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The concept of ‘heteromorph ammonoids’

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‘Heteromorph ammonoids’ encompass all ammonoid species whose shapes do not conform to a closely coiled planispiral shell. The term is useful as a broad description for such ammonoids. However, as a concept, ‘heteromorph ammonoids’ no longer has any scientific value or explanatory power. Although such ammonoids have traditionally been considered aberrant forms, they represent instead an integral part of the evolutionary history of the Ammonoidea. ‘Heteromorph ammonoids’, as a whole, are a polyphyletic group, consisting of a heterogeneous mixture of taxa without any phylogenetic, morphological or ecological coherence. Their treatment as a single entity risks conflating convergences and phylogenetic affinities. It also vastly oversimplifies the stunning array of morphologies and ecological niches occupied by these animals. Investigation into the uncoiling (and recoiling) of ammonoids is a legitimate and worthwhile enterprise, especially in view of the realization that this phenomenon occurred several times in the history of the Ammonoidea. However, few insights can be gained by treating ‘heteromorph ammonoids’ as a single entity. Studies of such ammonoids should focus on monophyletic groups within a well-constrained phylogenetic and stratigraphical framework to yield meaningful results. □ *Ammonoids, Ancyloceratina, heteromorphs, morphotype, Scaphitidae.*

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‘Heteromorph ammonoids’ have long fascinated scientists and collectors alike (Hyatt 1894; Schindewolf 1950; Wiedmann 1969; Kennedy 1977; Okamoto 1988; Grulke, 2014; Peterman *et al.* 2020; Hoffmann *et al.* 2021; Schaffert & Larson 2021). The term is a reference to shell morphologies that depart from a closely coiled spiral. ‘Heteromorph ammonoids’ appear in many families spanning the Devonian to the earliest Paleogene. These include hook-shaped *Scaphites*, straight shelled *Baculites*, torticonic *Nostoceras*, and gyroconic *Erbenoceras*. These shapes seemingly defy logic compared to the perfect logarithmic spiral of ‘typical’ ammonoids and Recent *Nautilus*.

To study ‘heteromorph ammonoids’ from a scientific point of view requires grappling with several issues. First, is the negative connotation that somehow these ammonoids are a distorted version of the ‘normal’ or ‘ideal’ ammonoid bauplan, as if this distinction merits special attention. Second, is that no single morphotype pertains to all or most ‘heteromorph ammonoids’, and that none of the various morphotypes is necessarily homologous to each other. Such a variety of disparate morphologies implies no ecological or developmental unity. Third, is that this grouping is neither monophyletic nor paraphyletic and, thus, has absolutely no systematic significance whatever.

Historical background

Part of the enduring curiosity about ‘heteromorph ammonoids’ stems from the old notion that they were poorly adapted organisms, and could barely function, at least as swimming creatures. They have traditionally been referred to as aberrant or bizarre forms, an idea that has intrigued many scientists up to the present day. This view reflects a pre-Darwinian taxonomic philosophy in which a group was divided into a normal platonic ideal form, almost always considered superior in some way, constituting the essential bauplan of the group. The rest of the group consisted of aberrant or retrograde forms, generally considered ill-adapted and ill-conceived.

This view fits neatly into the theory of racial senescence perpetuated by Alpheus Hyatt (1894) at the end of the 19th and beginning of the 20th centuries. Inspired by Louis Agassiz’s lectures at Harvard in the 1860s (Mayer 1911), Hyatt argued that the shell contortions of Late Cretaceous ‘heteromorphs’ were manifestations of their death throes, culminating in

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maladapted forms, and presaging their extinction. For example, Hyatt (1894, pp. 376–377) reflected thus on the fate of ammonoids at the end of the Cretaceous: ‘In the Trias and early Jura, pathologic uncoiled forms are rare among ammonoids, but in the Middle and Upper Jura they increase largely; and finally, in the Upper Cretaceous they outnumber the normal involute shells, and the whole order ceases to exist …This proves conclusively, that the degeneration was general, and affected all forms of Ammonoidea at this time; since the uncoiled forms are not confined to special localities, as in the Jura, but are found in all faunas as far as known’.

Similar theories about racial decline were expressed at the time by several prominent vertebrate palaeontologists including Henry Fairfield Osborn at the American Museum of Natural History (Rainger 1991). Unfortunately, and not surprisingly, he applied these concepts to human evolution, distinguishing between so-called pure and degenerate races. His views were showcased in an exhibit called the *Hall of the Age of Man*, which opened in time to coincide with a meeting of the International Eugenics Congress in New York in 1921. Osborn argued that his views were based on empirical observations of the fossil record but, of course, they reflected his prejudices about ‘racial mixing’ and ‘racial decline’. Needless to say, these views had disastrous consequences for humankind in the ensuing decades.

In Europe, these non-Darwinian ideas were embraced and elaborated on by the German palaeontologist Otto Schindewolf, among others. In his monumental *Basic Questions in Paleontology* (1950, translated into English, 1993), Schindewolf laid out his typostrophe, a cycle of evolutionary change with strong similarities to Hyatt’s evolutionary cycle. It was a non-Darwinian, anti-adaptationist, orthoselectionist outlook (Reif 1993; Korn 2003). The first phase of the cycle consisted of an explosive origin (typogenesis), characterized by the diversification of forms. This was followed by typostasis during which the group developed according to its own volition (orthogenesis) unconstrained by adaptation. The cycle culminated in typolysis characterized by overspecialization, decline, and degeneration ending in extinction.

For Schindewolf, ‘heteromorph ammonoids’ were graphic examples of his third and final destructive phase of evolution. He described the history of ammonoids in the following terms (Schindewolf, 1993, p. 143): ‘…after having experienced a *phase of explosive evolution* and a *long period of gradual progressive specialization*, they arrive at a *phase of overspecialization and decadence of form* [italics in the original] completely analogous to the one the Triassic representatives experience. The closer we get to the end of the Upper Cretaceous, to the final extinction of the ammonite stock, the more frequently we encounter degenerate forms: with the final whorl detached and showing many differences with regard to details of shape; with secondarily straight shells; with snail-type spirals; and finally, with shells all coiled together in a completely irregular tangle’.

Both Hyatt and Schindewolf knew that ‘heteromorph ammonoids’ became extinct at the end of the Cretaceous. These ‘heteromorphs’ are now included in the suborder Ancyloceratina. However, the three other suborders living at the same time (Lytoceratina, Phylloceratina, and Ammonitina), comprising exclusively closely coiled ammonoids, were equally affected by the catastrophic consequences of the Chixculub impact (Goolaerts 2010; Witts *et al.* 2021). New evidence suggests that some members of the Ancyloceratina may even have briefly survived the K-Pg extinction event (Machalski & Heinberg 2005). These ‘dead clade walking’ forms include several unrelated taxa such as straight shelled baculitids and recoiled (almost ‘normal’) scaphitids (Machalski *et al.* 2009). However, even this fortuitous outcome surely had nothing to do with their ‘heteromorph’ properties. These taxa were among the most common ammonoids at the end of the Maastrichtian, and their survival was undoubtedly related to such mundane factors as the breadth of their geographical distribution, nature of their habitat, and size of their population (Landman *et al.* 2014).

Many studies have recently appeared that counter the notion that ‘heteromorphs’ were ill-adapted. Although these ammonoid shapes depart from a closely coiled spiral, even the most unusually coiled forms follow a logical ontogenetic pathway, if we are only clever enough to discern it. Okamoto (1988) explained the seemingly irregular coiling of *Nipponites* as a response to maintain the same orientation of the aperture in the water column, with each turn of the shell. Peterman *et al.* (2020) analysed *Didymoceras* and concluded that these ammonoids maintained near neutral buoyancy throughout life. These and other studies underscore the fact that ‘heteromorphs’ struggled with the same constraints as closely coiled ammonoids: buoyancy, orientation of the aperture in the water column, and swimming capability. They may have been more limited in getting around than some of the more closely coiled taxa due to their poor streamlining, but they were not deficient in any way. The race for evolutionary and ecological success does not always belong to the swift of foot.

The reconstructions of 'heteromorph' life habits in Westermann (1996), Kakabadzé & Sharikadzé (1993), and Hoffmann *et al.* (2021), among others, demonstrate how these ammonoids formed an important component of the marine ecosystem for several hundred million years and underscore the fact that these taxa were an integral part of the Ammonoidea. 'Heteromorphs' are preserved in shallow and deep water facies, in sandstones, shales, marls, and chalks around the globe. The geologic duration of many of these 'heteromorph' taxa also demonstrates that the development of uncoiling did not in any way reduce their evolutionary longevity. Several families of the Ancyloceratina were long lived. For example, the Scaphitidae and Baculitidae ranged from the Albian to the early Danian, a duration of ~30 Myr. Both of these families were nearly global in their distribution, containing more than 100 species each. Thus, in contrast to Hyatt's and Schindewolf's interpretations, 'heteromorph ammonoids' were well-adapted forms belonging to evolutionarily successful lineages. The disparity of morphotypes among 'heteromorphs' suggests evolutionary experimentation and adaptive radiation, indicators of clade vitality, rather than maladaptation and senescence.

Phylogenetic context

'Heteromorph ammonoids' as a whole represent a polyphyletic mixture of heterogeneous forms without any phylogenetic coherence. They are neither monophyletic nor paraphyletic. They constitute a classic non-A group. Instead of a synapomorphy, the only character that they all have in common is what they lack, i.e. a closely coiled planispiral shell (the absence of a symplesiomorphy). The polyphyletic nature of 'heteromorph ammonoids' was emphasized by Wiedmann (1969) in his landmark paper in *Biological Reviews*. In it, he refuted the theories of Schindewolf who treated 'heteromorphs' as a distinctive entity to support his non-Darwinian theories about the history of life. Wiedmann pointed out instead that the various groups of ammonoids that we call 'heteromorphs' represent multiple taxa with no phylogenetic affinity.

'Heteromorph ammonoids' appear in multiple, unrelated lineages separated in time and space. Genera include Early Devonian *Anetoceras*, Late Triassic *Choristoceras* and *Rhabdoceras*, Middle Jurassic *Spiroceras* and *Parapatoceras,* Early Cretaceous *Protancyloceras*, and Late Cretaceous *Exiteloceras* and *Nostoceras*. These genera comprise a wide array of shell shapes (few of which are homologous to each other), a broad variation in adult size (ranging from a few centimetres to nearly 2 metres), and a multiplicity of ornamental types (including ribs, tubercles, and spines). Kakabadzé (1988) recognized 31 different morphotypes among 'heteromorph ammonoids' and divided them into four categories: 'symmetrical heteromorphs with planispiral, uncoiled second whorl; straightly uncoiled (directly after the first whorl), symmetric heteromorphs; symmetrical heteromorphs with contiguous early whorls; and asymmetrical heteromorphs'.

Many of the same shell shapes appear in different clades. As Raup (1967) pointed out years ago – the ammonoid tool box is limited and the potential variation in shell shape is not inexhaustible. Indeed, evolutionary convergence is a widespread phenomenon in the animal kingdom, with fusiform body shapes repeatedly appearing, for example, in coleoids, mammals, reptiles, chondrichthyans, and actinopterygians. At the same time, instances of convergence are never exact. Apparent similarities in 'heteromorph' shapes begin to break down on closer inspection, as emphasized by Kakabadzé (1988). The ontogenetic development of uncoiling does not follow the same pattern in all taxa with, for example, straight shafts followed by U-turns in some taxa (e.g. *Oxybeloceras*) versus straight shafts followed by trochospiral whorls in other taxa (e.g. *Didymoceras*).

The diverse phylogenetic make-up of 'heteromorphs' is also reflected in many other aspects of their morphology. For example, the buccal apparatus in most Late Cretaceous 'heteromorphs' consists of an aptychus-type lower jaw, a synapomorphy of the Aptychophora (Engeser & Keupp 2002). This feature is present in nearly all members of the Jurassic and Cretaceous Ammonitina and Ancyloceratina (Tanabe *et al.* 2015). However, it is possible that some 'heteromorphs' such as *Crioceratites* possess the more primitive anaptychus-type jaw, and are thus derived from lineages outside of the aptychophoran clade (Engeser & Keupp 2002). The shape and size of the embryonic shell also vary broadly across taxa (De Baets *et al.* 2012). For example, the embryonic shell consists of a large ovoid protoconch and elongate shaft in Early Devonian *Ivoites* whereas it consists of a small protoconch and a spirally coiled whorl in Late Cretaceous *Exiteloceras*. The same is true about the complexity of the suture. The primary suture in Early Devonian *Metabactrites* is trilobate whereas it is quadrilobate in Late Cretaceous *Scaphites*. Thus, with regard to almost every aspect of morphology, 'heteromorph ammonoids' do not represent a single monolithic morphotype.

Investigations into the uncoiling of ammonoids are a legitimate and worthwhile enterprise, especially in view of the fact that this phenomenon occurred several times in the history of the Ammonoidea. However, without a well-constrained phylogenetic and stratigraphical framework, a comparison of one group of uncoiled forms with another, unrelated, and morphologically different group of uncoiled forms risks conflating convergences and phylogenetic affinities, resulting in a misreading of evolutionary history and associated changes in habitat preference over time (Hoffmann *et al.* 2021). This cautionary note applies equally well to the study of clades that contain both coiled and uncoiled forms (e.g. the Scaphitidae). It is necessary to consider all taxa in such a clade to avoid paraphyletic misinterpretations. Indeed, 'heteromorph' blinders can be as misleading to our understanding of ammonoid paleobiology as investigations that focus exclusively on 'heteromorph' wastebaskets.

Examples

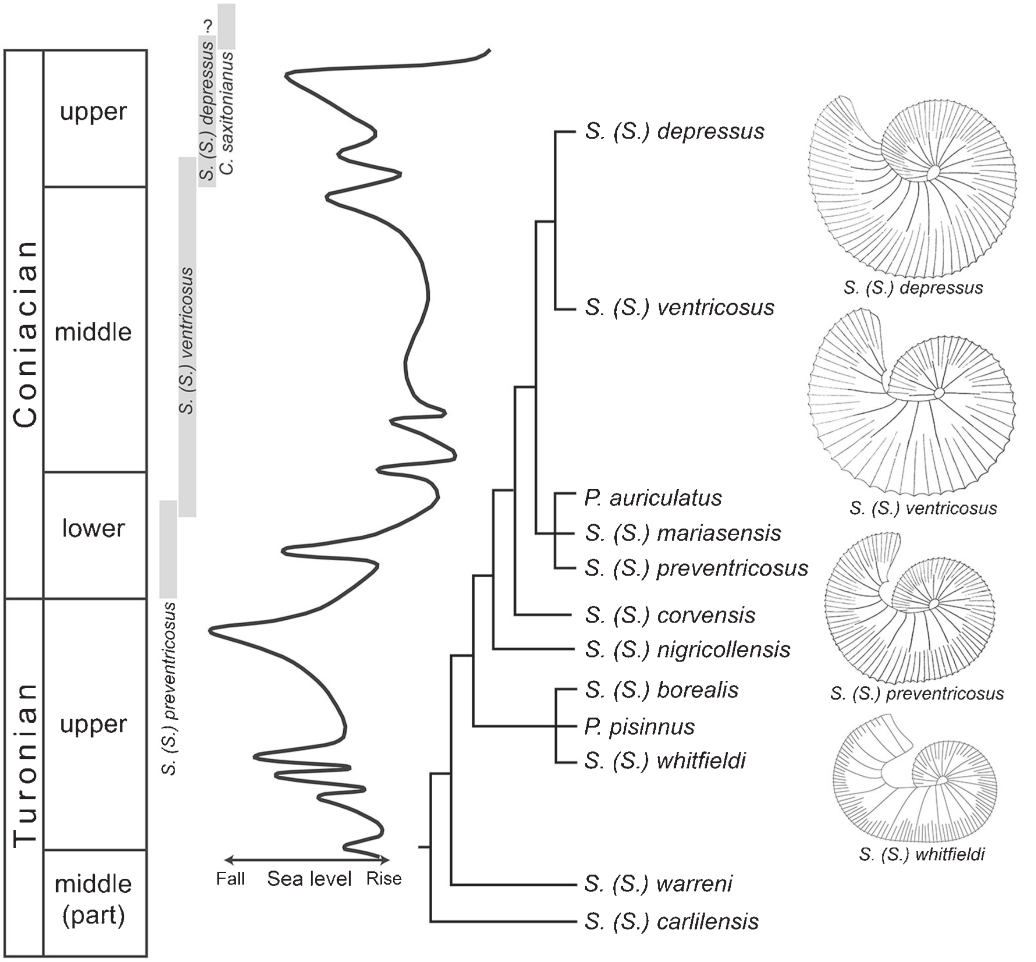
One of the most famous examples of changes in the mode of coiling is in the early evolution of the Ammonoidea, first described by Erben (1966). This evolutionary transition from uncoiled to closely coiled ammonoids was recently restudied by Klug *et al.* (2015). They documented a long-term pattern in the Early Devonian starting with orthoconic and cyrtoconic Bactritoidea, and culminating in the advolute Anarcestoidea, reflecting a brief window of expanded morphological disparity near the Emsian-Eifelian boundary (Whalen *et al.* 2020). These changes are associated with modifications in the shape of the aperture, the rate of whorl expansion, the size of the umbilicus, the degree of sutural complexity, and the length of the body chamber. Klug *et al.* (2015) concluded that these changes probably enhanced swimming ability and manoeuvrability and may also have contributed to higher reproductive fecundity.

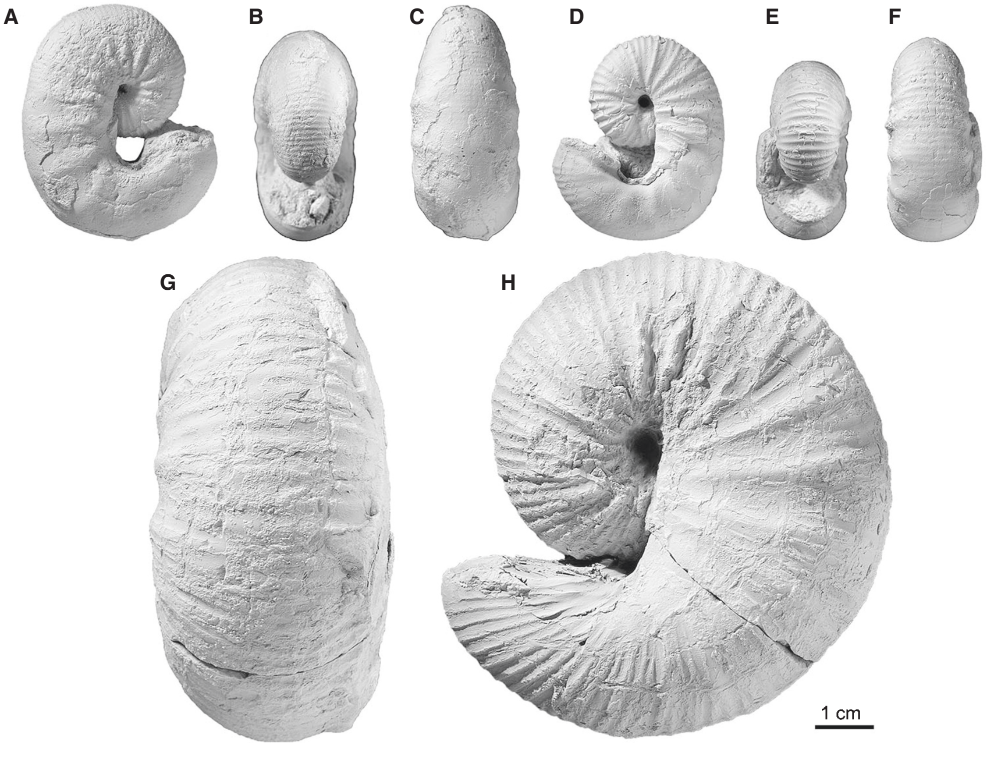
The appearance of the Ancyloceratina (Wiedmann 1966a,b, 1969) at the Jurassic-Cretaceous boundary (Tithonian/Berriasian) is another example of the importance of changes in shell coiling in the history of the Ammonoidea. The appearance of this suborder was sudden, with the development of uncoiled shell shapes in early ontogeny, without any record of transitional taxa. The suborder is characterized by a variety of forms, as measured by both diversity and disparity metrics, quite the opposite of Hyatt's racially charged conjectures. It includes both coiled and uncoiled forms and contains such iconic genera as *Ancyloceras*, *Crioceras*, *Baculites*, *Nostoceras*, and *Didymoceras*. These taxa were united into a single monophyletic clade based on similar sutural features in early ontogeny. As Wiedmann (1969, p. 584) stated 'the most essential criterion of homology, at least within the Cretaceous heteromorphs and ammonoids, proves not to be aberrant shell form but instead the suture line inclusive of its ontogenetic development'.

The radiation of the Ancyloceratina in the Cretaceous is no longer attributed to endogenous causes such as degeneration and depletion of the gene pool. Today, their radiation is mostly attributed to exogenous factors such as changes in the physical and biotic environment. For example, the rise of the Ancyloceratina may have been linked to the appearance of new predators such as teleost fishes and, as a consequence, these ammonoids may have exploited new niches in mid-water to avoid predators (Ward 1983). Equally, the appearance of the Ancyloceratina may have been related to the radiation of new groups of plankton, providing new sources of food coincident with the acquisition of the aptychus-type lower jaw (Cecca 1997; Mikhailova & Baraboshkin 2009; Fraaije *et al.* 2018).

Within the suborder Ancyloceratina, the Late Cretaceous Scaphitidae contain both closely coiled and uncoiled forms. The most primitive species are small (2 cm long) and develop a long shaft and recurved hook. However, a trend towards recoiling has been documented in the Turonian-Coniacian strata of North America (Cobban 1952; Kennedy 1977). This trend involved a reduction in the gap between the earlier formed, closely coiled spire and the recurved hook (Fig. 1). This trend is associated with an increase in adult size and degree of whorl depression. The increase in adult size was accommodated by the secretion of additional whorls rather than an increase in the degree of whorl expansion. Landman (1987)

Fig. 1. Top. Stratigraphical ranges of selected species of *Scaphites* plotted on the left side, next to a curve of the changes in relative sea level in the Western Interior Seaway during the Turonian-Coniacian. The evolutionary relationships proposed by Cobban (1952) are presented as a cladogram on the right side, showing the trend towards recoiling (reprinted from Landman *et al.* 2017). Bottom. A–F, *Scaphites* (*S.*) *whitfieldi* Cobban 1952, adults, Carlile Shale, Fall River County, South Dakota. A–C, AMNH 82696, macroconch, right, apertural, and ventral views. D-F, AMNH 82694, microconch, right, apertural, and ventral views. G, H, *Scaphites* (*S.*) *ventricosus* Meek & Hayden 1862, adult macroconch, TMP2016.041.0035, Wapiabi Formation, Alberta, ventral and left lateral views. Abbreviations: AMNH, American Museum of Natural History; TMP, Tyrell Museum of Paleontology.


Coniacian
upper
middle
lower
Turonian
upper
middle (part)
S. (S.) preventricosus
S. (S.) ventricosus
S. (S.) depressus ?
C. saxitonianus
Fall
Sea level
Rise
S. (S.) depressus
S. (S.) ventricosus
P. auriculatus
S. (S.) mariasensis
S. (S.) preventricosus
S. (S.) corvensis
S. (S.) nigricollensis
S. (S.) borealis
P. pisinnus
S. (S.) whitfieldi
S. (S.) warreni
S. (S.) carlilensis
S. (S.) depressus
S. (S.) ventricosus
S. (S.) preventricosus
S. (S.) whitfieldi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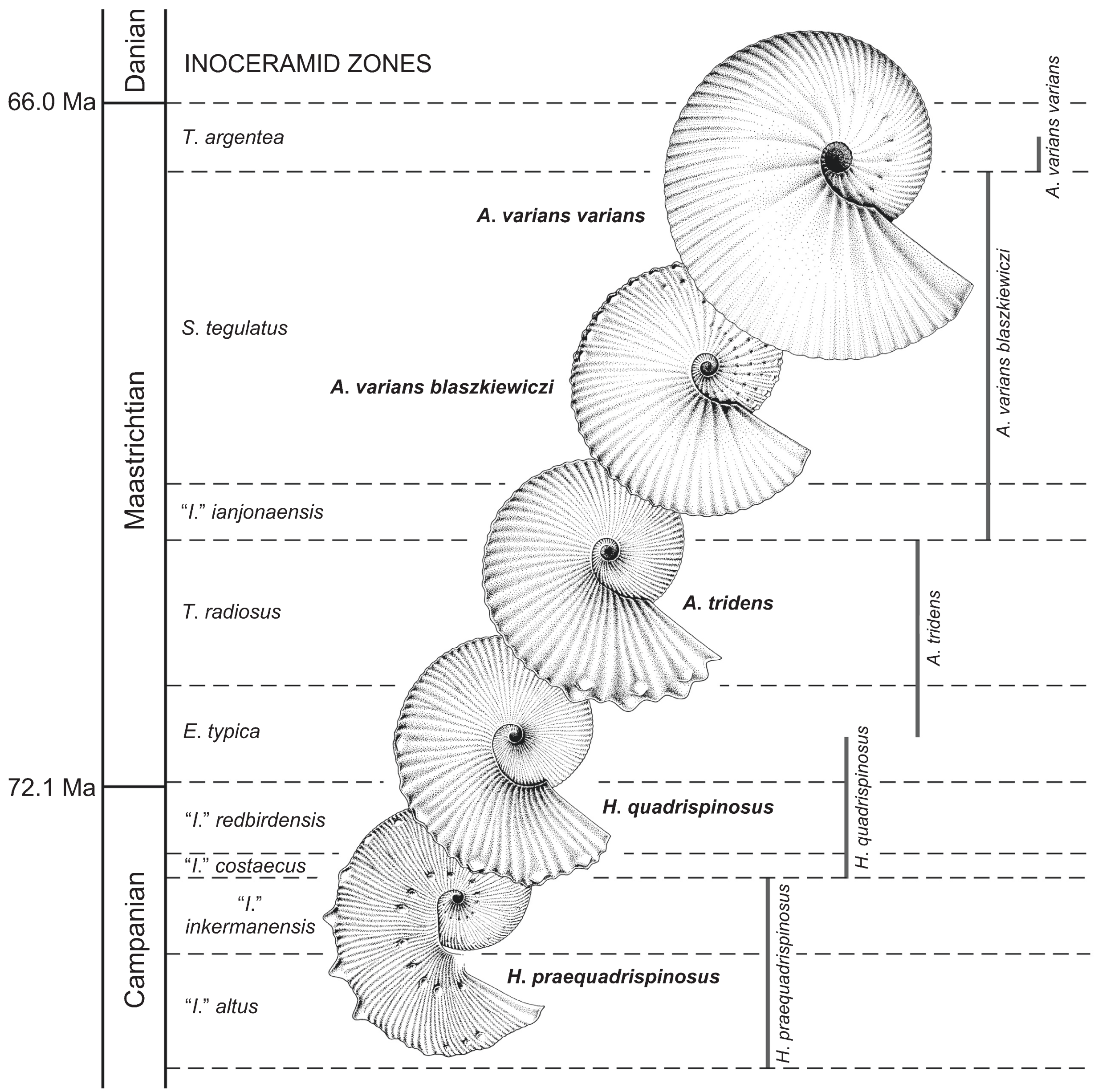

Fig. 2. Evolutionary lineage of giant scaphitids in the Campanian and Maastrichtian of Europe, based on Machalski (2019, and Machalski, unpublished), calibrated against the inoceramid zonation. Only macroconch specimens are illustrated. The inoceramid zonation is compiled based on Walaszczyk *et al.* (2016, fig. 3), Machalski & Malchyk (2016, fig. 4), Gale *et al.* (2020, fig. 27.9) and Ireneusz Walaszczyk (personal communication, 2021). Abbreviations: *H.*, *Hoploscaphites*; *A.*, *Acanthoscaphites*; *E.*, *Endocostea*; *T.*, *Trochoceramus*, *I.*, '*Inoceramus*'; *S.*, *Spyridoceramus*; *T.*, *Tenuipteria*.

attributed this increase in adult size to a delay in the timing of maturation (hypermorphosis), rather than a change in the rate of growth.

These changes in shape may have been associated with environmental changes in the Western Interior Seaway in which the ammonoids lived (Fig. 1). The Seaway expanded in size during this time due to a transgression, leading to an increase in the areal extent of muddy, offshore facies. Landman *et al.* (2017) hypothesized that the increase in the areal extent of muddy, offshore facies, associated with quieter water conditions, may have favoured longer-lived species with more depressed shell shapes. Interestingly, once the maximum size and closer coiling were attained in this evolutionary lineage, more derived species did not become more loosely coiled again even though they became smaller.

Similar trends towards recoiling are present in *Hoploscaphites* and *Acanthoscaphites* lineages from the Campanian-Maastrichtian of Europe. For example, Machalski (2019; unpublished data) reconstructed a lineage of giant scaphitids culminating in *A.* (*Euroscaphites*) *varians varians* (Łopuski, 1911) in which the shaft of the shell became shorter and the hook became more abbreviated (Fig. 2). These changes in shell shape probably enhanced swimming ability and manoeuvrability of these cephalopods, in analogy to the Devonian example of shell coiling mentioned above.

Conclusion

The concept of 'heteromorph ammonoids' is embedded in the scientific literature due to historical reasons. Once upon a time, the concept played a critical role in helping to illustrate theories of orthoselection, racial senescence, and departures from 'normality'. These theories have long since been abandoned (Wiedmann 1969; Kennedy 1977; Korn 2003) and, as a result, the concept of 'heteromorph ammonoids' has lost any explanatory power. Today, the concept has no biological meaning except as a broad descriptive term for a mixture of morphotypes that depart from a closely coiled shell. This mixture represents a heterogeneous assemblage of species with different ecologies and morphologies belonging to different families and time periods.

Thus, the concept of 'heteromorph ammonoids' fails on both epistemological grounds, as a useful means to test hypotheses, and on ontological grounds, as an attempt to portray reality. Continuing to employ this concept in investigative studies risks obscuring and muddling evolutionary patterns and processes. The challenge in the future is to examine morphological, functional and distributional data about uncoiled (as well as coiled) ammonoids within a well-constrained stratigraphical and phylogenetic context to more fully illuminate the evolutionary history of ammonoids and their associated changes in habit and habitat.

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