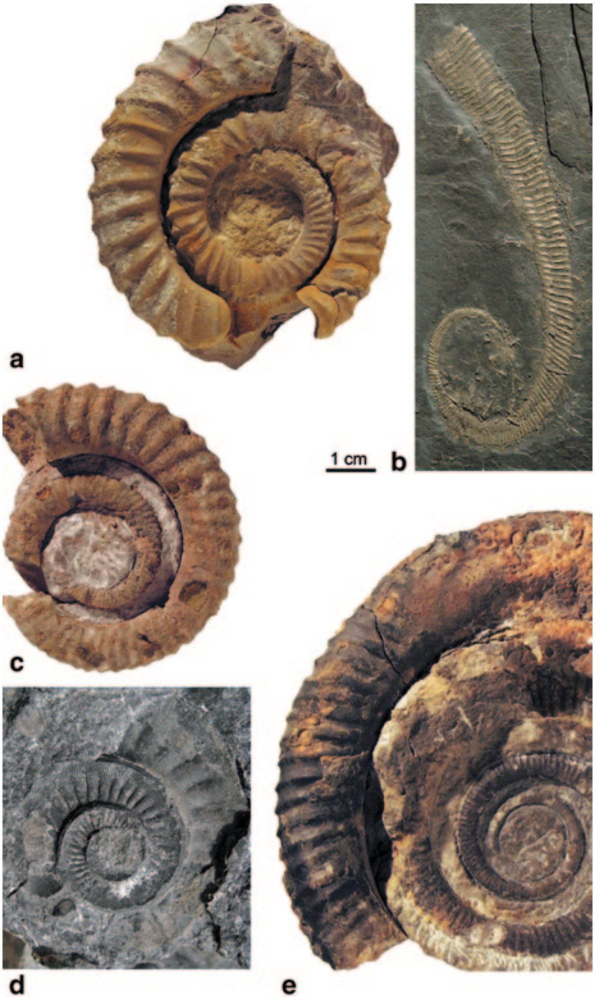

Fig. 1.6 Some ammonoids from the early Emsian, to illustrate morphological change early in ammonoid phylogeny. **a** *Erbenoceras solitarium*, GPIT 29789, Ouidane Chebbi, Morocco. **b** *Metabactrites fuchsi*, PWL2010/5251-LS, Bundenbach (Germany). **c** *Erbenoceras* cf. *solitarium*, GPIT 29806, Ouidane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

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

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

and Turek 1983; Bogoslovsky 1984; Klug 2001a, b; Klug and Korn 2002; Monnet et al. 2011; De Baets et al. 2013b).
3. Increase of the whorl height index from around 0.2 (e.g., in *Anetoceras* or *Erbenoceras*) to 0.5 (e.g., in *Celaeceras* or *Weyeroceras*; Klug 2001a, b; De Baets et al. 2010).
4. Increase in the ratio body chamber volume to diameter (Klug 2001a).
5. Initial decrease in the strength of ornamentation (De Baets et al. 2013b).
6. Increase in sutural complexity (Wiedmann and Kullmann 1980; García-Ruíz et al. 1990; Boyajian and Lutz 1992; Saunders and Work 1996; Daniel et al. 1997; Saunders et al. 1999; Gildner 2003; Ubukata et al. 2014).

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

1.3.2.2 Potential Consequences for the Mode of Life

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

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

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

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

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References

Bandel K (1982) Morphologie und Bildung der frühontogenetischen Gehäuse von conchiferen Mollusken. Facies 8:1–154

Becker RT, House MR (1994) International Devonian goniatite zonation, Emsian to Givetian, with new records from Morocco. Cour Forsch-Inst Senck 169:79–135

Bergmann S, Lieb B, Ruth P, Markl J (2006) The hemocyanin from a living fossil, the cephalopod *Nautilus pompilius*: protein structure, gene organization, and evolution. J Mol Evol 62:362–374

Bizikov VA (2008) Evolution of the shell in Cephalopoda. VNIRO, Moscow, pp 1–444

Bogoslovsky BI (1969) Devonskie Ammonoidei, I. Agoniatity. Trudy Paleont Zh 124:1–341

Bogoslovsky BI (1984) A new genus of the family Auguritidae and the ammonoids accompanying it from the Lower Devonian of the Zeravshan Range. Paleont J 1:30–36

Boletzky S von (2007) Origin of the lower jaw in cephalopods: a biting issue. Paläontol Z 81:328–333

Botting JP, Muir LA (2012) Fauna and ecology of the holothurian bed, Llandrindod, Wales, UK (Darriwilian, Middle Ordovician), and the oldest articulated holothurian. Palaeont Electronica 15:9A

Boyajian GE, Lutz TM (1992) Evolution of biological complexity and its relation to taxonomic longevity in the Ammonoidea. Geology 20:983–986

Brett CE, Walker SE (2002) Predators and predation in Paleozoic marine environments. Paleont Soc Pap 8:93–118

Brock GA, Paterson JR (2004) A new species of *Tannuella* (Helcionellida, Mollusca) from the Early Cambrian of South Australia. Mem Ass Aust Palaeont 30:133–143

Cecca F (1997) Late Jurassic and Early Cretaceous uncoiled ammonites: trophism-related Evolutionary processes. Earth Planetary Sci 325, 629–634

Chlupáč I, Turek V (1983) Devonian goniatites from the Barrandian area, Czechoslovakia. Rozpravy Ustředniho Ustavu geologickeho 46:1–159

Clausen CD (1969) Oberdevonische Cephalopoden aus dem Rheinischen Schiefergebirge. II. Gephuroceratidae, Beloceratidae. Palaeontogr A 132:95–178

Daniel TL, Helmuth BS, Saunders WB, Ward PD (1997) Septal complexity in ammonoid cephalopods increased mechanical risk and limited depth. Paleobiology 23:470–481

De Baets K, Klug C, Korn D (2009) Anetoceratinae (Ammonoidea, Early Devonian) from the Eifel and Harz Mountains (Germany), with a revision of their genera. N Jahrb Geol Paläont Abh 252:361–376

De Baets K, Klug C, Plusquellec Y (2010) Zlíchovian faunas with early ammonoids from Morocco and their use for the correlation of the eastern Anti-Atlas and the western Dra Valley. Bull Geosci 85:317–352

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) Evolutionary trends in ammonoid embryonal development. Evolution 66:1788–1806

De Baets K, Klug C, Monnet C (2013a) Intraspecific variability through ontogeny in early ammonoids. Paleobiology 39:75–94

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 299:1–114

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

Dzik J (1981) Origin of the Cephalopoda. Act Palaeont Pol 26:161–191

Dzik J (1984) Phylogeny of the Nautiloidea. Act Palaeont Pol 45:1–219

Dzik J (2010) Brachiopod identity of the alleged monoplacophoran ancestors of cephalopods. Malacologia 52:97–113

Engeser T (1990a) Major events in cephalopod evolution. In: Taylor PD, Larwood GP (eds) Major evolutionary radiations, Vol 42. Clarendon Press, Oxford

Engeser T (1996) The position of the Ammonoidea within the Cephalopoda. In Landman NH, Tanabe K, Davis RA (eds) Ammonoid Paleobiology. Plenum, New York

Erben HK (1960) Primitive Ammonoidea aus dem Unterdevon Frankreichs und Deutschlands. N Jahrb Geol Paläont Abh 110:1–128

Erben HK (1964a) Die Evolution der ältesten Ammonoidea. N Jahrb Geol Paläont Abh 120:107–212

Erben HK (1964b) Bactritoidea. In: Moore RC (ed) Treatise on Invertebrate Paleontology, Part K, Mollusca 3, Cephalopoda. GSA and the University of Kansas Press, Kansas, pp K491–K519

Erben HK (1965) Die Evolution der ältesten Ammonoidea (Lieferung II). N Jahrb Geol Paläont Abh 122:275–312

Erben HK (1966) Über den Ursprung der Ammonoidea. Biol Rev of the Cambridge Phil Soc 41:641–658

Evans DH (2005) The lower and middle Ordovician cephalopod faunas of England and Wales. Monogr Palaeontogr Soc 623:1–8

Firby JB, Durham JW (1974) Molluscan radula from earliest Cambrian. J Paleont 48:1109–1119

Frey L, Naglik C, Hofmann R, Schemm-Gregory M, Fryda J, Kröger B, Taylor PD, Wilson MA, Klug C (2014) Diversity and palaeoecology of Early Devonian invertebrate associations in the Tafilalt (Anti-Atlas, Morocco). Bull Geosci 89:75–112

Fuchs D (2006) Fossil erhaltungsfähige Merkmalskomplexe der Coleoidea (Cephalopoda)und ihre phylogenetische Bedeutung. Berliner paläobiol Abh 8:1–165

Gabbott S (1999) Orthoconic cephalopods and associated fauna from the late Ordovician Soom Shale Lagerstatte, South Africa. Palaeontology 42:123–148. doi:10.1111/1475-4983.00065

García-Ruíz JM, Checa A, Rivas P (1990) On the origin of ammonite sutures. Paleobiology 16:349–354

Gildner RF (2003) A Fourier method to describe and compare suture patterns. Palaeont Electron 6(1):1–12

Glaessner MF (1976) Early Phanerozoic annelid worms and their geological and biological significance. J Geol Soc London 132(3):159–215

Guex J (2006) Reinitialization of evolutionary clocks during sublethal environmental stress in some invertebrates. Earth Planetary Sci Lett 242:240–253

Holland CH (1987) The nautiloid cephalopods: a strange success. J Geol Soc 144:1–15

Holland B, Stridsberg S, Bergström (1978) Confirmation of the reconstruction of *Aptychopsis*. Lethaia 11:144

Horny R (1956) *Bojobactrites ammonitans* n. gen., n. sp. (Cephalopoda) from the Devonian of Central Bohemia. Sbornik Ústředntniho Ústavu Geologického. Oddíl paleontologicky 23:283–305

House MR (1988) Major features of cephalopod evolution. In: Wiedmann J, Kullmann J (eds) Cephalopods—present and past. Schweizerbart, Stuttgart

House MR (1996) Juvenile goniatite survival strategies following Devonian extinction events. Geol Soc London Spec Pub 102:163–185

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

Keupp H (2000) Ammoniten. Paläobiologische Erfolgsspiralen. Thorbecke, Sigmaringen

Klug C (2001a) Life-cycles of Emsian and Eifelian ammonoids (Devonian). Lethaia 34:215–233

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

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

Klug C, Korn D (2004) The origin of ammonoid locomotion. Acta Palaeont Pol 49:235–242

Klug C, Kröger B, Rücklin M, Korn D, Schemm-Gregory M, Mapes RH (2008a) Ecological change during the early Emsian (Devonian) in the Tafilalt (Morocco), the origin of the Ammonoidea, and the firs African pyrgocystid edrioasteroids, machaerids and phyllocarids. Palaeontogr A 283:1–94

Klug C, Meyer E, Richter U, Korn D (2008b) Soft-tissue imprints in fossil and recent cephalopod septa and septum formation. Lethaia 41:477–492

Klug C, Kröger B, Kiessling W, Mullins GL, Servais T, Frýda J, Korn D, Turner S (2010) The Devonian nekton revolution. Lethaia 43:465–477

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

Korn D (2001) Morphometric evolution and phylogeny of Palaeozoic ammonoids. Early and Middle Devonian. Acta Geol Pol 51:193–215

Korn D, Klug C (2002) Ammoneae Devonicae. Fossilium Catalogus 138. Backhuys, Leiden

Korn D, Klug C (2003) Morphological pathways in the evolution of Early and Middle Devonian ammonoids. Paleobiology 29:329–348

Korn D, Klug C (2012) Palaeozoic ammonoids—diversity and development of conch morphology. In: Talent J (ed) Extinction intervals and biogeographic perturbations through time: earth and Life (International Year of Planet Earth). Springer, Netherlands

Kröger B (2005) Adaptive evolution in Paleozoic coiled cephalopods. Paleobiology 31:253–268

Kröger B (2006) Early growth-stages and classification of orthoceridan Cephalopods of the Darriwillian (Middle Ordovician) of Baltoscandia. Lethaia 39:129–139

Kröger B (2007) Some lesser known features of the ancient cephalopod order Ellesmerocerida (Nautiloidea, Cephalopoda). Palaeontology 50:565–572

Kröger B (2008a) A new genus of middle Tremadocian orthoceratoids and the Early Ordovician origin of orthoceratoid cephalopods. Act Pal Pol 53:745–749

Kröger B (2008b) Nautiloids before and during the ammonoid origin in a Siluro–Devonian section of the Tafilalt (Morocco). Spec Pap Palaeont 79:1–110

Kröger B, Evans DH (2011) Review and palaeoecological analysis of the late Tremadocian–early Floian (Early Ordovician) cephalopod fauna of the Montagne Noire, France. Fossil Record 14:5–34

Kröger B, Lefebvre B (2012) Palaeogeography and palaeoecology of early Floian (Early Ordovician) cephalopods from the Upper Fezouata Formation, Anti-Atlas, Morocco. Fossil Record 15:61–75

Kröger B, Klug C, Mapes RH (2005) Soft-tissue attachment in Orthocerida and Bactritida of Emsian to Eifelian age (Devonian). Acta Palaeont Pol 50:329–342

Kröger B, Mapes RH (2007) On the origin of bactritoids. Paläontol Z 81:316–327

Kröger B, Servais T, Zhang Y (2009) The origin and initial rise of pelagic cephalopods in the Ordovician. PloS One 4 (9):e7262

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, Mapes RH, Pradel A (2014) New insights into the buccal apparatus of the Goniatitina: palaeobiological and phylogenetic implications. Lethaia 47:38–48

Kutscher E (1969) Die Ammonoideen-Entwicklung im Hunsrückschiefer. Notizbl Hess Landesa Bodenf 97:46–64

Landing E, Kröger B (2009) The oldest cephalopods from East Laurentia. J Paleontol 83:123–127

Landing E, Kröger B (2012) Cephalopod ancestry and ecology of the hyolith "*Allatheca" degeeri* s.l. in the Cambrian Evolutionary Radiation. Palaeogeogr Palaeoclim Palaeoeco 353:21–30

Lehmann J, Klug C, Wild F (2015) Did ammonoids possess opercula? Reassessment of phosphatised soft tissues in *Glaphyrites* from the Carboniferous of Uruguay. Paläontol Z 89:63–77. doi: 10.1007/s12542-013-0219-8

Mawson R (1987) Early Devonian conodont faunas from Buchan and Bindi, Victoria, Australia. Palaeontology 30:251–297

Mapes RH, Nützel A (2009) Late Palaeozoic mollusc reproduction: cephalopod egg-laying behavior and gastropod larval palaeobiology. Lethaia 42:341–356

Mazurek D, Zatoń M (2011) Is *Nectocaris pteryx* a cephalopod? Lethaia 44:2–4

Mehl J (1984) Radula und Fangarme bei *Michelinoceras* sp. aus dem Silur von Bolivien. Paläontol Z 58:211–229

Monnet C, Klug C, De Baets K (2011) Parallel evolution controlled by adaptation and covariation in ammonoid cephalopods. BMC Evolutionary biol 11(115):1–21

Mutvei H, Zhang Y-B, Dunca E (2007) Late Cambrian plectronocerid nautiloids and their role in cephalopod evolution. Palaeontology 50:1327–1333

Nixon M (1988) The buccal mass of fossil and recent cephalopoda. In: Clarke MR, Truman ER (eds) The Mollusca. Paleontology and neontology of cephalopods, vol 12. Academic, San Diego, pp 103–122

Ogura A, Yoshida M-A, Moritaki T, Okuda Y, Sese J, Shimizu KK, Sousounis K, Tsonis PA (2013) Loss of the six3/6 controlling pathways might have resulted in pinhole-eye evolution in *Nautilus*. Sci Rep 3:1432 (1–7)

Peel JS (1991) The classes Tergomya and Helcionelloida, and early molluscan evolution. Grønl Geol Unders Bull 161:11–65

Peterson KJ, Lyons JB, Nowak KS, Takacs C, Wargo MJ, McPeek MA (2004) Estimating metazoan divergence times with a molecular clock. PNAS 101:6536–6541

Pojeta J Jr (1980) Molluscan phylogeny. Tulane Studies in Geology and Paleontology 16:55–80

Raup DM (1967) Geometric analysis of shell coiling: Coiling in ammonoids. J Paleont 41:43–65

Ristedt H (1968) Zur Revision der Orthoceratidae. Akad Wiss Lit Mainz, Abh Math-Naturwiss Kl 1968:211–287

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. doi: 10.1111/jzo.12118

Runnegar B (2011) Once again: is *Nectocaris pteryx* a stem-group cephalopod? Lethaia 44:373–373

Sasaki T, Shigeno S, Tanabe K (2010) Anatomy of living *Nautilus*: Reevaluation of primitiveness and comparison with Coleoidea. In: Tanabe K, Shigeta Y, Sasaki T, Hirano H (eds) Cephalopods—present and past. Tokai University Press, Tokyo

Saunders WB, Shapiro EA (1986) Calculation and simulation of ammonoid hydrostatics. Paleobiology 12:64–79

Saunders WB, Work DM (1996) Shell morphology and suture complexity in Upper Carboniferous ammonoids. Paleobiology 22:189–218

Saunders WB, Work DM, Nikolaeva SV (1999) Evolution of complexity in Paleozoic ammonoid sutures. Science 286(5440):760–763

Shigeno S, Sasaki T, Moritaki T, Kasugai T, Kasugai T, Vecchione M, Agata K (2008) Evolution of the cephalopod head complex by assembly of multiple molluscan body parts: evidence from *Nautilus* embryonic development. J Morph 269:1–17

Shigeno S, Takenori S, Boletzky SV (2010) The origins of cephalopod body plans: a geometrical and developmental basis for the evolution of vertebrate-like organ systems. In: Tanabe K, Shigeta Y, Sasaki T, Hirano H (eds) Cephalopods—present and past. Tokai University Press, Tokyo

Smith MR (2013) Nectocaridid ecology, diversity, and affinity: early origin of a cephalopod-like body plan. Paleobiology 39: 297–321

Smith, MR, Caron J-B (2010) Primitive soft-bodied cephalopods from the Cambrian. Nature 465:469–472

Strugnell J, Jackson J, Drummond AJ, Cooper A (2006) Divergence time estimates for major cephalopod groups: evidence from multiple genes. Cladistics 22:89–96

Strugnell J, Nishiguchi MK (2007) Molecular phylogeny of coleoid cephalopods (Mollusca: Cephalopoda) inferred from three mitochondrial and six nuclear loci: a comparison of alignment, implied alignment and analysis methods. J Moll Stud 73:399–410

Teichert C (1948) Middle Devonian Goniatites from the Buchan District, Victoria. J Paleont 22:60–67

Turek V (1978) Biological and stratigraphical significance of the Silurian nautiloid *Aptychopsis*. Lethaia 11:127–138

Turek V, Marek J (1986) Notes on the phylogeny of the Nautiloidea. Paläontol Z 60:245–253

Ubukata T, Tanabe K, Shigeta Y, Maeda H, Mapes RH (2014) Wavelet analysis of ammonoid sutures. Palaeont Electron 17(1):9A (1–17 palaeo-electronica.org/content/2014/678-wavelet-analysis-of-sutures)

Ward PD (1979) Cameral liquid in *Nautilus* and ammonites. Paleobiology 5:40–49

Warnke KM, Meyer A, Ebner B, Lieb B (2011) Assessing divergence time of Spirulida and Sepiida (Cephalopoda) based on hemocyanin sequences. Mol Phylogenet Evol 58:390–394

Webers GF, Yochelson EL (1989) Late Cambrian molluscan faunas and the origin of the Cephalopoda. Geol Soc Lond Spec Pub 47:29–42

Wiedmann J, Kullmann J (1980) Ammonoid sutures in ontogeny and phylogeny. In: House MR, Senior JR (eds) The Ammonoidea. Academic Press, London

Witmer LM (1995) The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In: Thomason JJ (ed) Functional morphology in vertebrate paleontology. Cambridge University Press, Cambridge

Woodruff DS, Carpenter MP, Saunders WB, Ward PD (1987) Genetic variation and phylogeny in *Nautilus*. In: Saunders WB, Landman NH (eds) *Nautilus*, the biology and paleobiology of a living fossil. Plenum, New York

Woodward H (1885) On some Palaeozoic phyllopod-shields, and on *Nebalia* and its allies. Geol Mag 3:385–352

Yochelson E, Flower RH, Webers GF (1973) Bearing of new Late Cambrian monoplacophoran genus *Knightoconus* upon origin of Cephalopoda. Lethaia 6:275–309

Young RE, Vecchione M, Donovan DT (1998) The evolution of coleoid cephalopods and their present biodiversity and ecology. S Afr J Mar Sci 20:393–420