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Recent advances in heteromorph ammonoid palaeobiology

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ABSTRACT

Heteromorphs are ammonoids forming a conch with detached whorls (open coiling) or non-planispiral coiling. Such aberrant forms appeared convergently four times within this extinct group of cephalopods. Since Wiedmann's seminal paper in this journal, the palaeobiology of heteromorphs has advanced substantially. Combining direct evidence from their fossil record, indirect insights from phylogenetic bracketing, and physical as well as virtual models, we reach an improved understanding of heteromorph ammonoid palaeobiology. Their anatomy, buoyancy, locomotion, predators, diet, palaeoecology, and extinction are discussed. Based on phylogenetic bracketing with nautiloids and coleoids, heteromorphs like other ammonoids had 10 arms, a well-developed brain, lens eyes, a buccal mass with a radula and a smaller upper as well as a larger lower jaw, and ammonia in their soft tissue. Heteromorphs likely lacked arm suckers, hooks, tentacles, a hood, and an ink sac. All Cretaceous heteromorphs share an aptychus-type lower jaw with a lamellar calcitic covering. Differences in radular tooth morphology and size in heteromorphs suggest a microphagous diet. Stomach contents of heteromorphs comprise planktic crustaceans, gastropods, and crinoids, suggesting a zooplanktic diet. Forms with a U-shaped body chamber (ancylocone) are regarded as suspension feeders, whereas orthoconic forms additionally might have consumed benthic prey. Heteromorphs could achieve near-neutral buoyancy regardless of conch shape or ontogeny. Orthoconic heteromorphs likely had a vertical orientation, whereas ancylocone heteromorphs had a near-horizontal aperture pointing upwards. Heteromorphs with a U-shaped body chamber are more stable hydrodynamically than modern *Nautilus* and were unable substantially to modify their orientation by active locomotion, i.e. they had no or limited access to benthic prey at adulthood. Pathologies reported for heteromorphs were likely inflicted by crustaceans, fish, marine reptiles, and other cephalopods. Pathologies on *Ptychoceras* corroborates an external shell and rejects the endocochleate hypothesis. Devonian, Triassic, and Jurassic heteromorphs had a preference for deep-subtidal to offshore facies but are rare in shallow-subtidal, slope, and bathyal facies. Early Cretaceous heteromorphs preferred deep-subtidal to bathyal facies. Late Cretaceous heteromorphs are common in shallow-subtidal to offshore facies. Oxygen isotope data suggest rapid growth and a demersal habitat for adult *Discoscaphites* and *Baculites*. A benthic embryonic stage, planktic hatchlings, and a habitat change after one whorl is proposed for *Hoploscaphites*. Carbon isotope data indicate that some *Baculites* lived throughout their lives at cold seeps. Adaptation to a planktic life habit potentially drove selection towards

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smaller hatchlings, implying high fecundity and an ecological role of the hatchlings as micro- and mesoplankton. The Chicxulub impact at the Cretaceous/Paleogene (K/Pg) boundary 66 million years ago is the likely trigger for the extinction of ammonoids. Ammonoids likely persisted after this event for 40–500 thousand years and are exclusively represented by heteromorphs. The ammonoid extinction is linked to their small hatchling sizes, planktotrophic diets, and higher metabolic rates than in nautilids, which survived the K/Pg mass extinction event.

Key words: cephalopods, heteromorph ammonoids, palaeobiology, anatomy, geochemistry, facies distribution

CONTENTS

I. INTRODUCTION

Heteromorphs are ammonoids that are defined by detached whorls (open coiling) or non-planispiral coiling, and thus deviate from the monomorph bauplan. The oldest mention of the term 'heteromorph' in relation to ammonoid shell shape that we could identify is in Whitehouse (1926). Heteromorphy may occur at any growth stage and can be expressed throughout ontogeny or be restricted to a single or a few growth stages (*cf.* Wiedmann, 1969). Ammonoids with modified apertures or angular coiling at the very end of their body chambers due to morphogenetic countdown (*sensu* Seilacher & Gunji, 1993) are not classified as heteromorphs. Heteromorphy occurred in many evolutionary lineages, and thus by definition, the term 'heteromorph ammonoid' forms a polyphyletic 'grouping'. Heteromorphy appeared multiple times during the history of ammonoids, beginning with the first ammonoids in the early Devonian to their very end at the Cretaceous/Paleogene boundary (see Section VI). Heteromorphy was most common in the Cretaceous, which is the reason why many textbooks identify heteromorphs (only) as Cretaceous Ancyloceratina, and why most of the available data on their palaeobiology comes from Cretaceous examples. Only Cretaceous heteromorphs show an important modification of the suture line, namely a reduction from five to four lobes in the primary suture line, which was used by earlier workers to define them as a monophyletic group (Korn *et al.*, 2003), an outdated idea that is strictly rejected herein. It was also the diversity of 'aberrant' forms during the Cretaceous that was used in the outdated hypothesis of degeneration ('typolysis') to explain the cause of their extinction (Schindewolf, 1936; Wiedmann, 1969; Korn, 2003). Some of their complex conch shapes (conch refers to the entire skeleton, shell refers to the material) without apparent streamlining have been used to argue for an immobile benthic or pseudoplanktic life habit for ammonoids (Arkhipkin, 2014), an interpretation that was fuelled by the rapid replacement of loosely coiled (heteromorph) forms by tightly coiled (monomorph) ammonoids during their early evolution in the Devonian (e.g. Klug & Korn, 2004; De Baets *et al.*, 2012; Klug *et al.*, 2015*a*). It is now widely accepted that heteromorphs independently and convergently evolved from different phylogenetic lineages during the Triassic, Jurassic, and multiple times during the Cretaceous (Cecca, 1997). Evolutionary relationships within the heteromorphs, particularly during the Cretaceous, require refinement (Wright, Callomon & Howarth, 1996; Kaplan, 2002). To what degree heteromorphs had comparable life habits is still debated, but is crucial for understanding their radiations, evolutionary successes, and extinctions during each period.

Here, we review the currently known constraints of heteromorph palaeobiology and ecology using a wide range of approaches to disentangle the factors driving the organisation and evolution of heteromorph conch shapes within Ammonoidea.

II. SOFT BODY RECONSTRUCTION

Remains of soft parts are rarely preserved in ammonoids (e.g. Closs, 1967*a*,*b*). However, two reported cases come from heteromorphs, namely trochospiral *Allocrioceras* (Wippich & Lehmann, 2004; Keupp, Saad & Schweigert, 2016*b*) and orthoconic *Sciponoceras* (Klug, Riegraf & Lehmann, 2012; Klug & Lehmann, 2015). In these genera, remains of the digestive tract including the oesophagus (well preserved due to its original chitinous cover), crop, and stomach are preserved as thin organic sheets (Fig. 1).

Klug *et al.* (2012) and Klug & Lehmann (2015) proposed that structures surrounding the oesophagus of *Sciponoceras* might represent phosphatised parts of the cephalic cartilage with the eye capsules. Both phylogenetic bracketing with nautiloids and coleoids (Witmer, 1995; Klug *et al.*, 2015*a*, 2019; Shigeno *et al.*, 2018) and the limited fossil evidence suggest the presence of a well-developed brain in these heteromorphs. We speculate that the evolution of the nervous system in cephalopods was linked with the need to control their position in space and to handle information from sensory systems like eyes and statocysts (sensory receptors for balance and orientation).

Phylogenetically, ammonoids are positioned between nautilids with their pinhole camera eye and coleoids with a lens eye. The shared ancestry of ammonoids and coleoids (derived from bactritids; Kröger, Vinther & Fuchs, 2011), and their potential for a more active lifestyle similar to coleoids, suggests that ammonoids had lens eyes. Putative eye capsules are relatively large in *Sciponoceras*, suggesting the presence of large eyes in baculitids (Klug *et al.*, 2012; Klug & Lehmann, 2015), which is supported by deep lateral sinuses on their apertures providing structural space for large eyes useful for an active lifestyle.

The number, shape, and proportions of the arms ammonoids possessed are subject to ongoing debate. Structures anterior to the jaws in *Sciponoceras* (Klug *et al.*, 2012; Klug & Lehmann, 2015) might represent arm bases. Various authors have suggested that the arms of heteromorphs were short (Landman, Cobban & Larson, 2012*a*). Klug *et al.* (2015*a*) applied phylogenetic bracketing (Witmer, 1995), and argued that it is most parsimonious to assume that all ammonoids including heteromorphs had 10 arms (Klug & Lehmann, 2015). The same line of reasoning suggests that ammonoid arms lacked suckers and hooks (but see Section II.1*c*), and that they had no tentacles (extendable extremities longer than the arms), which is weakly supported by the absence of fossil evidence of these structures. Clements *et al.* (2017) found that members of the clade comprising modern 10-armed cephalopods (sepiids and squids) decompose faster as a function of their higher ammonia content, therefore connecting coleoid cephalopod taphonomy with physiology. Thus, the scarcity of soft-part preservation in ammonoids could be linked to both the ammonia content of their soft parts and that potentially preserved soft parts are often covered by shell remains.

Closs (1967*a*,*b*) interpreted ammonoids as possessing a hood, but re-examination of his Carboniferous material suggests a misidentification of a shell fragment situated near the aperture as a hood (Lehmann, Klug & Wild, 2015). Using phylogenetic bracketing and information from the embryonic development of modern nautilids Shigeno *et al.* (2008) and Shigeno, Sasaki & Boletzky (2010) suggest that the hood is derived from Anlagen (developmental foundation) of the arm crown which is absent in ammonoids.

(1) Buccal mass

(*a*) Jaws

The buccal apparatus is known for several Ancyloceratina, and in the Ammonitina for *Spiroceras* (Tanabe, Kruta & Landman, 2015*a*) (see online Supporting Information, Table S1). It follows the general pattern of ammonoid jaws: a smaller upper jaw nested within a larger lower jaw (Fig. 1E). The upper jaw is conservative in ammonoids and has a blunt rostrum with inner lamellae for the support of the muscular tissue split into two rounded wings (Tanabe *et al.*, 2015*a*). Lower jaws are morphologically variable with different shapes, ornamentation, and microstructure of the calcitic covering. Most heteromorphs have an aptychus-type jaw with a central commissure (symphysis) dividing the lower

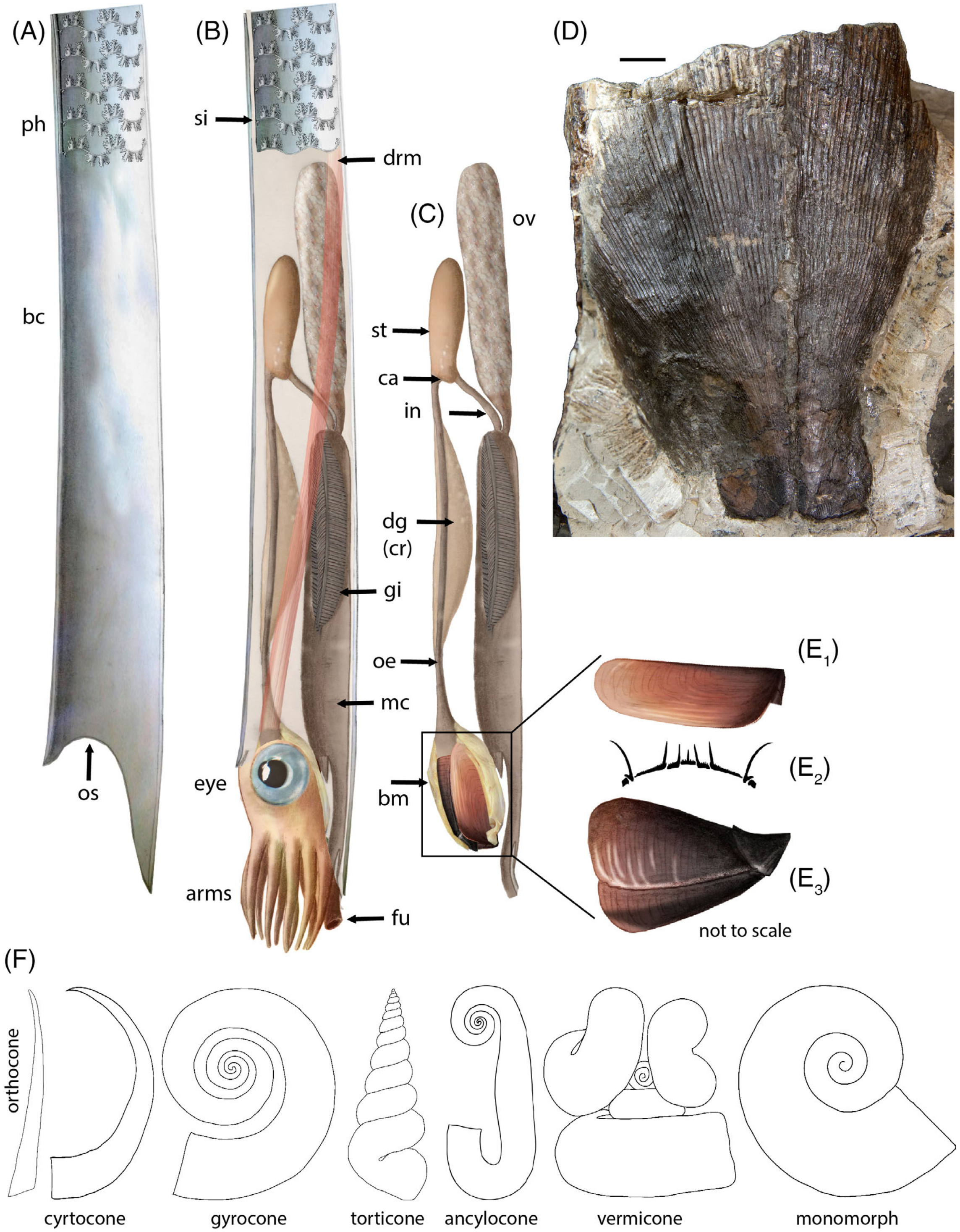

Fig. 1. Soft body reconstruction of an orthocone heteromorph. (A) Empty conch with body chamber and parts of the phragmocone. (B) Overlay image of conch and soft body with eyes and arms. (C) Reconstructed soft body with the digestive tract, buccal mass, and ovary. (D) Lower jaw of *Aegocrioceras* (Hauterivian, NW Germany). Scale bar = 1 cm. (E) Detailed parts of the buccal mass showing radula (E2) and upper and lower jaws (E1, E3). (F) Six morphological heteromorph archaetypes. Abbreviations used in A–C: arms, 10 arms of equal length without suckers or hooks; bc, body chamber; bm, buccal mass (see E for details); ca, caecum; cr, crop (covered by digestive gland); dg, digestive gland; drm, dorsal retractor muscle; fu, funnel; gi, gill; in, intestine; mc, mantle cavity; oe, oesophagus; os, ocular sinus; ov, ovary; ph, phragmocone; si, siphuncle; st, stomach.

jaw into two valves lacking a sharp rostral tip. In Crioceratidae, the symphysis is poorly expressed and due to this fact, their jaws are interpreted by some authors as an anaptychus-type jaw (Engeser & Keupp, 2002). In contrast to an anaptychus interpretation, Tanabe *et al.* (2015*a*) considered the crioceratid lower jaws as the inner chitinous lamella of the aptychus. Later, Rogov & Mironenko (2016) reported Hauterivian praestriaptychi associated with early crioceratids (*Criosarasinella* and *Crioceratites*) suggesting that one of these taxa had an aptychus-type jaw (praestriaptychus, see Table S1).

In the aptychus-type lower jaw, the surface is covered by a calcitic layer either with a striated surface (praestriaptychus and striaptychus) or with rugae (rugaptychus). The outline of the lower jaw spread open matches the shape of the whorl cross section (*Baculites*, *Scaphites*), which led to the suggestion that this structure had an opercular function. By contrast, Larson & Landman (2017) and Landman & Waage (1993*b*) argued that the jaws of *Baculites*, even when fully splayed out, did not touch the inner surface of the conch tube. Accordingly, they rejected an operculum function of the lower jaw in *Baculites*. Parent, Westermann & Chamberlain jr. (2014) suggested that lower jaw types like praestriaptychus and striaptychus could fulfill multiple functions: lower mandible, operculum, filtering device, flushing benthic prey, pumping for jet propulsion and stabilizing against pitching [for praestriaptychus see Parent *et al.* (2014) and Tanabe *et al.* (2015*a*)].

The microstructure of the calcitic covering of aptychi varies in ammonoids between tubular and lamellar [Farinacci *et al.* (1976); see Kruta *et al.* (2009) for heteromorphs]. The calcitic covering in all Cretaceous heteromorph jaws is lamellar. In *Baculites*, the calcitic covering can reach 1 mm in thickness and two main layers have been described (R1 and R2) consisting of overlapping thin (3 μm thickness) calcitic increments (Kruta *et al.*, 2009). The aptychus is 0.5 mm thick in *Hoploscaphites* and 0.03 mm in *Polyptychoceras* without ornamentation.

(*b*) Radula

The use of tomographic techniques on three *in situ Baculites* radulae allowed description of their jaw apparatus (Kruta *et al.*, 2011). The radular ribbon lies between the upper and lower jaws. Each tooth row of the radula is composed of nine elements (one central tooth, two pairs of lateral teeth, one pair of marginal teeth, and one pair of marginal plates) (Fig. 1E). The central rachidian tooth and the two pairs of lateral teeth are delicately multicuspidate, while the marginal tooth is long and sabre-like. The same radula composition and morphology was revealed for a baculitid (?*Sciponoceras*) from the Late Cretaceous of Germany (Klug *et al.*, 2012). Multicuspidate radular teeth found *in situ* in *Rhaeboceras* have been described by Kruta *et al.* (2013) and Kruta, Landman & Tanabe (2015). The only other report (see Table S1) of a radula from heteromorphs is from a *Spiroceras* (Tanabe *et al.*, 2015*a*) but the number of radular teeth per row and their morphology remains unknown.

(*c*) Enigmatic structures found in the body chamber

Cuspidate structures associated with jaws have been found in the body chamber of several species of well-preserved heteromorphs and re-coiled scaphitids. Landman & Waage (1993*b*) described bicuspidate structures in two Maastrichtian species from South Dakota: *Hoploscaphites spedeni* and *H. nicolletii*. Kennedy *et al.* (2002*b*) documented similar cuspidate structures in *Rhaeboceras halli*, a re-coiled scaphitid from the Campanian of Montana, and interpreted them as radular teeth. Kruta *et al.* (2013) rejected this interpretation after finding actual radular teeth in three specimens of *R. halli*. These *in situ* teeth match the size and morphology of radular teeth known from other aptychophoran ammonoids (Kruta *et al.*, 2015; Keupp *et al.*, 2016*a*). Landman *et al.* (2013) documented additional structures associated with *H. gilberti* from the Campanian of South Dakota. Ongoing studies are characterising the diverse morphology of these enigmatic structures in *R. halli* (Kruta *et al.*, 2019) and their function in scaphitids, e.g. hooks on the hectocotylised arm.

(2) **Muscle system**

Although there is no unequivocal report of fossilised muscles from ammonoids we can make inferences about their muscle system (Doguzhaeva & Mapes, 2015). Based on dimensions of attachment scars, the cephalic retractor muscles inserted at the largest postero-lateral attachment sites. However, Mironenko (2015*b*) argued that these muscles were attached dorsally with the nuchal retractors in Jurassic ammonoids like *Kachpurites*. In his opinion, the hyponome muscles inserted laterally in the annular elevation or the lateral sinus. Mironenko (2015*b*) proposed that the collar was attached laterally. Mironenko's (2015*b*) interpretation of their function and homology with muscles in nautilids and coleoids raises several questions, which cannot yet be fully answered given the paucity of available anatomical information.

1. Does the arrangement of the main muscles in ammonoids correspond to that of modern *Nautilus*? Jacobs & Landman (1993, p. 101) stated that *Nautilus* is in some respects "a poor model for the function and behaviour of ammonoids", but is the only living ectocochleate cephalopod for comparison. Nevertheless, in the absence of coleoids with chambered conchs and a long body chamber, *Nautilus* represents one of the most important living relatives used to reconstruct ammonoid palaeobiology. Jacobs & Landman (1993) support Mironenko's (2015*b*) interpretation of a dorsal insertion of retractor muscles. The muscle attachment patterns of *Audouliceras renauxianum* from the Russian Cretaceous figured in Doguzhaeva & Mapes (2015, Figs. 14.1–14.4) may support this hypothesis, because there are large dorsoventral (umbilical) 'tongue-like marks'. In this ancylocone, the adult body chamber forms a characteristic hook. To enhance efficiency of the retractor muscles, the distance to the head must be minimised. Due to the curve in the adult body

chamber, a posterior insertion of straight cephalic retractors is impossible. By contrast, an anterior insertion of retractor muscles would have reduced the length of these muscles, thereby increasing their efficiency. Nevertheless, this homologisation requires further evidence. Ultimately, we will have to await specimens preserving remains of the musculature.

(2) Are coleoid muscles homologous with ammonoid muscles? Homology of the mantle in coleoids (*cf.* Jacobs & Landman, 1993; Fuchs *et al.*, 2016) with that of ammonoids is likely. However, it is also probable that the ammonoid mantle could not serve the same purposes as in coleoids because of the external conch. The mantle secretes the mineralised hardparts (ectocochleate or endocochleate) in most cephalopods, except for *Argonauta*. Klug *et al.* (2008) proposed that the mantle musculature in ammonoids enabled the animal to move its soft parts within the body chamber. Jacobs & Landman (1993) suggested that the mantle played an active role in swimming. This assumption would support a moderately thick mantle with the potential to be fossilised, which has yet to be reported. The homologisation of other muscles would require soft tissue preservation.

(3) Did ammonoids have a collar like coleoids? Mironenko (2015*b*) found a lateral soft tissue attachment site close to the aperture and suggested that the collar and funnel-locking apparatus attached at this site. The soft tissues were presumably attached to the body chamber wall anteriorly and posteriorly. The presence of a nuchal and funnel cartilage in *Nautilus* and *Sepia* implies that these were also present in ammonoids. If we accept the intermediate position of ammonoids between nautilids and coleoids with respect to locomotory abilities, we can assume that the funnel was somewhat stiff and could be locked firmly near the aperture to maximise the thrust of the hyponomic water jet. Although fossil remains of the nuchal cartilage have been reported from coleoids (Klug *et al.*, 2016), they have not been found in ammonoids.

We conclude that ammonoids likely had paired cephalic and hyponome retractor muscles, a ventral muscle, and mantle musculature. Since ammonoid muscles are not preserved well enough (only a few doubtful remains), homologisation of ammonoid muscles and their attachment sites with those of coleoids and nautilids remains uncertain. Conch morphology of heteromorphs and the likely arrangements of muscles in their body chambers suggest that their locomotory abilities were limited compared to most modern coleoids because of the indirect action of the main muscles. Efficiency of the muscle system and the locomotory apparatus probably improved towards the end of their lives, which is achieved through the commonly widened body chamber and the more horizontal orientation of the adult aperture. This ontogenetic change in orientation allowed the approximate horizontal alignment of the jet with the centre of mass (e.g. Klug, 2001; Klug & Korn, 2004).

(3) Ink sac

There are four categories of colour or light display in animals: (*i*) pigments, (*ii*) bioluminescence, (*iii*) structural colours, and (*iv*) liquid crystals. While the ink of modern coleoids is made of the pigment melanin, coleoids also evolved bioluminescence such as in the photophore of *Spirula spirula*. Some cephalopod light organs are also situated within the ink sac, for example in *Sepiola atlantica* (Herring *et al.*, 1981). Structural colour is present as mirrors in photophores composed of collagen fibres forming a multilayer reflector e.g. in *Selenoteuthis*, *Abralia*, or *Enoploteuthis* (Parker, 2000). Reports on fossilised colour mostly refer to the presence of pigments in shells or the ink sac (e.g. Roy *et al.*, 2020).

Melanin macromolecules are classified into eumelanins (black) that contain nitrogen and pheomelanins (broad colour range: yellow-red-brownish) containing sulfur (Schäfer, 2013). Melanins are stored in melanosomes, specific cell organelles of pigment cells that share the size and shape of bacteria (Lindgren *et al.*, 2012). Identification of melanin based on structural information can be misleading. In addition, the presence of melanin in soft tissues such as visual systems (Schäfer, 2013), liver (Scalia *et al.*, 1990), or others (Wakamatsu & Ito, 2002) complicates the recognition of ink in fossil cephalopods.

Reports of ink sacs in ammonoids by Lehmann (1967) for *Eleganticeras*, Mathur (1996) for *Eopsiloceras*, and Wetzel (1969) for *Bochianites* have been discarded by subsequent researchers (Wippich & Lehmann, 2004; Klug & Lehmann, 2015). Doguzhaeva *et al.* (2004) interpreted bituminous matter in flattened ammonoid body chambers of *Austrachyceras* as ink sacs. This interpretation is rejected here because modern ectocochleate cephalopods lack an ink sac and melanin occurs in other ammonoid structures such as the black layer (Klug *et al.*, 2004). Unequivocal evidence for fossil ink and ink sacs are common in fossil coleoids from the Carnian Austrian Rheingraben Shale, the German Posidonia Shale (Toarcian), German plattenkalks (Kimmeridgian–Tithonian), and Lebanese plattenkalks (Cenomanian) as summarised by Schäfer (2013), but are absent in co-occurring ammonoids. Raman spectroscopy revealed the presence of the typical melanin spectra, revealing the effect of the carbonate matrix or the presence of iron on these spectra (Schäfer, 2013). This method is recommended to test for the presence of ink and related structures in heteromorphs (see Section II.5).

(4) Digestive tract

Fossil remains of the digestive tract (except the buccal mass; Section II.1; Fig. 1B, C) have been documented from the heteromorphs *Allocrioceras* (Wippich & Lehmann, 2004) and *Sciponoceras* (Klug *et al.*, 2012; Klug & Lehmann, 2015). In both cases, flattened specimens with dissolved conchs preserve organic remains of crop and stomach. In *Allocrioceras* (Wippich & Lehmann, 2004) from the Cenomanian of Lebanon, the remains of the digestive tract lie far behind the buccal mass, suggesting that it is the stomach and not the crop. In the case of *Sciponoceras* from the Cenomanian–Turonian boundary in Germany, carbonised impressions show details of the digestive tract (Klug *et al.*, 2012; Klug & Lehmann, 2015). It begins with the oesophagus, which was identified based on its elongate shape and its spatial association with the buccal mass. Posteriorly, the digestive tract displays a swelling, which probably represents the elongate crop, which is known to be large in cephalopods. The elongate crop in *Sciponoceras* is likely linked with the long body chamber in baculitids. A third, further posteriorly situated elongate structure found in *Sciponoceras* was interpreted as the stomach by Klug *et al.* (2012).

(5) Shell colour patterns

Shell colour patterns in molluscs can be the result of pigments or of structural colour (see Section II.3). Identification of true colour patterns including bands and spots is complicated by the existence of false colour patterns, which often run parallel to growth lines and shell thickening. Klug *et al.* (2012) reported on false colour patterns, which are related to growth halts (megastriae) accompanied by faint ribs and the secretion of melanin along transverse stripes (parallel to former apertures). Muscle attachment structures can also result in dark patches mimicking colour patterns regarded herein as pseudo colour patterns.

The oldest true colour patterns in ammonoids were described from a monomorph from the Early Triassic Crittenden Springs Lagerstätte (Mapes & Sneck, 1987), although there are reports of colour patterns for Palaeozoic nautiloids (Manda & Turek, 2009*a*,*b*, 2015) and one Devonian ammonoid (Ebbighausen *et al.*, 2007). In mollusc shells, polyenes like carotenoids represent most shell pigments as outlined by Hedegaard, Bardeau & Chateigner (2006) and Barnard & de Waal (2006) using *in situ* Raman spectroscopy. Mapes & Larson (2015) reported true colour patterns from *Hoploscaphites nicolletii* and *H. reesidei*. In both species, longitudinal iridescent bands are preserved in nacre. This colour pattern is a structural colour with multilayer reflectors, where the nanometer thick nacre tablets fulfill the Bragg condition for diffraction. Bragg diffraction by a crystal lattice occurs when radiation (e.g. X-rays or light) with a wavelength comparable to atomic spacing is scattered from the lattice plane undergoing constructive interference (Bragg & Bragg, 1913). These structural colours are comparable to the colours of butterfly wings, gold bugs, polychaetes, and fish (Parker, 2000; Parker & Martini, 2006). Based on transmission electron microscopy analyses, Snow *et al.* (2004) described a new type of structural colour of nacre, the edge-band structure, which produces interference colours. These are characteristic for different widths of the edge-band structure ranging from silver tones (74 nm) to creams (80 nm) to yellow and gold (90 nm) in bivalve pearls. The same phenomenon could be responsible for structural colours in ammonoids (Keupp, 2005; Mapes & Larson, 2015). Keupp (2005) suggested that spiral bands resulted from original pigment-based colour patterns in the outer prismatic layer. It is noteworthy that the polyene pigments in modern *Nautilus* are restricted to the outer prismatic layer (Fig. 2). These colour patterns can be traced in the uppermost part of the underlying nacreous layer due to minute differences in ultrastructure. This is important because most ammonoids lack a preserved outer prismatic layer. For example, spot patterns in Jurassic amaltheid ammonoids (Schindewolf, 1928, 1931) are visible after the dark (pyrite) spots are lost. Mironenko (2015*a*) reported on remnants of radial pigment-based colour patterns coinciding with temporary apertures, representing an example of false colour patterns.

Externally shelled (ectocochleate) cephalopods with longitudinal bands fall into the planktic–vertical migrant life habit. By contrast, spiral structural colour patterns, like in *Quenstedtoceras*, have been suggested to indicate a potential demersal life habit (Keupp, 2005). Relationships between conch form, biofacies, and colour patterns have been discussed for broad longitudinal colour patterns on orthocone Palaeozoic nautiloids (Manda & Turek, 2009*b*). Turek & Manda (2011) described zig-zag or wave-like transverse colour patterns of the cyrtoconic barrandeocerids *Peismoceras* and *Phragmoceras* as well as the oncocerids *Octameroceras* and *Pentameroceras*. Manda & Turek (2009*a*) figured a similar zig-zag or wave-like transverse colour pattern for the cyrtoconic Silurian oncocerid *Euryrizocerina*, which was likely demersal. A marked polymorphism in colour patterns has been described for modern *Nautilus* (Ward *et al.*, 1977), *Quenstedtoceras* (Keupp, 2005), and the Silurian nautiloid *Phragmoceras* (Turek & Manda, 2011) suggesting a camouflage function. In this regard, the suggestion by Balinski (2010) that marine invertebrates that exhibit colour patterns usually live no deeper than 200 m (photic zone) is convincing.

III. BUOYANCY AND LOCOMOTION

The bizarre morphology of many heteromorphs invites speculation on the function of these convoluted conchs, which are often considered to be poor swimmers that evolved from more streamlined monomorphs (Jacobs, Landman & Chamberlain, 1994; Monks & Young, 1998; Mikhailova & Baraboschkin, 2009). Functional morphological work has focused on buoyancy and hydrostatics to determine what life habits, typically adult, heteromorph conch shapes might have permitted. It is widely accepted that most ectocochleate cephalopods were nearly neutrally buoyant during life regardless of conch shape or ontogeny. This was controlled by adding fluid to a positively buoyant conch or counteracting slightly negative buoyancy through swimming (Denton & Gilpin-Brown, 1966; Klinger, 1981; Lukeneder, 2012; Hoffmann *et al.*, 2015; Lemanis *et al.*, 2015; Tajika *et al.*, 2015; Peterman, Barton & Yacobucci, 2019*a*; Peterman *et al.*, 2020*a*,*b*). Thus, neutral buoyancy is usually assumed for hydrostatic analyses, although some authors have proposed a mobile benthic to nektobenthic life habit for some heteromorphs (e.g. Wiedmann, 1973*b*;

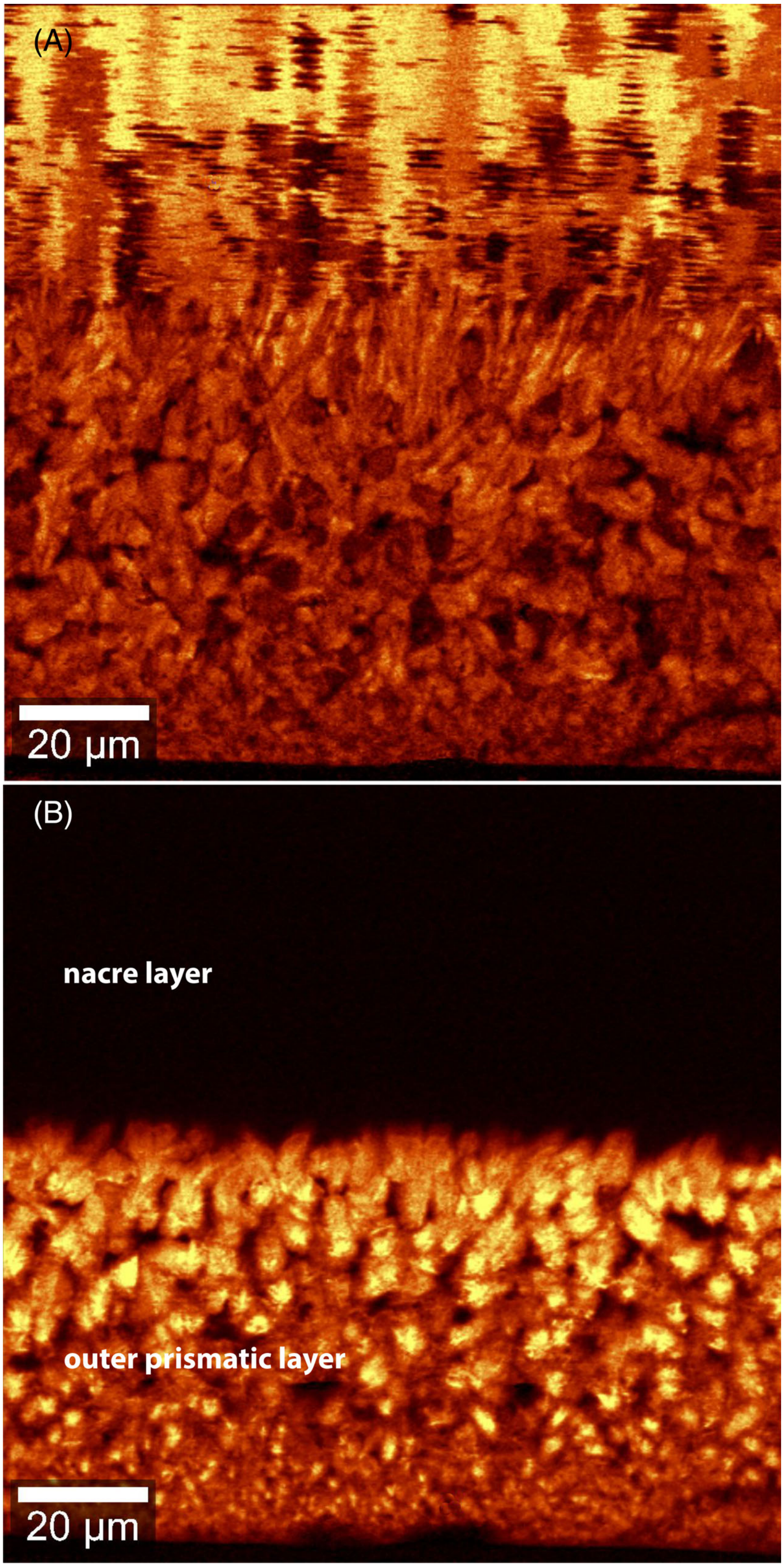

Fig. 2. Raman image showing the distribution of aragonite (A) and polyenes (B) in the shell of modern *Nautilus pompilius*. Shell colouration, i.e. distribution of polyenes within the shell, is limited to the outer prismatic layer.

Kakabadze & Sharikadze, 1993). These analyses can utilise both physical and virtual models.

(1) Physical models

Physical models include the construction of a physical replica of the conch that is immersed in fluid. Reyment (1973) was among the first to use physical models to examine static conch orientation, although these experiments were designed to understand *post-mortem* drift rather than life orientation, hence soft tissue was not considered. To determine life orientation, differentiation between phragmocone and body chamber densities must be replicated to reconstruct the positions of the centres of volume (buoyancy) and mass (gravity). Ward (1976) used microcrystalline sculpting wax to create models of the heteromorphs *Glyptoxoceras subcompressum*, *Didymoceras elongatum*, *Ryugasella ryugasensis*, *Pseudoxybeloceras nanaimoense*, *Baculites inornatus*, and *B. anceps pacificus*. Density differences were achieved by adding carborundum (silicon carbide), metal powder, and lead or solder strips to the wax. *G. subcompressum* likely had the most significant changes in aperture orientation in early ontogeny during a switch from orthoconic to torticonic to gyroconic coiling with less variation in aperture orientation in the gyroconic stage. *D. elongatum* showed a stable aperture orientation during the growth of the torticonic conch with the final growth stage showing a slight upwards turn of the aperture. The orthoconic *B. inornatus*, *B. anceps pacificus*, and ancylocone *R. ryugasensis* had a vertical conch orientation with the aperture directed downwards. *P. nanaimoense* with its ancylocone conch showed the greatest variation of orientation through ontogeny with the aperture changing by up to 180°, similar to the hamiticone *Dissimilites* that was investigated virtually (Lukeneder, 2012). A vertical orientation of orthoconic heteromorphs is a common result in both physical and virtual models (e.g. Trueman, 1941; Westermann, 1977; Peterman *et al.*, 2019*a*,*b*). A flooded apex of the phragmocone, however, might have allowed the animals to achieve a more horizontal orientation temporarily. This hypothesis was tested by Westermann (2013) using models of *Baculites* composed of plexiglass and styrofoam with iron weights used to simulate different weight distributions. Westermann (2013) confirmed the possibility of such conchs achieving a roughly horizontal orientation and proposed a potential ontogenetic shift from a vertical to a subvertical conch orientation following the growth of conch curvature and re-flooding of parts of the phragmocone. Peterman *et al.* (2019*b*) simulated an apically flooded *Baculites* that was not able to deviate from a vertical orientation while remaining neutrally buoyant. Experiments on physical models with the same hydrostatic properties as their virtual counterparts support a stable vertical posture. The models represent density-corrected, neutrally buoyant three-dimensional prints of reconstructed cephalopod conchs (Peterman *et al.*, 2019*a*,*b*, 2020*a*). These weighted models (Fig. 3) allow the approximate analysis of the restoring moment and hydrodynamic drag during rotational and translational movement. Changes in conch orientation during evolution from orthocones to early ammonoids were investigated by balancing sculpted models of the whole conch and the isolated body chamber to determine the relative positions of the centres of mass and buoyancy (Klug & Korn, 2004). They found an evolutionary shift from the aperture horizontally pointing downwards (Bactritida) *via* oblique apertures (early heteromorphs) to a near horizontal aperture facing upwards (derived monomorphs), which implies an increase in swimming velocity and manoeuvrability.

(2) Virtual models

Virtual models include mathematical models and simulated conchs, either generated *ex nihilo* or from tomographic data (Hoffmann *et al.*, 2014; Naglik *et al.*, 2015; Lemanis, Zachow & Hoffmann, 2016; Naglik, Rikhtegar & Klug, 2016; Hebdon, Ritterbush & Choi, 2020). Trueman (1941) first attempted to calculate the buoyancy and hydrostatic orientation of several heteromorph conchs, taking the body chamber length *versus* total conch length into account. Planispiral to gyrocone *Crioceras fissicostatum*, *C. duvali*, and *C. mulsanti* were calculated with a sub-vertical aperture orientation, whereas the planispiral *Macroscaphites yvani*, *Scaphites aequalis*, and *Oecoptychius* sp. were calculated with a near-horizontal aperture that pointed upwards. Trueman (1941) and later authors (e.g. Klinger, 1981; Westermann, 1996; Peterman *et al.*, 2020*a*) noted that the uncoiling of the conch has the tendency to increase the distance between the centre of buoyancy and the centre of mass, thereby increasing the conch's hydrodynamic stability (its tendency to resist changes in orientation). Tanabe (1975) calculated the buoyancy for *Otoscaphites* by volume approximations based on coiled conical geometries and the equations of Raup (1973). *Otoscaphites* had a negative buoyancy that was interpreted as a shift through the group's evolutionary history from a benthic to a nektoplanktic habitat. Ward & Westermann (1977) calculated the buoyancy of the vermicone *Nipponites occidentalis* based on conch length, radius, cross-sectional area, and several corrective factors to account for ornamentation, septa, and the siphuncle. They interpreted *N. occidentalis* as being planktic due to its near-neutral buoyancy, lack of hydrodynamic streamlining or perceived adaptations to a benthic life habit (shell thickening, reduction in sutural complexity). The assumption of neutral buoyancy has a strong impact on reconstructed orientations. This impact was shown for different heteromorphs with both neutral and negative buoyancy (Okamoto, 1988*b*; Okamoto & Shibata, 1997; Higashiura & Okamoto, 2012). On the basis of simulated conchs, Okamoto argued for a nektobenthic life habit, in some cases with the conch occasionally resting on the sea floor like the torticone *Eubostrychoceras muramotoi*, the ancylocone *Polyptychoceras pseudogaultinum*, and torticone nostoceratids (Okamoto, 1988*b*; Okamoto & Shibata, 1997; Higashiura & Okamoto, 2012). But he agreed with Ward & Westermann (1977) that *Nipponites* had a near-neutral buoyancy and a planktic life habit (Okamoto, 1988*a*).

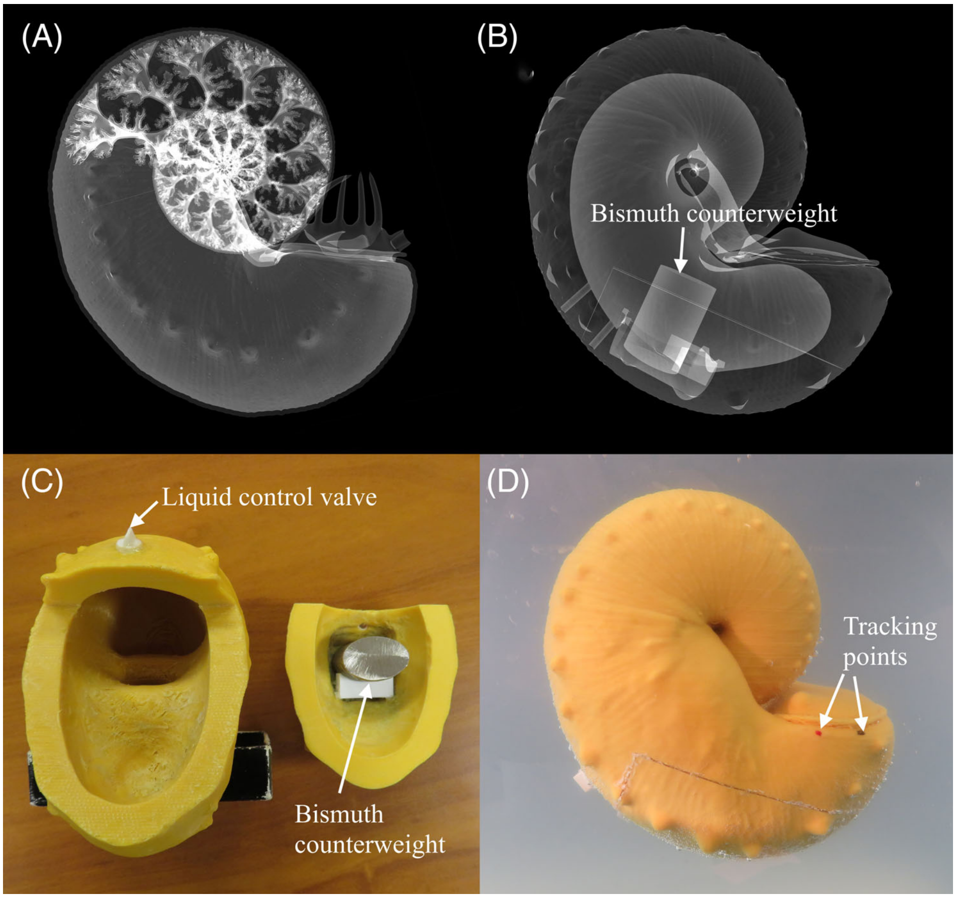

Fig. 3. Neutrally buoyant physical experiments on scaphitid heteromorph ammonoids. (A) Virtual model with complex internal geometry. (B) Modified virtual model for 3D printing. Bismuth counterweight corrects for differences in mass and stability between A and B. (C) 3D printed model showing counterweight and a control valve in case of flooding. (D) Neutrally buoyant model with proper hydrostastics and tracking points for hydrodynamic analyses. From Peterman *et al.* (2020*a*).

Olivero & Zinsmeister (1989) calculated a positive buoyancy and near-horizontal upwards aperture orientation for the heteromorph *Diplomoceras maximum*. *Diplomoceras* is a hamiticone (paperclip-like ancylocone subtype) heteromorph similar in morphology to the proposedly negatively buoyant *Polyptychoceras* (Okamoto & Shibata, 1997). The role of the U-shaped body chamber of some heteromorphs was tested by Kaplan (2002) who abstracted the complex conch shapes into simpler geometric forms (e.g. cones, cylinders, tori) to calculate volumes, surface areas, and centres of mass and volume. Kaplan (2002) also took into account the effect of partial phragmocone refilling and alterations of the centre of mass of the soft body due to movement within the body chamber (Monks & Young, 1998). Kaplan (2002) found that only heteroconic (combination of torticone and ancylocone) conchs could consistently attain an orientation that would allow them to feed on benthos; scaphiticones and praviticones (a combination of planispiral and ancylocone) showed limited access to benthos through manipulation of the fill fraction of the phragmocone, while ancylocones and hamiticones showed no easy access to benthic prey regardless of orientation modification. This analysis challenged the idea that the evolution of the U-shaped body chamber was an adaptation for a benthic life habit. Landman *et al.* (2012*a*) agreed with this interpretation by arguing for a more passive, filter-feeding strategy for *Scaphites*.

Heteromorphs with a U-shaped body chamber (nostocones, scaphiticones, ancylocones; Fig. 4) are more stable than modern *Nautilus* and are unlikely to be able to substantially modify their orientation by active swimming locomotion by jet propulsion (Peterman *et al.*, 2020*a*,*b*). The U-shaped body chamber distributes organismal mass away from the centre of buoyancy, while maintaining an upward-facing posture (as suggested by Trueman, 1941; Klinger, 1981; Westermann, 1996). Horizontal alignment of the hyponome with the centres of rotation, such as in ancylocones, suggests that more energy would be transmitted to translational movement with minimal rocking, i.e. these morphotypes are well suited for backwards horizontal swimming at maturity. Hydrodynamic efficiency was investigated for various scaphiticones (Peterman *et al.*, 2020*a*) and an ancylocone (Peterman *et al.*, 2020*d*). The uncoiled shape increases

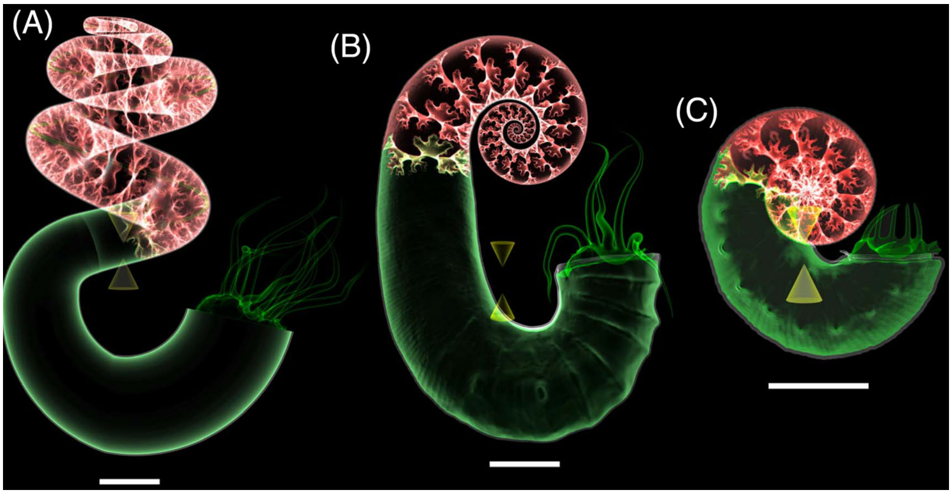

Fig. 4. Virtual hydrostatic models of heteromorphs with recurved body chambers at maturity. (A) *Didymoceras nebrascense* (Peterman *et al.*, 2020*b*). (B) *Audouliceras renauxianum* (Peterman *et al.*, 2020*d*). (C) *Hoploscaphites crassus* microconch (Peterman *et al.*, 2020*a*). Tip of upper yellow cone, centre of buoyancy; tip of lower yellow cone, centre of mass. Scale bars = 3 cm.

drag, but with *Nautilus*-like thrust values they were able to move horizontally backwards at velocities similar to *Nautilus* (when normalised by mass). Coleoid-like thrusts would have allowed them to surpass the velocities of similarly sized *Nautilus*. These calculations depend on the largely unknown ammonoid soft body morphology (see Section II). Thus, it remains unclear whether they are realistic. Aside from these open questions, the results of these studies contrast with the interpretation of such heteromorphs as being confined to benthic habitats and the interpretation of limited horizontal mobility (Westermann, 1996).

The adult change in coiling (U-shaped body chamber) brought the hyponome closer to the level of the centre of mass. This implies improved swimming capabilities. Klug (2001) and Klug & Korn (2004) found this phenomenon in several ammonoid clades and suggested that improved swimming capabilities represent selective advantages during reproduction particularly for the choice of mating partners and spawning grounds. Sexual selection is a strong evolutionary agent and might be the main driver behind the convergent evolution of more horizontally oriented apertures in adult conch forms in many ammonoid clades, including numerous heteromorphs.

IV. ECOLOGICAL INTERACTIONS

(1) Predators

Abnormal shell growth in modern and fossil molluscs, including ammonoids, is often the result of sublethal injuries, which may inform on predator–prey relationships (Keupp, 2012; Hoffmann & Keupp, 2015). Like modern cephalopods, ammonoids were an important part of marine food webs and served as prey for vertebrates and invertebrates. For food-web reconstructions, digestichnia (Vallon, 2012), including stomach contents, cololites, coprolites, regurgitalites, and palaeopathologies (Keupp, 2012) have been used. Since digestichnia including heteromorph remains were reviewed by Hoffmann *et al.* (2020) we herein focus on palaeopathologies. Various heteromorphs bear large (often hollow) spines which might have had a protective function against predators or encrusters (Klinger, 1981; Cecca, 1997) but other authors have speculated that these spines were too fragile and might have had other functions such as stabilizing the shell in the water column (Klinger, 1981; Ifrim, Bengtson & Schweigert, 2018).

Specific reactions of the prey often result in a characteristic abnormal growth of the repaired shell (symptoms). Assumptions about the ammonoid life habit including habitat depth and proximity to the seafloor are possible (Hoffmann & Keupp, 2015). However, sublethal injuries in cephalopods can be inflicted not only by predators, but also by the same species such as in *Nautilus* during mating (Ward, 1987) or by dangerous prey such as crustaceans [e.g. see Ward (1981) for *Nautilus* and Landman & Waage (1986) for scaphitids].

Pathologies have been primarily reported for Jurassic and Cretaceous heteromorphs (Table S2) but were also known from Devonian heteromorphs, which suggest damage caused by other cephalopods (Klug, 2007). The oldest known injured Mesozoic heteromorph is the Late Bajocian *Spiroceras* (Bayer, 1970: plate 8, Fig. 9; Dietl, 1978: Fig. 6f). Here, we document palaeopathologies for the Hauterivian *Aegocrioceras raricostatum* (Fig. 5B, G), Aptian *Proaustraliceras tuberculatum* (Fig. 5D), Albian *Pictetia astieriana* (Fig. 5A), Aptian *Ptychoceras minimum* (Fig. 5C, E), and *Ptychoceras renngarteni* (Fig. 5F).

Among Cretaceous heteromorphs, palaeopathologies are common and have been mostly reported for scaphitids (Landman & Waage, 1986; Hengsbach, 1996; Larson, 2002; Landman *et al.*, 2010*b*, 2012*a*, 2019; Keupp, 2012;

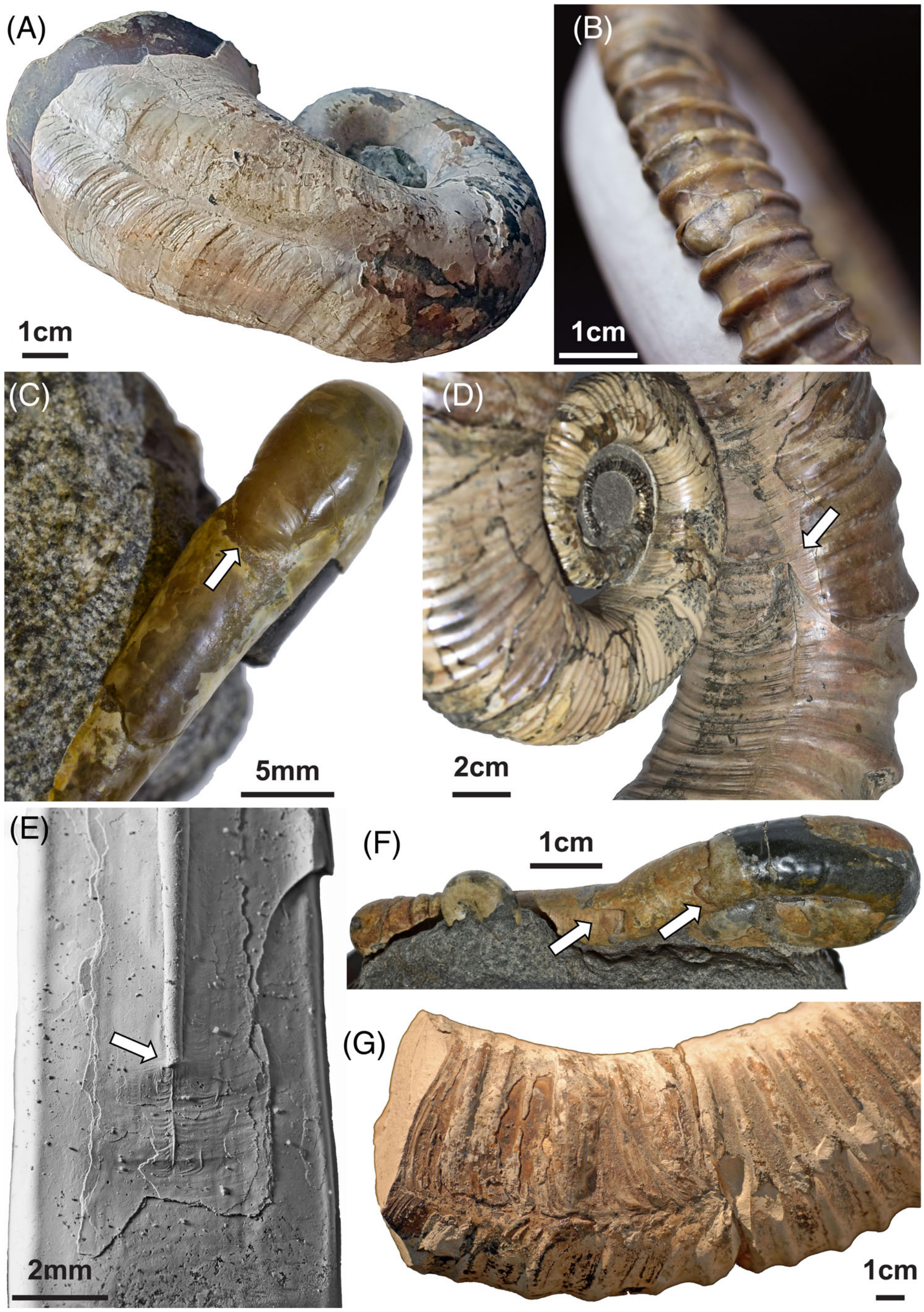

Fig. 5. Palaeopathologies of heteromorphs. (A) *Pictetia asteriana* (Early Albian, Madagascar) with a band-slit pathology potentially caused by a benthic crustacean suggesting a demersal life habit of the ammonoid. Private collection of Wolfgang Grulke (Dorset, UK). (B) *Aegocrioceras raricostatum* (Hauterivian, NW-Germany) with a bulbous shell breakage. (C) *Ptychoceras minimum* (Late Aptian, Krasnodar region, Russia). Geological institute RAS, No. GIN MPC 5/2. Arrow indicates a healed sublethal injury on the second shaft of the conch. Post-traumatic inflation indicates damage of the shell-secreting mantle edge. (D) *Proaustraliceras tuberculatum* (Early Aptian, Ulyanovsk region, Russia). Private collection of Dmitry Vinogradov (Moscow), specimen No. 438. Arrow indicates a healed sublethal injury on the dorsal side of the conch likely produced by durophagous fish. (E) *Ptychoceras minimum* (Late Aptian, Krasnodar region, Russia). Geological institute RAS, No. GIN MPC 5/5. Feather-like wrinkles on the dorsal surface of the second shaft that start at the point of truncation of the first shaft. (F) *Ptychoceras renngarteni* (Late Aptian, Krasnodar region, Russia). Geological institute RAS, No. GIN MPC 5/1. Arrows mark healed sublethal injuries on the second shaft of the conch. (G) *Aegocrioceras* sp. body chamber (Hauterivian, NW-Germany) with a band-slit.

Hoffmann & Keupp, 2015). Typically, injuries affected the margin of temporary apertures and usually occur in early ontogenetic stages (coiled conch part). Severe injuries of the shell-secreting mantle epithelium sometimes resulted in the disappearance of ventral tubercles (Hoffmann & Keupp, 2015: Fig. 21.8d). Crustaceans, fish, marine reptiles, coleoids, ammonoids, and nautiloids were discussed as potential producers of such damage (Landman & Waage, 1986; Hengsbach, 1996; Larson, 2002; Landman *et al*., 2010*b*; Keupp, 2012; Hoffmann & Keupp, 2015).

Orthoconic baculitids display palaeopathologies on their apertural edges of different growth stages (Klinger & Kennedy, 2001; Henderson, Kennedy & Cobban, 2002; Kennedy, Cobban & Klinger, 2002*a*). In some cases, the complete aperture was fragmented, presumably by pycnodontid fish (Kennedy *et al*., 2002*a*: plate 8, Fig. 9) or the conch had long and narrow V-shaped injuries on both flanks (Kennedy *et al*., 2002*a*: plate 8, Figs. 2–4, 6–8). For the latter, Kennedy *et al*. (2002*a*) suggested a coleoid attack, but Keupp (2012) argued for a benthic crustacean as the predator.

Palaeopathologies may help reconstructing the soft body organisation of the Aptian *Ptychoceras*. Doguzhaeva & Mutvei (1989, 1993, 2015) argued that *Ptychoceras* had an internal shell. Kakabadze & Sharikadze (1991, 1993) and Keupp (2012) rejected that interpretation based on similarities of *Ptychoceras* palaeopathologies with injuries found in other monomorph and heteromorph ammonoids. Injured and repaired temporal apertures (forma aegra *substructa*) of *Ptychoceras* caused a strong distortion of the subsequent shaft, indicating severe damage of the mantle edge (Fig. 5C, F). A healed ventral injury located behind the terminal aperture (forma aegra *fenestra sensu* Keupp, 2006) was found in another *Ptychoceras*. In all cases, the healed shell is attached to the inner surface of the preserved pre-traumatic conch wall like in other ammonoids and modern *Nautilus* with repaired injuries. No additional layers were secreted on top of the outer prismatic layer, as expected for an internal shell.

Truncation of shell is restricted to the first shaft in *Ptychoceras* (Doguzhaeva & Mutvei, 1989, 1993, 2015). Truncation also occurs in Palaeozoic nautiloids (e.g. Turek & Manda, 2012) and coleoids (Doguzhaeva, Mapes & Mutvei, 2002). Doguzhaeva & Mutvei (1989) suggested that the truncation in *Ptychoceras* occurred due to muscular action of the ammonoid body, during the formation of the second shaft. Kakabadze & Sharikadze (1993) assumed that the truncation could have occurred randomly during the formation of the first to the beginning of the second shaft. Reported fragments preserved in the partially broken phragmocone chambers near the point of truncation (Doguzhaeva & Mutvei, 1989, pl. 9, 10) support the hypothesis of Doguzhaeva & Mutvei (1989). The feather-like structure (Fig. 5E) implies the presence of the shell-secreting mantle edge and periostracum in *Ptychoceras*, which disproves the endocochleate hypothesis for this ammonoid.

Palaeopathologies of heteromorphs include various shell abnormalities and deformed suture lines. Pseudoinversion of suture lines refers to pointed saddles and rounded lobes. Pseudoinversion has been reported for the Late Cretaceous heteromorphs *Glyptoxoceras* (Westermann, 1975; Ward & Westermann, 1976) and *Baculites* (Henderson *et al*., 2002). Rogov (2018) found this in several Jurassic and Cretaceous monomorphs. Another internal abnormality of the ammonoid conch is sutural asymmetry relative to the venter, while the conch wall is unaffected [forma aegra *juxtalobata* (Landman & Waage, 1986; Keupp, 2012)]. In this case, the siphuncular tube moved out of its ventral central position. This type of palaeopathology occurs in both heteromorphs and monomorphs (Keupp, 2012). However, the question of what causes these pathologies remains unanswered. Various authors speculated that the asymmetries were caused either by the asymmetric development of reproductive glands due to parasites or due to 'epithelial diseases' (Keupp, 2012; De Baets *et al*., 2015*a*). 'Morton's syndrome' also affected conch symmetry, where the asymmetry is unrelated to external injuries and occurs in 3–6% of scaphitids from South Dakota (Landman & Waage, 1986). This phenomenon is widespread in keeled monomorphs, such as Jurassic *Graphoceras* and *Pleuroceras* (Morton, 1983; Keupp, 2012). As in many other cases of abnormalities with unclear aetiology, this asymmetry has been explained by parasitic infestation (Morton, 1983; De Baets, Keupp & Klug, 2015*b*), although traces of parasites have not been documented in asymmetric conchs.

(2) **Prey**

Reports of fossil cephalopod stomach contents are rare (Table S3). Planktotrophy was suggested for ammonoids that have aptychus-type, calcified lower jaws (Kruta *et al*., 2011, 2015; Tanabe, 2011; Tanabe *et al*., 2015*a*; Keupp *et al*., 2016*a*). This is supported by finds of stomach contents associated with a radula in *Baculites* (Kruta *et al*., 2011) and *Allocrioceras* (Wippich & Lehmann, 2004), a pelagic, aperture-upwards drifter that probably fed on echinoderms (comatulid crinoids or ophiuroids; Fig. 6). Diet remains from Jurassic and Triassic monomorphs comprise foraminifera, ostracoda, decapod crustacean, bivalves, aptychi, and crinoid hardparts (e.g. *Saccocoma*) in *Neochetoceras* and corroborate planktotrophy in ammonoids (Wippich & Lehmann, 2004; Ritterbush *et al*., 2014; Klug & Lehmann, 2015). Interestingly, the modern coleoid *Japetella* shares radular tooth morphology with some Jurassic ammonoids (Kruta *et al*., 2011; Keupp *et al*., 2016*a*), which have been regarded as microphagous planktotrophs.

Jurassic–Cretaceous heteromorphs are widely accepted as microphagous zoo-planktotrophic suspension feeders (Nesis, 1986, 2005; Kruta *et al*., 2011; Tajika, Nützel & Klug, 2018). Many heteromorphs reached large sizes (e.g. *Baculites grandis* with a conch length of 250 cm; N. Larson, personal communication) and are considered passive drifters with low manoeuvrability (Westermann, 1996; Mikhailova & Baraboschkin, 2009). Without direct evidence, Nesis (1986, 2005) suggested the presence of membranes between the arms or a special mucus web to collect planktic prey out of the water column. Heteromorphs likely lived in the water column (Cecca, 1997; Guex, 2006), i.e. with direct access to

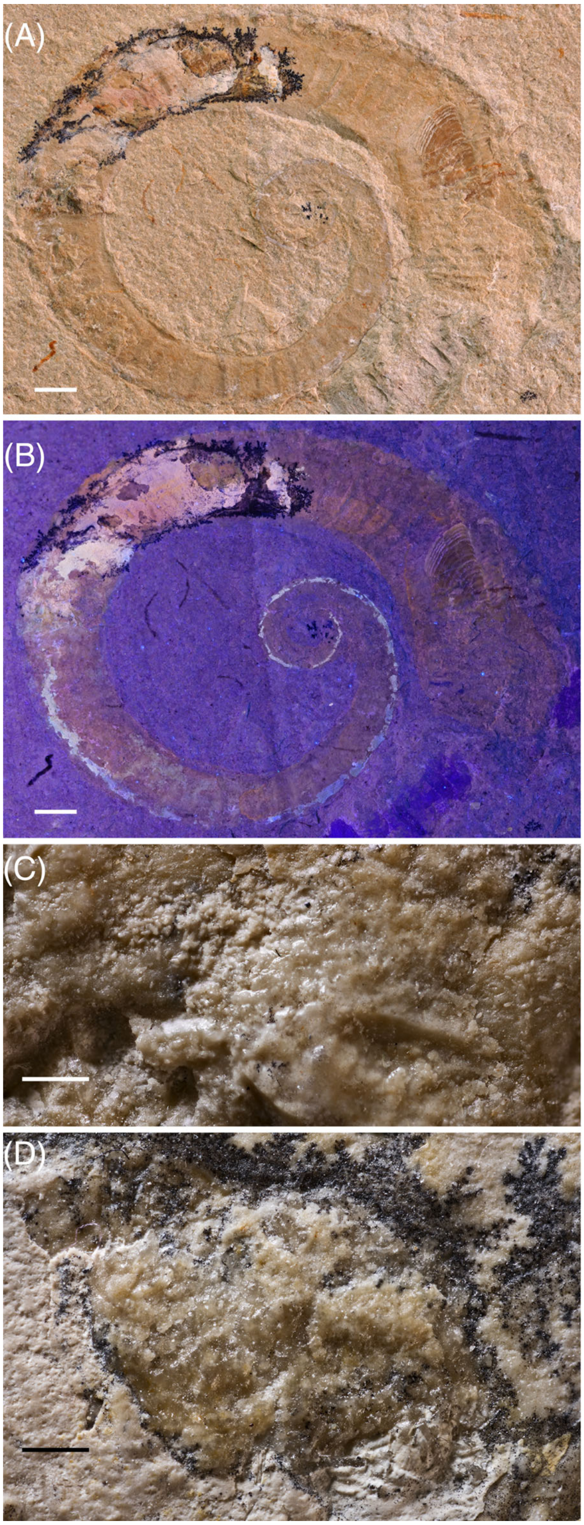

Fig. 6. Stomach content of *Allocrioceras* (specimen shown in Wippich & Lehmann, 2004). (A) Image taken under daylight. (B) Same specimen imaged under ultraviolet light showing preserved soft parts such as the siphuncle and remnants of the stomach. (C) Close up of assumed but unidentifiable stomach remains. (D) Stomach remains of planktic comatolids (crinoids). Scale bars: A and B = 5 mm, C and D = 0.5 mm.

meso- and microplankton. Based on the reconstructed swimming position for heteromorphs with U-shaped body chambers in which the aperture pointed upwards (Kaplan, 2002), it is assumed that their diet was composed of microscopic particles or organisms (Kruta *et al.*, 2011; Keupp, 2012; Ritterbush *et al.*, 2014; Klug & Lehmann, 2015; Keupp *et al.*, 2016*b*). Remarkably, the jaw morphology of modern coleoids does not entirely relate to diet (Clarke & Maddock, 1988). Jaw morphology only reflects the maximum size of prey and dictates the area for the insertion of mandibular muscles and hence its mass and biting force (Kear, 1994). All Cretaceous heteromorphs, except the crioceratids, share an aptychus-type lower jaw (Section II.1.*a*). The aptychus is potentially not involved in determining prey size but prey type. Accordingly, both the Crioceratidae with an anaptychus and other aptychus-bearing Cretaceous heteromorphs may differ in their food preferences.

All modern cephalopods are carnivores – ranging from active predators to more passive forms like *Vampyroteuthis* (Norman, 2000; Golikov *et al.*, 2019). Hanlon & Messenger (2018) documented cannibalism for every known species of modern coleoids except *Sepioteuthis sepoidea*. The occurrence of cannibalism appears to be related to poor food supply (Ennis & Collins, 1979). Research on stomach contents in modern cephalopods is difficult because the jaws reduce the prey to unidentifiable pieces. Hardparts needed for the identification of prey organisms are often regurgitated, leading to an underestimation of soft-bodied prey in estimations of diet (Rodhouse & Nigmatullin, 1996). This is because the oesophagus diameter is limited because it passes through the brain. This likely also applied to most extinct neocephalopod groups such as ammonoids (Engeser, 1996; Klug *et al.*, 2016, 2019). Modern cephalopod stomachs often contain skeletal parts of fish, crustaceans, and cephalopods (even from the same species). A shift of food resources during ontogeny is evident. The juveniles of most modern cephalopods feed on crustaceans and shift towards larger fish and other cephalopods later in ontogeny (Rodhouse & Nigmatullin, 1996). Only a few coleoids seem to be specialists; the majority appear to be non-selective in their choice of prey [e.g. Mather (1993) for observations on octopuses]. Rodhouse & Nigmatullin (1996) observed that squid and cuttlefish preying on pelagic crustaceans ingest the exoskeleton, whereas octopuses paralyse their prey with cephalotoxin, digest only the flesh and reject the exoskeleton. This is relevant for the reconstruction of predator–prey relationships in heteromorphs. This difference in behaviour might be related to the need to form a mineralised internal skeleton or other unknown factors. Larson (2002) speculated on canibalism in scaphitids. Based on their high demand for calcium, Larson (2002) postulated that ammonoids fed on crustaceans, echinoids, molluscs, and possibly fish.

(3) Epizoa, parasites, and commensalism

Syn vivo encrustations, i.e. epizoa (in contrast to *post-mortem* encrustation of dead shells – epicole; see Davis, Mapes &

Klofak, 1999), provide a unique source for palaeoecological reconstructions (Lukeneder, 2008). Some cases have been attributed to parasitism, while others might indicate *syn vivo* epizoism, which ranges from associations that might have been detrimental to both or beneficial for one or both organisms.

Four criteria have been applied to identify cases of *syn vivo* associations of epizoans with ammonoid conchs (see Keupp, 2012). (*i*) Associations found on both flanks, but not at the apertural region mostly refer to ectoparasites or epizoans [see exceptions in Mironenko (2016) and Landman, Slattery & Harries (2016*b*)]; in the case of disease or endoparasitism, no external injuries are visible, but pathologies develop within soft tissues. (*ii*) The growth of associated organisms stops precisely at a whorl or is otherwise outpaced by the conch growth of the cephalopod. (*iii*) Associated organisms show a growth direction consistent with shape and life position of the cephalopod and may follow changes in growth direction of the host. (*iv*) The cephalopod reacts to its epizoans by altering its conch form such as non-planispiral coiling, shortening of body chamber (Klug *et al.*, 2004), and other pathologies.

Cases of conch deformation or deviation from normal planispiral coiling caused by encrusters, which are still preserved, provide incontrovertible evidence for *syn vivo* encrustation in ammonoids (Ramming *et al.*, 2018). *Syn vivo* encrustations may result in monomorphs resembling heteromorphs (Checa, Okamoto & Keupp, 2002). Patterns related to criteria 1 and 3 are the only indicators useful to infer *syn vivo* encrustation when host growth has stopped, but could potentially develop in *post-mortem* sclerobiont attachment during necroplanktic drift (Stilkerich, Smrecak & De Baets, 2017). However, marked *post-mortem* drift is unlikely in the case of heavy encrustation and smaller conchs (Yacobucci, 2018; Wani et al. 2005). Furthermore, the conch might change orientation during *post-mortem* drift and due to added weight by epicoles. The orientation and position of encrusters during life could also support the idea that heteromorphs were nektoplanktic or at least neither demersal nor benthic.

Encrustation by cirripedes (Hauschke, Schöllmann & Keupp, 2011), brachiopods (Landman *et al.*, 2016*b*), and bivalves (Misaki *et al.*, 2014) have been reported on Cretaceous heteromorphs. Misaki *et al.* (2014) found anomiid bivalves on both sides of *Pravitoceras* conchs, suggesting these are epizoa. These heteromorphs come from mudstones without signs of strong currents or wave-induced transport. Misaki *et al.* (2014) suggested that *Pravitoceras* was neutrally buoyant and could move vertically, thus contradicting the hypothesis of a benthic life habit (Matsumoto *et al.*, 1981*b*).

Syn vivo encrustation of a Palaeozoic *Ivoites* specimen by hederelloids (?phoronids) caused trochospiral instead of gyrocone coiling (Stilkerich *et al.*, 2017). The pathological specimen survived into adulthood despite multiple encrustations (Stilkerich *et al.*, 2017). If cephalopods reached adulthood showing such deformations, these may not have altered ammonoid health substantially, irrespective of whether such trochospiral coiling was a normal variant or pathological. Regular covariation patterns might relate to structural constraints and may provide information about growth. Highly irregular patterns within the same specimen might indicate a lack of morphogenetic constraints.

Associations between heteromorphs and algae have been suggested repeatedly. Arkhipkin (2014) suggested that *Spiroceras* was associated with macroalgae and that adult life stages of Cretaceous heteromorphs (e.g. scaphitids) clung to macroalgae with their umbilical opening [see also Vašíček & Wiedmann (1994) for Leptoceratoidinae such as *Karsteniceras*]. However, direct evidence for such associations has not been found yet, rendering this idea speculative (Landman *et al.*, 2016*a*). The fossil record of non-calcified macroalgae is sparse; potential biomarkers like sterols may help to identify their presence.

Hatchlings of the trochospiral *Mariella* or orthoconic *Scipnoceras* have been interpreted as semi-sessile based on associations with algal mats (Stinnesbeck, Frey & Zell, 2016). However, this is likely a taphonomic artefact and solid evidence for this life habit is needed because such life habit is unknown in modern cephalopods.

V. HABITAT RECONSTRUCTION

(1) Taphonomic controls on facies distributions

The relationship between heteromorphs and facies has been debated due to *post-mortem* drift. This issue stems from externally shelled cephalopods having phragmocones, which can remain gas-filled after death allowing the conch to float and drift varying distances away from the living animals' habitat [Fig. 7; Reyment (1958, 1973, 2008); for alternative perspectives see Wani & Gupta (2015) and Yacobucci (2018)]. However, numerous studies have argued that *post-mortem* drift was rare among ammonoids, and that their fossils closely reflect their life distributions (e.g. Kennedy & Cobban, 1976; Tanabe, 1979; Chamberlain, Ward & Weaver, 1981; Wani *et al.*, 2005; Wani & Gupta, 2015; Yacobucci, 2018). These interpretations are based on the low frequency of encrusters, degree of shell breakage, frequency of preserved jaws in body chambers, size–frequency distribution of conchs, low drift potential of numerous conch morphotypes, and geographic distribution patterns. Kennedy & Cobban (1976) proposed that facies independence and broad geographic ranges as well as distinct facies associations and limited ranges should reflect high and low *post-mortem* drift, respectively. They state that the large numbers of unbroken, well-preserved ammonoids at many localities represent autochthonous assemblages, which cannot be explained by *post-mortem* drift. This is supported by taphonomic and experimental studies of modern nautilid conchs, which revealed that drifted conchs show signs of fragmentation and encrustation (Wani, 2004; Reyment, 2008). Yacobucci (2018) argues that most ammonoid conchs, except for highly inflated monomorphs, were unlikely to undergo long-distance *post-mortem* drift. This study

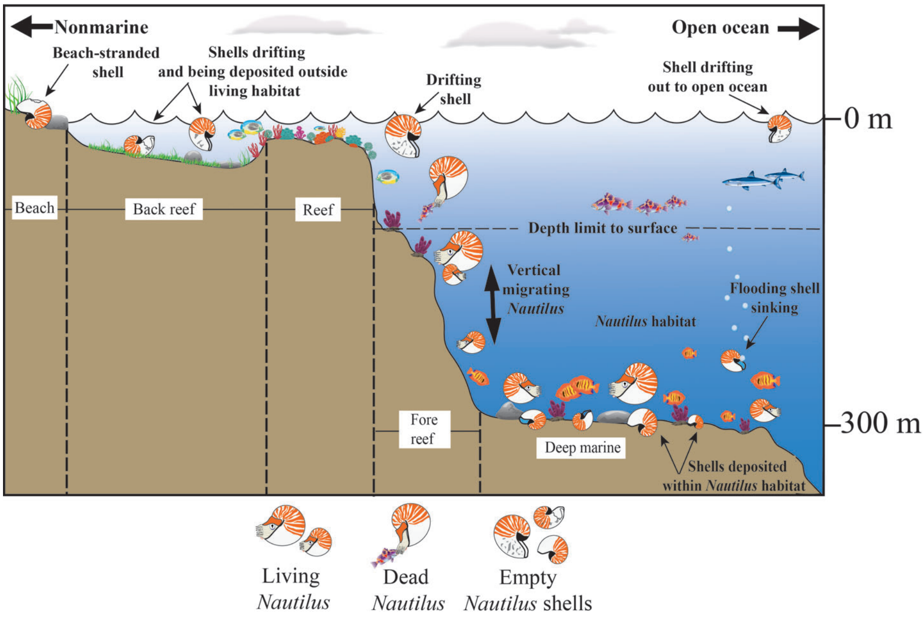

Fig. 7. Potential taphonomic pathways of modern *Nautilus* prior to burial (modified from Maeda & Seilacher, 1996; Mapes *et al.*, 2010*a*,*b*). *Nautilus* habitat ranges from 20 to 600 m depth; however, most live within a few meters of the seabed. The 'Depth Limit to Surface' is the theoretical limit where an empty conch cannot ascend to the sea surface because hydrostatic pressure forces water into the phragmacone and causes the conch to become negatively buoyant and sink.

also shows that most Cretaceous ammonoids, even those with conch forms conducive to *post-mortem* drift, rarely had substantial biogeographic ranges (i.e. basinwide, intercontinental), which would be expected if they were floating over great distances after death.

Post-mortem drift in heteromorphs has not been considered to the same extent as for monomorphs; the latter being morphologically more like nautilids, which are assumed to be reasonable analogs. However, the few available studies suggest that the impact of *post-mortem* drift on heteromorph spatial distributions is minimal (Tanabe, Obata & Futakami, 1978; Tanabe, 1979; Kawabe, 2003; Reboulet, Giraud, & Proux, 2005; Landman *et al.*, 2010*b*, 2019; Landman & Klofak, 2012; Misaki *et al.*, 2014; Slattery, Harries & Sandness, 2018). Stable isotopic analysis of heteromorphs and associated benthic faunas provides evidence for limited *post-mortem* drift. These studies reveal that the δ^{18}O and δ^{13}C composition of scaphitids, baculitids, and nostoceratids more closely match the isotopic composition of associated benthic faunas than known planktic organisms. This has been interpreted as an indication that they were living near where they were collected (Tsujita & Westermann, 1998; He, Kyser & Caldwell, 2005; Landman & Klofak, 2012; Landman *et al.*, 2012*b*; Sessa *et al.*, 2015).

Berry (2018*a*,*b*) and Landman *et al.* (2019) are among the few studies to suggest that some heteromorph conchs could undergo long-term and/or long-distance *post-mortem* drift. Berry (2018*a*,*b*) utilised changes in both bryozoan zooid size and the direction of growth in colonies encrusting the internal body chambers of *Baculites* and *Scaphites* to suggest that these heteromorphs experienced long-term *post-mortem* drift. Landman *et al.* (2019) argued that the occurrences of North American *Hoploscaphites* in Europe are best explained by long-distance *post-mortem* drift due to their rarity. However, Machalski *et al.* (2007) suggested that North American *Hoploscaphites* and *Discoscaphites* in Europe are more likely related to immigrant populations rather than *post-mortem* drift due to the greater potential for small cephalopod shells to be buried close to their habitats.

(2) Life habit controls on facies distributions

The association of water-column-dwelling ammonoids with a benthic bio- and lithofacies or a lack thereof is likely due to their preferred habitats and positions in the water column (Ziegler, 1967; Kennedy & Cobban, 1976; Batt, 1986, 1989; Westermann, 1996; Lukeneder, 2015). They would have tracked these environmental preferences both spatially and temporally, which in turn would be expressed in the stratigraphic record as changes in faunal occurrences and/or ranges. Environmental changes in the upper water column would be expressed in the stratigraphic record as changes in occurrences and abundances of nektic and planktic organisms (e.g. ammonoids, fish, planktic foraminifera, nannoplankton), while potentially showing no concomitant pattern among benthic organisms, or lithofacies [Soule & Kleppel (1988) and references therein]. Nektic (i.e. actively swimming in the water column), nektoplanktic (i.e. passively floating in the water column), and vertically migrating (i.e. moving vertically through the water column) ammonoids likely tracked their preferred ecological conditions and food sources through the water column. This would have decoupled them from benthic faunas, environments, and facies, unless their prey was tied to a benthic environment (Westermann, 1996). By contrast, nektobenthic (i.e. living near the sea bottom) ammonoids would have been influenced by the same conditions (e.g. oxygen, turbidity) that controlled the distribution of benthic organisms, which explains the association of many ammonoids with specific benthic bio- and/or lithofacies (e.g. Tsujita & Westermann, 1998; Landman *et al.*, 2012*b*; Slattery *et al.*, 2018). Documenting changes in heteromorph occurrences and abundances across benthic bio- and lithofacies can reveal important details about their preferred habitats, specifically when examined within a sequence stratigraphic framework. Kennedy & Cobban (1976) showed that occurrences of Cretaceous ammonoids, including heteromorphs, rarely exhibit discernable lithofacies patterns. However, they also noted that there are obvious changes in abundances among taxa across lithofacies. Variation in heteromorph abundances has also been documented across benthic biofacies, which are attributed to changes in marine environmental conditions (e.g. oxygen) that are independent of lithofacies (e.g. Lukeneder, 2003, 2004, 2005; Slattery *et al.*, 2018).

Heteromorphs are known from an array of facies spanning tidally influenced littoral to oceanic environments (Fig. 8; Westermann, 1996). Most heteromorphs occur in shallow-subtidal to offshore facies deposited in neritic (i.e. open-ocean-facing seas) and epeiric seas (i.e. seas covering continental interiors). They are common in continental slope facies, but rare in bathyal, foreshore, and littoral facies (Westermann, 1996). Most heteromorphs preferred epipelagic depths (0–200 m), and for certain taxa, upper mesopelagic depths (200–600 m) due to depth limitations imposed by the strengths of their shells (Hewitt, 1996). Taxa found in oceanic facies were likely living within a few meters of the continental slope and/or in the water column well above the slope and bathyal seafloor at epi- and/or upper mesopelagic depths (Hewitt, 1996; Westermann, 1996). The few examples of heteromorphs in foreshore and littoral facies (e.g. Hoganson & Murphy, 2002) are likely due to *post-mortem* transport *via* drift or storms.

Devonian, Triassic, and Jurassic heteromorphs show a preference for deep-subtidal to offshore facies but are rare in shallow-subtidal, slope, and bathyal facies (Fig. 8A; Table S4; Dietl, 1978; Laws, 1982; Chlupáč & Turek, 1983; www.paleodb.org). The rarity of Pre-Cretaceous heteromorphs in shallow-subtidal, slope, and bathyal facies suggests that these ammonoids did not inhabit these environments but were transported into these settings *via* storms or *post-mortem* drift from their epipelagic, deep-subtidal to offshore habitats.

Early Cretaceous heteromorphs preferred deep-subtidal to bathyal facies (Fig. 8B; Table S4). Barragan, Gonzalez-Arreola & Villaseñor (2004) documented distributions of Barremian ammonites in Mexico, which were controlled by water-column oxygenation and the preferred water depth of each species. They suggest that ancylocone heteromorphs were nektic or nektoplanktic based on their abundance in anoxic facies, which indicates a preference for offshore settings (Barragan *et al.*, 2004). Lukeneder (2003, 2004, 2005) suggested that the Barremian ancyloceratid *Karsteniceras* preferred low-oxygen conditions based on its mass occurrences in dysoxic facies. Marcinowski & Wiedmann (1990) noted that Albian heteromorphs in Poland are restricted to clay- and marlstones rather than sandstones, which suggests that these ammonites preferred offshore facies rather than subtidal facies. Reboulet *et al.* (2005) studied Albian ammonite occurrences and abundances across Oceanic Anoxic Event 1d in the Vocontian Basin (France) and found that most heteromorphs are associated with offshore neritic to oceanic facies. For example, the baculitid *Lechites* is most abundant in continental-slope facies. The torticones *Turrilitoides* and *Mariella* as well as the hamiticones *Anisoceras* and *Hamites* are associated with offshore neritic and oceanic facies. Tajika *et al.* (2017) showed that Cretaceous cephalopod associations of Switzerland, including heteromorphs (e.g. *Emericiceras*, *Mariella*), are dominant in deep-subtidal to offshore facies and rare to absent in shallower, carbonate facies. Several studies suggest that bochianitids are deeper-water indicators due to their abundances in limestones and claystones deposited in continental slope facies (>200 m) and absence in neritic as well as epeiric facies (Company, 1987; Reboulet & Atrops, 1997; Baraboschkin & Enson, 2003; Reboulet *et al.*, 2005; Arkadiev, 2008; Lukeneder, 2015).

Late Cretaceous heteromorphs have a preference for shallow-subtidal to offshore facies, but are rare in slope and bathyal facies (Fig. 8C; Table S4). Baculitids are broadly distributed with juveniles being common in well-oxygenated, shallow- to deep-subtidal facies and adults being common in well-oxygenated, deep-subtidal to anoxic, offshore facies (Fig. 9; Tsujita & Westermann, 1998; Kawabe, 2003; Slattery *et al.*, 2018). The earliest juvenile *Baculites* have been recorded in shallow-subtidal to offshore facies, which indicates that they might have been more facies independent and/or more subject to drift as compared to more mature individuals (Landman & Klofak, 2012; Slattery *et al.*, 2018; N.H. Landman, personal communication; Rowe *et al.*, 2020). The giant baculitid *Pseudobaculites* is common in subtidal facies but rare in offshore facies (W.A. Cobban, personal communication). Turrilitids, scaphitids, diplomoceratids, and nostoceratids are typically associated with well-oxygenated, subtidal to offshore facies due to their nektobenthic life habit (Fig. 9; Scott, 1940; Kennedy & Cobban, 1976; Tanabe *et al.*, 1978; Tanabe, 1979; Matsumoto *et al.*, 1981*a*; Batt, 1986, 1989; Tsujita & Westermann, 1998; Kawabe, 2003; Landman *et al.*, 2012*b*; Slattery *et al.*, 2012, 2018; Olivero & Raffi, 2018; Rowe *et al.*, 2020; J. S. Slattery, personal observations). The scaphitid *Worthoceras* likely inhabited the middle to upper water column based on their broad distribution in well-oxygenated, subtidal to anoxic, offshore facies (Scott, 1940; Batt, 1986, 1989). Several nostoceratids in North America are common in shallow-subtidal facies but rare to absent in deep-subtidal to offshore facies (Table S4; Fig. 9; Kennedy & Cobban, 1976, 1994;

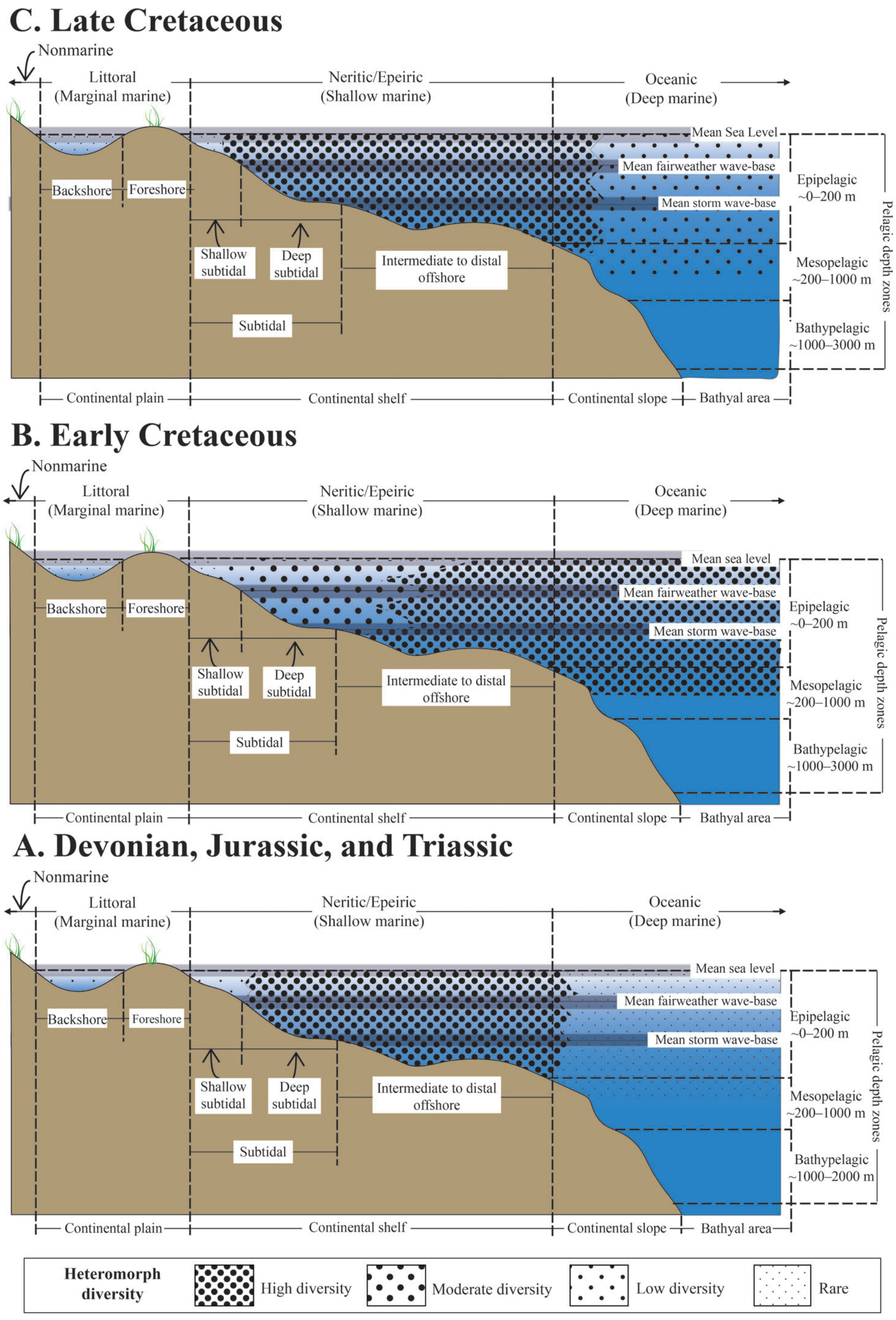

Fig. 8. Heteromorph distributions across marine environments and depth zones during the (A) Devonian, Triassic, and Jurassic, (B) Early Cretaceous, and (C) Late Cretaceous. Based on data from Table S4.

Cobban, 1993; Cobban *et al.*, 1993; Kennedy, Cobban & Scott, 2000*a*,*b*). Hamitids and anisoceratids are commonly restricted to well-oxygenated, subtidal facies, however, the hamitid *Stomohamites* and anisoceratid *Allocrioceras* have broad distributions ranging from well-oxygenated, subtidal to anoxic, offshore facies (Kennedy & Cobban, 1976; Batt, 1986, 1989). The increase in heteromorph diversity in shallow-subtidal settings during the Late Cretaceous likely reflects an evolutionary shift among Ancyloceratina to shallower-water settings.

(3) Ecological requirements based on shell geochemistry

Stable isotope proxy systems provide information on habitat depth, depth change through ontogeny, and growth rates of individual monomorphs and heteromorphs (e.g. Moriya *et al.*, 2003; Lukeneder *et al.*, 2010; Fig. 10). Most analyses to date have been focused on baculitids and scaphitids from the Late Cretaceous (He *et al.*, 2005; Landman *et al.*,

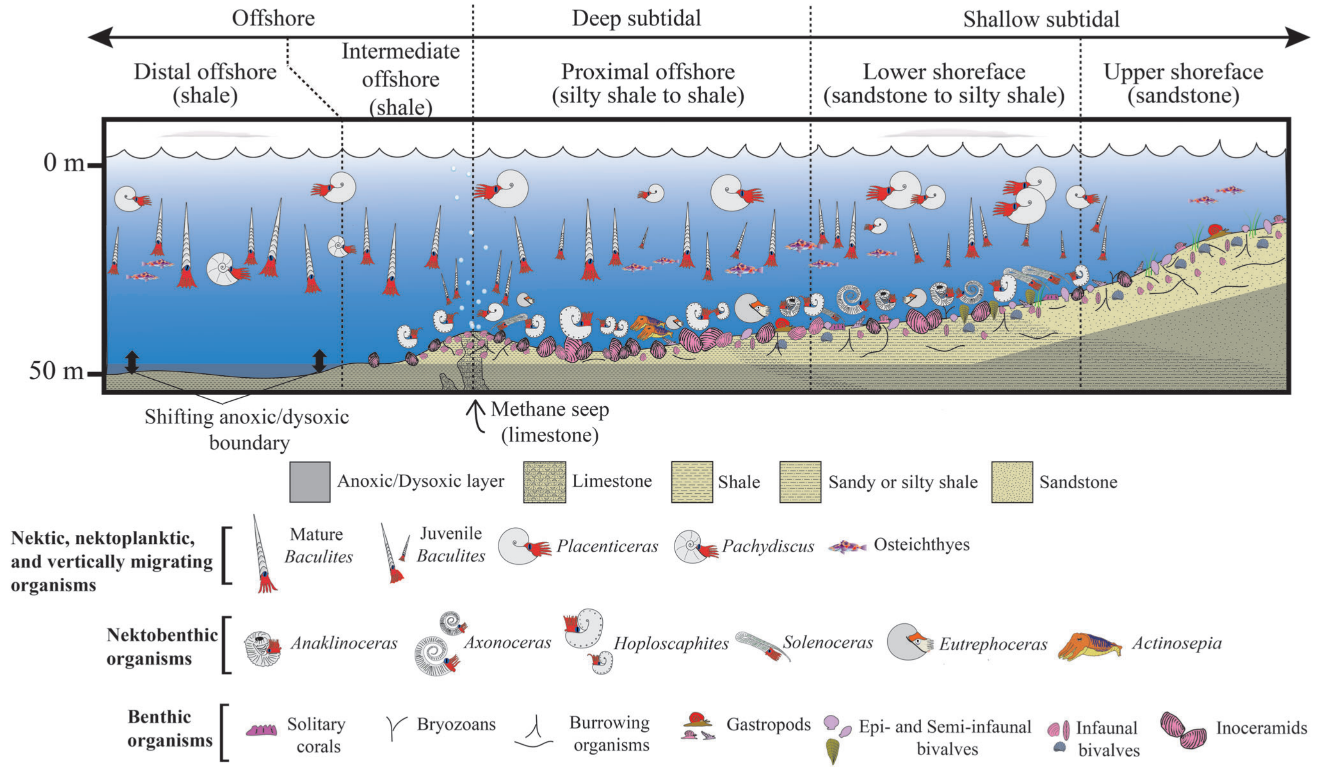

Fig. 9. Shoreface to offshore ammonoid facies and habitat distributions in the late Campanian *Baculites compressus* Biochron (Late Cretaceous) in the Western Interior Seaway. Based on data from: Kennedy & Cobban (1976); Cobban, Kennedy, & Scott (1993); Cobban *et al.* (1993); Larson *et al.* (1997); Landman & Klofak (2012); Landman *et al.* (2012*a*); and Meehan & Landman (2016).

2012*b*). Variation in the oxygen isotope ratio (δ^{18}O) reflects changes in temperature or the oxygen isotope ratio of sea water, which often covaries with salinity (Mátyás *et al.*, 1996). Combined temperature and salinity gradients create a variable profile in δ^{18}O between surface water and bottom water, which is recorded in shell carbonate precipitated in equilibrium with those waters. Seasonal variation in these parameters can impart sinusoidal variation and therefore a chronometer in the shells and aptychi of heteromorphs (Fatherree, Harries & Quinn, 1998; Kruta, Landman & Cochran, 2014; Ellis & Tobin, 2019), although swimming behaviour and growth rate can complicate these patterns in ammonoids (Linzmeier, 2019). Cephalopods are thought to precipitate shell aragonite in oxygen isotope equilibrium with ambient seawater stable oxygen isotope composition ($\delta^{18}O_{SW}$) and temperature (Landman *et al.*, 1994). Stable carbon isotope ratios (δ^{13}C) record a mixture of carbon dominated by dissolved organic carbon from water and minor respired carbon (McConnaughey & Gillikin, 2008). Therefore, the habitat depth of modern cephalopods can be directly inferred from measured carbonate oxygen isotope ratios of their aragonitic shell or calcitic aptychi (Auclair *et al.*, 2004; Lukeneder *et al.*, 2008; Kruta *et al.*, 2014; Lukeneder, 2015; Linzmeier *et al.*, 2016). To interpret habitat depth or growth rate from δ^{18}O and δ^{13}C of fossils, additional isotopic information derived from co-occurring benthic and planktic organisms is required.

The habitats of Late Cretaceous heteromorphs have been studied using stable isotope analyses. *Discoscaphites* and *Baculites* from Mississippi show δ^{18}O values that are more similar to both benthic molluscs and foraminifera than to planktic foraminifera (Sessa *et al.*, 2015). Individuals have consistent δ^{18}O through the gerontic whorl, supporting an interpretation of rapid growth and consistently benthic habitat (Ferguson *et al.*, 2019). Analysis of the earliest whorls of *Hoploscaphites* from South Dakota suggest a benthic embryonic development, planktic hatchlings, and a habitat change after about one whorl (Linzmeier *et al.*, 2018). These data may also suggest seasonally protracted spawning like some modern cephalopods (Rocha, Guerra & González, 2001). Other work spanning multiple Campanian ammonoid zones from the Western Interior Seaway suggests *Didymoceras* was living in warmer or more brackish water than co-ocurring *Scaphites* and *Baculites* (He *et al.*, 2005).

The interpretation of δ^{13}C in heteromorphs, like other marine molluscs, reflects the δ^{13}C of dissolved inorganic carbon (DIC) (McConnaughey & Gillikin, 2008). In the modern ocean, the δ^{13}C varies with changes in the ratio of respiration to photosynthesis and proximity to sources of unusual δ^{13}C from DIC (e.g. methane seeps). Analyses of *Baculites* from the Western Interior Seaway (WIS) suggest that some heteromorphs lived on or close to cold seeps throughout their lives and exploited the diverse prey available at the seeps

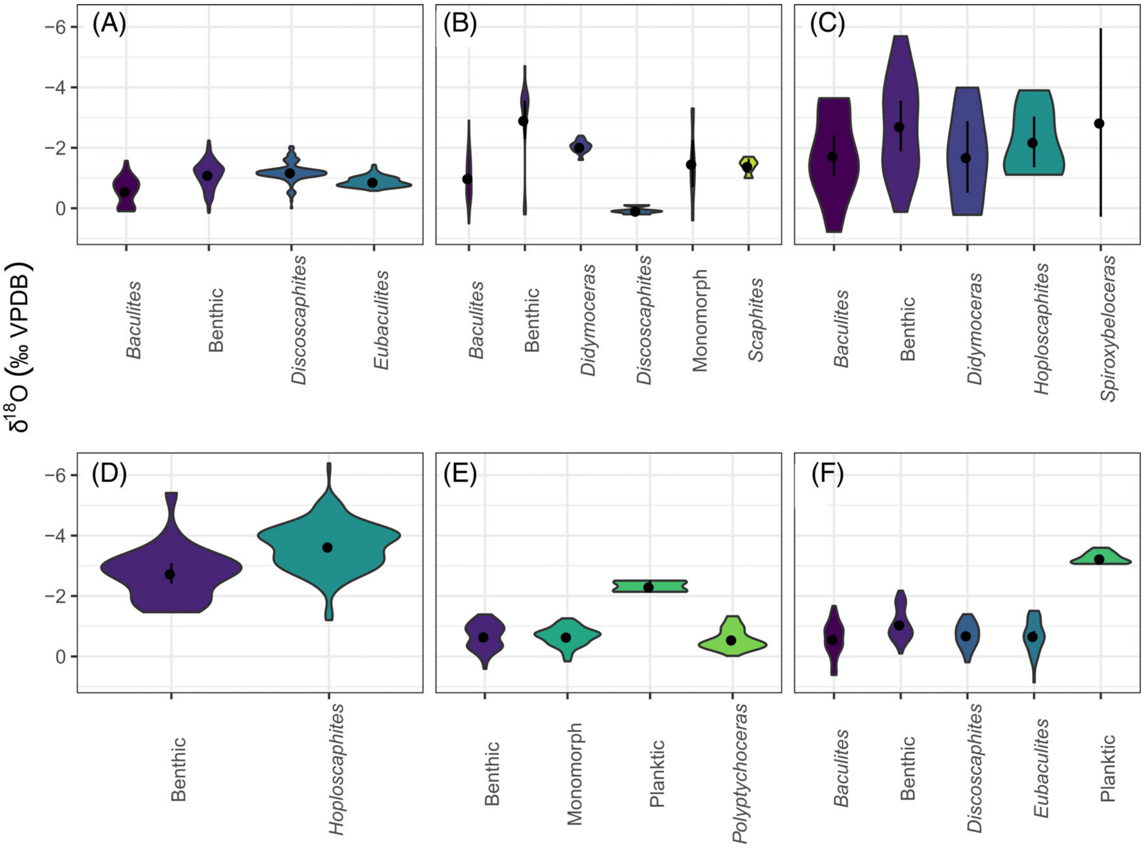

Fig. 10. Habitat depth reconstruction based on oxygen isotope ($\delta^{18}O$) values collected from well-preserved, coeval monomorphs, heteromorphs, benthic faunas, and planktic faunas. Modified after (A) Ferguson *et al.* (2019), (B) He *et al.* (2005), (C) Landman *et al.* (2012*b*), (D) Linzmeier *et al.* (2018), (E) Moriya *et al.* (2003), and (F) Sessa *et al.* (2015), VPDB, Vienna Pee Dee belemnite.

(Landman *et al.*, 2018). *Hoploscaphites* and *Didymoceras* also appear to use methane seep habitats both as adults (Landman *et al.*, 2012*b*) and juveniles (Rowe *et al.*, 2020).

The growth rates of *Baculites* have been estimated using stable isotopic methods. Their orthoconic conchs are relatively easy to sample serially. By interpreting the pronounced sinusoidal pattern in $\delta^{18}O$, Fatherree *et al.* (1998) inferred a growth rate of 33 cm/year for a subadult *Baculites compressus*. Sampling of other *Baculites* suggest similarly high growth rates if interpreting sinusoidal variability in either $\delta^{18}O$ or $\delta^{13}C$, although there are caveats about geographic differences in both isotope proxies that could reflect migration (Ellis & Tobin, 2019). Future investigation of heteromorph living depths and growth rates using stable isotope methods will yield important information that cannot be gathered from other methods.

(4) Reproduction

Early ammonoids (Anetoceratinae) have slightly curved embryonic conchs, which are among the largest of all ammonoids (De Baets *et al.*, 2013*a*; De Baets, Landman & Tanabe, 2015*c*). They range from about 6 mm in *Metabactrites* to 5 mm in *Ivoites* to 3.7 mm in *Erbenoceras*. This, together with their small body chamber volume, implies low fecundity (35–500 eggs). De Baets *et al.* (2012) argued that increased coiling and a reduction in embryonic conch size with an increase in adult size affected fecundity. To date, no embryonic conchs of Triassic heteromorphs have been reported (De Baets *et al.*, 2015*c*; Laptikhovsky, Nikolaeva & Rogov, 2018), but adults are generally small suggesting low fecundity. The size of *Spiroceras* hatchlings is 0.8 mm (Landman, Tanabe & Shigeta, 1996) and falls within the 95% confidence interval for all Jurassic ammonoids (De Baets *et al.*, 2015*c*). Heteromorphs have the smallest embryonic conchs of all Cretaceous ammonoids with median measurements of 0.8 mm, which are smaller than in Ammonitina (0.9 mm), Phylloceratina (0.9 mm), and Lytoceratina (1.2 mm; De Baets *et al.*, 2015*c*). It is tempting to attribute this to constraints imposed by adult size and mobility, which probably drove selection towards an increasing number of smaller hatchlings that are better adapted to a planktic life habit (e.g. Laptikhovsky *et al.*, 2018; Tajika *et al.*, 2018, 2020). However, additional data comparing adult and embryonic sizes and distributions will be necessary to corroborate this hypothesis.

(5) Intraspecific variability

Herein, we use the six archetype morphologies (orthocone, gyrocone, cyrtocone, ancylocone, torticone, and vermicone) rather than the 44 subtypes distinguished by Kakabadze

(2015); Figs. 1F, 11; see also Section III). Phenotypic variation in conch shape, ornamentation, size, and suture line is common in ammonoids (De Baets *et al.*, 2015*a*). Intraspecific variation rarely has been considered in ammonoid taxonomy, even less so in heteromorphs (Ropolo, 1995; Kakabadze, 2004, 2015; Witts *et al.*, 2020), where it might partially relate to difficulties in quantitatively analysing and comparing shape variation in orthoconic, gyroconic, or torticonic forms. As in monomorphs, intraspecific variation can be continuous between two or more extremes (e.g. De Baets, Klug & Monnet, 2013*b*) or discontinuous between two or more morphs (e.g. Bert, 2013). More general principles like an association between strength of ornamentation and whorl cross section (Buckman's law of covariation) illustrate common ancestry and growth principles among ammonoids and molluscs as a whole (Monnet, De Baets & Yacobucci, 2015*b*). Various authors have argued that intraspecific variation might be higher in heteromorphs than in their monomorph relatives (e.g. Dietl, 1978; Kakabadze, 2004; De Baets *et al.*, 2013*b*). This might make sense as coiling in heteromorphs is less constrained by the previous whorl and might even deviate from the planispiral plane as in gastropods. In the most extreme examples like *Spiroceras*, orthoconic, crioconic, and trochospiral coiling occurs within one species (e.g. Dietl, 1978). The large degree of variation and differences between different sites have been used to argue that *Spiroceras* was pseudoplanktic (Westermann, 1996). Various environmental factors could explain the degree of phenotypic plasticity, and the association of the mode and degree of variation in relationship to environmental factors, partially reflected in the litho- and biofacies, still need to be analysed quantitatively. Differences in coiling and ornamentation occur in gastropods, even within the same species, and are related to differences in environmental factors (Urdy, 2015). Novel methods will allow us to study intraspecific variation quantitatively in orthoconic, gyroconic, and vermiform shapes (Okamoto, 1988*ab*,*c*, 1996; Tsujino, Naruse & Maeda, 2003; De Baets *et al.*, 2013*a*; Urdy, 2015; Ward *et al.*, 2015; Hoffmann *et al.*, 2019). Even taxa that seemingly grow chaotically like *Nipponites* have been demonstrated to have a regular growth pattern consistent with a free-living, pelagic life habit (Okamoto, 1988*c*; Peterman, Mikami & Inoue, 2020*c*). In many cases, more traditionally defined species have been synonymised, leading to more comprehensive analyses of drivers of the mode and degree of intraspecific variation in different taxa (Ward *et al.*, 2015; De Baets *et al.*, 2015*b*; Hoffmann *et al.*, 2019).

Ammonoid conch characters vary ecophenotypically with environmental factors such as water depth and energy (Landman, n.d.; Landman & Waage, 1993*a*; Jacobs *et al.*, 1994; Ikeda & Wani, 2012; Yahada & Wani, 2013; Lukeneder, 2015; Klein & Landman, 2019). Among heteromorphs, only scaphitid conch characters have been quantitatively shown to vary with environment, which is likely linked to their nektobenthic life habit (Landman *et al.*, 2012*a*). Other clades, such as baculitids, appear to show variation in conch characters with facies but this remains to be explored in detail (N.H. Landman, personal communication). Jacobs *et al.* (1994) documented the degree of whorl compression within Turonian *Scaphites whitfieldi* in near- and offshore facies in the WIS. They show that whorls are more compressed in nearshore facies, and that compressed whorls were hydrodynamically more efficient in these higher-energy environments. Landman (n.d.) showed that *Hoploscaphites* became more compressed and nodose in response to a late Campanian to early Maastrichtian shift from lower-energy offshore to higher-energy nearshore environments in the WIS. Landman & Waage (1993*a*) showed how several different conch characters vary within late Maastrichtian *Hoploscaphites* and *Discoscaphites* in near- and offshore facies in the WIS. *Hoploscaphites* in nearshore facies are less umbilicate, more nodose, and have more compressed whorl sections compared to specimens in offshore facies (Landman & Waage, 1993*a*). *Discoscaphites* are also more nodose in nearshore than in offshore facies (Landman & Waage, 1993*a*). These facies-linked patterns indicate that intraspecific variation in conch characters reflect local adaptations of populations to the differing environments associated with the nektobenthic life habit across a spectrum from shallower to deeper habitats. Jacobs *et al.* (1994) hypothesised that iterative evolutionary changes in ammonoid lineages might be driven by selection for conch characters specifically adapted to environments that fluctuate through time with sea level.

VI. HETEROMORPHS THROUGH TIME

(1) Devonian heteromorphs

Ammonoids originated from orthoconic orthoceratids *via* cyrtocone bactritoid ancestors during the Early Devonian (Kröger & Mapes, 2007; Kröger *et al.*, 2011; De Baets *et al.*, 2013*a*; Klug *et al.*, 2015*a*). This is based on a stratigraphically consistent record of evolutionary transitions in both embryonic and later ontogenetic stages within these lineages (De Baets *et al.*, 2013*a*; Klug *et al.*, 2015*a*). Ammonoids completing at least one whorl evolved only once (Anetoceratinae ranging from loosely coiled *Metabactrites* to coiled *Erbenoceras* and closely related forms). However, multiple bactritoid lineages evolved loosely coiled representatives including a lineage leading to *Kokenia* and a lineage including *Cyrtobactrites* and *Pseudobactrites* with a mix of morphological characters. Irrespective of these iterative coiling trends in bactritoids around the origin of ammonoids, heteromorph ammonoids have a short (about 6 million years) appearance during the Palaeozoic (Klug *et al.*, 2015*a*). Early Devonian ammonoids show a rapid trend towards increased coiling in embryonic and post-embryonic development (Klug & Korn, 2004; De Baets *et al.*, 2012). This rapid coiling trend has been linked to increased swimming velocity and manoeuvrability in the face of increased predation pressure (Klug & Korn, 2004; Klug, 2007), although the coiling of the early whorls and

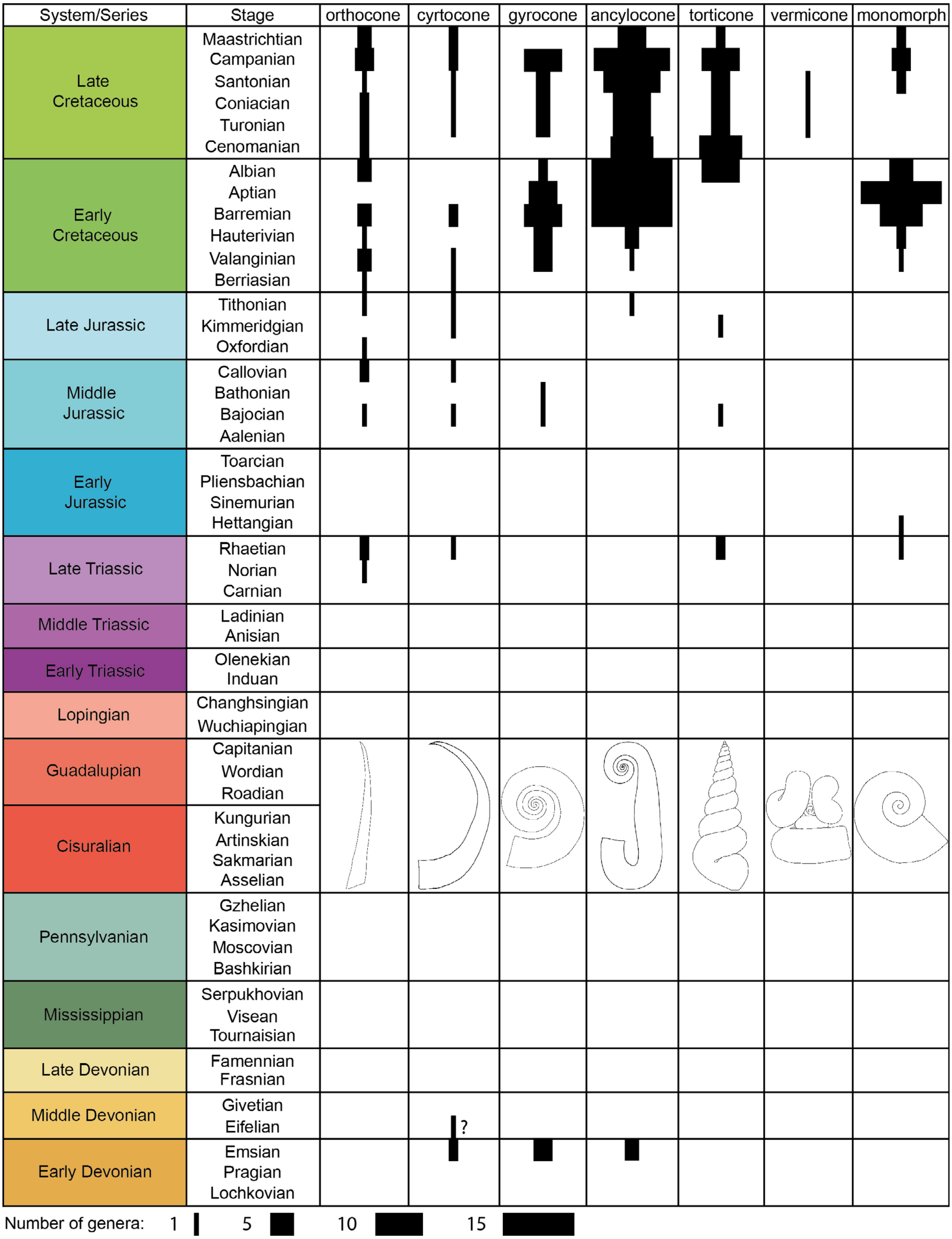

Fig. 11. Stratigraphic distribution of the six arche-morphotypes of heteromorphic conchs from the Devonian, Triassic, Jurassic, and Cretaceous. Also shown are secondarily monomorphic forms derived from heteromorphs. After Wright *et al.* (1996).

increased body chamber volume also influenced fecundity and reproductive strategies (De Baets *et al.*, 2012; Klug *et al.*, 2015*a*). Constructional constraints might also have played a role (Monnet, De Baets & Klug, 2011). Both biotic and abiotic factors impacted this trend as there are both convergent coiling trends within lineages and the preferential extinction of loosely coiled ammonoids during Devonian extinction events (House, 1996; De Baets *et al.*, 2012).

Mesozoic heteromorphs repeatedly underwent convergent uncoiling trends, which is the inverse to that observed in post-embryonic Devonian ammonoids (Fig. 11). These forms were not an evolutionary end stage as some show secondary trends back to planispiral forms such as scaphitids or douvilleiceratids (Wiedmann, 1969; Korn, 2003). Embryonic conchs of all Mesozoic heteromorphs are planispirally coiled unlike those of most Early Devonian ammonoids. Torticone conchs did not exist among Palaeozoic ammonoids. The only exception is a slightly trochospirally coiled *Ivoites* (De Baets *et al.*, 2013*a*), which is interpreted as a pathological phenomenon related to *in vivo* encrustation (Stilkerich *et al.*, 2017).

Early Devonian gyroconic (subtype: crioconic) heteromorphs (Anetoceratinae) are palaeogeographically widely distributed from about 30°N in the Kolyma basin to 45°S in the Anti-Atlas, i.e. a similar range to normally coiled ammonoids. Other ammonoids and loosely coiled bactritoids have a more endemic distribution, which likely indicates poorer dispersal abilities and *K*-strategy selective reproduction (De Baets *et al.*, 2012). These differences could also relate to collection or preservation artefacts. Fragments of loosely coiled and flattened ammonoids are not considered here as they are difficult to identify or to compare with better preserved specimens. The oldest heteromorphs occur 404 million years ago (Ma) during the early Emsian, and these lineages disappear 398 Ma at the beginning of the late Emsian (Klug *et al.*, 2015*a*). Advolute ammonoids with a closed umbilical appear 396 Ma, while advolute forms with an open umbilicus disappear 390 Ma in the early Eifelian. *Kokenia*, another loosely coiled form, is known from the late Eifelian but is usually considered to be a bactritoid due to the age gap as well as differences in morphology. Loosely coiled Palaeozoic ammonoids are therefore maximally distributed for about 16 million years (Myr) and do not reappear for over 170 Myr until the Late Triassic [late Norian, at the beginning of the Sevatian following Jenks *et al.* (2015)].

In summary, loose coiling was successful for a short period in the Palaeozoic (Fig. 11) probably because it provided limited swimming capabilities. Early heteromorphs represent evolutionarily transitional forms to the fully coiled monomorphs. Later, specific environmental or ecological conditions allowed the convergence and longer evolutionary success of heteromorphs in the Mesozoic. However, this was only a post-embryonic phenomenon, highlighting the evolutionary importance of, and constraints related to, a coiled embryonic conch.

(2) Triassic heteromorphs

Triassic heteromorphs rarely attain sizes larger than 30 mm, possess a coarse ornamentation comprised of simple straight ribs, and have low diversity (about 30 species) and disparity (morphologically stable: semi-evolute, orthocone, cyrtocone, torticone, or monomorph trochospiral; Fig. 11) compared to Jurassic and Cretaceous heteromorphs (Monnet, Brayard & Brosse, 2015*a*). Wiedmann (1973*a*) considered the Triassic four-lobed heteromorphs (Choristoceratidae) as a monophyletic family of ceratitic ammonoids (Wiedmann, 1969; Shevyrev, 2005). Choristoceratidae contains the subfamilies Rhabdoceratinae including *Rhabdoceras* and *Peripleurites*, Choristoceratinae with *Choristoceras* and *Vandaites*, as well as Cochloceratinae comprising *Cochloceras* and *Paracochloceras* (Shevyrev, 2005). Krystyn & Wiedmann (1985) regarded the Clydonitidae (*Pseudothetidites praemarshi*) from the Late Norian Hallstattkalk facies as direct ancestors of the Choristoceratidae, a viewpoint rejected by Shevyrev (2005). Based on a quadrilobate suture, coarse ribs, and with *Rhabdoceras* as its oldest representative, Shevyrev (2005) suggested the family Cycloceltitidae (*Ophiorhabdoceras* – a small, monomorphic, coarsely ribbed form) as potential ancestors of Triassic heteromorphs. The first *Rhabdoceras* occurred at the base of the Sevatian, a time interval that is characterised by decreasing ammonoid diversity (Jenks *et al.*, 2015). Wiedmann (1973*a*) highlighted the differences in morphological variability between the highly variable Jurassic spiroceratids and the less variable Triassic heteromorphs.

Triassic heteromorphs occur during the Late Norian and persist into the Rhaetian (Marshi Zone) (Fig. 11). These occurences range from 209 to 201 Ma (aged according to Ogg, Ogg & Gradstein, 2016) and are geographically restricted to the Tethyan realm. Most reports come from Europe and the Pacific coast of North and South America (Yukon Territory to central Argentina; Shevyrev, 2005). The paucity of reports of Late Triassic heteromorphs prevented Brayard *et al.* (2015) from developing a biogeographical reconstruction for these ammonoids.

A life habit similar to spiroceratids was suggested for the choristoceratids (Wiedmann, 1969, 1973*a*). This viewpoint changed based on the co-occurrences of heteromorphs together with monomorphs (phylloceratids, arcestids, megaphyllitids), making it likely that choristoceratids were capable of active swimming. Based on the absence of gastropods, Laws (1982) concluded that Triassic heteromorphs from Nevada (USA) were epibenthic scavengers or micropredators that occupied the same ecological niche as gastropods. Wiedmann (1973*a*) argued that reduced selective pressure on the suture line occurred during the change from a nektic to a vagile benthic life habit, expressed as reduced complexity of suture lines. Such reduction in complexity is documented in all heteromorphs from this period, inferring a benthic life habit.

The extinction of choristoceratid heteromorphs is likely related to the Rhaetian marine regression, which is associated with a sharp negative excursion in the stable carbon isotope curve (Pálfy, Demény & Haas, 2001; Ward, Haggart & Carter, 2001; Guex *et al.*, 2003, 2004; Ward, Garrison & Haggart, 2004). This agrees with their gradual disappearance during the Rhaetian (Shevyrev, 2005). The last Triassic heteromorph *Choristoceras*, went extinct together with other monomorph ceratitids at the Triassic–Jurassic boundary. Increased volcanism (i.e. flood basalts) at the Central Atlantic Magmatic Province during the break up of Pangea (Cohen &

Coe, 2002; Guex *et al.*, 2004) likely resulted in the release of sulfate aerosols and other pollutants. These pollutants reduced the effect of solar radiation, causing short-term cooling, while the release of greenhouse gases (carbon dioxide) could have led to long-term warming. We assume that these pertubations had their largest effect in the uppermost water column causing a plankton crisis. This crisis eventually affected marine ecosystems on a global scale. Some tropitids and choristoceratids survived into the earliest Jurassic based on rare occurrences from basal Hettangian strata (Longridge & Smith, 2015). Choristoceratids have been reported from Hettangian strata in North and South America (Guex, 1995; Guex *et al.*, 2004, 2012) and ?Tibet (Yin *et al.*, 2007).

(3) Jurassic heteromorphs

Parapatoceras distans and other spiroceratids (Dietl, 1978, 1981) have a higher intraspecific variability compared to Triassic heteromorphs (Jain, 2018). Accordingly, their coiling mode is insufficient to characterise species. Two pathways from planispiral to orthocone conchs have been documented for spiroceratids (Fig. 11), including radial and axial uncoiling. The recognition of large intraspecific variability resulted in a significant reduction in the number of species from 38 to 12 (Dietl, 1978). Jurassic heteromorphs are often preserved as fragments or small specimens. Dietl (1978) reported a fragment of 40 mm whorl height indicating that they could grow to large sizes. Similar to Triassic choristoceratids, their sutures are simplified, and ornamentation comprises simple straight ribs (Jain, 2018). Rows of tubercles suggest the presence of lateral and ventral spines. Mitta (2017) reported on micro- and macroconchs with preserved apertures (lappets) in *Spiroceras* (Jain, 2018).

The Spiroceratidae is composed of the two subfamilies Spiroceratinae with *Spiroceras* and Parapatoceratinae, including *Parapatoceras*, *Paracuariceras*, and *Acuariceras*. Due to morphological resemblance, Mitta (2017) regarded *Bajocia rarinoda* as potentially ancestral to *Spiroceras* aff. *fourneti*. Jain (2018) discussed the descent of the oldest spiroceratids from either *Strenoceras* or *Bajocia*, favouring the former. Jain (2018) suggests that *Spiroceras* gave rise to *Parapatoceras*, and that *Parapatoceras* gave rise to *Epistrenoceras* (a secondary monomorph) and *Paracuariceras*, with the latter being the ancestor of *Acuariceras*. This phylogeny contrasts with the hypothesis that spiroceratids and parapatoceratids had independent origins (Besnossov & Kutuzova, 1990; Mitta, 2017; Galácz, 2019), but produced morphologically similar convergent forms. Besnossov & Kutuzova (1990) argued that the late Bajocian heteromorph genera *Apsorroceras* and *Spiroceras* represent macroconchs of the monomorphs *Pseudogarantiana* and *Strenoceras* and that all four genera evolved from the monomorph *Caumontisphinctes* as members of the Spiroceratidae. Galácz (2019) introduced the genera *Kumetaceras* and *Sikeliceras*, which he regarded as microconchs and possible ancestors of *Parapatoceras*.

The first Jurassic heteromorphs appear during the late Middle Bajocian (Arkelli/Bremeri Zone) with the genus *Spiroceras* and disappear with the extinction of *Acuariceras* during the Early Oxfordian (Collotiformis Subzone, Athleta Zone). According to Jain (2018) and Bert & Courville (2016), Jurassic heteromorphs range from 169.5 to 163 Ma (aged according to Ogg *et al.*, 2016). The Tithonian *Protancyloceras* is hypothesised as the ancestor of Early Cretaceous heteromorphs (Wierzbowski, 1990; Sarti, 1999). Some species of the genera *Spiroceras* and *Parapatoceras* are distributed worldwide, such as *S. orbignyi* and *S. annulatum*. The latter was recently reported from Kenya by Galácz (2017), whereas others are more geographically restricted.

The global distribution of some species has been explained by a planktic life habit of their hatchlings. Genera such as *Paracuariceras* and *Acuariceras* are only known from France, Germany, and Romania (Jain, 2018). These heteromorphs occur frequently in clays ('Hamitentone') and their conchs show substantial morphological variability. This led to the hypothesis that spiroceratids inhabited calm water (Dietl, 1978). A vagile benthic life habit was inferred by the large variability of conch morphology from planispiral *via* helicoid to rhabdoceratid, i.e. from bilaterally symmetric to asymmetric forms within a single species. Specifically, crawling locomotion on plants was suggested due to associated findings of the bivalve '*Posidonia*' (*Bositra*), which are thought to have lived in 'macroalgae forest' (Dietl, 1978).

A benthic life of spiroceratids is contradicted by records of spiroceratids within sideritic beds devoid of benthos except for abundant *Ophiopinna elegans* (ophiuroids) in the clays of La Voulte (Dietl & Mundlos, 1972). Shevyrev (2005) revived the benthic habitat hypothesis for spiroceratids with their biotopes in dense algal thickets. He argued that their hydrostatic apparatus enabled them to change their position within these algal mats. Since spiroceratids rarely co-occur with planispiral ammonoids, Shevyrev (2005) speculated that they lived in cracks in the sea bottom in calm water. Mitta (2017), however, found spiroceratids in Bajocian siltstone nodules together with *Baculatoceras*, *Calliphylloceras*, *Holcophylloceras*, *Pseudophylloceras*, and *Megalytoceras*, i.e. forms that inhabit the pelagic realm. Herein, spiroceratids are regarded as having a pelagic-nektoplanktic life habit.

The higher-level systematics of Jurassic and Cretaceous heteromorphs remains problematic. Different schemes are available but there is no consensus. Arkell, Kummel & Wright (1957) included all heteromorphs in the Lytoceratina. Wiedmann (1966*a*,*b*) then included them in the Ancyloceratina. Subsequently, they were split into the Turrilitina and Ancyloceratina (Doguzhaeva & Mikhailova, 1982; Besnossov & Mikhailova, 1983), which was accepted by most subsequent workers (see Wright *et al.*, 1996). Later, Shevyrev (2006) assigned them to the Lytoceratoidea and Ammonitida. Vermeulen (2005) added the Protancyloceratina. These examples reflect the complexity of the interpretation of their polyphyletic origin and evolutionary record (Matsukawa, 1987; Monks, 1999, 2000*a*).

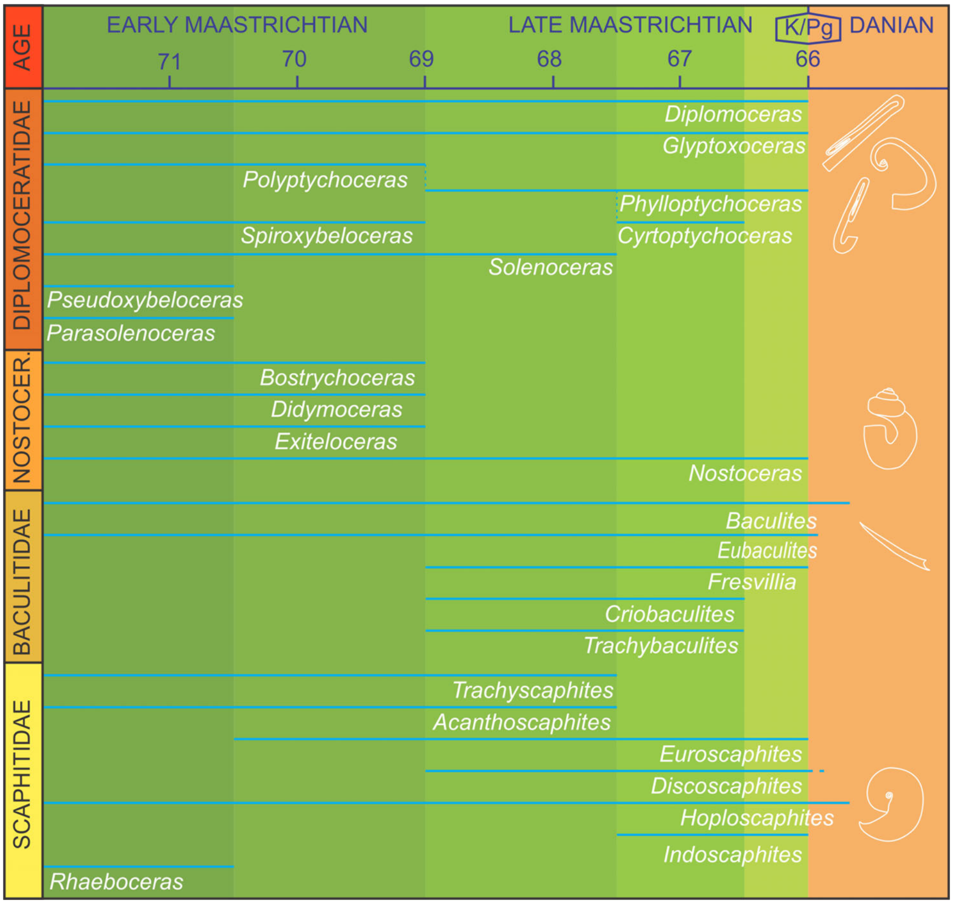

Fig. 12. Ranges of Maastrichtian to earliest Danian heteromorph genera. Taxonomy after Wright *et al.* (1996), with the omission of *Jeletzkytes* and *Karlwaageites* following Landman *et al.* (2010*b*), *Ponteixites* following Grier *et al.* (2007), and the subgenus *Tovebirkelundites* following Kennedy & Jagt (1998). In the absence of a fully integrated stratigraphic scheme for the subdivision and correlation of all basins, the division of the Maastrichtian into the five bins (early early, late early, early late, late late, and last 0.5 million years) is arbitrary. Phylogenetic relationships between scaphitid genera differ among authors (e.g. Cooper, 1994; Monks, 2000*a*), and are therefore not included.

(4) Cretaceous heteromorphs and ammonoid extinction

Heteromorphs have been classically linked to the extinction of the ammonoids (Wiedmann, 1969). Their 'aberrant' conch shapes were often related to degeneration and phylogenetic extinction (e.g. Dacqué, 1935; Schindewolf, 1936, 1945; Müller, 1955). The fact that they are a dominant faunal element in many Late Cretaceous ammonoid faunas might have sustained this hypothesis. However, Mesozoic heteromorphs were successful, particularly in the Cretaceous (Fig. 11), as evidenced by their high abundance, generic diversity, and morphological disparity (Seilacher, 2013). Elevated generic diversity is recognised during the late Hauterivian to Aptian, late Albian, and Coniacian to Campanian, with peaks in the late Barremian, late Albian, and early Campanian (Klein *et al.*, 2007; Mikhailova & Baraboschkin, 2009). A wide variety of heteromorph conch shapes developed in the Cretaceous, but the most complex three-dimensional shapes evolved within the Nostoceratidae with genera like *Nipponites*, *Pravitoceras*, *Eubostrychoceras*, *Didymoceras*, and *Anaklinoceras* (Wiedmann, 1969; Wright *et al.*, 1996).

Heteromorphs are the most abundant faunal element (mostly scaphitids and baculitids) documented at 29 out of 31 sites preserving a record from the last 0.5 Myr of the Cretaceous (Landman *et al.*, 2014, 2015). New genera within the Diplomoceratidae, Baculitidae, and Scaphitidae evolved during the Maastrichtian (Fig. 12). The diversity of Nostoceratidae declined during the late Maastrichtian with only two *Nostoceras* specimens known from the Maastrichtian type area (van der Tuuk & Zijlstra, 1979).

Goolaerts (2010) concluded that the cause of the extinction of ammonoids must have been a catastrophic event affecting both heteromorph and monomorph diversity on a global scale, in colder and warmer waters, in shallow and deeper settings, and for a wide variety of taxa exhibiting different food and life strategies. The Chicxulub impact at the Cretaceous/Paleogene (K/Pg) boundary (66 Ma; Schulte *et al.*, 2010) is currently regarded as the most probable trigger for ammonoid extinction (Ward, 1996; Goolaerts, 2010; Landman *et al.*, 2014, 2015; Petersen, Dutton & Lohmann, 2016; Witts *et al.*, 2016; Tobin, 2017).

Ammonoids have been reported from beds above the K/Pg boundary. Most of these records reflect reworked specimens or resulted from an erroneously placed K/Pg boundary level (Sadler, 1988; Landman, Johnson & Edwards, 2004*a*,*b*; Landman *et al.*, 2007*a*). However, some may belong to possible extinction event victims or even were true short-term survivors. At Tanis, North Dakota, the monomorph *Sphenodiscus* is the only ammonoid recorded from beds directly correlated to the Chicxulub impact (De Palma *et al.*, 2019).

In Denmark, ammonoids from the Cerithium Limestone were considered as reworked until Machalski & Heinberg (2005) reported early Danian age infilling of the conchs, which favoured the short-term survivor hypothesis for *Hoploscaphites constrictus johnjagti* and *Baculites vertebralis* (Machalski *et al.*, 2009). The Cerithium Limestone was deposited between 40 and 500 kyr after the K/Pg boundary (Rasmussen, Heinberg & Håkansson, 2005).

In the type Maastrichtian area (The Netherlands, Belgium), ammonoids were found up to 2 m above the K/Pg boundary (Goolaerts, 2010; Jagt *et al.*, 2013; Vellekoop *et al.*, 2020). The fauna consists exclusively of heteromorphs: *Eubaculites latecarinatus*, *Baculites* spp. and *H. constrictus johnjagti* (Landman *et al.*, 2014, 2015). These are regarded as true survivors (Vellekoop *et al.*, 2020), but in contrast to Denmark, the ammonoids range in age from hundreds to thousands of years after the K/Pg boundary.

In New Jersey (USA), non-reworked ammonoids were found above an iridium anomaly, which likely represents the K/Pg boundary (Landman *et al.*, 2007*a*, 2010*a*, 2012*c*, 2014, 2015). In the *Pinna* Layer, which contains the iridium anomaly at its base, the fauna is dominated by the heteromorphs *Discoscaphites* and *Eubaculites*. In the overlying Burrowed Unit, *Discoscaphites* and *Eubaculites* have also been recorded.

Tajika *et al.* (2018, 2020) discussed the ecological framework of the ammonoid extinction at the K/Pg boundary. Tajika *et al.* (2018) suggested ecological replacement of the micro- to mesoplanktic ammonoid (and belemnite) hatchlings by holoplanktic gastropods in the Paleogene. Tajika *et al.* (2020) hypothesised that a combination of higher metabolic rates, a microphageous diet, and small hatchling size (i.e. limited resources) likely caused the selective extinction of the ammonoids. By contrast, nautilids and coleoids with different metabolism, macrophageous to scavenging diets, and varying reproductive strategies survived the K/Pg mass extinction.

VII. CONCLUSIONS

(1) This review of published data on the soft body, conch organisation, habitat, and palaeoecology of heteromorph ammonoids has resulted in a detailed and robust reconstruction of their palaeobiology. It should provide a useful background for those studying the life habits of extinct animals and more specifically heteromorphs.

(2) The digestive tract of heteromorphs with an oesophagus, crop, and stomach, follows the molluscan U-shaped bauplan. Their brain was likely well developed as in other cephalopods, because of the need to control their position in the water column and to process information provided from their lens eyes and statocysts. Based on phylogenetic bracketing, we assume that heteromorphs had 10 arms and lacked suckers, hooks, and tentacles (extendable arms). Heteromorphs had no hood and ink sac but probably had ammonia in their soft tissues, which resulted in the rapid decay of soft parts, explaining their absence in the fossil record.

(3) The buccal apparatus in heteromorphs shares the general pattern of ammonoid jaws: a smaller upper jaw inserted into a longer and larger lower jaw. All Cretaceous heteromorphs share an aptychus-type lower jaw with a lamellar calcitic covering. Aptychi may have fulfilled multiple functions: lower jaw, operculum, filtering device, flushing benthic prey, pumping for jet propulsion, regulating conch position, and stabilisation against rocking.

(4) Differences in the morphology and size of radular teeth reported for heteromorphs suggest preferences for microphagous prey (i.e. zooplankton).

(5) Based on functional morphological and phylogenetic constraints, the presence of muscles such as the cephalic retractors, hyponome retractors, ventral muscle, and mantle musculature are assumed for heteromorphs. Homologisation of ammonoid muscles and their attachment sites with those of coleoids and nautilids will require soft tissue preservation.

(6) Heteromorphs could achieve nearly neutral buoyancy regardless of conch shape or ontogeny. This was potentially achieved by adding fluid to a positively buoyant conch or counteracting slight negative buoyancy through swimming. Encrustation by epizoans like barnacles, brachiopods, and bivalves supports the buoyant heteromorph hypothesis and contradicts the idea of a benthic habitat.

(7) A vertical orientation for orthoconic heteromorphs has been proposed based on physical and virtual models. Ancylocone conchs likely had a near-horizontal aperture pointing upwards. Heteromorphs with a U-shaped body chamber (nostocones, scaphiticones, and ancylocones) are more stable hydrodynamically than modern *Nautilus* and were unable to modify substantially their orientation by active locomotion, i.e. had no or limited access to benthic prey. These forms have their hyponomes horizontally aligned with their centres of rotation, allowing more energy to be transmitted to translational movement with minimal rocking, i.e. these morphotypes are well suited for backwards horizontal swimming at maturity.

(8) Pathologies reported for ancylocone scaphitids were likely inflicted by crustaceans, fish, marine reptiles, and other cephalopods. Injuries in baculitids have been assigned to pycnodontid fish, coleoids, and benthic crustaceans. Pathologies of *Ptychoceras* corroborate an external shell and reject the endocochleate hypothesis for this taxon.

(9) Stomach contents of Cretaceous heteromorphs comprise planktic crustaceans, gastropods, and crinoids suggesting a zooplanktic diet. Forms with a U-shaped body chamber (ancylocone) are regarded as suspension feeders, whereas orthoconic conchs might have had access to benthic prey. A carnivorous diet for heteromorphs is supported by the fact that all modern cephalopods are carnivorous.

(10) Heteromorphs are known from a broad range of litho- and biofacies. These facies associations change through time among and within respective clades. Devonian, Triassic, and Jurassic heteromorphs show a preference for deep-subtidal to offshore facies but are rare in shallow-subtidal, slope, and bathyal facies. Early Cretaceous heteromorphs preferred deep-subtidal to bathyal facies but are rare in shallow-subtidal facies. Late Cretaceous heteromorphs are common in shallow-subtidal to offshore facies but rare in slope and bathyal facies. The increase in heteromorph species in shallow-subtidal settings during the Late Cretaceous likely reflects an evolutionary shift to shallower-water environments.

(11) Adult *Discoscaphites* and *Baculites* show oxygen isotope values supporting an interpretation of rapid growth and a demersal habitat. Analyses of the earliest whorls of *Hoploscaphites* suggest a benthic embryonic stage, planktic hatchlings, and a habitat change after about one whorl. Carbon isotope values derived from *Baculites* from the Western Interior Seaway indicate that some heteromorphs lived on or close to cold seeps throughout their lives and likely exploited the diverse prey available at the seeps.

(12) Heteromorphs have the smallest hatchlings of all Cretaceous ammonoids. Constraints imposed by adult size and mobility potentially drove selection for more and/or smaller hatchlings adapted to a planktic life. This implies high fecundity and an ecological role of the hatchlings as micro- and mesoplankton.

(13) Various environmental factors, partially reflected in the litho- and biofacies, explain the large degree of intraspecific variation in heteromorphs. So far, only scaphitid conch characters have been shown to vary with environment, in accordance with their nektobenthic life habit, e.g. whorls being more compressed, more umbilicate, and less nodose in nearshore facies compared to specimens from offshore facies.

(14) The Maastrichtian is noted for the evolution of new ammonoid genera and at many latest Cretaceous localities, heteromorphs are the most abundant macrofaunal element. The cause of the extinction of ammonoids must have been a catastrophic event affecting their diversity on a global scale and for a wide variety of organisms exhibiting different life habits. The Chicxulub impact at the K/Pg boundary (66 Ma) is the likely trigger for their final extinction.

(15) Post-K/Pg-boundary ammonoid survivors are all heteromorphs, which likely survived up to 40–500 kyr after the mass extinction event.

(16) The heteromorph and monomorph ammonoid extinction is linked to their small hatchling sizes, planktotrophic diets, and high metabolic rates. The end-Cretaceous event caused a collapse of marine primary producers, which allowed only cephalopods with sufficient energy reserves, macrophageous diet, and low metabolic rates to survive.

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X. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Known occurrences of upper and lower jaws and radulae in heteromorph ammonoids.

Table S2. Distribution of palaeopathologies of ammonoid heteromorphs in chronological order.

Table S3. Heteromorph ammonite stomach content.

Table S4. Published facies distributions of Devonian, Triassic, Jurassic, and Cretaceous heteromorph ammonoids.

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