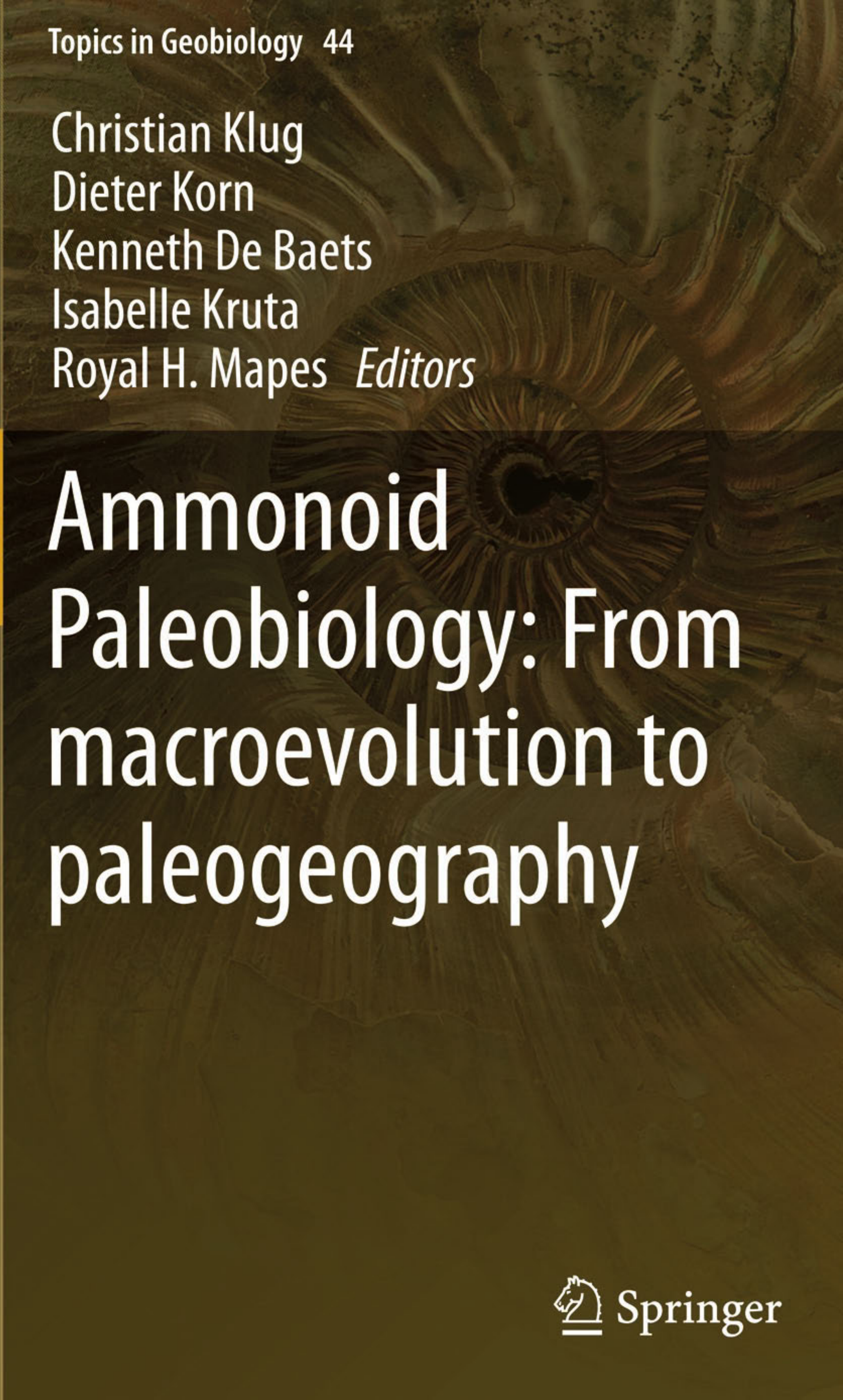

Topics in Geobiology 44

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

Ammonoid Paleobiology: From macroevolution to paleogeography

Springer

Topics in Geobiology

Volume 44

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

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

Christian Klug • Dieter Korn • Kenneth De Baets
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Editors

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Dedication

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

(24. February 1925 to
26. April 2014)

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

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

Seilacher (1989, p. 67)

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

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

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Foreword to the First Edition: Ammonoids Do It All

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

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

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

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

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

The American Museum of Natural History
New York, New York

Niles Eldredge

Foreword to the New Edition

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

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

Preface

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

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

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

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

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

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

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

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

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Part I
Macroevolution

Chapter 1
Ancestry, Origin and Early Evolution of Ammonoids

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

1.1 Introduction

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

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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

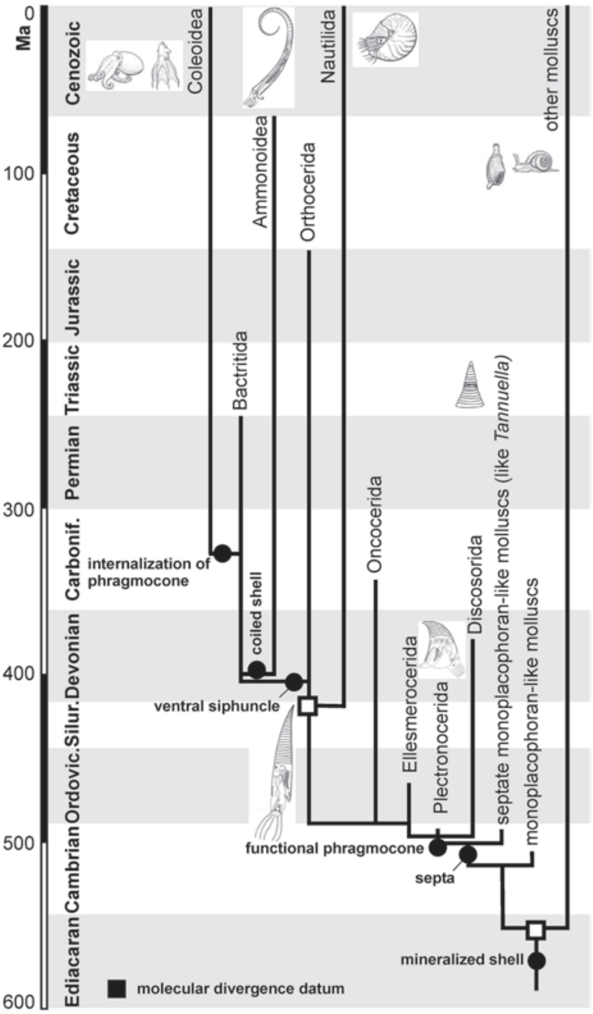

Fig. 1.1 Cephalopod phylogeny (modified after Kröger et al. 2011)

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-

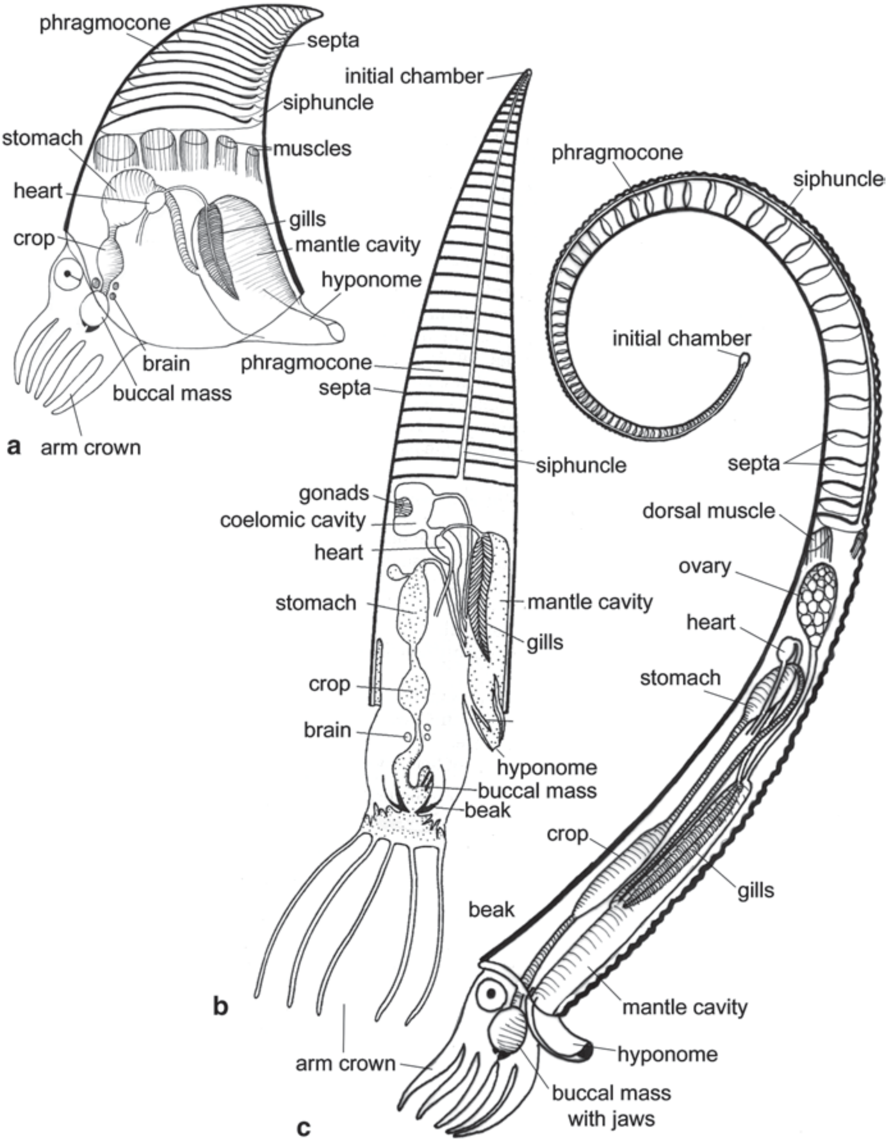

Fig. 1.2 Hypothesized Bauplan of **a** an ancestral cephalopod like *Plectronoceras* (based on Kröger 2007), **b** the HASC, modified after Engeser (1996) and **c** an ancestral ammonoid like *Metabactrites fuchsi* (De Baets et al. 2013b)

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).

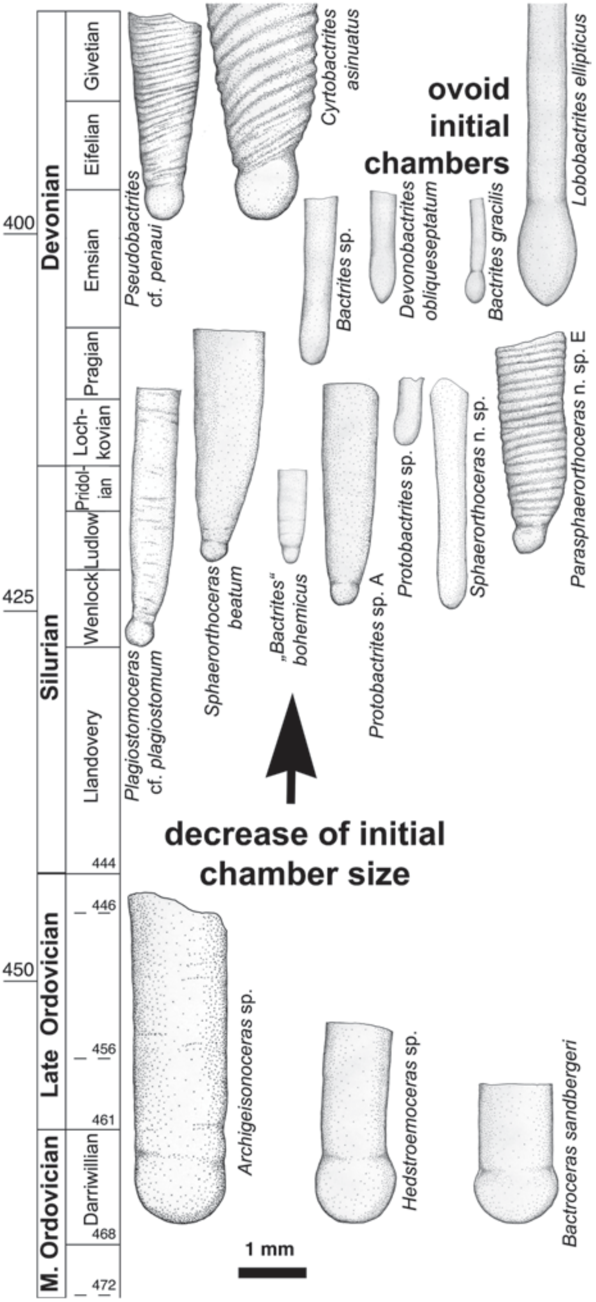

Fig. 1.3 Occurrences of embryonic shells of orthocerids and bactritids in the Paleozoic (modified after Kröger and Mapes 2007)