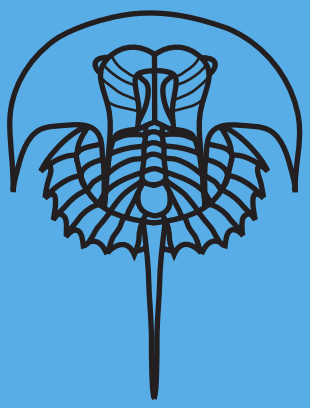

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Ammonites and Octopuses

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PART M, CHAPTER 18: AMMONITES AND OCTOPUSES

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THE *ARGONAUTA* PROBLEM

The unique shell of the female *Argonauta*, and its external resemblance to some ammonite shells, give rise to questions that have puzzled paleontologists and biologists from time to time, and that have not been satisfactorily resolved.

The shell is present in the female only. The male is dwarf and does not have a shell. Arms of pair I (the dorsal pair) of the female are expanded into thin flaps of tissue that cover the shell (Fig. 1), which is secreted at the anterior margin by glands along the edge of the arm flap. The shell (Fig. 2–3) is made of calcite with a high proportion of organic matter. Solution of the calcite in dilute HCl leaves behind the organic matter, having the form of the shell but no stiffness.

Argonauta is the only Recent genus placed in the family Argonautidae. Other pelagic octopods (families Alloposidae, Ocythoidae, Tremoctopodidae) do not secrete a shell and do not have the modified arm pair I.

Fossil argonauts show greater diversity than living ones. Miocene forms comprise four genera placed in two subfamilies. The extinct Mizuhobariinae have smooth shells, and indeed, *Obinautilus* was originally described as a nautilid. There is some reason to think that *Argonauta* is a relict genus like *Nautilus*, though it is much more widely distributed and appears to be successful.

The shell ornament of Argonautinae commonly consists of sinuous, bifurcating ribs on the side, ending in sharp, elongated tubercles flanking a smooth venter. There is a range of types of ornament. At least one species, *A. nodosa*, has tuberculate ribs. A large number of specific names has been proposed for argonauts on the basis of different forms of the shell (Robson, 1932), the animal being unknown for most of these. Norman (2003, p. 190) stated that there are at least five species, of which three are well known.

ARGONAUTS AND AMMONITES

The similarity between *Argonauta* shells and those of some ammonites has struck many workers. The most common comparison is made with some of the Cretaceous Hoplitaceae but there are also resemblances to other groups, such as the Jurassic schlotheimiid *Angulaticeras*, and the Triassic Trachyceratidae, in the case of shells with tuberculate ribs.

The shell of *Argonauta* is not chambered. The ammonite shell is composed of aragonite, and is presumed to have been secreted by the mantle, while that of *Argonauta* is calcite and is formed by the arms. These differences render it difficult to propose that the shell of *Argonauta* is homologous with that of the ammonites and other ectocochleate cephalopods.

However, authors have, from time to time, suggested that the ammonite shell was internal or at least partly enveloped by the mantle. The most recent are Doguzhaeva and Mutvei (1989), who provided evidence from the Lower Cretaceous (Aptian) heteromorph ammonoid *Ptychoceras*, that the outermost shell layer was secreted from the outside, and hence the shell was at least partly covered by living tissue. In 1991, they provided similar evidence for *Aconeceras*, a normally coiled ammonite (also Cretaceous:

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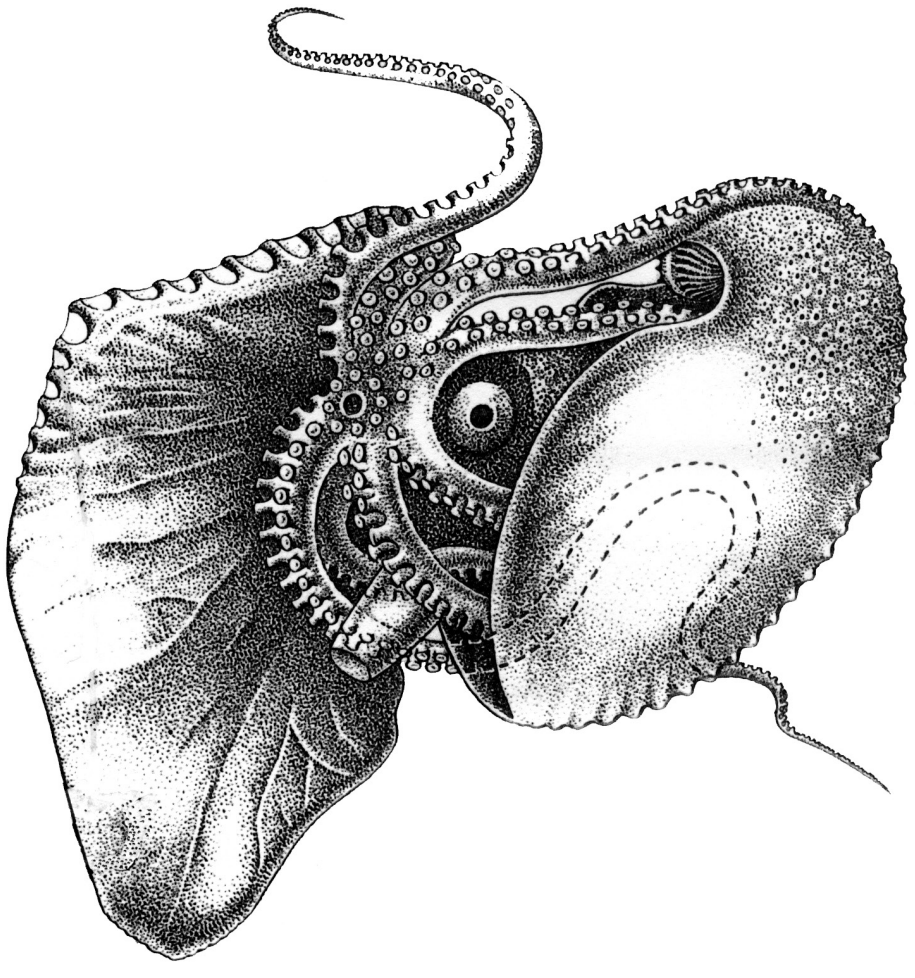
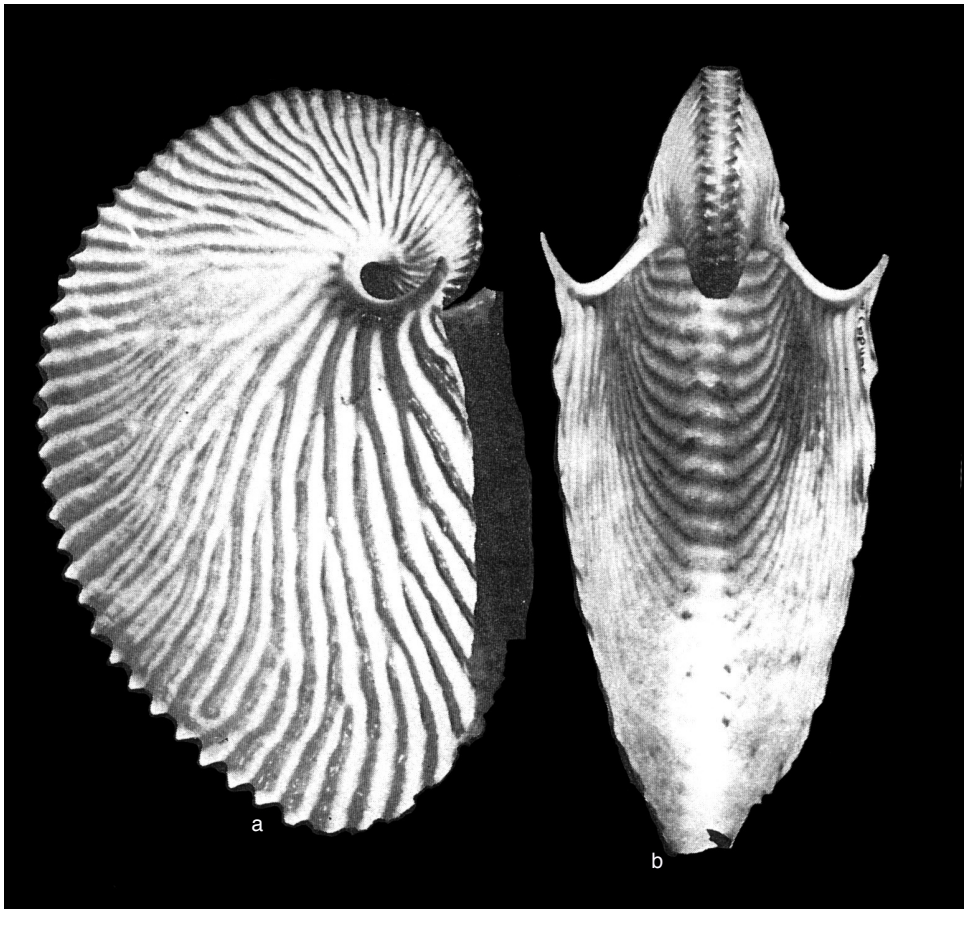


FIG. 1. *Argonauta argo* L., female in shell. Left arm I covers shell, of which earliest part is visible; right arm I is against side of tank, approximately ×0.5 (Young, 1960).

Aptian). It is possible that this external shell layer was secreted by arms rather than mantle, and if so, one could argue that the *Argonauta* shell represented this layer only in the ammonites, the original external shell having been lost in the course of evolution. The form of the ammonite arm crown remains unknown.

OCTOPOD ORIGIN IN AMMONITES

Johann REINECKE (1818), who wrote a book on some ammonites found near Coburg, Germany, seems to have believed that ammonites were fossil *Argonauta* shells, though he does not discuss the question in detail. SUESS (1865, p. 74) remarked on the similarity between the shell of *Argonauta* and that of *Ammonites aon* (i.e., the Triassic *Trachyceras*), and in 1870 (p. 319), SUESS suggested that the ammonites are represented today by the octopods and that the *Argonauta* shell was "eine rudimentäre Ammonitenschale." Dictionaries translate rudimentäre as rudimentary or vestigial, and the latter meaning was presumably intended by SUESS.



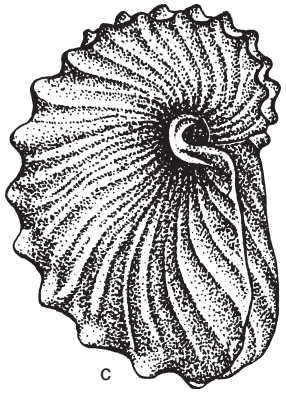


FIG. 2. *a–b, Argonauta argo* L., shell, right lateral and apertural views, ×0.8 (Dell, 1952); *c, A. hians* SOLANDER, shell, ×1 (Nesis, 1982).

Suess's idea was developed by Steinmann (1888), who studied a large collection of *Argonauta* shells and found that they fell into three groups. He suggested that these three groups of Recent *Argonauta* species had descended from different ammonite stocks.

Schwarz (1894) referred to a paper by Perrier and Rochebrune (1894) on a new species of octopus that laid eggs in bivalve shells, and lived in the shell itself, in Schwarz's words, probably "a return to former habits." Schwarz (1894, p. 92) thought that the octopods, in the process of losing their ammonitic shells, passed though a stage in which "some retained their original covering while others were free; some of the latter . . . would feel the loss of the shell which their near relatives possessed" and look for empty shells.

Haeckel (1896) likewise accepted the derivation of octopods from an ammonoid stem, the two groups forming for him a separate clade from Decapoda. Accordingly, he grouped the Ammonoidea (Ammonitaria) with the Octopodaria in his order Octolenae. In contrast to earlier authors, he derived the octopod stock from goniatites; that is, an early ammonoid group that existed from the Devonian to the Permian (see *Treatise*, Part L, Mollusca 4, revised, volume 2, 2009).

John (1909, p. 14) was cited by Spath (1933, p. 459) as discussing the question of "passage forms" between ammonites and coleoids. I have not been able to see John's dissertation. He seems to be otherwise unknown in cephalopod literature.

Naef (1923, p. 783) rejected Steinmann's (1888) derivation of *Argonauta* from the ammonites. He put forward (1922, p. 292; 1923, p. 781–783) his own theory as a "tentative" explanation of the similarity between *Argonauta* and some ammonoid shells. He noted that, in *Ocythoe tuberculata*, which he regarded as the closest living relative of *Argonauta*, the male takes possession of an empty "shell" of the tunicate *Salpa* and drifts about in it like a "pelagic Diogenes" (Naef, 1922, p. 291). He proposed that the ancestral argonauts adopted empty ammonite shells in which to lay their eggs. The eggs were fixed to the inner surface of the shells using the secretions of the skin glands, and the same secretions were used to enlarge the adopted shell. He recalled that the sea anemone *Adamsia* adds material to the aperture of the gastropod shell that it shares with a hermit crab, though this analogy does seem far fetched. In due course, the adopted shell was merely the nucleus of the shell produced by the cephalopod and finally became dispensable, so that when the ammonites became extinct, the argonauts no longer had need of them. Strugnell and others (2006, p. 95) thought this "perhaps a fanciful explanation." The similarity of argonaut to ammonite shells may have been due to "some kind of transfer of plastic sense" (Naef, 1922, p. 294), though Naef admitted that this was a metaphysical concept and not a scientific hypothesis (translations from the English edition, 2004).

Pia (1923, p. 70), remarking that only a minority of authors had supported Steinmann's ideas, wrote that, nevertheless, they should not be discarded out of hand. He listed six reasons for taking the hypothesis seriously. Finally, Pia (1923, p. 72) wrote that the conclusion that all octopods originated in ammonites was "unavoidable." Pia (1923, p. 73) noted that Naef's book Die fossilen Tintenfische (Naef, 1922) had been published while his own paper was in press and could not therefore be given proper consideration.

Steinmann (1925b) returned to his hypothesis of a polyphyletic genus *Argonauta* and developed it in some detail, ignoring Naef's rejection of his ideas. Following his division of argonaut shells into three groups (in Steinmann, 1888), he proposed new generic names: *Argonautina* (for *Argonauta hians* Solander) for species supposedly like hoplitid ammonites, and *Argonautella* (for *A. tuberculosa* Schumacher), for shells with tuberculate ribs. *Argonauta* was restricted to shells that Steinmann compared with the Jurassic *Angulaticeras* and the Cretaceous

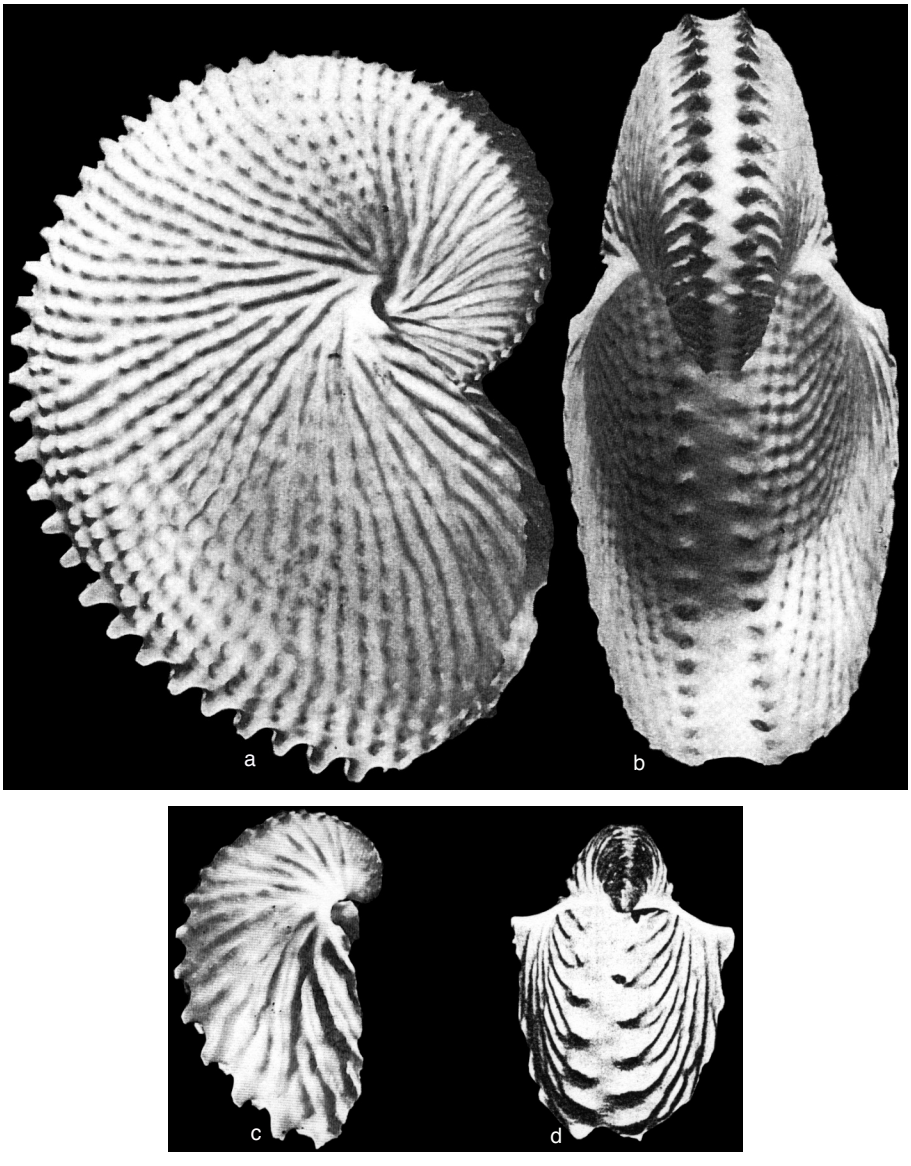


FIG. 3. *Argonauta nodosa* SOLANDER; *a–b,* adult shell, ×1; *c–d,* early part of shell showing nontuberculate stage, ×1 (Dell, 1952)

Forbesiceras. This generic subdivision has not been adopted by workers on Recent octopods.

ROBSON (1932, p. 61) rejected a genetic connection between ammonites and octopods and summarized (1932, p. 27) previous views that the octopods were derived from an early, or ancestral, decabrachian stock. He discussed NAEF's theory of the origin of the argonaut shell and rejected it also. He thought that the octopod arms, being homologous with the gastropod foot, might "retain the capacity to reproduce spiral calcareous plates" like the gastropod operculum, and

that two such plates "might . . . produce a structure simulating an Ammonite shell, the secondary ornamentation being . . . due to the presence of the suckers." This is not much more plausible than NAEF's idea.

SPATH (1933, p. 457–459), in his long paper on cephalopod phylogeny, considered whether the late Cretaceous heteromorph ammonites (Baculitidae) could have had shell-less descendants, and seem to think that this was possible, but he did not offer a clear opinion.

J. Z. YOUNG (1960) returned to the possibility previously entertained by NAEF, that the argonautids had passed through an evolutionary stage living in borrowed shells, noting that octopuses, in general, are in the habit of living in cavities (however, this is true of the benthic Octopodidae rather than the pelagic families). Neither he nor NAEF went as far as SCHWARZ (1894), whose work they probably did not know, in seeing such a habit as evidence of the evolutionary origin of octopods in ammonites.

EBEL (1985), developing his earlier calculations on the buoyancy and limited swimming abilities of ammonites, suggested a benthic mode of life for them, and, in 1992, he published reconstructions of heteromorph ammonoids as benthic creatures, in which a large part of the body was permanently outside the shell. Clearly, such a mode of life could prefigure the octopod condition, although it must be stated that EBEL's opinions differed from those of most workers on ammonoids, who regarded the majority of ammonoids as having been pelagic animals.

DOGUZHAEVA and MUTVEI (1990), in a brief paper in Russian, figured the radula of *Aconeceras* with that of the Recent *Eledonella* for comparison. In 1992, they described the *Aconeceras* radula in English and noted its similarity to that of the pelagic bolitaenid octopods. They noted the possibility that "ammonoids with an *Aconeceras* type of radula are phylogenetically related to bathypelagic incirrate octopods" (p. 175) but also that the similarity may be caused by convergence. DOGUZHAEVA and MUTVEI (1993, p. 113) repeated the suggestion that the similarity of radulas "may reflect the phylogenetic relationship between octopods and certain ammonoid groups."

The latest author to support the origin of *Argonauta* and related octopods in the ammonites was LEWY (1996). He did not mention the earlier authors cited above, and may, therefore, have originated the idea independently, although he did mention the ideas of NAEF (1922) and J. Z. YOUNG (1960). LEWY (1996) laid stress on the supposed similarity between the reproductive strategies of ammonites and octopods. He also cited DOGUZHAEVA and MUTVEI (1993) as suggesting a relationship between Cretaceous ammonites and some octopods on the basis of the structure of the radula.

In 2002, LEWY published two further papers, both primarily concerned with ammonoids. LEWY (2002a) discussed the functional interpretation of the complex septa possessed by many ammonoids. He also repeated NAEF's hypothesis that ancestral argonautids used empty ammonite shells as egg cases and were able to repair or modify them, becoming able to secrete complete shells after the ammonites became extinct. He thought that the similarity of argonaut shells to Cretaceous ammonites "seemed to reflect" a "phylogenetic relationship" (LEWY, 2002a, p. 65). In the second paper, LEWY (2002b) considered the ammonite mode of life and evolution, at the end of the paper referring again to the ammonite-octopod relationship, claiming that puzzling features of ammonoids were "clarified when the anatomy and skills of octopods were applied to the ammonoids. . . ." (LEWY, 2002b, p. 136).

LEWY's two papers provoked comment from researchers on ammonoids who thought that his interpretations were unconvincing. Both CHECA (2003) and HEWITT and WESTERMANN (2003) discussed LEWY's views on the ammonoid septum, and HEWITT and WESTERMANN also examined reproductive strategy, the supposed similarity between ammonoids and octopods that had been used

by LEWY in support of the ammonite-octopod phylogenetic relationship. They found the argument to be flawed. LEWY (2003), in reply, claimed that he had been misunderstood or misrepresented.

The present writer once discussed the possibility that the octopods might be ammonites that had lost their shells with the late Hans GRÜNEBERG, a paleontologist who became a geneticist, and he did not see anything improbable in such an evolutionary change from the genetic point of view (GRÜNEBERG, personal communication, 1977).

PLAUSIBILITY OF THE HYPOTHESIS OF AMMONITE ANCESTORS FOR OCTOPODS

The implications of the ammonite descent theory for *Argonauta* may now be examined. The little that we know about the soft parts of ammonites does not contradict the idea. The radula was similar to that of coleoids, and the jaws were of general coleoid type. However, these are plesiomorphic character states for Coleoidea, and the radula shows a limited range of variation.

The octopods appear to be a sufficiently compact group to necessitate a common origin for all of them (though ROBSON, 1932, p. 34, thought that the "homogeneity of the Incirrata is questionable"). The so-called internal shell of octopods cannot be easily homologized with those of decapodan coleoids (though BIZIKOV [2004, p. 81] has suggested a morphological series), and this could be advanced as an argument in favor of an origin of the octopods being well separated from the decapodan stem. As noted above, PIA (1923) concluded that all Octobrachia had evolved from ammonites, though whether as a series of separate lineages (as STEINMANN thought) he did not say.

STEINMANN's proposal of polyphyly of *Argonauta* has, in any case, to be rejected. It is most improbable that three widely separated groups of ammonites would have given rise to descendants that are placed in a single genus by zoologists. His hypothesis of three separate lines of descent of argonauts from different ammonites may have been credible when he first proposed it in 1888. By the time of his last paper (STEINMANN, 1925b), however, many detailed studies of ammonites, for example, SPATH's (1923–1943) monograph on English Gault (Cretaceous: Albian) ammonites, had shown that most Mesozoic ammonite genera had very short ranges in time, and the concept of deriving a living octopod genus from an early Jurassic ammonite, for example, was no longer plausible.

NAEF was the first author with detailed knowledge of living and fossil Coleoidea, including embryology and life history of Recent forms, to attempt a phylogeny in some detail that gave consideration to the geological sequence (NAEF, 1922, fig. 101, p. 297). NAEF considered the Coleoidea to have originated from a single lineage. Paleontologists (SPATH, 1933; JELETZKY, 1966), probably influenced by NAEF, have taken the same view. Major reviews by zoologists (VOSS, 1977; MANGOLD & PORTMANN, 1989; SWEENEY & ROPER, 1998; NIXON & YOUNG, 2003) have all accepted Coleoidea, by implication a monophyletic group, and all have ignored the possibility of an independent origin for the Octobrachia.

In the last couple of decades, attempts at detailed phylogenies have followed cladistic practice, pioneered by BERTHOLD and ENGESER (1987), for the fossils, and by BONNAUD, BOUCHER-RODONI, and MONNEROT (1994) for living forms, and have mostly ignored the ammonite-octopod hypothesis. ENGESER (1990, p. 131), in a very detailed study, was at pains to detail the monophyly of the Coleoidea; he mentioned STEINMANN (1925b) (ENGESER, 1990, p. 161), only to note that his proposal of *Argonautina* and *Argonautella* had been neglected by later workers. ENGESER (1990) did not discuss STEINMANN's hypothesis, but he rejected it by implication. In a recent cladistic study, STRUGNELL and others (2006, p. 95) estimated that the argonaut

lineage originated in the Jurassic, as a sister-group of Octopodidae.

A fact that does not seem to have been considered is the lack of an ink sac in ammonites (reviewed by DONOVAN, 1993, p. 4–5). An ammonite origin for octopods would require that the ink sac has evolved independently in the group. The evolutionary origin of the ink sac in coleoids has not received much attention, but its independent origin in Decabrachia and Octobrachia is highly unlikely.

To conclude, the ammonite origin of octopods is not generally accepted, either by neontologists or palaeontologists.

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