Journal of Paleontology

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Invited Article

Cite this article: Klug C., Hoffmann R., Rouget I., Pohle A., Rowe A.J., Fuchs D., Peterman D.J., Iba Y., Aubrechtová M., Kröger B., De Baets K., Tajika A., Kruta I., and Yacobucci M.M. 2026. Cephalopod paleobiology and evolution: new insights, rising problems, and perspectives. *Journal of Paleontology*, 1–23
https://doi.org/10.1017/jpa.2026.10256

Received: 28 February 2026 UTC
Revised: 11 April 2026 UTC
Accepted: 22 April 2026 UTC

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Guest Editor:
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Cephalopod paleobiology and evolution: new insights, rising problems, and perspectives

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Abstract

In times when science, including paleontology, is being questioned by some, the rising interest in the paleontology and paleobiology of the most intelligent invertebrates, namely cephalopods, may raise the hope for a brighter future. Here we provide an overview of some exciting fields in cephalopod research, where (in our biased opinion) the most impressive advances have been made. These are, in roughly stratigraphical order: the phylogeny of early cephalopods (using Bayesian approaches); the origin of ammonoids; functional morphology of ammonoids (using ammonoid robots, grinding tomography, finite element analyses); stable isotope geochemistry of Mesozoic–Cenozoic cephalopods; ammonoid reproduction (based on exceptionally preserved fossils and substantive fecundity estimates); ammonoid morphological evolution and biodiversity dynamics; early coleoid evolution (multispectral imaging, RTI); new coleoid systematics; coleoid anatomy (synchrotron, UV); coleoid diversity in the Cretaceous ("digital fossil mining," i.e., a system that excavates all fossils embedded in rocks through a combination of automated grinding tomography and artificial intelligence); food-web positions of various cephalopods (as prey or predator); and nautiloid evolution. Furthermore, we highlight some fields that require research focus and discuss threats and problems impacting research on fossil cephalopods.

Non-technical Summary

Today, cephalopods include octopuses, squids, cuttlefish, and pearly nautilus. In the geological past, numerous other groups of cephalopods existed, which have received quite some attention, partly because they were used to date rock layers. In recent decades, new discoveries were made, partially owing to the rapid development of new technologies such as tomography (synchrotron, CT, and by grinding specimens). Here we summarize recent developments concerning cephalopod origin and early evolution, origin of ammonoids, biology of ammonoids, geochemistry of cephalopod skeletons, ammonoid conch shape, evolution of octopus and squid ancestors and their systematics, diversity and anatomy, the ecological role in food webs, and the evolution of nautiloids. We also describe potential topics for future research and some problems that research on fossil cephalopods is facing.

Introduction

Cephalopod mollusks have a history of about half a billion years. Although there are currently 863 accepted living species (octobrachians: 321; decabrachians: 415; nautilids: 7; MolluscaBase, 2026), fossil species outnumbered them by at least one, but probably rather two or potentially even three, orders of magnitude. In addition, several cephalopod groups occurred in great numbers, which suggests that some of these extinct species produced a significant biomass not just as adults, but also as hatchlings; an estimate for a layer particularly rich in ammonoids was presented by Greif et al. (2022). Throughout their evolutionary history, cephalopods have played

an important ecological role as both predator and prey in marine food webs as they still do today, where their role is threatened by global changes (Piatkowski et al., 2001; Boavida-Portugal et al., 2022; Borges et al., 2023). Here we provide an overview of recent research and briefly discuss fields requiring research and problems that our research community encounters.

Materials

Since this is a review article, most materials presented here have been published before. Hence, no new materials were gathered, and no new permits were needed.

Repositories and institutional abbreviations. Specimens displayed in the figures are stored at the Muséum d'Histoire Naturelle in Paris (abbreviation: MNHN.F.) and in the Staatliches Museum für Naturkunde, Stuttgart (abbreviation: SMNS).

Phylogeny of early cephalopods

For several reasons, the opinions on early cephalopod evolution greatly differed between researchers. This is related to the origin of cephalopods themselves and to the phylogenetic relationships of the main early Paleozoic cephalopod groups. A considerable temporal gap exists between the earliest known unambiguous cephalopod occurrence (the latest Cambrian *Plectronoceras*; Kröger et al., 2011; Pohle et al., 2024) and estimates based on molecular analyses, which suggest an early Cambrian divergence date (Kocot et al., 2020; Song et al., 2023; Chen et al., 2025). Most candidate occurrences older than *Plectronoceras* have been shown to be either a stem chaetognath (Vinther et al., 2025) or a hyolith chimaera (Landing et al., 2023). It is worth considering that the oldest cephalopod (i.e., directly after the divergence from other mollusks) would not be recognizable as such as the molecular divergence dates allow no conclusions about the origin of diagnostic morphological structures.

For cephalopods, the unequivocal diagnostic character is the phragmocone, which may not have been present in the earliest members of the cephalopod lineage or in the lineage leading there. These mollusks would be difficult to distinguish from various Cambrian mollusks considered as possible cephalopod ancestors such as *Tannuella* or *Knightoconus* (Kröger et al., 2011).

The rapid diversification of cephalopods during the latest Cambrian and Early Ordovician led to a dramatic richness in forms and to an expansion in habits and habitats (Kröger and Zhang, 2009; Kröger et al., 2009). By the Late Ordovician, cephalopods reached peak diversities and disparities, especially in low-paleolatitude shallow-water environments (Kröger, 2013; Kröger, 2025).

The phylogenetic relationships and systematics of these early Paleozoic cephalopods were largely unresolved until a few years ago. Researchers of previous generations purported that fossil cephalopod taxa did not preserve enough characters for meaningful cladistic analyses (Neige et al., 2007). Furthermore, many of the characters that were preserved were typically homoplastic. Over the past two decades, however, several attempts have been made to apply new phylogenetic methods to cephalopods (Korn, 2001; Rouget et al., 2004; Monks, 2002; Cecca and Rouget, 2006; Kröger and Mapes, 2007; Yacobucci, 2012; Bardin et al., 2014, 2017a, 2017b; Fang et al., 2021; Kröger and Pohle, 2021; Pohle et al., 2022, 2025b; Stevens et al., 2023). Another problem is that the diversity of some of the earliest cephalopods from the late Cambrian of China was overestimated, partly on the basis of misoriented sections (Chen and Teichert, 1983); this led to an over-splitting on several systematic levels. The resulting confusion was clarified by comparing the Chinese material with the latest Cambrian specimens from Australia, which had partially silicified siphuncles (Pohle et al., 2024). Along with previous research (Mutvei et al., 2007; Mutvei, 2020), these specimens revealed that the siphuncle structure of plectronoceratids, the oldest cephalopods, is rather complex, and two-dimensional sections are challenging to interpret (Pohle et al., 2024).

Disagreement also existed over the phylogenetic meaning of morphological characters. While Mutvei (2015) relied entirely on siphuncular structures, King and Evans (2019) preferred to include muscle-scar patterns, and still other authors used the morphology of the embryonic shell and juvenile growth stages (Kröger and Mapes, 2007; Manda and Turek, 2019).

A major step in disentangling the evolutionary relationships of these groups was undertaken by Pohle et al. (2022), who assembled a large character matrix for Cambrian and Ordovician cephalopods. Using Bayesian inference and the fossilized birth–death model (Wright et al., 2022), they suggested a framework for higher-level phylogenetic relationships and classification. This resulted in the recognition of three major clades of early Paleozoic cephalopods: Endoceratoidea, Multiceratoidea, and Orthoceratoidea (Pohle et al., 2022). The Orthoceratoidea group is likely ancestral to coleoids (including ammonoids; see Hoffmann et al., 2022), while the origin of the Nautiloidea sensu stricto is most likely to be found within the Multiceratoidea, although an origin from the Orthoceratoidea may also be considered (King and Evans, 2019; Pohle et al., 2022). Further research is needed to clarify remaining uncertainties, in particular at the basal divergence between the major clades close to the Cambrian–Ordovician transition.

It will also be interesting to see how the increasing understanding of biomineralization of the conch (Immenhauser et al., 2016; De Baets and Munnecke, 2018), including cameral and endosiphuncular deposits (Turek and Aubrechtová, 2024; Pohle et al., 2025a; Peterman et al., 2026), fits within this phylogeny. Descriptions of additional material can only further improve this endeavor (Cichowolski et al., 2023; Aubrechtová and Korn, 2025; Fang et al., 2025; Kröger, 2025).

Understanding has also improved about the early Paleozoic origin (Manda and Turek, 2019; Turek and Manda 2026) and later "explosion" of diversity and disparity (Korn, 2025; Korn and Ghaderi, 2025) of the Nautiloidea. This group is important because, in the restricted sense (Pohle et al., 2022), it contains the single order Nautilida, including the only extant representatives, *Nautilus* and *Allonautilus.* An unresolved problem, however, is the existing gap between the oldest unambiguous occurrence of nautiloid fossils (Dzik and Korn, 1992) in the Devonian and the Silurian molecular divergence date (Kröger et al., 2011; Tanner et al., 2017; Uribe and Zardoya, 2017; Chen et al., 2025). A Silurian divergence would also imply that the Nautilida can have originated only from the Orthoceratoidea since the Multiceratoidea diverged at the latest during the Early Ordovician (Pohle et al., 2022). Nevertheless, more research using molecular clocks is needed as these studies typically contain wide uncertainty margins (±60 Myr in Kröger et al., 2011) and strongly depend on fossil calibrations and underlying model assumptions (Warnock et al., 2012; O'Reilly and Donoghue, 2016; Budd and Mann, 2024).

Origin of ammonoids

While the transition from orthoceratids via bactritids to ammonoids and coleoids started crystallizing in the literature much earlier (Schindewolf, 1935; Erben, 1964, 1965, 1966), a mix of new

discoveries, application of cladistic methods, and morphofunctional studies led to the emergence of a clearer and more coherent picture. Some important steps were the discovery of: (1) the oldest bactritids (Cichowolski and Rustán, 2017), (2) soft-tissue attachment structures in orthoceratids and bactritids (Kröger et al., 2005), (3) new early ammonoid faunas in Morocco (Klug, 2001; De Baets et al., 2010; Becker et al., 2019) and Uzbekistan (Kim et al., 2007; Naglik et al., 2019), as well as the revision of the Hunsrück Slate ammonoids (De Baets et al., 2013). On the basis of comparative anatomy, the phylogenetic transformations (Fig. 1) are now quite well understood (Kröger et al., 2005). It is also well documented that ammonoids rapidly explored the range of possible shapes during their initial radiation and that morphological disparity is partially decoupled from taxonomic diversity (Allaire et al., 2023, 2025).

In one of the first studies that applied cladistical methods to cephalopods, Korn (2001) focused on Devonian ammonoids and found some support for the following early groups: Agoniatitina (paraphyletic), Gephuroceratina (monophyletic), Anarcestina (paraphyletic), and Pharciceratina (monophyletic).

Korn and Klug (2003) and Klug and Korn (2004) examined the morphofunctional meaning of the evolutionary innovations that occurred in Early and Middle Devonian ammonoids (Fig. 1). Likely drivers for the transition from orthoconic, via cyrtoconic and gyroconic, to fully coiled conchs is the shift in aperture orientation from a vertically downward position to a horizontally upward position, the proximity of the hyponome's position transitioning from downward (below the center of mass), to oblique downward (at an angle below the center of mass), and finally to being aligned horizontally with the center of mass, as well as the increasing compactness of the conch (Tendler et al., 2015; Klug et al., 2016a).

Morphogenesis and functional morphology of the ammonoid phragmocone

The quintessential question in ammonoid research has always been about the evolution and function of the complexly frilled septa in derived ammonoids (Klug and Hoffmann, 2015). Many different explanations have been proposed, including, in no particular order: to increase hydrostatic strength of the phragmocone, to accelerate the chamber-emptying process by increasing the pellicle-covered wettable surface, to accommodate muscle attachment in the frills to operate a non-mineralized "pre septum" (Cartesian diver), to allow for faster phragmocone growth, to increase mechanical strength of the phragmocone against predation, and to optimize buoyancy regulation by accelerating the filling and emptying processes. This list might be incomplete, but it comprises the main ideas (more details and references are provided by Klug and Hoffmann, 2015). In the following discussion, we focus on only a few of these hypotheses because they have received some recent attention and new results have been published.

In a series of papers, Lemanis and co-authors (Lemanis et al., 2015, 2016; Lemanis and Zlotnikov, 2023) assessed the functional morphology of septa. While septa doubtlessly also served to withstand hydrostatic pressure, it is likely that other factors were more important in terms of enhancing positive selection for increased septal frilling. In their brilliant paper, Lemanis and Zlotnikov (2023) examined the mechanical properties of virtual models of phragmocone segments using finite element analysis (FEA). They convincingly demonstrated that complex ammonite septa were optimized to withstand point loads, a good indication that they protected the ammonoid phragmocone against damage by teeth or beaks of predators.

In contrast to mechanical hypotheses, a physiological function was explored in experiments by Peterman et al. (2021). These experiments used three-dimensional (3D) printed models to isolate the variables of septal complexity while holding septal spacing and chamber shape constant (Fig. 2). Furthermore, these experiments were conducted across scales, spanning a broad range of chamber sizes (whorl heights spanning 25 to 90 mm). These 3D-printed models demonstrate that more complex septa have increased capillary potential, readily accepting or holding droplets of liquid in the folded septal margins. Furthermore, the fractal-like scaling of ammonitic septa improves capillary potential across scales. That is, lower-order folds increase capillary potential in smaller chambers while higher-order folds increase capillary potential in larger chambers. These results suggest that septal complexity could have influenced the buoyancy regulation and/or growth of the conch by increasing fluid retention or chamber refill potential. However, more work is required to better understand these physiological mechanisms.

Since evolution can act only on structures that exist, the question for the origin of the complexity arises. The tie-point model by Seilacher (1975) suggested a link with muscle insertion in the frills. Self-organization was at play as suggested by self-similarity, especially in some of the more complex suture types. The viscous-fingering model of Checa and Garcia-Ruiz (1996) represented an incorrect analogy in their opinion (Lemanis and Zlotnikov, 2023). Another explanation was provided by Klug and Hoffmann (2015). They argued that the gradual ontogenetic increase in folding and frilling of ammonoid septa is best explained by a moderately stiff septal mantle, which keeps the shape of the preceding mineralized septum. Since the new septum had to cover a larger area, it had to grow outward and follow the inclination of the frills of the preceding septum. Like the leaf of a Lollo Rosso salad, the frilling intensified, eventually forming intensely folded sutures, especially in some Mesozoic forms. Tighter coiling and strong whorl overlap strengthened the effect (Monnet et al., 2011), hence the strongly folded septa in oxycones such as *Augurites*, *Celaeceras*, and *Pinacites* (as early examples) or *Pinacoceras*, *Ptychites*, and *Sphenodiscus* as Mesozoic examples.

Importantly, the discussion about ammonoid habitats is intimately linked with the question of whether the phragmocone was a buoyancy apparatus. Repeatedly, it was suggested that ammonoids were actually benthic, which is unlikely in the light of the steadily increasing (with rare evolutionary pseudo-inversions toward simpler septa) sutural complexity in ammonoids and the complete absence of ammonoid walking or crawling traces.

Grinding tomography (alternating grinding and scanning of specimens with subsequent segmentation of the image stack) yielded the first empirical data on ammonoid buoyancy. Naglik et al. (2016) and Tajika et al. (2015a, 2015b) reconstructed conchs of Devonian, Carboniferous, and Jurassic ammonoids. They quantified volumes and masses of the shell volume, gas volume, and body-chamber volume. They could demonstrate that, in the absence of chamber water, each examined conch would have been positively buoyant; like modern nautilids, they require some chamber liquid to attain neutral buoyancy. Furthermore, they established the positions of the centers of mass and buoyancy and thereby the resting position of the animal. As predicted by theoretical models presented in several seminal papers by Saunders and Shapiro (1986), Raup and Michelson (1965), and Raup and Chamberlain (1967), the conch orientation and hydrostatic stability depended on coiling and body-chamber

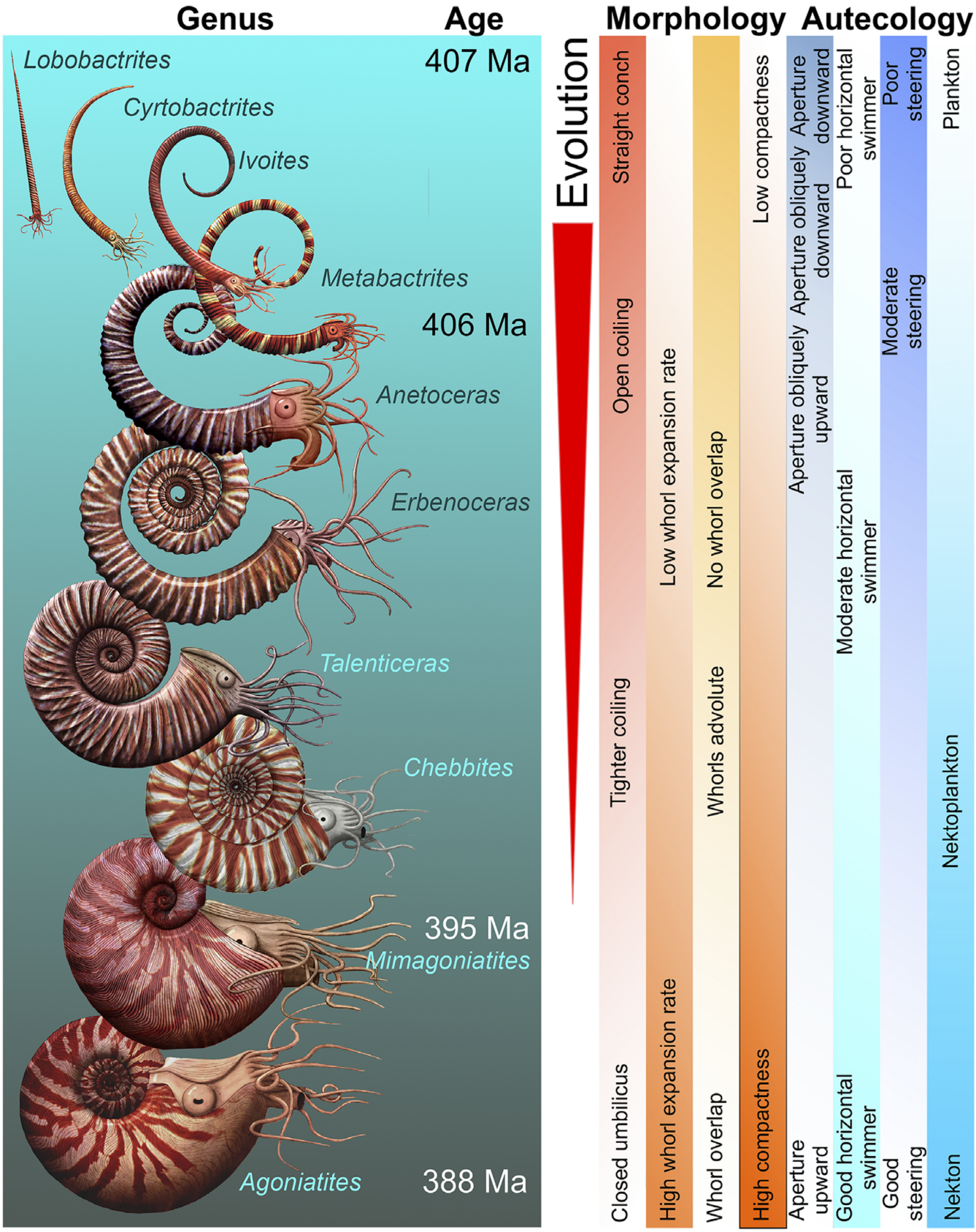

Figure 1. Morphological changes during the evolution from bactritids (top) to the first and slightly derived Devonian ammonoids and changes in ecology. Modified after Klug and Korn (2004).

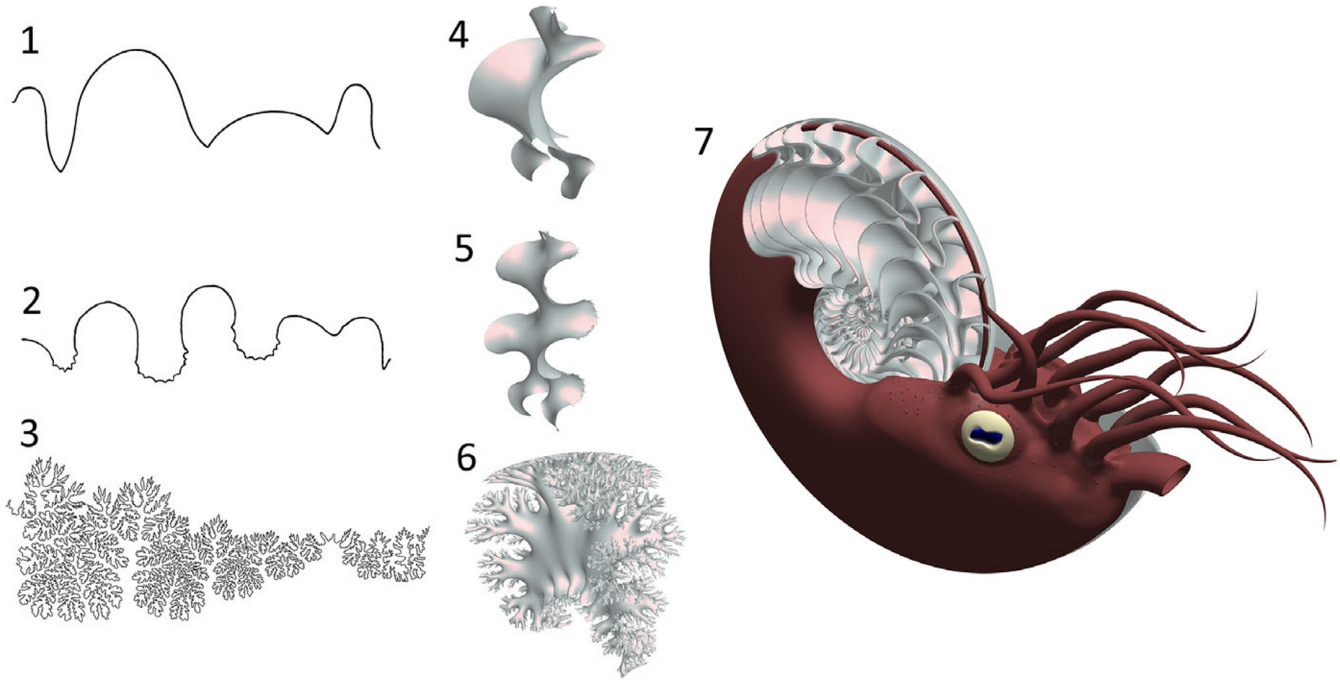

Figure 2. (**1–3**) Ammonoid suture patterns. (**4–6**) Septa. (**7**) Conch anatomy. (**1, 4**) Goniatitic suture pattern (**1**) and septum (**4**) of *Manticoceras* sp. (suture modified from Arkell et al., 1957). (**2, 5**) Ceratitic suture pattern (**2**) and septum (**5**) of *Xenaspis* sp. (suture modified from Arkell et al., 1957). (**3, 6**) Ammonitic suture pattern (**3**) and septum (**6**) of *Menuites oralensis* Cobban and Kennedy, 1993 (both modified from Peterman et al., 2021). (**7**) Reconstruction of *Manticoceras* sp. with half of the external shell removed to reveal internal contents (soft body and goniatitic septa).

length. Similar results were obtained for a Callovian *Cadoceras* hatchling using computed-microtomography. Lemanis et al. (2015) found that the hatchling had neutral to positive buoyancy with three to five chambers. Moreover, it was shown that the animal could also overcome negative buoyancy through swimming, similar to modern squid hatchlings, through hop–sink motion. This makes the hatching of approximately neutrally buoyant ammonites with three or fewer chambers likely. In this regard, it is interesting to note that many nektic and planktic animals are slightly negatively buoyant. These two approaches (grinding and computed tomography) are based on real shell and chamber dimensions instead of mathematical approximations and challenge former reconstructions of ammonite life habits. In addition, the calculations for *Cadoceras* support a planktic dispersal strategy of ammonite hatchlings (Lemanis et al., 2015).

The next step in this research was taken by the researchers Kathleen Ritterbush and David Peterman and their teams, who put a tremendous effort in creating virtual models and physical models, including free-swimming robots (Peterman et al., 2019b, 2020a, 2020b, 2025; Peterman and Ritterbush, 2021, 2022a, 2022b). Like the models produced by serial grinding and computed tomography, they constructed virtual models of cephalopod conchs purely from mathematical expressions of their coiling. These conch models were then populated with internal components (soft body, chamber liquid, and gas) to explore various functional constraints that acted on these once-living animals. Such models enable the calculation of various syn-vivo properties, including the conditions for neutral buoyancy, life orientation, hydrostatic stability, and how jet thrust was transmitted into directional movement. Using dense counterweights, physical models were produced to match these hydrostatic properties despite having different internal geometries and material properties (Peterman et al., 2020a, 2020b, 2025; Peterman and Ritterbush, 2021, 2022a, 2022b). Such models allow hydrodynamics to be explored alongside these hydrostatic constraints, enabling comprehensive analyses of the fundamental properties that govern swimming performance (Fig. 3). Some physical models were equipped with motorized water pumps, microcontrollers, and sensors to produce free-swimming, untethered robots (Peterman and Ritterbush, 2022a). These physical models and robots were chosen to represent some key ammonoid shell forms, namely the serpenticone, oxycone, sphaerocone, and cadicone conch morphologies. Their experiments revealed considerable differences in swimming performance between these different conch shapes. Specifically, these cephalopods encountered harsh physical tradeoffs between stability and maneuverability in both static and dynamic settings (Peterman and Ritterbush, 2022a, 2022b; Ritterbush and Hebdon, 2023). First-order conch morphology alone can produce differences in hydrostatic stability spanning about one order of magnitude and differences in turning maneuverability spanning half an order of magnitude (Peterman and Ritterbush, 2022a, 2022b). Subsequent experiments explored second-order conch morphology (i.e., various types of shell sculpture; Peterman et al., 2025). These more nuanced morphological characteristics were found to strongly influence the rocking of the cephalopods in the water. Coarser ribbing patterns progressively attenuated rocking motions. Intermediate forms were able to attenuate rocking without incurring extra hydrodynamic drag while swimming. Finally, the hydrodynamic efficiency of certain conch shapes across a biologically relevant range of sizes and speeds has been explored through fluid flow simulations (i.e., computational fluid dynamics; Hebdon et al., 2020a, 2020b, 2022; Peterman et al., 2025). Ultimately, these integrative approaches confirm that the morphological disparity displayed by ammonoids reflects a broad range of specializations, thereby explaining why these cephalopods

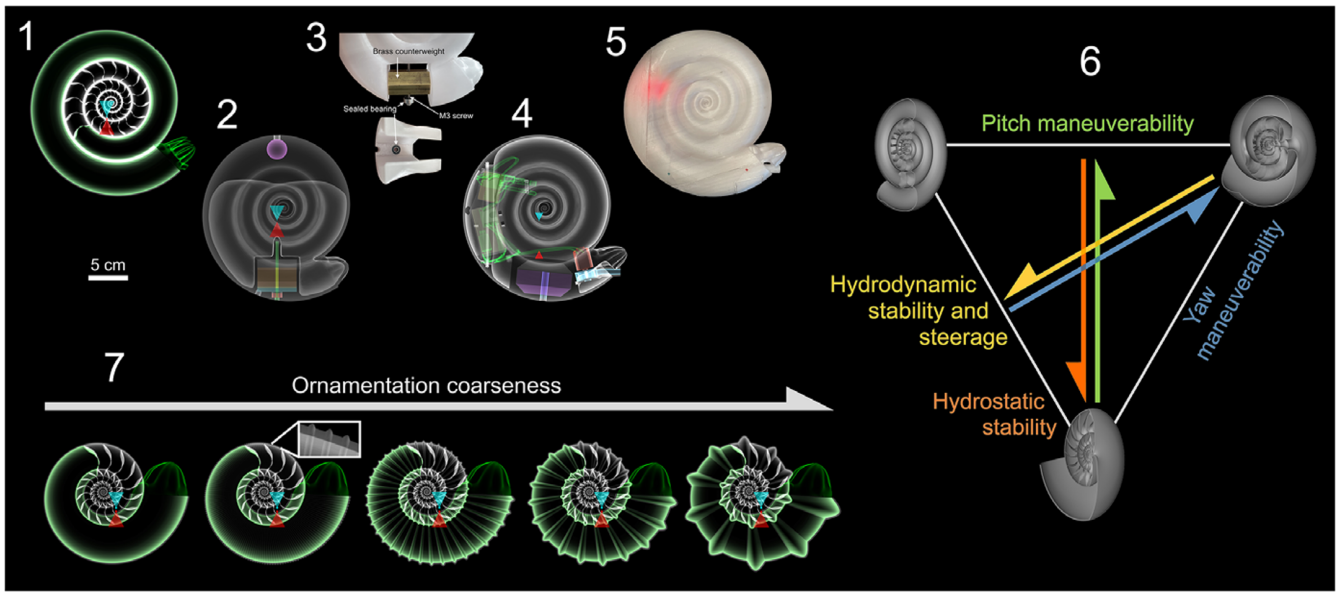

Figure 3. Virtual and physical biomechanical models of ammonoids. (**1**) Virtual hydrostatic model used to determine buoyancy, orientation, stability, and so on. (**2**) Schematic illustration of a physical model that matches the physical properties in (**1**). (**3**) Physical model weighted to produce the same hydrostatics as a living ammonoid. (**1–3**) Modified from Peterman and Ritterbush (2022b). (**4**) Schematic illustration of an ammonoid robot. (**5**) Self-propelling, untethered ammonoid robot. (**4, 5**) Modified from Peterman and Ritterbush (2022a). (**6**) Fundamental physical tradeoffs experienced by planispiral ammonoids (modified from Peterman and Ritterbush, 2022b). (**7**) Theoretical morphologies showing a continuum of increasing ornamentation coarseness and correspondingly increased rocking attenuation (modified from Peterman et al., 2025).

were so diverse, even within assemblages. These morphological expressions reflected lifestyle adaptations, including stability, maneuverability, passive and active orientation control, and swimming efficiency. This association also implies that some of the highly diverse ammonoid assemblages did not achieve their diversity by over-splitting but by a primary specialization of the various species.

Geochemistry of Mesozoic–Cenozoic cephalopods

Biogenic carbonate hard parts such as the aragonitic ammonite shell or the calcitic belemnite rostrum are regarded as archives or recorders of past environments and climates. From these archives, several proxy data can be extracted. Traditional proxy data are, for example, strontium-, carbon-, and oxygen isotopes or element-to-calcium ratios. Non-traditional proxy data are calcium, magnesium, nitrogen, lithium, or sulfur isotopes or the relatively new clumped isotope method (Immenhauser et al., 2016). An extensive overview on the application of stable isotopes to reconstruct ammonoid ontogeny and habitat was provided by Lukeneder (2015). Because calcite is the diagenetically more stable calcium carbonate polymorph, belemnite rostra are, by far, the most often used cephalopod archive material (Hoffmann et al., 2021a). However, interpretation of these proxy data can be complicated by (1) diagenetically overprinting, (2) unrecognized vital effects (maybe species specific) affecting specific proxy data, (3) petrographic microstructure of carbonate hard parts, and of specific interest, (4) migration pattern of mobile mollusks. For diagenesis screening techniques, required before conducting geochemical analyses, the reader is referred to Ullmann and Korte (2015).

For belemnite rostra, the degree of diagenetic alteration is difficult to assess since modern cephalopods do not produce comparable structures. Moreover, the biomineralization pathways are still poorly understood. In their thorough examination, Stevens et al. (2017) compared belemnite rostra with modern calcitic argonaut shells and revealed that both blueish and orange luminescence of growth increments could represent a primary (not diagenetic) feature in belemnite calcite. Evidence for vital effects affecting carbon and oxygen stable isotope signatures potentially due to a combination of metabolic and kinetic fractionation was presented in the same study. Comparable vital effects have been detected using the more advanced clumped isotope method in modern *Nautilus* and *Sepia* shell carbonate that is seemingly influenced by salinity changes of cameral fluid, dehydration of HCO_3^-, and/ or isotopic fractionation during CO_2 diffusion across cell walls (Davies et al., 2021). Therefore, this modern approach should be applied with caution to cephalopod hard parts. While hampering the reconstruction of paleoclimate, the geochemical composition of the rostra of different belemnite taxa can be used to reconstruct their paleobiology. In this regard, Pohle et al. (2025b) published a stimulating paper using Bayesian phylogenetic tools to test evolutionary constraints on element-to-calcium ratios, based on a phylogenetic tree established by Stevens et al. (2023). A strong taxonomic signal was found for Mg/Ca and Sr/Ca ratios, for which the term phylogeochemistry was coined. Again, this study highlights the interplay of evolutionary, ontogenetic, environmental, and diagenetic effects on biogenic proxy data.

For example, the recognition of a two-phase composition of belemnite rostra and high-resolution oxygen isotope data sampling revealed an offset between both phases of about 4‰, which would translate into a temperature difference of about 16°C in sample spots only 25 µm apart (Hoffmann et al., 2021a). This together with an observed temperature lead–lag signal of about 100 to 150 µm along a cross-section transect cast doubt on published temperature estimates based on belemnite calcite, which are sometimes cooler than values derived from contemporaneous benthic organisms (Veizer and Prokoph, 2015). Furthermore, Stevens et al. (2022) documented a range of microstructures (porous, organic-rich, or

fine-grained) from belemnite rostra that deserve consideration before geochemical analyses.

Interpretation of isotopic data derived from cephalopods is generally more difficult than from benthic organisms such as bivalves or brachiopods because the measured isotopic values combine both seasonal change and lateral or vertical migration pattern over the life of an individual in free-swimming cephalopods (Linzmeier, 2019). This complexity casts doubt on serial sampling (sclerochronology) as the sole growth chronometer in cephalopods, highlighting the need for other methods for age determination. In addition, the simple translation of reconstructed paleotemperatures to water depth could be misleading (Lukeneder, 2015). Therefore, Hoffmann et al. (2019), in a novel multi-proxy approach, combined oxygen isotope data with petrographic proxy data, here nacre table thickness of the septa named nacre-tablet-paleobathymetry, and Westermann morphospace to more accurately reconstruct ammonoid habitat depth. The study is based on cephalopods extracted from a singly sedimentary block (lower Albian, Madagascar) and comprising the nautiloid *Cymatoceras* as well as the ammonites *Cleoniceras*, *Desmoceras*, and *Eogaudryceras*. *Cymatoceras*, regarded as a vertical migrant, had a maximum habitat depth of 250 m and a mean habitat temperature of 20–21°C. Using geochemical criteria, *Cleoniceras*, *Desmoceras*, and *Eogaudryceras* with their platycone to planorbicone shell morphology share a demersal mode of life, with a maximum habitat depth of 450 to 500 m and water temperatures of 19–21°C for *Cleoniceras* and *Desmoceras* and a water depth of 525 m and water temperature of 14°C (deepest and coolest) for *Eogaudryceras*. Landman et al. (2018) successfully applied isotope sclerochronology to Late Cretaceous *Baculites* from methane seeps in the Western Interior Seaway. It was shown that *Baculites* lived at temperatures of 16 to 28°C. Furthermore, methane fluids significantly affected seawater chemistry and provided suitable habitats for ammonites. Regarding the ammonite life habit, they proclaim that, although ammonites were mobile animals, they probably exploited a low-energy mode of life, remaining at the same general vicinity for long periods. When exploring early cephalopod ontogeny on the basis of isotopes, the amount of shell material required for this method is too small to be practical. However, other special methods are useful, namely, ion microprobe stable isotope analyses. Due to the small quantities of shell material available, Linzmeier et al. (2018) applied the method to learn about early ontogenetic ammonite habitat and mode of life from *Hoploscaphites* specimens (Upper Cretaceous, Fox Hills Formation, South Dakota, USA). Because oxygen isotope ratios resembled those of benthic bivalves, the team supposed that *Hoploscaphites* laid its eggs on the seafloor. Hatchlings immediately migrated into shallower, warmer water masses. After approximately one whorl was completed, some individuals migrated back toward cooler water masses, potentially establishing a demersal mode of life.

Besides environmental or climate reconstructions, some proxy data, such as nitrogen or calcium isotopes, can be used to infer trophic levels. While an attempt to explore calcium isotope data shows no evidence for a significant control by trophic levels (e.g., lack of ontogenetic shift in *Nautilus*), nitrogen isotope data are promising in this regard (Hoffmann et al., 2021b). Note that the nitrogen isotope composition of biogenic carbonate reflects intercrystalline soluble organic matter. Nonetheless, nitrogen isotopes are known to be strongly affected during the decomposition of organic material, which renders their application to fossil shells difficult (Ohkouchi et al., 2013). On the basis of exceptionally well-preserved material, Ward et al. (2023) collected nitrogen data for extinct nautilids (*Aturia*, *Cimomia*, *Eutrephoceras*) as well as ammonites providing a first glimpse on their trophic positions, where nautilids may have had lower levels than ammonoids.

Ammonoid reproduction

Recently, ammonoid reproduction has been assessed in different ways. (1) Rock samples, with small ammonoids in rock-forming numbers, were prepared completely until only the ammonoids remained. This enabled an assessment of the number of individuals per rock volume and the estimation of the minimum number of ammonoids for the corresponding stratigraphic unit. (2) Fecundity estimates have been made by measuring body chamber volumes relative to ovary and embryonic conch (ammonitella) sizes in modern coleoids. (3) Exceptionally preserved soft tissues, specifically the reproductive organs, of two Late Jurassic ammonoids provided direct information on the sex of these ammonoids. In addition, one of the specimens helped to determine the fecundity of the species.

Greif et al. (2022) prepared 1,393 small ammonoids out of five rock samples from a stratigraphic unit in the Famennian (Late Devonian) in the eastern Anti-Atlas (1). Using estimates for the layer thickness and the surface area of these two small basins, they calculated that "the estimated numbers of ammonoids within the whole area with a layer thickness of 1000 mm is estimated to range from 30.9×10^{13} to 19.4×10^{14} ammonoids and an annual conch accumulation of 15.4×10^{9} to 97.1×10^{10}. The annual biomass ranges from 25,954 to 47,058 t" (Greif et al., 2022, p. 15). This is even more impressive when considering that these are likely low estimates and that these species attained only small adult sizes and therefore also had rather low offspring numbers. This study shows how important it is to assess abundances to get a better idea of aspects such as biomass in the fossil record.

After the origin of ammonoids, ammonitella size was quickly reduced by increasing coiling and closure of the umbilical window (2). Simultaneously, the ratio of body-chamber volume to conch diameter rose markedly. Assuming a constant ovary-to-body-chamber-volume proportion was maintained, an increase in fecundity was hypothesized. The estimates provided by De Baets et al. (2012) verified this hypothesis. From the earliest ammonoids to large Late Devonian forms, the reproductive rate (assuming semelparity) increased by at least three orders of magnitudes (from less than 100 to over 200,000). When applying the same metrics to more derived ammonites, such as the currently largest known species, *Parapuzosia seppenradensis* (Landois, 1895), the reproductive rates may have reached tens of millions (Tajika et al., 2018a). This large number of offspring is important because it identifies ammonoid juveniles as an important part of the small zooplankton from the Devonian to the Cretaceous.

Lastly, three exceptional fossils were discovered in the past decade that gave us direct insight into ammonite fecundity, sex, and reproduction. Unfortunately, the soft tissues of ammonoids have been documented from only a very small number of specimens. This is likely linked to various factors: (1) where preserved, the shell (independent of whether it is still aragonitic or recrystallized) can cover the soft body; (2) the chemical composition of the ammonoid body may be more prone to decay than that of, e.g., coleoids (Clements et al. 2017, 2022, 2026); (3) due to the often open marine habitat, ammonoid carcasses may have drifted for some time until the phragmocone was sufficiently waterlogged to sink (Yacobucci 2018), and during that time, decay and scavenging likely caused the partial or complete loss of soft parts. Soft tissues may also have been removed from the conch through predation

(Klug et al., 2021a, 2021d). Mironenko and Rogov (2016) presented a stunning example of an aragonitic adult female conch of the Aptian species *Sinzovia sazonovae*. In the posterior part of the body chamber, numerous minute ammonites are preserved, also in aragonite. Importantly, there are no signs of predation and most of them preserve their jaws in situ. Since their conch size slightly exceeds ammonitella size, Mironenko and Rogov (2016) proposed that these ammonites could have been ovoviviparous. Importantly, about 200 of these ammonite babies were present, providing a minimum fecundity estimate for this species (compare Tajika et al., 2018).

Later, Klug et al. (2021d) published a less beautiful but similarly interesting specimen from the Late Jurassic of the famous Konservat-Lagerstätte of Solnhofen. This specimen consists of fossilized soft tissues with the aptychus, which rendered a taxonomic assignment possible in the absence of the conch. The authors managed to identify most of the main organs; for example, one pair of gills confirms that ammonites were really dibranchiates. In addition, they could identify the male reproductive organs, which confirmed the assumption that microconchs were the males.

Some years later, another Solnhofen soft-tissue specimen turned up. This time, the imprint of the flattened conch was preserved, and several organs displayed details, which were then interpreted as various growth stages of embryonic conchs (Klug et al., 2025b). As in the case of the *Sinzovia* specimen, a count of the embryonic conchs permitted a fecundity estimate that ranges between 640 and about 50,000 eggs. Together with the more theoretical, size-based fecundity estimates, we can now estimate reproductive rates of ammonoids using the relation between their embryonic and adult conch sizes, with a maximum of 10 million eggs for the world's largest ammonite, *Parapuzosia*.

Evidence for reproductive strategies in fossil non-ammonoid cephalopods is even rarer. In one example, Pohle et al. (2020) suggested that at least some Devonian oncoceratids, which are presumably more closely related to *Nautilus* than they are to coleoids, had a semelparous lifestyle, because of frequent clustering in pairs. This implies that the evolution of reproductive strategies was complex, and the common assumption that ammonoids and coleoids share an r-strategy while all other cephalopods are K-strategists is likely too simple (Walton et al., 2010; Fuchs et al., 2020b), which aligns with the diversity of reproductive strategies seen among living cephalopods (Rocha et al., 2001; Vidal and Shea, 2023).

Ammonoid morphological evolution and biodiversity dynamics

Ammonoid cephalopods are renowned for their rapid rates of evolution and extinction, making them a model organism for exploring the processes governing morphological evolution, speciation, and extinction dynamics (Kennedy and Cobban, 1976; House, 1988; Page, 1996; Yacobucci, 2005, 2015, 2016; Brayard and Bucher, 2015; Monnet et al., 2015c; Neige and Rouget, 2015; De Baets, 2024; Korn et al., 2025; Neige and van Tiel, 2026). Allaire et al. (2025) demonstrated that this evolutionary volatility is seen even in the early radiation of ammonoids during the Devonian, and rates of biotic turnover remained high in most ammonoid groups up to their final demise at the end of the Cretaceous.

Ammonoid morphologies were constrained by functional, morphogenetic–developmental, and phylogenetic processes (Seilacher, 1970). Innovative new work on ammonoid functional morphology (described above) has shown that the range of ammonoid shell forms reflects adaptations to different locomotory styles and habitats. Numerous studies have documented linkages between shell shape, shell ornamentation, and sutural complexity, known as Buckman's rules of covariation, with most workers proposing that these correlations are due to constructional constraints on how ammonoids grow their shells (Monnet et al., 2015a; Erlich et al., 2016). These constraints have led to extensive homeomorphy in ammonoid shells, with similar shell forms evolving repeatedly (Monnet et al., 2011, 2015b; Bert et al., 2023). However, some ammonoid species show remarkable degrees of intraspecific variability (De Baets et al., 2015); there are even examples of right and left sides of the shell of a single ammonoid looking entirely different (Jattiot et al., 2019). Finding ways of addressing homeomorphy and intraspecific variability are ongoing challenges to conducting quantitative parsimony-based or Bayesian phylogenetic analyses on ammonoid clades (Neige et al., 2007; Yacobucci, 2012; Bardin et al., 2014).

Even considering some degree of oversplitting due to their stratigraphic utility, there is no question that ammonoid clades could rapidly produce many new species. Explanations for how and why ammonoids speciated so readily must integrate external factors (e.g., environmental fluctuations, formation of new habitats and their patchiness) with factors related to ammonoid paleobiology, such as their dispersal ability, reproductive strategies, and ability to generate morphological variations (Yacobucci, 2016). We know that ammonoids rapidly rediversified after mass extinctions, for example, filling Early Triassic seas when most other marine groups were still utterly decimated by the Permo–Triassic mass extinction event (Brayard et al., 2006; Nicholls et al., 2026). It is likely that these rapid radiations were at least partly driven by the availability of empty ecosystems in which new groups could evolve and persist. Yacobucci (2016) proposed a more general model for ammonoid speciation that linked the formation of shallow epicontinental seaways during times of sea-level rise with the inherent ability of ammonoids to easily generate new shell forms via developmental plasticity.

Just as with their rapid speciation, a variety of explanations have been proposed for why ammonoid species became extinct so readily. Old ideas about biological "senescence" have long been set aside, and it is likely that the drivers of extinction varied in different ammonoid groups and between background and mass extinction events. For example, recent work by Miao et al. (2024) has linked more-complex shell ornamentation in Jurassic and Cretaceous ammonoids with higher rates of both speciation and extinction, while Neige and van Tiel (2026) recently showed that increased ecological specialization, as reflected by morphological disparity, in the early Jurassic family Dactylioceratidae was followed by their (background) extinction. By contrast, Tajika et al. (2025a) found no strong relationship between intraspecific variation in shell form and stratigraphic range in several Late Cretaceous ammonoid species, and Raia et al. (2015) found that sutural complexity across 241 ammonoid genera was not strongly correlated with extinction resistance. Furthermore, Yacobucci (2017) and Flannery-Sutherland et al. (2024) both found that speciation and extinction patterns in Late Cretaceous ammonoids were quite spatially and temporally variable, all of which highlights the broad range of causal processes that could drive ammonoids to extinction. Other well-supported explanations for ammonoid extinction are their planktic pseudolarval stage early in ontogeny and their relatively high (at least compared with nautilid cephalopods) metabolic rate, requiring a robust planktic food web. These ties to planktic habitats may have doomed ammonoids during (or shortly after) the end-Cretaceous asteroid impact (Landman et al., 2014; Tajika et al., 2018, 2020a, 2023; Machalski et al., 2025).

Early coleoid evolution

The fossil record of coleoids is patchy, but it has also yielded some spectacularly preserved materials from the Carboniferous (Fuchs, 2006b, 2007; Fuchs et al., 2009, 2010, 2016, 2020a, 2021; Fuchs and Larson, 2011a, 2011b; Donovan and Fuchs, 2016; Clements et al., 2017, 2022, 2026; Klug et al., 2019, 2021b, 2023a, 2023b; Whalen and Landman, 2022). However, despite the wealth of anatomical information, misinterpretations can occur. For example, the supposedly oldest octobrachian has been recently re-identified as a nautilid (Clements et al., 2026). Similarly, for several specialists, the seemingly oldest vampyromorph, *Syllipsimopodi*, is likely a junior synonym of *Gordoniconus*, an important stem-coleoid (Klug et al., 2019; 2023b).

A re-investigation of the type material (Landman and Davis, 1988) and new specimens of *Gordoniconus beargulchensis* Landman and Davis, 1988 from Bear Gulch using state-of-the-art methods such as multispectral imaging, synchrotron, and reflectance transformation imaging revealed a series of new anatomical details, including the arm crown, the brain, and gills (or ovaries?; Klug et al., 2019). Importantly, this work provides a clear picture of an early coleoid, which still shares a lot of conch characters with bactritids such as the low apical angle, the small initial chamber and likely small embryonic conch, the simple dome-shaped septa, and the narrow ventral siphuncle. Remarkably, none of the specimens of this species preserves an ink sac. Klug et al. (2019) interpreted this as an indication for the following sequence of evolutionary events. First, the shell sac was retained during embryogenesis, which introduced one of the most important characters, the internal conch. Second, the endocochleate state implies that the mantle was exposed to predators and parasites. A secondary defense mechanism was needed, and soon thereafter, the first coleoids with ink sacs appeared (Mapes et al., 2010). Only later, the apical angle grew, and the rostrum, which was secreted from the now externally located mantle inward, became thicker and eventually started serving the function of a counterweight, enabling a horizontal body posture (Jenny et al., 2019). It is not clear when and how fins evolved (Fuchs, 2006b; Donovan and Fuchs, 2016; Klug et al., 2016c).

Coleoids became more abundant and diverse during the Triassic, which represents a crucial time during their evolution as the origin of the coleoid crown group is estimated during the Permian or Triassic, according to molecular clock estimates (Kröger et al., 2011; Tanner et al., 2017; Uribe and Zardoya, 2017; López-Córdova et al., 2022; Chen et al., 2025). Recent studies have documented a considerable diversity of Triassic coleoids, including aulacoceratids with an aragonitic rostrum (Niko and Ehiro, 2018), the oldest belemnites with calcitic rostra (Iba et al., 2012; Niko and Ehiro, 2022; Ma et al., 2023), rostrum-less phragmoteuthids (Lukeneder and Lukeneder, 2022; Lukeneder et al., 2024), and the enigmatic, similarly rostrum-less "mojsisovicsteuthid-group" with unknown affinities (Košťák et al., 2024; Lukeneder et al., 2024; Pohle and Klug, 2024).

New coleoid systematics

The classic system divided the Coleoidea into two subgroups: the extinct Belemnoidea (Paleocoleoidea) and the living Neocoleoidea. The arms of belemnoids carried hooks, and those of neocoleoids were equipped with suckers. This subdivision was challenged by discoveries of suckers associated with a pair of hooks in some belemnoid taxa (Fuchs et al., 2010). This inconsistency led contemporary workers to reactivate an older classification (Naef, 1922), which considered the hook-bearing orders Belemnitida and Diplobelida as stem groups of crown Decabrachia (Hoffmann et. al., 2022). The taxon Neocoleoidea is monophyletic only when Belemnitida and Diplobelida are included.

Further research on the coleoid soft-part morphology initiated by Bandel and Leich (1986) impacted another systematic issue. Mesozoic gladius-bearing taxa, earlier known as "fossil teuthids," were revealed to possess eight (rather than 10) arms. This insight supported by other characters such as the type of muscular mantle attachment led to an enormous diversity of octobrachians and simultaneously the seeming absence of squids in Mesozoic localities. Recently, Ikegami et al. (2025) could demonstrate the presence of a previously hidden diversity of decabrachians in the Cretaceous.

The Triassic was a time when stem coleoids (Aulacoceratida), stem neocoleoids (Phragmoteuthida), and crown coleoids (Belemnitida, Octobrachia) coexisted. The critical character in these taxa is the state of the body chamber. In aulacoceratids, it is cylindrical; in phragmoteuthids, it was ventrally reduced; and in belemnitids and octobrachians, even lateral shell walls were lost. Along with this gradual reduction of the body chamber (= development of a proostracum) goes a gradual decrease in mineralization peaked in a fully unmineralized gladius in the Octobrachia. Ventral and lateral shell parts were substituted by muscular mantle, which in turn enabled proostracum-bearing coleoids a significantly improved jet propulsion (Fuchs et al., 2016).

Coleoid anatomy

As mentioned, coleoid fossils from Konservat-Lagerstätten such as Holzmaden (Germany), La Voulte-sur-Rhône (France), Solnhofen with Eichstätt and Painten (Germany), and Haqel as well as Hadjoula (Lebanon) show stunning morphological details of the phragmocone and gladius, as well as soft-tissue anatomy (Donovan and Fuchs, 2016; Fuchs, 2016; Kruta et al., 2016; Rowe et al., 2022, 2024). While some of these features are visible to the naked eye, others have been revealed by a wide range of imaging techniques, including ultra-violet light, micro-X-ray fluorescence (μXRF) mapping, and high-resolution X-ray-based imaging techniques. We list only some examples here. The three-dimensionally preserved coleoids from the Callovian of La Voulte-sur-Rhône were examined using propagation phase contrast synchrotron X-ray microcomputed tomography (PPC-SR-μCT) at the European Synchrotron Radiation Facility (Kruta et al., 2016, Rowe et al., 2022, 2024; Klug et al., 2023a). Almost all major soft tissues are visible in the synchrotron imagery, including arm musculature, arm nerves, cirri, suckers with their ganglia, eyes, cephalic cartilages, digestive tracts, ink sacs, fins, and even bio-luminescent organs (Figs. 4–6). Holzmaden yielded new belemnites with soft tissues (Klug et al., 2021c) and vampyromorphs with their filaments (Klug et al., 2021b), musculature, and so on. The Fossillagerstätten in Lebanon delivered the best soft-tissue preservation of the Cretaceous age. Although preserved in two dimensions, fossils from Hjoula, Haqel, and Sahel Alma greatly benefit from advanced imaging techniques, including μXRF, ultraviolet light observation, and reflectance transformation imaging (Fig. 5). The abundant fauna of vampyromorphs show details of the arm crowns such as suckers, brachial nerves, and musculature. Furthermore, details of the eyes, the gills with the branchial hearts, components of the digestive system, and many other tissues have been documented (Fuchs, 2006a, 2006b, 2007; Fuchs and Weis, 2009; Fuchs et al., 2009, 2010, 2016, 2021; Fuchs and Larson, 2011a, 2011b;

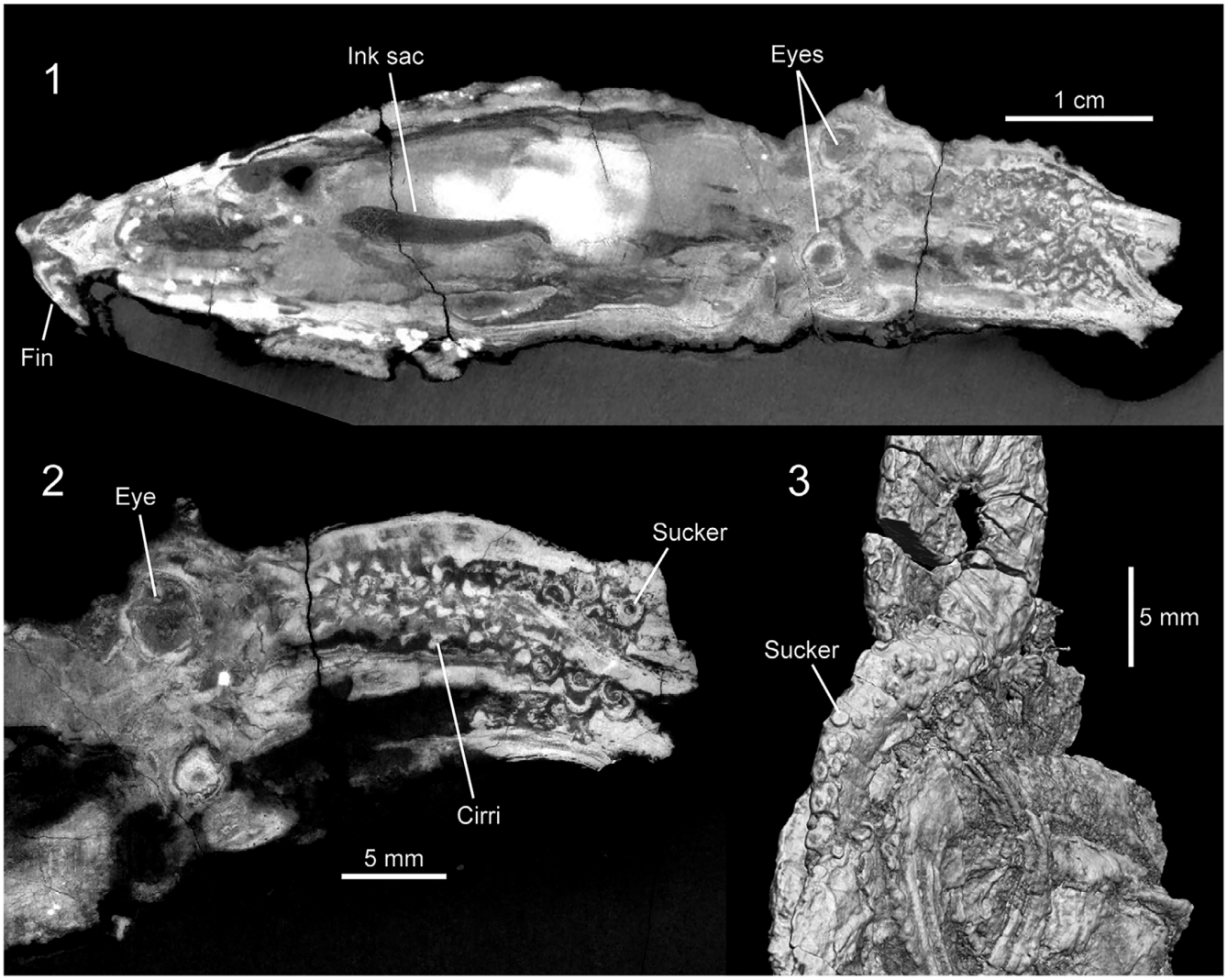

Figure 4. (**1, 2**) PPC-SR-μCT slices of *Vampyrofugiens atramentum* Rowe et al., 2023 (MNHN.F.A32491) from La Voulte-sur-Rhône: (**1**) binned dataset, voxel size 25, 28 μm); (**2**) close-up of cephalic region; binned dataset, voxel size 7 μm. (**3**) 3D rendering of the arms of *Proteroctopus ribeti* Fischer and Riou, 1982 from La Voulte-sur-Rhône (Kruta et al., 2016; supplementary material). PPC-SR-μCT scan data are available at http://paleo.esrf.fr/.

Jattiot et al., 2015; Lukeneder and Lukeneder, 2024; Rowe et al., 2025). The accumulation of data now enables the investigation of intraspecific variability in these gladius-bearing coleoid cephalopods and provides a stronger basis for assessing taphonomic biases affecting soft-tissue preservation (Donovan and Fuchs, 2016; Rowe et al., 2024, 2025).

More broadly, these technological breakthroughs represent a decisive step forward in our understanding of coleoid cephalopod evolution. They enhance access to knowledge of fossil soft tissues, enabling much more refined comparisons with extant coleoids. The implications extend well beyond descriptive insights: they shed light on the lifestyle and morphofunctional characteristics of fossil species and should, in the future, substantially improve phylogenetic reconstructions integrating both living and extinct coleoid taxa.

Evolution of modern-type coleoids in the Cretaceous

A recent study shed light on the diversity of non-belemnoid coleoids in the Cretaceous. Previously, this fossil record was limited to a few exceptionally preserved sites such as the Cenomanian of Lebanon (Naef, 1922). Decabrachians are absent from such sites because their high ammonia content inhibits calcium phosphate replacement (Clements et al., 2017). These limitations have long prevented decoding branching patterns of crown decabrachians and thus the evolutionary history of soft-bodied, modern-type cephalopods.

The workgroup of Yasuhiro Iba developed digital fossil mining, a system designed to excavate all fossils embedded in rocks through automated, high-resolution grinding tomography (Ezaki et al., 2023; Iba et al., 2025; Ikegami et al., 2025; Kubota et al., 2025 ; Takeda et al. 2026). In its latest development, zero-shot learning, artificial intelligence (AI) was integrated to enable training-free segmentation and unbiased extraction of fossils (Ikegami et al., 2026; Sugiura et al., 2026). Applying these approaches to whole-rock samples from the Cretaceous of Japan (Ikegami et al., 2025) and the USA (Sugiura et al., 2026), they recovered hundreds of coleoid jaws. Because coleoid jaws have high fossilization potential and are useful for taxonomic identification, they represent one of the few reliable keys to reconstructing the evolutionary history of soft-bodied groups (Tanabe et al., 2015b). Many of the recovered jaws were extremely small and fragile, making physical and

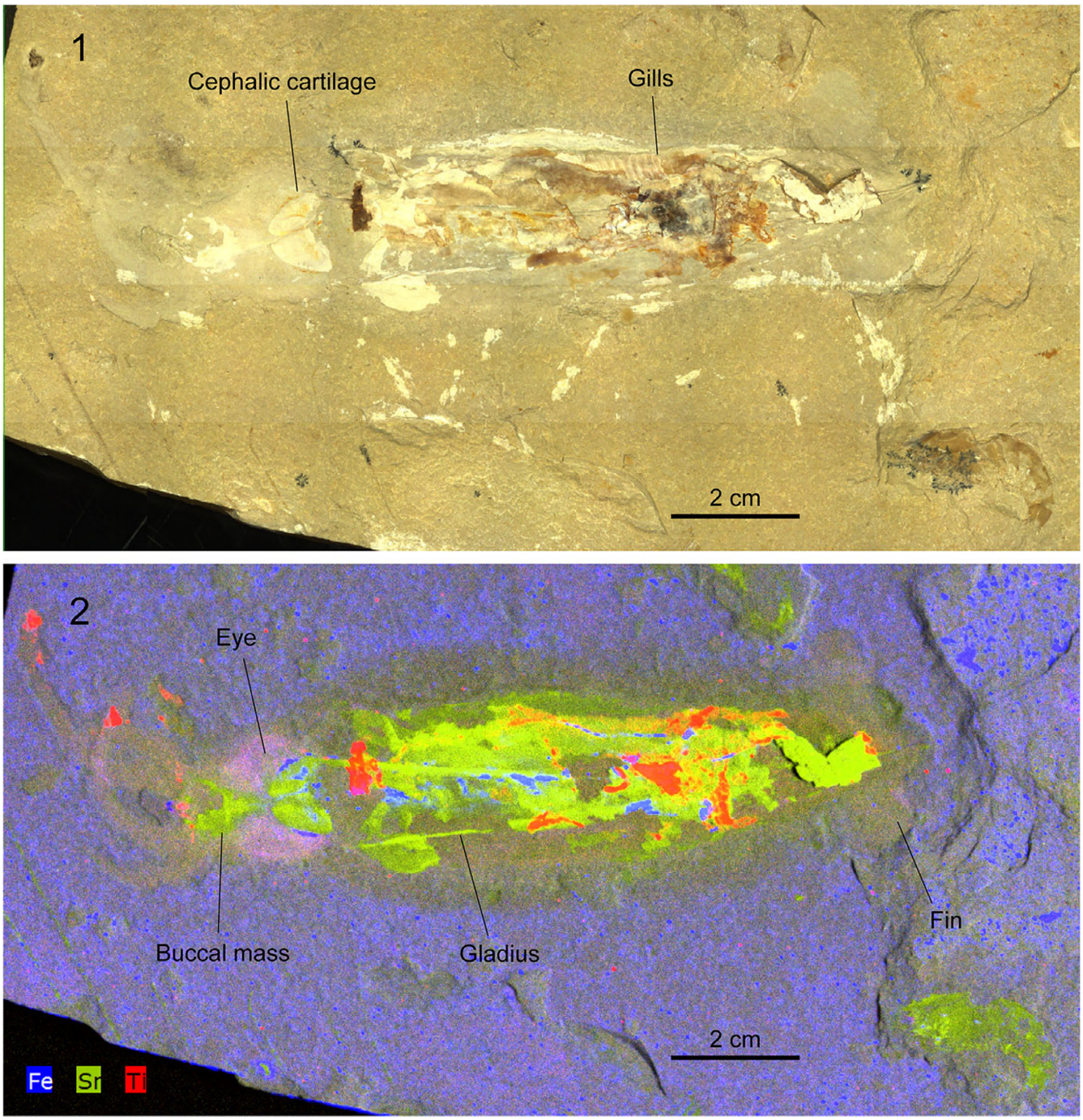

Figure 5. *Dorateuthis syriaca* Woodward, 1883 MNHN.F. 88589 from Hjoula, Cenomanian, Lebanon. (**1**) Overview. (**2**) μXRF overall of titanium (red), yttrium (green), and iron (blue) distribution (M6 Jestream Bruker XRF, UAR 3224 CRC, MNHN). See Rowe et al., 2024, 2025 for discussion.

chemical preparation nearly impossible, and other tomographic methods were ineffective due to low density contrast.

In these studies, more than 40 new species were introduced and assigned to various coleoid clades previously undocumented from the Cretaceous (Ikegami et al., 2025; Sugiura et al., 2026). The results indicate that squids (orders Oegopsida and Myopsida) originated at the Early/Late Cretaceous boundary in the Northwest Pacific (Ikegami et al., 2025), coinciding with regional belemnite extinction in the broader North Pacific (Iba et al., 2011). This temporal coincidence suggests a faunal turnover from shelled to derived soft-bodied coleoids (Ikegami et al., 2025). At least in the taphonomically controlled and high-resolution record of the Northwest Pacific, Late Cretaceous squids surpassed co-occurring ammonites and bony fishes in relative abundance and estimated body length, suggesting substantial biomass. As bony fishes and marine mammals radiated after the Cretaceous–Paleogene mass extinction, these findings suggest that squids were pioneers representing intelligent, fast-swimming predators that contributed to the emergence of the modern-type marine ecosystem (Ikegami et al., 2025). Studies comparing cephalopod statoliths with fish otoliths

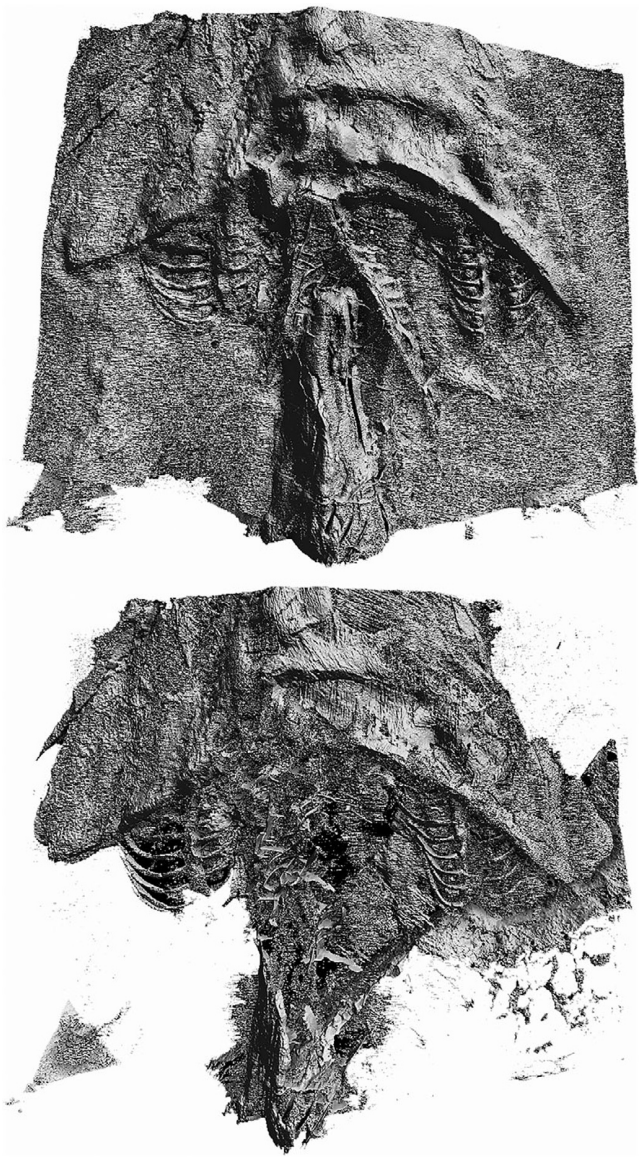

Figure 6. *Phragmoteuthis conocauda* (Quenstedt, 1846–1849), SMNS 61129, Toarcian, Holzmaden. In this specimen, the gills are well preserved. Computed tomography makes it possible to visualize such organs better. Top: rendering with sediment; bottom: only the soft parts.

have suggested a relative decline of stem-decabrachians, probably assigned to belemnites, from the Late Jurassic to the Early Cretaceous (Pindakiewicz et al., 2022, 2025). Together, the jaw and statolith records indicate that belemnite-dominant Jurassic faunas were followed by the rise of modern-type nekton, such as squids, in the Cretaceous. In this context, it is, however, worth mentioning that a recent study found supporting evidence for an older idea whereupon some lineages of belemnites may have survived until the Eocene (Galácz, 2026). A rapid mid-Cretaceous radiation of decabrachians was recently also documented by molecular clock estimates (Sanchez et al., 2026).

Food-web positions of various cephalopods

In recent years, trophic interactions have been documented for a series of cephalopods. These are predominantly from the Mesozoic. By contrast, Paleozoic interactions are known exclusively from healed shell breakages (Kröger, 2004; Keupp, 2012; Manda and Turek, 2025). Notably, no cephalopod beaks or soft-body remains are known from pre-Devonian cephalopods, despite intensive search in potential Lagerstätten with frequent cephalopod occurrences. Hence, reconstructions of early cephalopod feeding habits remain largely speculative and based on indirect evidence (Petermann et al., 2019a; Mironenko, 2020).

Of particular interest are examples of fossilized behavior where the prey animal is still preserved in the arm crown or mouth of the cephalopod. Recent work has also yielded independent evidence of predatory behavior from heavily worn fossil jaws. Most examples involve a coleoid.

Cephalopods as predators. Several Early Jurassic diplobelids have been described holding small bony fish in their arm crown, which is equipped with hundreds of pointy arm hooks (Hart et al., 2020; Jenny et al., 2019). Therefore, not only uniform hooks but specialized forms depending on their arm position have been developed. On the basis of elliptic Fourier shape analyses of the diplobelid *Chondroteuthis*, four different micro-hook morphotypes and their distribution within a single arm crown have been documented (Hoffmann et al., 2017). Smaller hooks were positioned close to the mouth and at the arm tips, while the largest hooks were found at the midarm region. In addition, arm-specific hook equipment was shown. Remarkably, even behavioral details are fossilized. For example, Jenny et al. (2019) provided evidence that the diplobelid first cracked the vertebral column to paralyze the fish during predation. Klug et al. (2021b) documented a case where a larger vampyromorph caught a smaller vampyromorph; the predator was possibly so excited about its success that it did not pay attention to water depth, sank into oxygen-depleted deeper water layers, and suffocated. Modern *Vampyroteuthis* has been recently shown to be at least in part a low-oxygen detritivore (Hoving and Robison, 2012; Gollikov et al., 2019), suggesting this mode of life may at least have been a post-Jurassic development if this is not opportunistic (Klug et al., 2021b; Košťák et al., 2021; Rowe et al., 2022). Ammonoids are generally accepted as secondary consumers feeding on primary consumers (i.e., micro- and mesozooplankton, 0.2–20 mm in size, microcarnivory; Kruta et al., 2011; Klug and Lehmann, 2015; Keupp et al., 2016; Hoffmann et al., 2021b).

New evidence from the Late Cretaceous expands the trophic roles known in cephalopods. Ikegami et al. (2026) documented extensive wear on the huge jaws of *Nanaimoteuthis*, a finned octopus of the suborder Cirrata. The wear includes chipping, scratches, and polishing, which caused substantial loss of the rostral tip and jaw edges. It was interpreted as the result of repeated crushing of hard prey. Digital fossil mining and AI for large-scale data visualization were also applied in this study. These approaches enabled the discovery of new jaws of Cirrata and a precise three-dimensional evaluation of wear patterns. Asymmetric wear on the jaw edges suggests lateralized behavior, which is related to advanced cognitive abilities. Body-size estimates indicate total lengths of approximately 7–19 m. These results suggest that some Cretaceous finned octopuses functioned as invertebrate top predators with body sizes and ecological roles comparable to those of coeval giant vertebrates.

Cephalopods as prey. Among ammonoids, indications for predation are often indirect, such as lethal or sublethal injuries. Already in 1960, Kauffman and Kesling unambiguously demonstrated that the pattern of tooth marks in an ammonoid shell was produced by the

mosasaur *Prognathodon*, and even pterygoid tooth marks could be identified (Kauffman, 2004). For example, a Middle Jurassic ammonite preserves the imprint of teeth that are quite characteristic, and a pycnodontiform fish could be identified as the culprit (Richter, 2009) although other predators cannot be ruled out entirely. Only on rare occasions can stomach contents help identify predators; for example, Keupp (2000) reported an ammonite lower jaw lying within the rib cage of a pycnodontiform fish, *Gyrodus*, from the Late Jurassic platy limestones of Solnhofen. Cooper and Maxwell (2023) described an ammonite conch in a Toarcian bony fish.

Two cases have been reported where the soft parts of ectocochleate cephalopods had been torn out of their conch and then possibly dropped by the predator accidentally. In both cases, this soft-body-only preservation enabled unique insights into the anatomy of Mesozoic cephalopods. The first case is a Late Jurassic ammonite (Klug et al., 2021d) whose soft parts were assigned to a perisphinctid on the basis of the aptychi that were still associated. This specimen displays the complete digestive tract and, importantly, the male reproductive organs, confirming that microconchs were the males. In addition, one pair of gills is preserved, corroborating the dibranchiate nature and closer relationship of ammonoids to coleoids rather than the superficially similar nautilids. The second case is a Cenomanian nautilid, which preserves a shadow of its eyes, the jaw, mantle musculature, and renal concrements (Klug et al., 2021a). These "kidney stones" serve as a calcium reservoir for the construction of new septa during growth (Ward et al., 2014).

Evidence of teuthophagous feeding strategies is common in the fossil record (Weis et al., 2024; Fischer et al., 2025 and literature therein). A quite spectacular specimen of *Plesioteuthis* from the Late Jurassic of Solnhofen preserves a tooth of the pterosaur *Rhamphorhynchus* in its mantle musculature (Hoffmann et al., 2020a). This confirms that the pterosaur hunted marine soft-bodied organisms that inhabited the upper part of the water column and correspondingly informs us about such a habitat for *Plesioteuthis*, a common squid from that region.

Both forms of digestichnia—regurgitalites and coprolites—bear additional information (Klug and Vallon, 2019). Some fossil oral ejecta (regurgitalites) from the Late Jurassic Solnhofen platy limestones were composed exclusively of calcified lower ammonite jaws (aptychi). These regurgitalites have been assigned to coleoids with an opportunistic diet by Hoffmann et al. (2020b), taking functional considerations, vomiting behavior, stomach fluid pH, and published reports on predator–prey relations into account. Cephalopod onychites (arm hooks) as well as an orthoceratoid shell were found in coprolites from the Lower Triassic of Spitsbergen attributed to fish and temnospondyls as well as ichthyopterygians (Simonsen et al., 2026).

Pathologies are, although indirect, a complementary approach to understanding the evolution of ecological interactions between cephalopods and their prey, pathogens, or competitors (Keupp et al., 2020; De Baets et al., 2022a).

Indirect evidence of predator–prey interactions has also been documented. Injuries to ammonoid body chambers have often been reported from the Mesozoic, and several authors have interpreted these as (sub-)lethal damage inflicted by crustaceans, coleoid cephalopods, and mosasaurs (Tsujita and Westermann, 2001; Klompmaker et al., 2009; Keupp, 2012, Takeda and Tanabe, 2014; Hoffmann et al., 2021c, Tajika et al., 2025b). There is the tendency for the shell wall of the phragmocone to preserve the outline of mosasaur teeth better than that of the body chamber, in agreement with the notion of the frilled septa having the function of supporting the shell wall (Lemanis and Zlotnikov, 2023). Jain et al. (2025) suggested a pliosaur as the culprit to have produced two large holes in the conch of a Jurassic nautilid.

Nautiloid evolution

Studies of extant nautiloids have provided a basis for understanding the ecology and evolution of extinct shelled cephalopods. Although an increasing number of genetic, ecological, and morphological studies on modern nautilids have been published over the past few decades (Combosch et al., 2017; Tajika et al., 2017, 2021, 2022a, 2022b; Tajika and Klug, 2020; Zhang et al., 2021; Barord et al., 2023; Doriath-Döhler et al., 2026), comparatively few studies have examined nautiloid paleobiology and evolution (Ward et al., 2026). Their ontogenetic trajectory of shell formation appears to have been conservative throughout nautilid evolution (Wani and Mapes, 2010; Tajika et al., 2020b). However, the factors controlling conch morphology remain unknown. In addition, although we have begun to understand the early evolution of ectocochleate cephalopods (Pohle et al., 2022), the systematics and taxonomic status of extinct and extant nautiloids remain largely unresolved (Ward et al., 2016). Geochemical evidence suggests that the basal metabolic rate of modern nautilids and some extinct taxa, such as the Cretaceous *Eutrephoceras*, was broadly similar to and lower than that of ammonoids and coleoids (Tajika et al., 2023). A recent paleogeographic study of *Nautilus* and its potential competitors suggests that the restriction of modern *Nautilus* to the Indo-Pacific was likely driven by the spread of pinnipeds during the Cenozoic, in combination with predation by short-snouted whales in the Oligocene (Kiel et al., 2022).

Future directions and unresolved questions

New methods to study cephalopod evolution are in development and are constantly being improved. A good example is computed tomography. Refined micro-synchrotron tomography is improving, allowing us to visualize structures that were impossible to see due to low contrast and other factors just a decade ago. The digital fossil-mining method enables researchers to perform all processes, from fossil discovery to analysis, in cyberspace. In this digital environment, segmentation enhanced by zero-shot-learning AI enables visualization of morphologies or taxa previously unknown (Sugiura et al., 2026). Virtual modeling methods have also significantly improved, which will be beneficial to study evolution, phylogeny, function, and ecology (Morón-Alfonso et al., 2020, 2021, 2024; Peterman et al., 2021, 2025).

Taxonomic revisions are urgently needed for most groups of fossil cephalopods. This is a daunting task given the many described taxa. Similarly, there are plenty of undescribed faunas, particularly when it comes to Paleozoic nautiloids and other non-ammonoid and non-coleoid cephalopods. Ammonoids are in some cases oversplit, especially since ontogenetic change has often been neglected in more historical studies. An improved understanding of intraspecific variation, including ontogenetic, sampling, and taphonomic aspects, is needed for such revisions to become meaningful and, in most cases, will result in a reduction of valid species (De Baets et al., 2013, 2015, 2022b; Weinkauf et al., 2021; Bert et al., 2023; Shigeta et al., 2025).

A more comprehensive phylogeny for cephalopods, including all major fossil lineages, is also sorely needed to understand their evolution and ecology. Achieving this goal is not straightforward given the different diagnostic traits and their varying preservation

within and between groups. This problem is nicely illustrated for the evolution of cephalopod body size (Klug et al., 2025a) where size estimates differ between the group and their common preservation. Size proxies, which may work well within particular lineages, such as the volume of the rostrum solidum within belemnites (Rita et al., 2019; De Baets et al., 2021; Nätscher et al., 2021), cannot be used across all cephalopods. On the basis of estimates on entire skeleton length and volume, Klug et al. (2025a) showed that maximum size increased in ammonoids and coleoids over their stratigraphic range, while patterns of nautiloids and orthoconic cephalopods differed. A more comprehensive and detailed phylogeny would help to test these patterns more explicitly, particularly within paraphyletic groups such as early externally shelled orthoconic cephalopods. In addition, finding how jaw size relates to body size may help to fill gaps in our knowledge of groups lacking skeletal representation (Tanabe et al., 2015a; Hoffmann et al., 2020b; Ikegami et al., 2025, 2026).

The integration of fossil constraints in divergence time estimates is also crucial to understand large-scale patterns in evolution (Barido-Sottani et al., 2023) but is not necessarily straightforward given the vastly different traits used, needed, or commonly preserved in different cephalopod lineages (externally shelled cephalopods versus coleoids; Paleozoic versus Mesozoic or Cenozoic externally shelled cephalopods). Traits range from soft-tissue characters preserved only under exceptional conditions (Clements et al., 2016) to shells or other biomineralized structures (e.g., statoliths; Neige et al., 2016) differing in composition between aragonite and calcite to more resistant organic remains such as jaw remains (Klug et al., 2016b) and onychites (belemnoid hooks; Hoffmann et al., 2017).

The application of Bayesian modeling approaches for testing phylogenetic hypotheses and estimating rates of character evolution, speciation, and extinction is rapidly growing within the paleontological community (Pohle et al., 2022; Wright et al., 2022; Stevens et al., 2023; Mulvey et al., 2025). As robust morphological datasets for fossil cephalopods are compiled, they can be combined with stratigraphic range to conduct Bayesian analyses that will help us test a variety of hypotheses, ranging from how fast and when different traits evolved to how rates of evolution and extinction correlate with climate and oceanographic perturbations. Adding paleobiogeographic data will allow us to test the relative importance of vicariance versus dispersal in cephalopod cladogenesis and connect phylogeography with ecology (Lamsdell et al., 2026).

Advances in additive manufacturing, miniaturization of electronic components, digital imaging, computer modeling techniques, and simulations will continue to reshape how we study functional morphology and paleoecology (Johnson and Carter, 2019; Johnson et al., 2022; Perricone et al., 2022; Ishida et al., 2024; Aish et al., 2025). In the past few decades, these approaches have become more sophisticated and accessible, enabling multi-disciplinary investigations of cephalopod biomechanics and their corresponding paleoecological constraints. Consequently, we highlight a few future directions that deserve more attention. The physics of swimming strongly depends on size and speed (Reynolds number: the ratio of inertial to viscous forces). While hydrostatic properties such as orientation and stability scale to any size, hydrodynamics (interactions with fluid) do not. This scale dependence is particularly relevant for understanding the ontogeny of ammonoids and other ectocochleates. Most planispiral cephalopods swam, partially or fully, in an intermediate Reynolds number regime (where neither inertial nor viscous effects can be neglected; Hebdon et al., 2020a, 2020b, 2022; Peterman et al., 2025). However, at earlier life stages, they occupied lower Reynolds number settings and gradually started to live life in this transition zone. Thus, ontogenetic changes in conch morphology may have impacted how these animals dealt with certain swimming constraints at different scales. Advances in smart materials such as magnetic elastomers (Lin et al., 2023) present new avenues to mimic cephalopod locomotion (i.e., compressive mantle cavities). Such materials can produce more life-like robots made of composite components. Advances in high-performance computing will continue to reduce simulation processing time, enabling higher throughput for biomechanical tools such as computational fluid dynamics (Rahman, 2017; Hebdon et al., 2020a, 2020b, 2022) and finite element analysis (Lemanis et al., 2015, 2016; Lemanis and Zlotnikov, 2023), among others. Advances in digital imaging and growing use of these techniques further valorize museum collections by increasing the availability of high-quality 3D morphological data. Such data can produce virtual and physical biomechanical models that closely resemble a particular specimen. Furthermore, large datasets can capture the morphological disparity across numerous taxa, informing the construction of theoretical morphologies while isolating specific variables of interest (Peterman et al., 2025). Last, extinct cephalopods have much potential in the growing field of paleobioinspiration (Ishida et al., 2024; Aish et al., 2025). The fossil record serves as a vast library of morphologies, with many forms absent in the modern biosphere. Throughout their evolutionary history, any group of aquatic animals has experienced similar functional constraints to those faced while designing aquatic vehicles. Ectocochleates may offer insight into the design of remotely operated underwater vehicles (ROUVs) with rigid bodies. Coleoid cephalopods (extinct and extant) have a complex arrangement of control surfaces that can be explored through soft robotics. Ultimately, cephalopod fossils play a key role in the investigation of fundamental questions in aquatic biomechanics. Such investigations synergistically identify constraints on the life habits and ecological roles of these enigmatic animals.

The morphogenetic development of incirrate and cirrate octopuses (in detail, the successive derivation of their gladius vestige from a teudopseid gladius during the Jurassic/ Cretaceous) is well understood (Fuchs et al., 2020a) while the origin of the decabrachian crown groups (hence the different decabrachian shell types) is still enigmatic, mainly because both morphological and phylogenomic analyses produced poorly supported resolutions at ordinal levels within the Decabrachia (Anderson and Lindgren, 2021). As a result, it is extraordinarily difficult to link Mesozoic decabrachians (Belemnitida, Diplobelida) with their descendants. Regardless, evidence suggesting that Spirulida and Sepiida, respectively, arise from longibelid and conoteuthid diplobelids directs our focus on the Diplobelida. Detecting the roots of myopsids and oegopsids will be one of our future challenges. Chronologically and geographically comprehensive documentation of jaw fossils, which strongly reflect the phylogenetic relationships of decabrachians, is expected to provide an alternative constraint for solving these problems (Ikegami et al., 2025; Sugiura et al., 2026).

Last, colleagues have often refrained from attempting to quantify cephalopod abundance in the fossil record. We feel that the fear of false results due to the incompleteness of the sedimentological record is, on the one hand, justified, but on the other, it has kept us from trying to create a database that at least approximates minimum values, such as those shown in the study by Greif et al. (2022). Relative abundance has been shown to be important to understand fluctuations in belemnite body size and diversity across the Pliensbachian–Toarcian crisis (Rita et al., 2019; De Baets et al., 2021). As the digital fossil-mining method can visualize all fossils inside rocks, it will provide precise, quantitative data on abundance, which can be

compared with that of other organisms (Iba et al., 2025). The more of this type of data we gather, the better our knowledge of both the minimum values and the error will get, and eventually we can attempt to quantify abundances more reliably, including biomass of certain taxa in certain regions through deep time.

Threats to cephalopod research

Funding for taxonomic work and science more generally is currently under threat around the world, and this disproportionally felt more among small disciplines such as paleontology (Smith et al., 2025). The impact of this reduced funding support could be counteracted by international and interdisciplinary collaborations and coordinated community efforts, as illustrated also for cephalopod research (Hoffmann et al., 2021a, 2021b; Pohle et al., 2022; Klug et al., 2025a; Sugiura et al., 2026; this paper). Nevertheless, fewer positions for fossil cephalopod researchers also poses big challenges for the long-term survival of our community. Research databases and novel methods have revolutionized our work and may make some aspects more efficient or feasible (De Baets, 2021; Foxon, 2021; Dowding et al., 2026; Sugiura et al., 2026), but they cannot replace work that is critically built on careful field, preparation, taxonomic, and collection endeavors and the innovative minds of researchers (Engel et al., 2021; De Baets, 2021, 2025; Ikegami et al., 2025; Takeda et al., 2026).

Conclusion

Over the past decades, cephalopod paleobiology has seen some remarkable advances, which is often linked with the progress of known methods (e.g., refined isotope analyses and imaging), the development of new methods, (e.g., clumped isotopes), or the application of methods developed in other research fields (e.g., computed tomography from medicine). In particular, computed tomography, synchrotron tomography, grinding tomography, and zero-shot-learning AI for segmentation have produced valuable datasets, which have significantly advanced our knowledge of aspects of certain groups, including anatomy, paleobiodiversity, and paleoecology. Ongoing excavations and fieldwork, as well as museum work, have also brought forth excellent materials that have furthered our knowledge.

While plenty of research questions remain open and possibilities are vast, our community is shrinking. We hope that our contribution will help stimulate new interest in the wonderful group of fossil cephalopods and our field will flourish again.

Acknowledgments. C.K., A.T., and A.P. received funding for cephalopod research from the Swiss National Science Foundation (project numbers 200021_113956, 200021_14911, 200021_169627, 3200-0-242879). A.T. received additional funding from the Japan Society for the Promotion of Science (KAKENHI; project numbers 21K14028, 22KJ0493, 23K26977, 24K17158). For the coleoid anatomy section, we acknowledge the ESRF for the provision of synchrotron radiation facilities (proposal ES36) and thank P. Tafforeau (Grenoble) for assistance with Beamline ID19, as well as D. Germain (CR2P) for his help during the acquisition session. We thank S. Charbonnier (Paris) and P. Abi Saad (Byblos) for providing the specimen MNHN.F.A88589, and M. Radepont and O. Belhadj (Paris) for the µXRF acquisition (UAR 3224 CRC, MNHN) of this specimen, supported by the Paris Île-de-France Region (DIM PAMIR – IDF DIM PAMIR-2023-4-028). We also thank A. Doriath-Döhler and R. Piguet-Ruinet (Paris) for their initial investigations of the specimen and A. Lethiers (UMR CR2P) for assistance in producing the figures. For the evolution of modern-type coleoids section, Y.I. received funding from the Japan Society for the Promotion of Science (project numbers 23K17274, 25K22459, 26K00821). We were very pleased by the highly positive and benevolent reviews of R. Lemanis (Bonn) and C.J. Tsujita (London, Ontario).

Competing interests. The authors declare none.

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