Swiss J Palaeontol (2015) 134:177–186
DOI 10.1007/s13358-015-0091-0

Early ideas about fossil cephalopods

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Received: 23 March 2015 / Accepted: 16 June 2015 / Published online: 22 July 2015

Abstract Ammonites and belemnites are among the most celebrated invertebrate fossils, and both groups played a crucial role in the early history of palaeontology. This article gives an overview of the sometimes twisted roads that led from the first descriptions and illustrations of ammonites and belemnites in the 16th century to the picture that emerged in the early 19th century. The pearly *Nautilus* served as modern analogue for ammonites since the late 17th century, and the organic nature of the ammonites and their kinship to *Nautilus* became established shortly thereafter. For belemnites, the lack of a suitable modern analogue led to a much longer phase of speculation in which belemnites were assigned to many different groups of organisms, or even to the inorganic/mineralogic world. The apparent lack of both groups in today's seas led to various explanations including migration into the deep-sea. For ammonites, however, transmutation into the tiny foraminifers seemed at one time a likely explanation. Extinction only became widely accepted after the protozoan nature of the foraminifers was established, and the great deep-sea expeditions failed to recover ammonites or belemnites.

Keywords History of palaeontology · Ammonites · Belemnites · Living analogue · Extinction

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Introduction

Between 1768 and 1773, the monumental "Naturgeschichte der Versteinerungen" (Natural History of Petrifications; Walch 1768, 1769, 1771, 1773a, b) was published, probably the first fully illustrated treatise of palaeontology. All groups of fossils that were then known were treated on more than 1000 pages of text and illustrated with around 270 beautiful coloured plates. Cephalopods received ample space in part 2 (Walch 1768, 1769): ammonites (including Nautilites but without Orthocerates and Lituitids) were treated on 17 pages, belemnites were discussed on 39 pages. A few years earlier, the first comprehensive dictionary of palaeontology (and mineralogy) was published: Elie Bertrand's "Dictionnaire Universel des Fossiles…" (Bertrand 1763). The "Corne d'Ammon" were treated on seven pages, whereas belemnites received with 25 pages much more space. This contrasts of course markedly with the treatment of those two groups in more modern textbooks. Moore et al. (1952) had 26.5 pages for ammonites and only five for belemnites. In Piveteau (1952), we find 197 pages for ammonites and only 37 for belemnites; in Ziegler (1991), 35 pages for ammonites and 18 for belemnites and other coleoids; in Müller (1994), 164 pages for ammonites and 14 for belemnites; in Clarkson (1998), 14 pages for ammonoids, four pages for belemnites and other coleoids.

The reasons why ammonites receive much more space than belemnites in recent textbooks and treatises are quite obvious. First, ammonites are much more diverse than belemnites. Second, we have quite a clear conception what a belemnite animal looked like and how it lived. They were pelagic predators with ten arms with hooks and a mostly streamlined body, quite comparable to modern squid. We are much more insecure about ammonites. Our knowledge of their soft-part anatomy is rudimentary at most, and with respect to the number and form of the arms and the anatomy of the eyes, we are left with little more than educated guesses. Furthermore, many have, compared to modern cephalopods, unusual jaws, and in part a very peculiar sexual dimorphism. Therefore, there is much more argument about their ecological role. Third, ammonites proved to be fossils which were preeminently suited for distinguishing strata of different ages. Their important role in the emerging field of biostratigraphy led to a boost in new descriptions and monographs. Yet it is also clear why belemnites required much more space in the books of 1770. There was still considerable disagreement whether belemnites were the remains of organisms (and if yes, remains of what organisms) or rather inorganic/mineralogical products.

In the following, the history of research for both groups between the 16th and the early 19th century is investigated. In this context, three concepts are employed:

- The concept of easy and difficult fossils, introduced by Rudwick (1972)
- The concept of a modern analogue and its use in establishing biological relationship (thereby becoming "homologues") for controversial fossils
- The concept of phases of perception, in which a phase of speculation, a phase of decision, and a phase of consolidation are distinguished.

Establishing an organismic origin

The first detailed descriptions of ammonites and belemnites in printed books appeared in the 16th century. Especially influential were Agricola (1546), who also introduced the term "fossilium", and Gessner (1565), who produced the first fully illustrated book on fossils (Fig. 1). At that time, the term "fossil" encompassed everything that was dug out of the ground, including minerals, stones and artefacts. Both authors treated ammonites and belemnites, describing their form and appearance and making references to works of the ancients, mainly Pliny. Fossils were not seen as remains of biological objects but rather as oddities of nature that had grown in the rocks by the action of a formative force ("vis plastica"; see Hölder 1960; Rudwick 1972; Ellenberger 1996). For ammonites, Gessner noted similarities with marine snails, also with coiled snakes (an idea he probably had from Albertus Magnus; personal communication Dieter Korn, September 2014), but these similarities were not used to postulate an organic origin. Belemnites were seen either as mineralogical precipitations like stalagmites, or as remains of thunder bolts, or as petrified lynx' urine. These interpretations prevailed for most of the 17th century as can be seen in the works of Aldrovandi (1648), Worm (1655), Mercati (1719) and others.

Belon was the first to figure the shell of *Nautilus* in his monograph of marine organisms (Belon 1553), and Worm was the first to directly compare *Nautilus* with an ammonite (Worm 1655). Yet the latter concluded that the ammonite rather imitated the skeleton of a snake (!), and no relationship to *Nautilus* was proposed. The first to suggest an organic origin for ammonites and to interpret them as "some kind of nautili" was Hooke (Fig. 2; 1665, and much more detailed in the posthumous work 1705). Around this time, various Italian authors also proposed an organic origin for ammonites (Romano 2015) but without linking them to *Nautilus*. For Hooke, it appeared obvious that ammonites and *Nautilus* were essentially of the same kind (Rossi 1984). Yet for his contemporaries, it was not: ammonites were some sort of imitations of *Nautilus*, and not even good ones, that were produced in the soil and in the rocks as "lapides sui generis" by yet unknown forces (e.g. Lister 1671; see Rossi 1984). Yet Hooke had made the link, and with the advent of the diluvial theory and the broad acceptance that fossils were the remains of ancient organisms around 1700, the ammonites were accepted as variants of the modern analogue *Nautilus*.

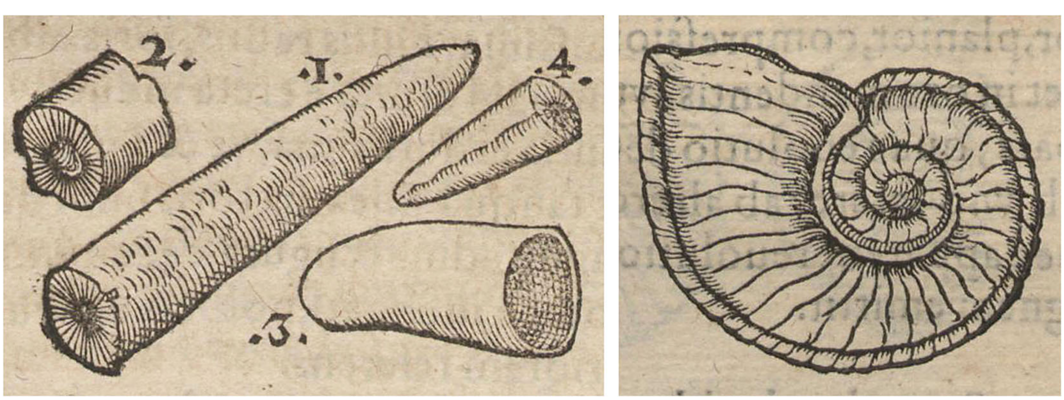

Fig. 1 The first illustrations of belemnites and ammonites in a printed work were published in 1565. From Gessner (1565)

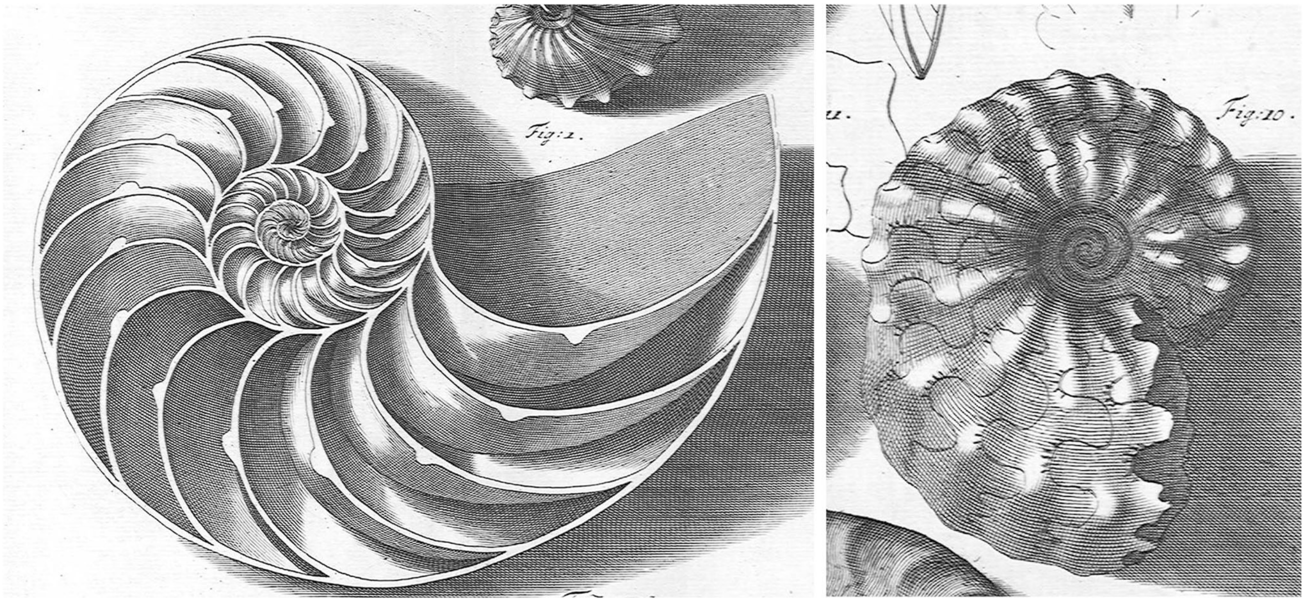

Fig. 2 Here for the first time, illustrations were used to directly compare a *Nautilus* shell with ammonites. From Hooke (1705)

For belemnites on the other hand, such a modern analogue was missing, and in the early 18th century, there was still a heated debate whether they had an organic origin or were rather mineralogical precipitates (see Bertrand 1763; Walch 1769). It should be noted in this context that both ammonites and belemnites are "difficult" fossils. They could not readily be compared to modern organisms and shells occurring in modern seas. "Easy" fossils like Neogene gastropods and bivalves found in Italy or France proved to be almost identical with species that are still frequently found on the coasts of the adjacent Mediterranean Sea. This led quite early to the assumption that these fossils were the remains of organisms that once lived in the sea (e.g. unpublished notes of Leonardo da Vinci; Palissy 1580; see Hölder 1960; Rudwick 1972; Gohau 1987; Ellenberger 1996; Romano 2015). Belemnites proved to be the more difficult fossils than the ammonites; yet in the early 18th century, the majority of naturalists started to accept an organic origin even for that group. There was also growing evidence that they must have been some sort of marine organisms as they were always associated with other marine shells (Erhart 1724, 1727; Wittmann 1979).

Establishing the biological kinship

The diluvial theory was instrumental for the proposition of an organismal origin of fossils. When it gained wide acceptance around 1700, promoted mainly through the works of John Woodward and Johann Jakob Scheuchzer, the relationship of ammonites to the pearly *Nautilus* was almost immediately accepted. They were thus very early included in the group of the cephalopods (although that term was only later introduced by Cuvier). In 1705, the first description of *Nautilus* soft-parts was published (Rumpf 1705) and confirmed what was previously only assumed by analogy with *Argonauta*: that *Nautilus* indeed belonged to the cephalopods. For the belemnites, the biological affinities remained controversial for much of the 18th century. It is really astounding how many different and fanciful proposals were made for the belemnites' affiliation. In this respect, they are only rivalled by the conodonts. It is beyond the scope of the present study to give an exhaustive overview of all the different opinions. For a full coverage, the reader is referred to Bertrand (1763), Walch (1769) and Blainville (1827).

A variety of isolated arguments were used to support specific placements. Helwing (1717) held the opinion that all belemnites originally were pointed at both extremities (an idea that was later revived by Vialet (1761), and placed them among the zoophyta, i.e. the corals. Such a placement was also favoured by Stobæus (1752) but this time the polyp was situated in the alveola. Quite popular was the rather indeterminate proposal that belemnites were tubular marine shells (e.g. Lhwyd 1699; Klein 1731; Breyn 1732) like tusk shells, serpulids, or clavagellid bivalves. Based on the external form, a relationship with pholadid bivalves or *Lithophaga* was postulated (Brückmann 1728), or based on the fibrous internal structure a relationship with pen shells was assumed (e.g. Cesalpino 1596). Echinoid spines were another widely discussed and obvious possibility (Klein

1731; Ritter 1741; Beudant 1810), not least because they also showed a radial internal structure. Assigning belemnites to the holothurians (Capeller 1740) seems today quite odd. Yet it was argued that the gelatinous fibrous nature of a holothurian might, through the action of petrifying fluids, fossilize to the massive fibrous structure of belemnites (Wallerius 1747, 1750; Bertrand 1763). In addition, both belemnites and holothurians lacked a head.

Belemnites as remains of vertebrates were also proposed by some, e.g. as teeth of the narwhale or horns of ungulates (see Blainville 1827) but the latter was already then seen as implausible because belemnites appeared to be remains of marine organisms (see above; Erhart 1724, 1727). Yet the pointed tip and the alveola corresponded rather well to the form of teeth of large whales, perhaps sperm whales, or crocodiles (Bourguet 1729), although differences in the internal structure were noted.

Matters got further complicated by the fact that it remained disputed for a long time whether all belemnites had an alveola, and whether the chambered part (phragmocone) belonged to another organism. Isolated phragmocone chambers might have been limpet-like gastropods (see Blainville 1827), and whole phragmocones were perhaps stacks of such organisms as is known from slipper shells. Phragmocones were also seen as shrimp tails (Swedenborg 1722), a relationship that was already stated by Gessner (1565). Yet shrimp tails should be semicircular, whereas belemnite phragmocones were circular (e.g. Blainville 1827).

When alveola and guard were considered in conjunction but without the assumption that they were the remains of the same animal, some new perspectives opened up. The belemnite proper (guard) was interpreted as an echinoid spine that was infected by a parasite (alveola) at its base (Raspail 1829). Earlier it was suggested that the belemnite proper was a voracious holothurian (!) that had engulfed its prey, the phragmocone (perhaps some sort of gastropod; Capeller 1740).

The first to propose a cephalopod origin for the belemnites was Erhart (1724, 1727; see Wittmann 1979) in his dissertation on Swabian belemnites. In his very thoughtful work, he first assembled many arguments which proved that belemnites were the remains of marine organisms. He then showed that the chambered phragmocone is an integral part of the shell. For the guard, he demonstrated that this structure grew by accretion on the surface, and that it must therefore have been an internal skeleton. The structure of the phragmocone led Erhart first to see *Nautilus* as the best analogue for belemnites (Erhart 1724). Yet in the second edition of his work, he favoured *Spirula* as the closest relative (Erhart 1727). Only a few years before, the shell of *Spirula* had been described (Rumpf 1705), and in contrast to *Nautilus,* it showed a marginal sipho which corresponded better with the situation in belemnites (Fig. 3).

A cephalopod kinship for belemnites was also proposed independently by Rosinus and based on the same reasonings as those of Erhart but only published posthumously (Rosinus 1728, 1751). Although the arguments of those two workers appear absolutely convincing to us, this was not the case during much of the 18th century. As an example might serve a review of Erhart's work in a conchyliological journal in the late 18th century (Schröter 1776). The reviewer came to the conclusion that the argumentation for a marine origin of belemnites was quite convincing. But when *Nautilus* or *Spirula* were treated as modern analogues, this "seemed definitively far-fetched" (Schröter 1776). In his dictionary, Bertrand (1763) also did not subscribe to the ideas of Erhart and Rosinus. Walch (1769) and Guettard (1786), on the other hand, fully supported the position of Erhart, although they had to admit that the missing of modern belemnites posed a problem.

This lack of a suitable modern analogue was the reason why the phase of speculation lasted for belemnites almost 100 years longer than for ammonites. During much of the 18th century, new descriptions of belemnites appeared (e.g. by Scheuchzer, Lang, Klein, Breyn, Walch and others; see Blainville 1827), but no real progress with respect to the biological affinities was made. In the 13th edition of Linné's Systema naturae (Gmelin 1793), the belemnites were placed directly after the nautilites, ammonites, lituites and orthoceratites. Yet discussions about their kinship continued. Towards the end of the century, the Cephalopoda (as order) was erected (Cuvier 1797), but without discussing the fossil forms. The phase of decision was then rather short and not based on additional evidence. It was in fact the authority of the eminent zoologists Cuvier and Lamarck who placed, in their general works, the belemnites without further discussion within the cephalopods (Cuvier 1817; Lamarck 1822). With very few exceptions (e.g. Raspail 1829), no "heretical" views were expressed afterwards.

In the subsequent phase of consolidation, the first large monographs (Blainville 1827; Voltz 1830, 1840) and soft-part reconstructions appeared (Fig. 4; Miller 1826; Orbigny 1840). These were in part influenced by finds of fossil coleoids which showed soft-part preservation from such famous Lagerstätten like Holzmaden/Boll and Lyme Regis, in part from analogy with modern squids like *Ommastrephes*. The first functional interpretations in these publications saw the guard mainly as protective organ for the backward swimming animal (Orbigny 1840). The question of buoyancy was also addressed, in part with experiments (Miller 1826), although it remained contentious whether the guard was originally massive or only became so during fossilization.

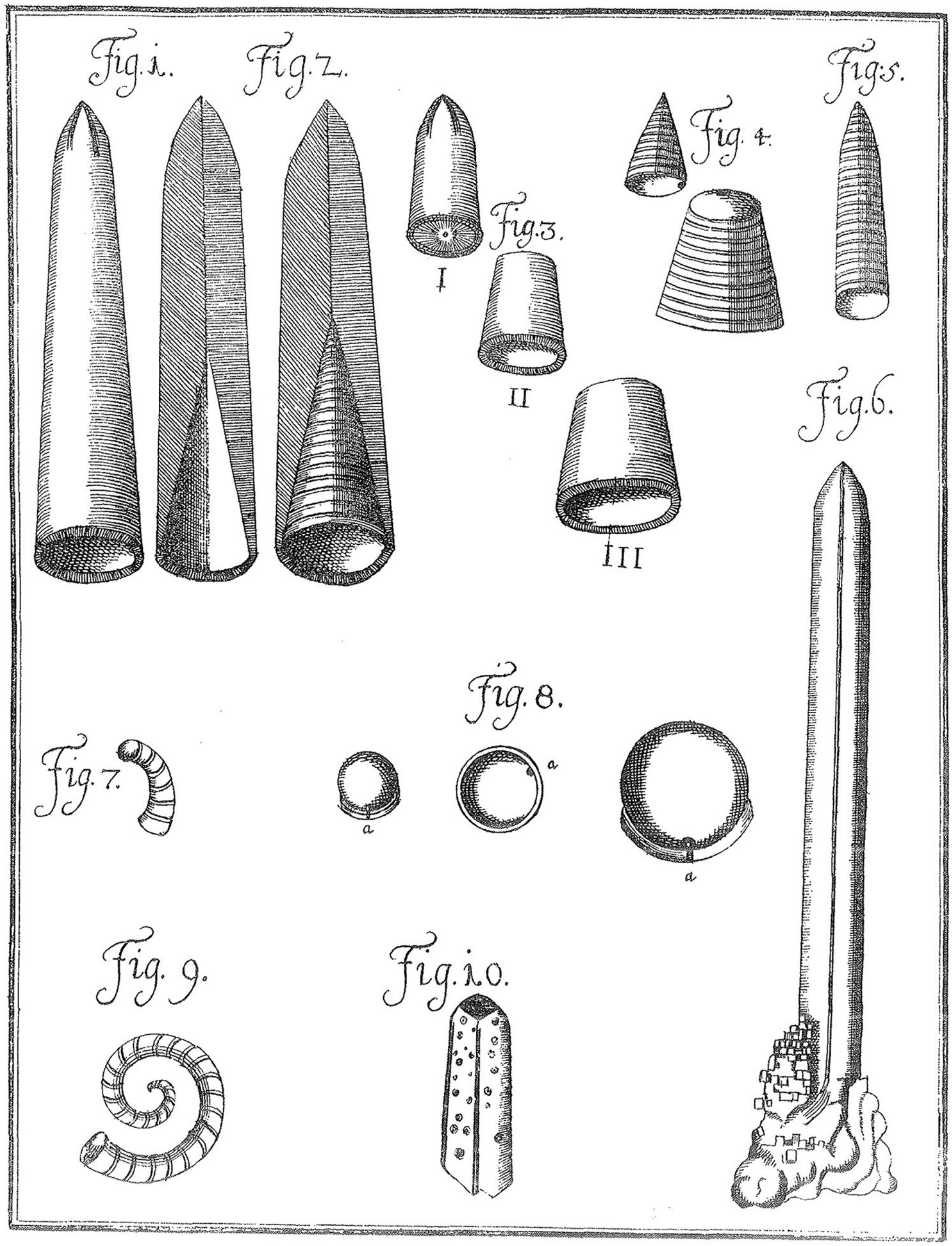

Fig. 3 Detail from the plate in Erhart's 2nd edition (1727) of his work on Swabian belemnites. They were here for the first time compared to *Spirula*

For ammonites, the phase of consolidation started early in the 18th century. Various authors described many different forms in the subsequent decades, although the concept what a "species" should be greatly differed between the authors (Nelson 1968). In the late 18th century, when Walch finished his treatise on petrifactions, around 300 different taxa had been erected (Nelson 1968). Yet most of these did not meet the standards of Linnean nomenclature and are no longer in use. In the early 19th century, systematic treatments increasingly placed emphasis on the description of new species *and* the strata where these ammonites came from (Sowerby 1812, 1823; Reinecke 1818; Young and Bird 1822; Phillips 1829; Zieten 1830; De la Beche 1830; Münster 1831, 1834; Buch 1832; Orbigny 1840, 1842; Quenstedt 1843, 1846). These descriptions became thus instrumental for the development and refinement of the new field of biostratigraphy.

An important difference between *Nautilus* and ammonites seemed that in the former the last whorl encompassed all previous ones, whereas in ammonites, the inner whorls were visible. Both Cuvier and Lamarck appeared to have favoured *Spirula* as the best modern analogue for the ammonites. They thus saw the ammonite shell as internal (Nelson 1968) which, however, was not widely accepted and definitively rejected by Buch (1832).

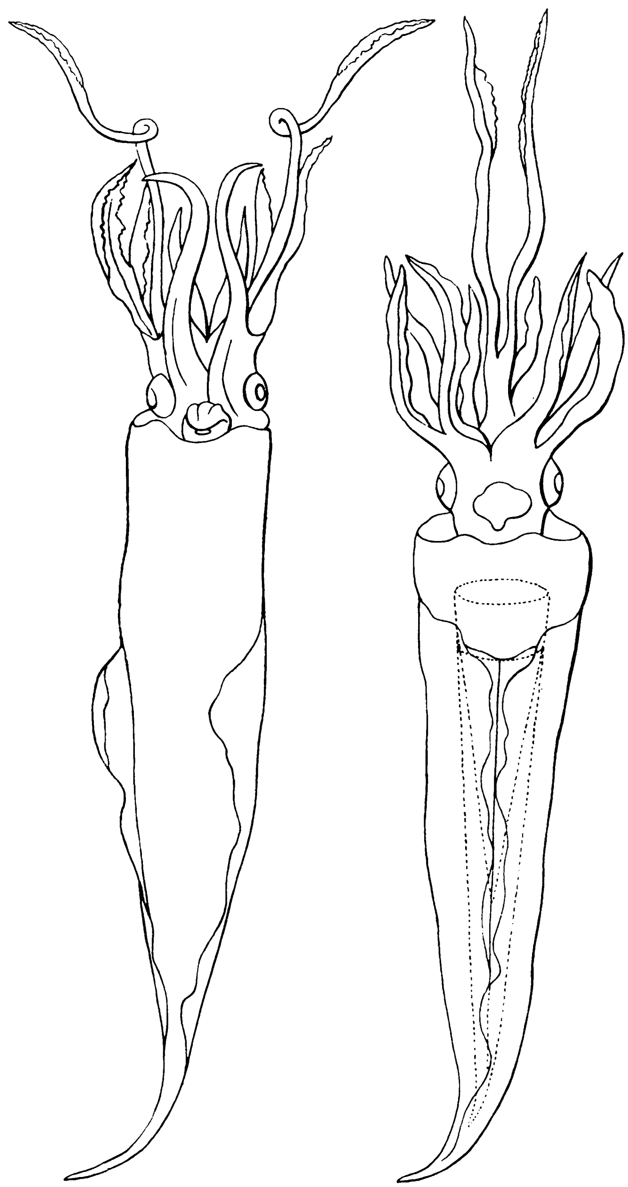

Fig. 4 Detail from plate IX in Miller (1826). This was the first pictorial soft-part reconstruction of a belemnite

In this time period, the first life reconstructions of ammonites were circulated (Fig. 5; De la Beche 1830; Goldfuss 1831; see Rudwick 1992, 2008). These oriented themselves on the living paper nautilus *Argonauta* (see e.g. Montfort 1802), and ammonites were consequently shown sailing across the surface waters of Mesozoic seas, with the two enlarged tentacles serving as sails. At first sight, this seems odd because ammonites were already before classified much closer to *Nautilus* than to *Argonauta*. But live specimens of *Argonauta* had been observed on the sea surface, whereas sightings of living *Nautilus* had not yet been published. The description of *Nautilus* soft-parts by Rumpf (1705) was notoriously devoid of details, and up to the early 19th century, it was assumed that *Nautilus* had a similar anatomy and mode of life as *Argonauta* (e.g. Montfort 1802). Only after a much more detailed description of *Nautilus* was published (Owen 1832), it became clear that there were fundamental differences in the shape of the head, the eyes, the number of tentacles, etc. *Nautilus*-like ammonite reconstructions were drawn only afterwards but for quite some time still sailing on the sea surface (e.g. Figuier 1862; Flammarion 1886; Fig. 6).

The question of disappearance/extinction

With both groups placed within a systematic framework, there remained one big unanswered question: Why can they not be observed in today's seas? This question had been of course already asked in the late 17th and early 18th century when the organismal nature of ammonites and belemnites gained wider acceptance (e.g. Hooke 1705; Erhart 1724, 1727). The two groups were obviously missing as shells on the coasts of the known seas which had made them difficult fossils (see above). The question became more urgent in the late 18th and early 19th century when it was realized that both ammonites and belemnites were missing not only on today's coasts but also in sediments above the chalk and other younger deposits. There were three possible categories of explanation why these fossils were not encountered in today's seas (Rudwick 2005): 1. Migration; 2. Transmutation and 3. Extinction.

Migration

By 1750, not all the marine realm had been charted and there remained the possibility that ammonites or belemnites might linger in some distant seas. Much more popular, however, was the notion that these organisms had migrated into the deep-sea (Hooke 1705; Erhart 1724, 1727; Walch 1769). As a matter of fact, most spectacular finds of "living fossils" had been made in these times. Stalked crinoids were brought to the surface from deep waters in the Caribbean and described (Guettard 1761; Ellis 1762). This provided the solution of the enigma of starstones and trochites. It also showed that these fossils that were so commonly found in older (i.e. Palaeozoic and Mesozoic) strata belonged to organisms that were still among us but now confined to the remote deep-sea. These and other finds led later in the 19th century to an agenda that tried to promote deep-sea expeditions with the explicit expectations to find more "living fossils".

Migration into the deep-sea remained the most popular explanation for the apparent absence of ammonites and belemnites in modern coastal and shallow seas well into the 19th century. Even on the eve of the great Challenger

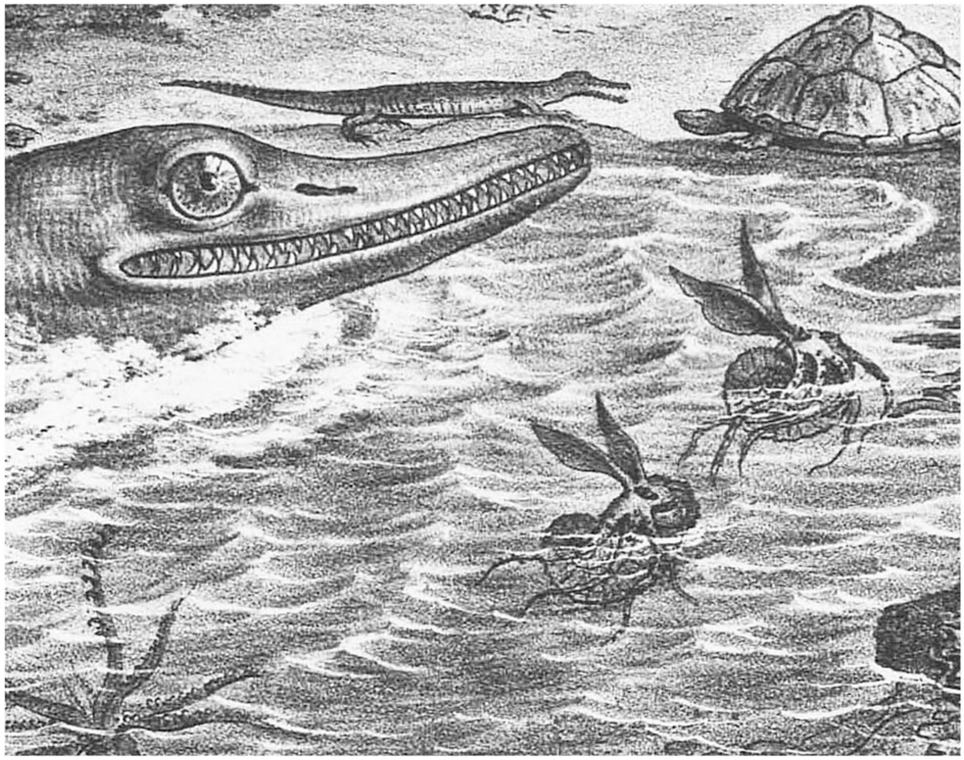

Fig. 5 Early life reconstruction of ammonites. This is a detail of the frontispice of (Goldfuss 1826–1831) appearing in the last part of the first volume of “Petrefacta Germaniae” (1831). It was obviously drawn after De la Beche (1830)

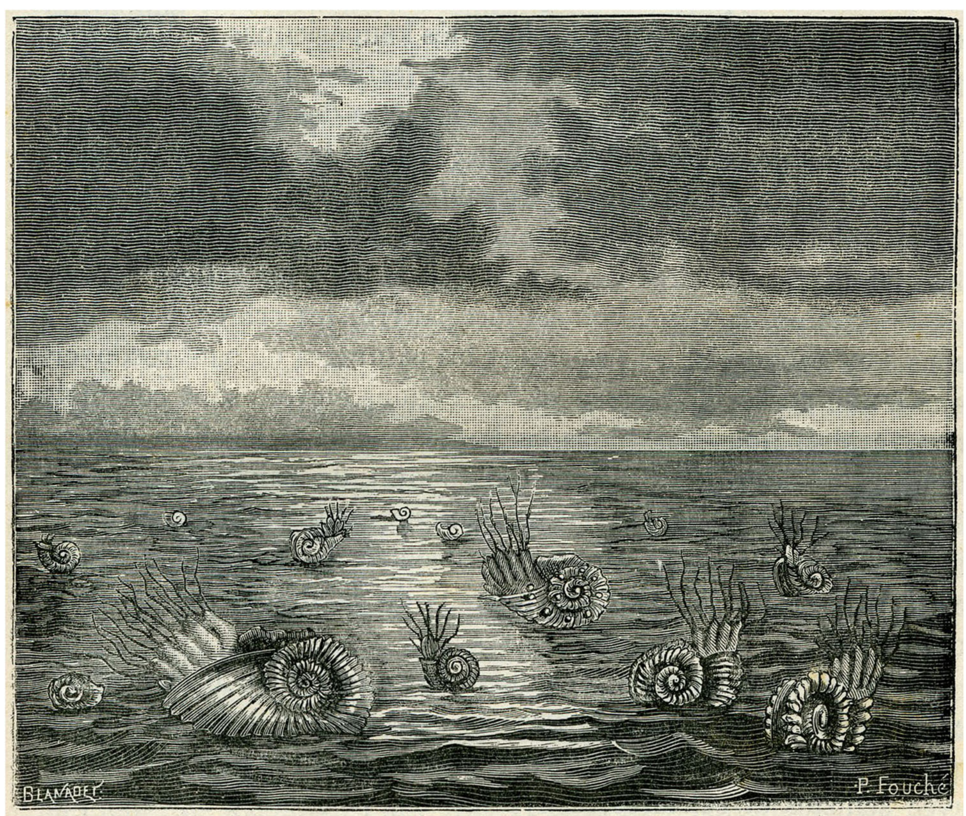

Fig. 6 Ammonites floating on the surface of the sea, with soft-parts reconstructed in *Nautilus*-like manner. This figure is from Flammarion (1886) but a very similar figure appeared already in Figuier (1862)

expedition, expectations were high what to find in deep-sea dredgings: "The Mollusks will, no doubt, afford a rich harvest… a variety of Nautiloid Cephalopods may be discovered… Belemnitic Squids would appear natural…" (Agassiz 1872).

Transmutation

Although a general theory of evolution was clearly heretic in the early 18th century, transmutation (i.e. change) for certain forms appeared possible (Rudwick 2005, 2014). Perhaps some of these cephalopod fossils had changed their form or size. For the ammonites, a whole new perspective opened when small planspiral and multilocular shells became known, first from marls around Bologna (Beccarius 1731), then from modern beach sands in Rimini (Plancus 1739). These shells appeared like miniaturized ammonites and seemed to prove that they had not vanished but instead transmuted into small forms (Romano 2015).

These descriptions were immediately welcomed by the large majority of authors working on the subject. It turned out that there were not only tiny ammonites and nautilites among these forms, but also orthoceratids and lituitids and other fossil chambered cephalopods seemed to have their corresponding miniatures. They appeared in all the treatises from 1750 onwards as belonging to the same group as *Nautilus* and ammonites (Linné 1758; Gmelin 1793; Montfort 1808; Cuvier 1817; Lamarck 1822; Blainville 1825). Many new species were erected early in the 19th century (Montfort 1808; Orbigny 1826) but only then the fundamental differences between the tiny forms and their larger counterparts emerged. Orbigny (1826) erected the order Foraminifera (corresponding in part to the Asiphonoïdei of Haan 1825) for those small shells. They were distinguished from the ammonites and nautilites by the absence of a syphon. Instead they had numerous pores between the chambers. Yet Orbigny retained them within the shell-bearing multilocular cephalopods.

When living specimens were observed, these tiny forms showed some sort of tentacles which seemed to link them further with the cephalopoda. Yet it was shown that foraminifers were unicellular organisms and that those tentacles were filamentous extensions of the protoplasm (Dujardin 1835a, b). Except for a superficially similar shell form, they had absolutely nothing in common with the cephalopod molluscs. The transmutation theory thus became obsolete at this time.

Extinction

Extinction was certainly not foreseen in any biblical approach to earth history that prevailed until the early 18th century. Even in the late 18th century, the search for modern belemnites and ammonites (see Walch 1768, 1769) stood high on the agenda, and the persistent classification of the tiny foraminifers amongst the cephalopoda testified to the hesitation to see extinction as a (common) possibility. Yet in the late 18th and early 19th century, it became apparent that extinction was real and had affected many different groups of organisms (Rudwick 2005, 2014). The proof, however, did not come from the cephalopods but rather from large terrestrial vertebrates (Cuvier 1799, 1806).

When Reinecke exclaimed in his work on the ammonites of the Coburg region (Reinecke 1818) "Where are they now?" and subsequently answered that they are gone (although he also admitted transmutation), he was a pioneer in the field (Pompeckj 1926). But the number of those who saw extinction as a reality was quickly growing. Extinctions of course became a serious possibility after Darwin (1859) had shown not only how new species could originate but also that organismal lines could end.

The big deep-sea expeditions of the late 19th and the 20th century failed to reveal any ammonites or belemnites. It thus became less and less likely that ammonites and belemnites had migrated into the deep-sea (although the case of the Monoplacophora should be kept in mind; Lemche 1957). After the foraminifers had been shown to be no cephalopods, extinction thus remained not only as the most probable but as the only explanation why we do not encounter ammonites and belemnites any more in modern seas.

Conclusions

The perception of the ammonites and belemnites during the past 500 years differed considerably between the two groups. No living representatives were encountered in modern shallow seas or their coasts which made both groups difficult fossils. Yet Hooke proposed already in 1665 that the modern *Nautilus* was a suitable analogue for the ammonites, a proposal that was after initial hesitation mostly accepted after 1710. The lack of a comparable analogue for belemnites led to a much longer phase of speculation for the latter, in which the belemnites were assigned to almost any animal phylum. The phase of decision for that group occurred early in the 19th century when they were placed in a definitive manner in the Cephalopoda. This was no majority rule or the inclusion of new evidence such as preserved soft-parts (which was so crucial in the conodonts) but rather an authoritative decision by leaders in the field. The extinction of both groups only became accepted in the 19th century when it was shown that the tiny foraminifers were not transmuted ammonites but totally unrelated protozoans, and that there were no ammonites or belemnites lingering in the remote deep-sea.

Acknowledgments The paper benefited from discussions with various experts at the 9th International Symposium "Cephalopods—Present and Past" in September 2014. The author also wishes to thank for the thoughtful comments and emendations made by Isabelle Rouget and an anonymous reviewer.

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