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The erroneous distinction between tetrabranchiate and dibranchiate cephalopods

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ABSTRACT:

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The informal subclass name Dibranchiata is still attributed to extant coleoids, referring to the possible taxonomic significance of the gill number in cephalopods. Ammonoids and the dibranchiate octopods exhibit a remarkable similarity in breeding strategies and an ammonite shape of argonautid egg cases, suggesting close phylogenetic relationships in which octopods are nude ammonoids, and accordingly reflect the dibranchiate anatomy of ammonoids. All these cephalopods descended from the Paleozoic nautiloids, which are represented today by two genera with a tetrabranchiate gill structure and other anatomical features, which differ from those in extant coleoids. The physiology of extant nautiloids enables them to survive in waters with low oxygen content at a few hundred meters depth, toward where the nautiloids withdrew. The two pairs of gills, which occur in extant nautilids only, are suggested to reflect a minor anatomical modification to improve respiration in low oxygen settings by the duplication of the cephalopod initial single pair of gills, and are thus of no taxonomic significance.

Key words: Cephalopoda, Dibranchiata, Tetrabranchiata, Extant Nautiloids.

INTRODUCTION

All extant nautiloid species belong to the genera *Nautilus* and *Allonautilus* (WARD & SAUNDERS 1997) in a single family Nautilidae within the superfamily Nautilaceae, which appeared in the Upper Triassic (KUMMEL & *al.* 1964; TEICHERT & MATSUMOTO 1987). The phylogenetic scheme of these nautiloids suggests that they, like all other fossil and extant cephalopods, descended from the same Late Cambrian ancestral organism (YOCHELSON 1973). Anatomical and skeletal features in extant cephalopods were assumed to be of phylogenetic significance for the subdivision of the class Cephalopoda into subclasses. Extant nautiloids have an external conch and two pairs of gills (ctenidia), for which they and the fossil nautiloids were attributed to subclass Ectocochlia or Tetrabranchiata respectively (MILLER & FURNISCH 1957a). The extant coleoids lack an external conch (a few have variably-shaped, internal, rudimentary skeletal features), posessing a single pair of gills only, for which they were distinguished as subclass Endocochlia or Dibranchiata respectively (*ibid.*). OWEN (1832) applied this anatomical criterion for the systematic subdivision of fossil cephalopods as well, and included in the Tetrabranchiata the extinct nautiloids and ammonoids. Later (in SWEET 1964, p. K10) he assigned the extinct belemnoids to the Dibranchiata. These subclass names were commonly used in the literature despite the awareness of scientific uncertainties (MILLER & FURNISH 1957a, p. xxii, 1957b, p.

L2). This superficial differentiation, whereby the fossil nautiloids were emplaced within the Tetrabranchiata (=Tetrabranchia), led to the conclusion that the two pairs of ctenidia (Tetrabranchia) represent the primitive anatomy of the cephalopods (NAEF 1913, 1926). YONGE (1964, p. I32) rejected this interpretation and suggested that the early cephalopods were probably slow moving dibranchiates, which with the increase of activity and rate of metabolism duplicated the ctenidia to improve respiration. The external conch prohibits the expansion of the mantle cavity of cochleate cephalopods. Probably the conchless coleoids regulate the intensity of the water circulation better than the cochleate cephalopods, and therefore these coleoids retained the initial cephalopod single pair of gills, which was sufficient for the respiration of these highly active creatures (*ibid.*).

The assumption that all fossil ectocochleate cephalopods were tetrabranchiate, and the endocochleate or conchless coleoids were dibrachiate like their extant relatives was recently questioned. LEWY (1996) compared the breeding strategies of octopods and ammonoids, and concluded that octopods are nude ammonoids and reflect the dibranchiate anatomy of the latter. This conclusion needs further elaboration and substantiation by additional evidence to examine the systematic significance of the number of gills in cephalopods.

CLOSE RELATIONSHIP BETWEEN AMMONOIDS AND OCTOPODS

Some mature ammonoids modify their terminal body chamber, constrict the aperture or add to it various appendages. Apertural appendages occur mainly in microconchs, the probable male form of a pair of sexual dimorphs (*e.g.*, COBBAN & KENNEDY 1976). Many large ammonites slightly uncoil, inflate the terminal body chamber, and constrict the aperture (Fig. 1.1). Others change mode of coiling and develop a terminal hooked body chamber (Fig. 1.2-5). The aperture in some of these latter heteromorphs faced the preceding whorl (Fig. 1.2-5), which prevented the extension of the body for swimming and hunting. When these conchs were in floating orientation the aperture faced upward (Fig. 1), restricting lateral movement and predation (LEWY 1996). Therefore, the heteromorph ammonites were suggested to change from predating to feeding on planktic organisms while moving vertically through the water column (*e.g.*, SEILACHER & LABRBERA 1995; WESTERMANN 1990). This awkward explanation overlooks the functional morphology of the modified terminal body chamber and aperture, which in many cases must have resulted in the ultimate death of the ammonoid. These pre-death, fatal modifications had a crucial function in the life cycle of these ammonoids, which is successful breeding. The apertural appendages in male microconch probably were involved in copulation (COPE 1967), whereas the terminal body chamber of female macroconchs changed into a boat-like, or hook-shaped egg case.

Thousands of minute embryonic shells of ammonoids occur in the body chambers of 15 mature macroconchs of the Upper Turonian *Scaphites ferronensis* (COBBAN), and in the adhering matrix (collected by W.A. COBBAN; LANDMAN 1985). These macroconchs must have sunk to the bottom where part of their content fell out of the conch. The two early growth stages represented by these ammonitellae evidence the presence in the conch of pre-hatched ammonitellae together with

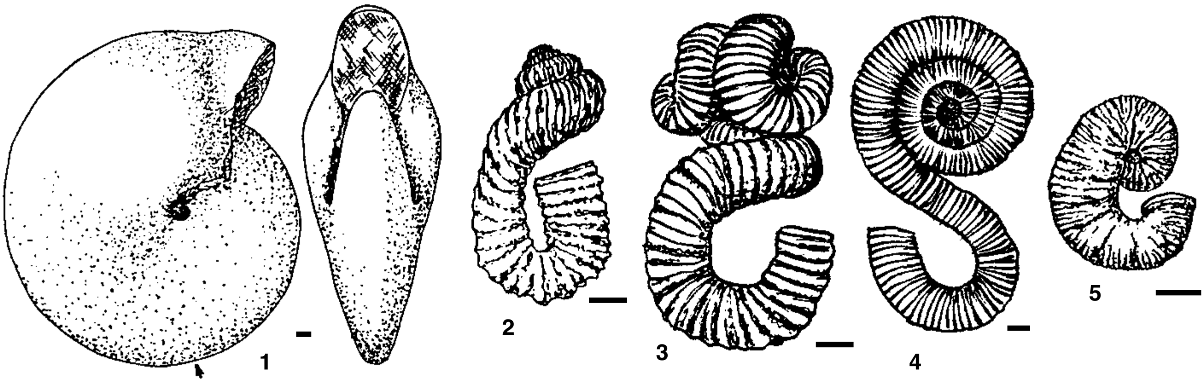

Fig. 1. Examples of ammonite modified terminal whorl and aperture, which restricted the activity of the ammonoid, resulting in the death of some by starvation; this modification turned the terminal body chamber into a floating egg case; 1. *Neoptychites*; 2. *Nostoceras*; 3. *Nipponites*; 4. *Pravitoceras*; 5. *Scaphites*; scale bar 1 cm

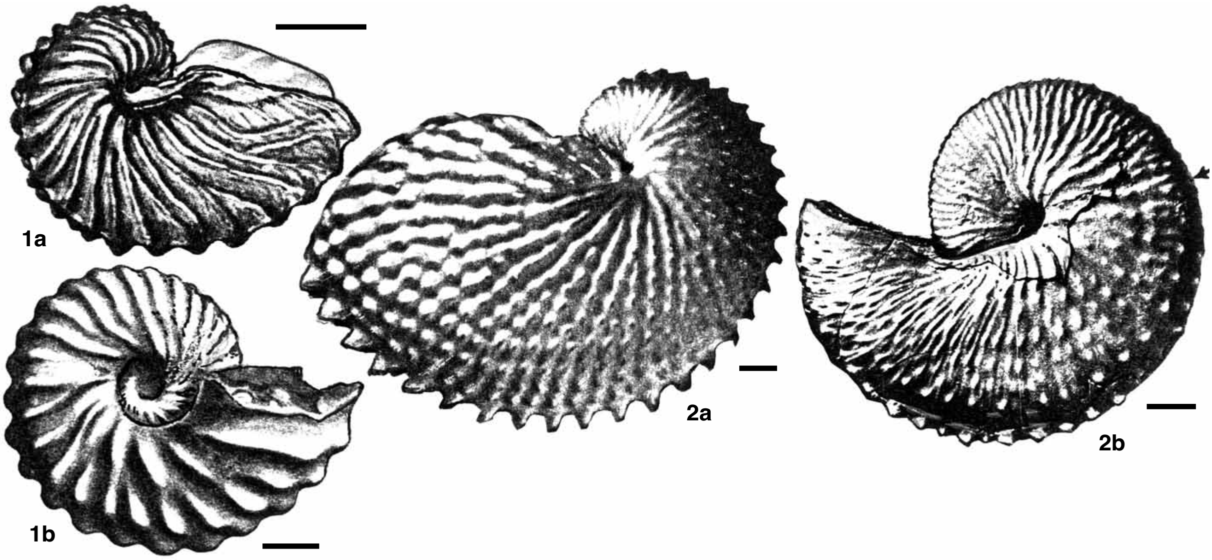

Fig. 2. Argonautid egg cases resembling Upper Cretaceous ammonites; the constricted aperture in some conchs was opened and enlarged; 1a. *Argonauta hians* LIGHTFOOT (from ABBOTT, 1968); 1b. *Hoplitoplacenticeras* (From PAULCKE, 1907); 2a. *Argonauta nodosa* LIGHTFOOT; 2b. *Jeletzkytes nebrascensis* (Owen) (from LANDMAN & WAAGE, 1993)

just hatched ones. Such mode of breeding in a floating egg case is exclusively exhibited by octopod argonautids. The sexually mature female *Argonauta* secretes from her pair of enlarged arms a fragile calcitic shell, in which it sits and lays numerous, tiny, spherical eggs, similar to those found fossilized in a few ammonite body chambers (LEHMANN 1981).

Fossil argonautid egg cases are known from the Oligocene onward probably because of the rare preservation of these fragile conchs (HOLLAND 1988), which did not protect the brood from predators. Perhaps therefore, more efficient and "economic" modes of pelagic breeding were developed by related octopods, which carry their tiny eggs in modified arms (BOLETZKY 1986, p. 223). The development of eggs in floating egg cases has the advantage that it disperses the brood and increases its chances of survival compared to stationary egg concentrations. The motion of the drifting egg case probably aerated the tiny eggs and prevented their encrustation by algae and fungi (indirect brood care; LEWY 1996).

The remarkable similarity between extant and fossil argonautid egg cases to Upper Cretaceous ammonites (Fig. 2), such as *Hoplitoplacenticeras,* the scaphitids *Jeletzkytes* and *Discoscaphites* and *Phylloceras,* strengthens the above discussed similarity between ammonoids and octopods. NAEF (1922) suggested that Cretaceous ancestral argonautids used to lay eggs in empty ammonites, which they partly modified for this purpose. The absence of ammonites in the Cenozoic required the argonautids to secrete a complete egg case in the shape that their ancestors learned to emend in the Upper Cretaceous. However, the need of the ancestral argonautids to lay the eggs in a floating case rather than in a stationary protected site, remained unexplained.

The remarkable physiological and morphological similarities between octopod and ammonoid cephalopods suggested that octopods are nude ammonoids which lost their conch, and hence the egg case, during the Mesozoic (LEWY 1996). They were physiologically forced to perform either the pelagic (in a floating egg case) or the stationary mode of breeding. During the Jurassic and Cretaceous ammonoid empty conchs were available to serve as egg cases for the conchless octopods. To enter, for example, a scaphitid conch (Fig. 2.2b) they had to break the constricted part of the terminal body chamber and enlarge the conch to contain themselves and the eggs. The constructional modifications may have started with organic components and later these octopods developed means to secrete calcareous (calcitic) complementary parts of the empty ammonite which they favored to occupy. The lack of an exoskeleton improves mobility, and hence competition on food and life territory, and to escape from predators. Because of these functional advantages the octopod-ammonoids survive the K/T biological turnover, whereas the slow-moving cochleate ammonoids went extinct, probably through overpredation (*e.g.*, by crustaceans; RADWAŃSKI 1996). The scarcity of empty floating nautiloid conchs in Cenozoic times forced the surviving octopod argonautids to produce a complete egg case. Such egg cases were constructed in the form of the empty ammonite conchs, which were preferably occupied, modified and enlarged by the ancestral argonautids.

According to the advocated relationships between octopods and ammonoids, the former exhibit the dibranchiate anatomy of ammonoids. Thus the living and probably all fossil coleoids, together with the ammonoids were dibranchiate, all of which evolved from Paleozoic nautiloids through the bactritoids. Therefore, it seems reasonable to assume that all cephalopods descended from dibranchiate nautiloid ancestors. The extant tetrabranchiate nautiloid species are assumed to represent an evolutionary duplication of the number of ctenidia under the strong ecological stresses to which extant nautilids had to adapt.

PREDATION ON NAUTILOIDS

The nautiloids nearly disappeared at the end of the Cretaceous, when the cochleate ammonoids became extinct. Survivors temporarily revived the nautiloid stock in the early Tertiary, but with limited success, as evidenced by the two extant genera. While the ammonoids thrived in the Mesozoic oceans they did not avoid preying on their own young (LEHMANN 1973, 1981), and may have fed on small nautiloids as well, which occupied the same living niches as the ammonoids. SAUNDERS & *al.* (1987) described extant *Nautilus* conchs with octopod borings as evidence for octopod predation on nautilids. This observation can be extended to fossil octopods and their cochleate form the ammonoids, even though the feeding strategy has changed. Ammonoids broke conchs and swallowed skeletal particles such as ammonoid aptychi, bivalves, echinoderm fragments and periopods of small decapod crustaceans (LEHMANN 1973, 1981; RIEGERAF & *al.* 1984; JÄGER & FRAAYE 1997). However, the extant octopods bore into the exoskeleton by radular rasping, and inject a venum to kill the prey (SAUNDERS & *al.* 1978). No such octopod borings were hitherto recorded from fossil conchs (BISHOP 1975, p. 274). It may be speculated that this latter mode of feeding was probably acquired not long ago, and that the Mesozoic octopods broke exoskeletons and swallowed hard parts as the cochleate ammonoids did.

Ammonoids probably increased in diversity and quantity during the Mesozoic through the oppression of the nautiloids, and the resulting expulsion of the latter into marginal, less hazardous habitats. Most of the fossil endocochleate cephalopods such as the teuthids and the belemnoids had probably ten arms as their extant relatives have, two of which were longer and modified to skillfully catch prey, such as the slow moving nautiloids. These latter, together with the ectocochleate ammonoids, were also intensively hunted by marine reptiles and fish, as well as by other predators (SAUNDERS & *al.* 1987; RADWAŃSKI 1996). Nevertheless the Mesozoic ammonoids and related cephalopods contributed to nautiloid ultimate withdrawal to less dangerous living niches, such as in dark, “deep” waters, as exemplified by the species of the extant *Nautilus* and *Allonautilus*. However, the gradual diversification and increase in size of the Cretaceous marine predators likewise affected the slow-moving, nekto-benthic cochleate ammonoids.

ADAPTATION TO LOW-OXYGEN SETTINGS

Live nautiloids occur confined to a small bioprovince extending from the offshore of Burma and Australia in the Indian Ocean to the east and south, off the Fiji Island in the western Pacific Ocean and off Japan in the north (SAUNERS 1981). During daytime they stay in rather cool waters at depths of 400-600 m (*e.g.*, ROUX & *al.* 1991). They rise to shallower waters of about 100 m to search for food during the night (STENZEL, 1964 p. K92). This few hundred meters thick water column comprises oxygen depleted zones in which the live nautiloid survives in its daily trips by “depressing its metabolic rate to match the amount of ambient oxygen available” (BOUTILLER & *al.* 1996, p. 534; see BALDWIN 1987, and HOCHACHKA 1987). “*Nautilus* is unique amongst the cephalopod molluscs in having the capacity to survive prolonged periods of low oxygen levels”, which may be the result of a physiological modification of the blood circulation, and the possible utilization of oxygen contained in the buoyancy chambers to help sustain aerobic metabolism (BOUTILLER & *al.* 1996, p. 536). Thus the present nautiloid is a hypometabolic, hypoxic animal, which moves slowly in deep waters, mainly vertically (O’DOR & *al.* 1993). Physiologically it must considerably differ from its Paleozoic and Mesozoic relatives, which were active marine predators mainly in shallow waters (common in reefal and carbonate platform sediments). The few Upper Cretaceous and Tertiary nautiloid genera are frequently found in outer shelf and pelagic sediments. This profound reduction in diversity and the preference of deeper marine settings than in earlier times resulted from the threat of numerous, more skillful marine predators. The gradual adaptation of the nautiloids to the harsh ecological settings in these deep marine waters was probably achieved through physiological modifications such as the suppression of metabolic rates. The retraction into less menacing niches started already in Late Mesozoic times, and thus proceeded for more than 65 million years. This time span is more than necessary in evolutionary processes to result in the anatomical modifications, whereby extant nautilids differ from other living cephalopods (*e.g.*, STENZEL 1964). It is suggested that among these evolutionary modifications is the duplication of the single pair of cephalopod ctenidia into the tetrabranchiate anatomy of extant *Nautilus* and *Allonautilus* species to improve respiration in oxygen-depleted waters in which they live. Accordingly, the two pairs of gills in extant nautiloids are merely an anatomical modification of the basic dibranchiate anatomy of all extant and fossil cephalopods. Hence, the term Dibranchiata should not be used, even as an informal characterization of the endocochleate and conchless cephalopods, as the exocochleate were dibranchiate as well, apart from the Recent and perhaps some earlier (Pleistocene, Neogene?) nautiloids. In this aspect of taxonomy it is suggested (LEWY 1996) to transfer the octopods (at least the Incirrata) from the Coleoidea to the Ammonoidea.

CONCLUSIONS

The close similarity in modes of breeding and shape of the egg case between ammonoids and extant octopods suggests that octopods are nude ammonoids, and hence reflect the dibranchiate anatomy of the latter. These dibranchiate ammonoids and extant coleoids descended from Paleozoic nautiloids, which were supposed to be tetrabranchiate as their extant relatives were. This assumption overlooks the remarkable ecological change that the nautilids underwent in Cenozoic times by adapting through profound physiological and anatomical changes to waters of a low oxygen content. The duplication of the cephalopods initial pair of gills in extant nautilids is regarded as another minor anatomical modification to withstand these harsh settings, and has no taxonomic significance.

REFERENCES

ABBOT, R.T. 1968. Seashells of North America. 280 pp. *Golden Press*; New York.

BALDWIN, J. 1987. Energy metabolism of *Nautilus* swimming muscles. *In*: W.B. SAUNDERS & N.H. LANDMAN, (*Eds*), Nautilus: the biology and paleobiology of a living fossil. *Topics in Geobiology*, **6**, 325-329. *Plenum Press*; New York.

BISHOP, G.A. 1975. Traces of predation. *In*: R.W. FREY (*Ed.*), The study of trace fossils, pp. 261-281. *Springer-Verlag*; New York.

BOLETZKY, S. v. 1986. Encapsulation of cephalopod embryos: a search for functionalcorrelations. *American Malacological Bulletin,* **4**, 217-227.

BOUTILIER, R.G., T.G. WEST, G.H. POGSON, K.A. MESA, J.W. WELLS, & WELLS, M.J., 1996. *Nautilus* and the art of metabolic maintenance. *Nature,* **282**, 534-536. London.

COPE, J.C.W. 1967. The palaeontology and stratigraphy of the lower part of the Upper Kimmeridge Clay of Dorset. *Bulletin of the British Museum (Natural History),* Geology, **15**, 1-79. London.

HOCHACHKA, P.W. 1987. Oxygen conformity and metabolic arrest in *Nautilus*. Analysis of mechanisms and functions. *In*: W.B. SAUNDERS & N.H. LANDMAN (*Eds*), Nautilus: the biology and paleobiology of a living fossil. *Topics in Geobiology*, **6**, 331-338. *Plenum Press*; New York.

HOLLAND, C.H. 1988. The Paper Nautilus. *New Mexico Bureau of Mines & Mineral. Research Memoire* **44**, 109-114. Socorro.

JÄGER, M. & Fraaye. R. 1997. The diet of the Early Toarcian ammonite *Harpoceras falciferum*. *Palaeontology,* **40**, 557-574. Oxford.

KUMMEL, B., *with* FURNISH, W.M. & GLESNISTER, B. 1964. Nautiloidea-Nautilida, K383-K457. *In:* R.C. MOORE (*Ed.*), Treatise on Invertebrate Paleontology, Pt. K, Mollusca 3: *Geological Society of America and University of Kansas Press*; New York.

LANDMAN, N.H. & WAAGE, K.M. 1993. Scaphitid ammonites of the Upper Cretaceous (Maastrichtian) Fox Hills Formation in South Dakota and Wyoming. *Bulletin of the American Museum of Natural History,* **215**, 1-257. New York.

LEHMANN, U. 1973. Zur Anatomie und Ökologie von Ammoniten: Funde von Kropf und Kiemen. *Paläontologische Zeitschrift,* **47**, 69-76. Stuttgart.

— 1981. The ammonites. Their life and their world. 246 pp. *Cambridge University Press*; Cambridge.

LEWY, Z. 1996. Octopods: Nude ammonoids that survived the Cretaceous-Tertiary boundary mass extinction. *Geology,* **24**, 627-630. Boulder.

MILLER, A.K. & FURNISH, W.M. 1957a. Introduction to Cephalopoda, xx-xxii. *In:* R.C. MOORE (*Ed*.), Treatise on Invertebrate Paleontology, Pt. L, Mollusca 4. *Geological Society of America and University of Kansas Press*. New York.

— & — 1957b. Introduction to Ammonoidea. L1-L2. *In:* R.C. MOORE (*Ed*.), Treatise on Invertebrate Paleontology, Pt. L, Mollusca 4. *Geological Society of America and University of Kansas Press*; New York.

MOORE, R.C., LALICKER, C.G. & FISCHER, A.G. 1952. Invertebrate fossils. 766 pp. *McGraw-Hill Book Comp*; New York.

NAEF, A., 1913, Studien zur generellen Morphologie der Mollusken, 1. *Ergebnisse und Fortschritte in Zoologie,* **3**, 73-164. Jena.

— 1922. Die fissilen Tintenfische. Verlag von Gustav Fischer, 1-322. Jena.

— 1926. Studien zur generellen Morphologie der Mollusken, 3. *Ergebnisse und Fortschritte in Zoologie,* **6**, 27-127. Jena.

O'DOR, R.K., J. FORSYTHE, D.M. WEBBER, J. WELLS & WELLS, M.J. 1993. Activity levels of *Nautilus* in the wild. *Nature,* **362**, 626-628. London.

OWEN, R. 1832. Memoir on the pearly nautilus (*Nautilus pompilius*, LINN.) with illustrations of its external form and internal structure. Royal College of Surgeons, 1-68. London.

PAULCKE, W. 1907. Die Cephalopoden der oberen Kreide Südpatagoniens. *Berichte der Naturforschenden Geselschaft zu Freiburg i. Br.,* **15**, 1-82. Freiburg.

RADWAŃSKI, A. 1996. The predation upon, and the extinction of, the latest Maastrichtian populations of the ammonite species *Hoploscaphites constrictus* (J. SOWERBY, 1817) from the Middle Vistula Valley, Central Poland. *Acta Geologica Polonica,* **46** (1-2), 117-135. Warszawa.

RIEGRAF, W., G. WERNER & LÖRCHER, F. 1984. Der Posidonienschifer. Biostratigraphie, Fauna und Fazies des südwestdeutschen Untertoarciums (Lias epsilon). 195 pp. *Enke*; Stuttgart

SAUNDERS, W.B. 1981. The species of living *Nautilus* and their distribution. *The Veliger* **24**, 8-17. Berkeley.

SAUNDERS, W.B., C. SPINOSA & DAVIS, L.E. 1987. Predation on *Nautilus*. *In:* SAUNDERS, W.B. & LANDMAN N.H. (*Eds*), Nautilus: the biology and paleobiology of a living fossil. Topics Geobiology, **6**. Plenum Press, 201-212. New York .

SEILACHER, A. & LABARBERA, M. 1995. Ammonites as cartesian divers. *Palaios* **10**, 493-506. Tulsa.

STENZEL, H.B. 1964. Living Nautilus, K59-K93. *In:* MOORE, R.C. (*Ed*.), Treatise on Invertebrate Paleontology, Pt. K, Mollusca **3**. *Geological Society of America and University of Kansas Press*. New York.

SWEET, W.C. 1964. Cephalopoda - General features. K4-K13. *In:* MOORE, R.C. (*Ed*.), Treatise on Invertebrate Paleontology, Pt. K, Mollusca 3. *Geological Society of America and University of Kansas Press*; New York.

TEICHERT, C. & MATSUMOTO, T. 1987. The ancestry of the genus *Nautilus*. *In* SAUNDERS, W.B. & LANDMAN, N.H. (*Eds*), Nautilus: the biology and paleobiology of a living fossil. *Topics in Geobiology*, **6**, 25-32. *Plenum Press*; New York.

WARD, P.D. & SAUNDERS, W.B. 1997. *Allonautilus*: a new genus of living nautiloids cephalopod and its bearing on phylogeny of the Nautilida. *Journal of Paleontology,* **7**, 1054-1064. Tulsa.

YOCHELSON, E.L. 1973. The bearing of the new Late Cambrian monoplacophoran genus *Knightoconus* upon the origin of the Cepalopoda. *Lethaia,* **6**, 275-310. Oslo.

YONGE, C.M. 1964. General characteristics of Mollusca, I3-I36. *In:* MOORE, R.C.(*Ed*.), Treatise on Invertebrate Paleontology, Pt. I, Mollusca 1. *Geologica Society of America and University of Kansas Press*; New York.

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