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Vol. 114, No. 7

POST-TRIASSIC NAUTILOID GENERA

BY BERNHARD KUMMEL

WITH TWENTY-EIGHT PLATES

CAMBRIDGE, MASS., U.S.A.

PRINTED FOR THE MUSEUM

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AT HARVARD COLLEGE

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INTRODUCTION

Studies on tetrabranchiate cephalopods have added much data to our understanding of the patterns and modes of evolution as displayed by fossil animals. Few invertebrate phyla show such marked periods of expansion in evolutionary intensity contrasted with periods of extreme contraction to the point of near extinction. The generalized evolutionary history of the ammonoids with periods of near extinction at the end of the Paleozoic and again at the end of the Triassic, and their final extinction at the end of the Cretaceous is well known. Among the nautiloid cephalopods a similar evolutionary history exists but with some important differences.

The nautiloid cephalopods had their greatest radiation soon after their first appearance in the Upper Cambrian, that is in the Ordovician. In this early phase of their history numerous distinct phyletic trends are well established. However, by Silurian time there is already a marked decline in the number of genetic groups. This decline in the viability of the nautiloids continued, until today we have only a single genus (*Nautilus*) living as a relic form in the southwest Pacific. In this long, gradually diminishing diversity the nautiloids nearly became completely extinct in the late Triassic, a period of extinction coinciding with a similar phase in the evolution of the ammonoids. A single stock derived from the Triassic Syringonautilidae survived into the Jurassic. From this surviving stock all post-Triassic nautiloids are directly or indirectly derived.

The purpose of this study is to analyze the evolutionary history of the family Nautilidae which includes the surviving stock from the Triassic and all post-Triassic nautiloid genera. This phyletic group is of particular interest since it includes an evolutionary complex which has survived a period of near extinction of the class, went through a minor eruptive phase in the development of new adaptive types, and is now represented by a single genus. No explanation is given as to the cause of the

decreasing viability of the nautiloids, but the patterns and modes of evolution of this declining group are instructive.

Post-Triassic nautiloids have received but scant attention, most workers having merely referred all species to the genus *Nautilus*. In 1927, L. F. Spath presented a very comprehensive, but short, review of post-Triassic nautiloids and proposed a taxonomic scheme including many new genera. In 1951, I spent eight months at the British Museum of Natural History, and at that time had the opportunity of studying the very large and excellent collections of that institution including the types of many of the genera proposed by Spath. At the time Spath (1927a) proposed his taxonomic scheme for post-Triassic nautiloids he did not give any diagnosis of his genera or illustrations of his type species, many based on Sowerby species not previously illustrated except in woodcuts. In the present report all genera of post-Triassic nautiloids are diagnosed and illustrated. An intensive search has been made of the literature to bring together, as far as possible, all species names that have been proposed over the past hundred odd years. In this way data was obtained on the variability, geologic range and geographic distribution of each generic group.

This study is an outgrowth of the preparation of a chapter on Mesozoic nautiloids for the Treatise on Invertebrate Paleontology, edited by R. C. Moore. A similar study on Carboniferous to Triassic nautiloids has already been published (Kummel, 1953c). I wish to express my very sincere appreciation to Dr. L. F. Spath for many long hours of stimulating conversations and for facilitating in every way my work at the British Museum. Fruitful discussions with Dr. Curt Teichert and Dr. Ernest Williams on taxonomic and evolutionary problems were most helpful.

CLASSIFICATION OF POST-TRIASSIC NAUTILOIDS

The only previous comprehensive discussion of post-Triassic nautiloids is that of L. F. Spath (1927a). In recent years several large works on Tertiary nautiloids have been produced by Miller which have included descriptions of many new Tertiary faunas. Spath's discussion of post-Triassic nautiloids was only a small and incidental part of his brilliant work on the famous Jurassic

fauna of Kachh (Cutch). Even so, he laid the framework for future work on these animals.

Nautiloids of Mesozoic age and, until recently, Tertiary age have received only brief incidental treatment in paleontological publications. For one thing post-Triassic nautiloids are not common fossils compared to the contemporaneous ammonoid, pelecypod, or gastropod faunas. They likewise are seemingly not nearly so diverse. The evolutionary decline of the nautiloids, already very marked in the Silurian, progresses steadily towards the Recent. Thus in studying Mesozoic and Tertiary nautiloids we are closely examining the decline and near extinction of a large animal group.

Until the contribution by Spath (1927a) there had been few genera proposed for post-Triassic nautiloids and most of these were not generally accepted or used. The most common practice was to place all post-Triassic species in the genus *Nautilus*. Those genera that had been proposed before Spath's 1927 revision include *Nautilus* Linné, 1758, *Bisiphytes* Montfort, 1808, *Cenoceras* Hyatt, 1883, *Eutrephoceras* Hyatt, 1894, *Digonioceras* Hyatt, 1894, *Angulithes* Montfort, 1808, *Hercoglossa* Conrad, 1866, *Pseudonautilus* Meek, 1876, *Cimomia* Conrad, 1866, *Cymatoceras* Hyatt, 1883, *Tithonoceras* Retowski, 1893, *Carinonautilus* Spengler, 1910, and *Aturia* Bronn, 1838. As mentioned above, most of these genera were never used after their original proposal; however, such generic names as *Eutrephoceras*, *Hercoglossa*, *Cymatoceras*, and *Aturia* are fairly common in the early literature. Most of these genera were considered as members of the Nautilidae.

In his revision of post-Triassic nautiloids Spath (1927a) proposed 16 new genera and adopted 5 families, namely the Nautilidae d'Orbigny, 1840, the Hercoglossidae Spath, 1927, the Cymatoceratidae Spath, 1927, the Paracenoceratidae Spath, 1927, and the Aturidae Hyatt, 1894. On a straight morphological basis, the Nautilidae include those genera directly or indirectly in the main stock giving rise to *Nautilus*. The Hercoglossidae include those genera with "goniatitic" or very sinuous sutures. The Cymatoceratidae include those stocks characterized by ribbing—the only stock of post-Triassic nautiloids with any ornamentation. The Paracenoceratidae are characterized by differentiation of the periphery, and the Aturidae are characterized by

the unique and peculiar dorsal siphuncle.

There have been no significant changes made to this taxonomic arrangement since its proposal in 1927. Restudy of the large nautiloid collections in the British Museum and the Museum of Comparative Zoology plus a comprehensive review of the literature have brought forth further data on the range of variation within the various genera, and also new data on the geographic and stratigraphic range of most of the species described.

The nautiloids reflect no significant change in their evolutionary development from the late Paleozoic into the Triassic. In fact, the evolutionary pattern of Triassic nautiloids is merely a culmination of trends begun back in the Carboniferous (Kummel, 1953c). Towards the end of the Triassic most of the long-lived stocks became extinct. A single persisting stock represented by *Cenoceras* survived the Triassic, and it represents the root form from which, directly or indirectly, all post-Triassic nautiloids are derived. On examination of the available data on post-Triassic nautiloids, one is impressed by the essential homogeneity of the group. Distinctive radiations are recognizable, each representing an elaboration of particular morphological characters. Homeomorphous developments within the group and with pre-Jurassic genera are common. The time-space relationships of the post-Triassic nautiloid "species" and their morphological modifications, interpreted in terms of adaptive radiation, make possible a constructive phylogenetic interpretation of the group. The interpretation presented in this report gives a much clearer understanding of the various generic groups and the kinds and ranges of variation within the groups. The classification adopted reflects the phylogeny of post-Triassic to Recent nautiloids. The classification used in this report is as follows:

Family Nautilidae d'Orbigny, 1840

Subfamily Nautilinae d'Orbigny

Genus *Nautilus* Linné, 1758

Type species: *Nautilus pompilius* Linné

Genus *Cenoceras* Hyatt, 1883

Type species: *Nautilus orbignyi* Prinz

Genus *Eutrephoceras* Hyatt, 1894

Type species: *Nautilus dekayi* Morton

Genus *Pseudocenoceras* Spath, 1927

Type species: *Nautilus largilliertianus* d'Orbigny

Genus *Carinonautilus* Spengler, 1910

Type species: *Carinonautilus ariyalurensis* Spengler

Genus *Obinautilus* Kobayashi, 1954

Type species: *Obinautilus pulchra* Kobayashi

Subfamily Pseudaganidinae nov.

Genus *Pseudaganides* Spath, 1927

Type species: *Nautilus kutchensis* Waagen

Genus *Pseudonautilus* Meek, 1876

Type species: *Nautilus geinitzi* Oppel

Subfamily Paracenoceratinae Spath, 1927

Genus *Paracenoceras* Spath, 1927

Type species: *Nautilus hexagonus* J. de C. Sowerby

Genus *Aulaconutilus* Spath, 1927

Type species: *Tautilus sexcarinatus* Pictet

Genus *Somalinautilus* Spath, 1927

Type species: *Nautilus antiquus* Dacqué

Genus *Tithonoceras* Retowski, 1894

Type species: *Tithonoceras zitteli* Retowski

Subfamily Cymatoceratinae Spath, 1927

Genus *Cymatoceras* Hyatt, 1883

Type species: *Nautilus pseudoelegans* d'Orbigny

Genus *Procymatoceras* Spath, 1927

Type species: *Nautilus subtruncatus* Morris and Lycett

Genus *Cymatonautilus* Spath, 1927

Type species: *Nautilus julii* d'Orbigny

Genus *Paracymatoceras* Spath, 1927

Type species: *Nautilus asper* Oppel

Genus *Syrionutilus* Spath, 1927

Type species: *Nautilus libanoticus* Foord and Crick

Genus *Anglonautilus* Spath, 1927

Type species: *Nautilus undulatus* J. Sowerby

Genus *Eucymatoceras* Spath, 1927

Type species: *Nautilus plicatus* Fitton

Genus *Heminautilus* Spath, 1927

Type species: *Nautilus saxbii* Morris

Genus *Deltocymatoceras* n.gen.

Type species: *Nautilus leiotropis* Schlüter

Genus *Epicymatoceras* n.gen.

Type species: *Nautilus vaelensis* Binckhorst

Subfamily Hercoglossinae Spath, 1927

Genus *Hercoglossa* Conrad, 1866

Type species: *Nautilus orbiculatus* Tuomey

Genus *Cimomia* Conrad, 1866

Type species: *Nautilus burtini* Galeotti

Genus *Angulithes* Montfort, 1808

Type species: *Nautilites triangularis* Montfort

Genus *Aturoidea* Vredenburg, 1925

Type species: *Nautilus parkinsoni* Edwards

Subfamily Aturinae Hyatt, 1894

Genus *Aturia* Bronn, 1838

Type species: *Nautilus aturi* Basterot

Because of the essential homogeneity of post-Triassic nautiloids their grouping into a single family — Nautilidae — seems most appropriate. Thus each of the distinctive radiations from the main evolving stock is reflected at the subfamily level and the radiations within the subfamilies are expressed at the generic level.

Several genera that have been proposed are considered to be synonyms of previously described forms. *Bisiphytes* Montfort, 1808, is suppressed because of the great ambiguity connected with the type species. *Sphaeronautilus* Spath, 1927, *Digonioceras* Hyatt, 1894, *Ophionautilus* Spath, 1927, and *Nautilites* Prinz, 1906, are considered to be synonyms of *Cenoceras*. *Hercoglossoceras* Spath, 1927, is considered to be a synonym of *Pseudaganides* Spath. The single species assigned to *Neocymatoceras* Kobayashi, 1954, falls within the range of variation of *Cymatoceras* and the genus is suppressed. *Vorticoceras* Scott, 1940, was established before its author knew of *Heminautilus* Spath, 1927, and was suppressed by Scott at a later date (Scott, 1943). *Platynautilus* Yabe and Ozaki, 1953, is a perfect synonym of *Heminautilus*. *Deltoidonautilus* Spath, 1927, is a synonym of *Angulithes* Montfort, 1808 (Kummel, 1953a). *Enclimatoceras* Hyatt, 1883, is a synonym of *Hercoglossa* Conrad, 1866 (Spath, 1927a). *Woodringia* Stenzel, 1940, also is here considered a synonym of *Hercoglossa*. *Paraturia* Spath (1927) was proposed prior to his (Spath's) knowledge of *Aturoidea* Vredenburg, 1925, and was shortly thereafter properly suppressed for *Aturoidea* which has priority.

The basic framework of the above classification is the work of Spath (1927a) but differs in some important aspects involving the general interpretation and phylogenetic relationships of post-Triassic nautiloids. Spath (1927a) originally proposed his major units as families, but later (1935b) he did use a subfamily rank while describing a species of *Paracenoceras* (Paraceno-

ceratinae). Within the Nautilinae the main difference in the above classification from that of Spath is placing *Angulithes* in the Hercoglossinae, and including *Carinonautilus* in the Nautilinae, which Spath had placed in the Paracenoceratinae. Also several genera of Spath's Nautilidae (*Bisiphytes*, *Sphaeronautilus*, *Digonioceras*, and *Ophionautilus*) are suppressed or placed in synonymy of other genera.

The Pseudaganidinae is a new subfamily proposed to differentiate those nautiloids with sinuous sutures that arose as a separate phyletic stock in the early Jurassic, and are distinct from the Cretaceous-Tertiary radiation including *Hercoglossa* etc. Spath (1927a) had included the two genera of the Pseudaganidinae (*Pseudaganides* and *Pseudonautilus*) in the Hercoglossidae. From Spath's Paracenoceratidae are removed *Carinonautilus* to the Nautilinae and *Heminautilus* to the Cymatoceratinae. The subfamily Aturinae includes only the genus *Aturia*. The Cymatoceratinae remains essentially as conceived by Spath except for the inclusion of *Heminautilus* and two new genera described in this report.

The relative rarity of post-Triassic nautiloids has led to a situation where most species have been described on the basis of one or very few specimens. To my knowledge, no large collection representing a population has ever been assembled from a single horizon and locality nor are any known where the fossils are sufficiently well preserved to allow a thorough study of intra-specific variation. The great majority of species are defined in terms of being slightly thinner, fatter or more involute or evolute than other already established species; or there are slight variations in the whorl shape or character of the suture. However, in none of these species is the range of variations in any of their morphological features known. Because of these factors, the so-called species of Mesozoic and Tertiary nautiloids have little reality in terms of our concepts of neontological species. Thus, in attempting to decipher the evolutionary patterns and modes of these nautiloids, it is impossible to use the species as a working unit. One's thinking and correlation of data need to be at the generic level. The species (representing the named units accumulated in the literature) when brought together in generic groups give very useful data in regard to range and direction of variation, and relative abundance of the various

adaptive types. Since so many of the so-called species are merely descriptions of specimens, they are here treated as examples of morphologic types brought together into genera — which are the only feasible taxonomic units to handle with this sort of material. Another difficulty is the complete lack of understanding of the adaptive values of the various morphological features. Most features of the conch are thought to be adaptive, but the exact nature of this adaptation is not known.

To properly appraise the evolutionary history of post-Triassic nautiloids it was essential that all of the named units be brought together and placed in generic groups. Thus, through the named units (species), the geologic history and range of variation, origin, and evolution of each generic group could be interpreted in terms of the whole nautiloid fauna. In assembling a list of described species, there are numerous problems of synonymy and other taxonomic irregularities that cannot possibly be determined just from the literature, and it is doubtful at this stage if such efforts would be worthwhile. Thus in compiling a list of the species of post-Triassic nautiloids most names that have been introduced are listed, except for several very obvious and long recognized cases of synonymy. The following list of 531 species of post-Triassic nautiloids gives the units upon which much of this study is based. Because of the great difficulty in tracking down many of these forms the author, date, original generic assignment, and the present generic assignment are given. The list is reasonably complete but even after several years of accumulating these data it is certain that there are still species that have escaped my attention. This list of forms does represent the great majority and from it certain interesting observations on relative abundance of the various adaptive types can be made. This problem will be discussed later.

SPECIES OF POST-TRIASSIC NAUTILOIDS

- Nautilus* (*Paracenoceras*) *acklini* Jeannet, 1951 — *Paracenoceras*
N. adneticus Pia, 1914 — *Cenoceras*
N. (Hercoglossa) aegyptiacus Foord, 1891 — *Angulithes*
N. affinis Chapuis and Dewalque, 1853 — *Cenoceras*
N. aganiticus Schlotheim, 1820 — *Pseudaganides*
N. ahltensis Schlüter, 1876 — *Eutrephoceras*
N. alabamensis Morton, 1834 — *Aturia*

- Aturia alaskensis* Schenck, 1931 — *Aturia*
N. albensis d'Orbigny, 1850 — *Cymatoceras*
Eutrephoceras aloesense Reeside, 1927 — *Eutrephoceras*
N. allani Fleming, 1945 — *Eutrephoceras*
N. allioni Michelotti, 1840 — *Eutrephoceras*
N. altavensis Pomel, 1889 — *Cymatoceras*
N. altifrons Chapman, 1915 — *Eutrephoceras*
N. altisiphites Prinz, 1906 — *Cenoceras*
N. amasianus Gugenberger, 1928 — *Cenoceras*
N. ammoni Loesch, 1912 — *Pseudaganides*
N. amorettii Parona, 1897 — *Cenoceras*
Cymatoceras andranofotsyense Collignon, 1951 — *Cymatoceras*
N. anguliferous Schlüter, 1876 — *Cymatoceras*
N. angustata Conrad, 1849 (in Dana) — *Aturia*
N. angustus Blanford, 1861 — *Cimomia*
N. anomphalus Pia, 1914 — *Cenoceras*
N. antiquus Dacqué, 1910 — *Somalinautilus*
N. applanatus Wanner, 1902 — *Pseudocenoceras*
N. arariformis Pia, 1914 — *Cenoceras*
N. araris Dumortier, 1869 — *Cenoceras*
N. aratus Quenstedt, 1846 — *Cenoceras*
N. archiacianus d'Orbigny, 1840 — *Eutrephoceras*
N. arcuatus Deshayes (in Leymerie, 1842) — *Angulithes*
N. arduennensis Loesch, 1914 — *Paracenoceras*
N. argoviensis Loesch, 1912 — *Pseudaganides*
Carinonautilus ariyalurensis Spengler, 1910 — *Carinonautilus*
N. arthaberi Gugenberger, 1928 — *Cenoceras*
N. articulatus Pulteney, 1813 (in Cox, 1940) — *Cymatoceras*
N. asper Oppel, 1865 — *Paracymatoceras*
N. astacoides Young & Bird, 1828 — *Cenoceras*
N. atlas Whiteaves, 1876 — *Cymatoceras*
N. aturi Basterot, 1825 — *Aturia*
N. aturioides Pictet, 1867 — *Pseudonautilus*
Aturia australis McCoy, 1867 — *Aturia*
N. austriacus Hauer, 1856 — *Cenoceras*
N. averilli Anderson, 1938 — *Cymatoceras* ?
N. baberi Morris & Lycett, 1850 — *Procymatoceras*
N. baconicus Vadász, 1911 — *Cenoceras*
Deltoidenautilus bakeri Teichert, 1947 — *Angulithes*
N. balcombensis Chapman, 1915 — *Eutrephoceras*
N. balsamocrivellii Parona, 1897 — *Cenoceras*
Aturia basteroti Benoist, 1888 — *Aturia*
N. bayfieldi Foord and Crik, 1890 — *Cymatoceras*

- N. begudensis* Kilian and Reboul, 1915 — *Anglonautilus*
N. bellerophon Lundgren, 1867 — *Eutrophoceras*
N. berriasensis Pictet, 1867 — *Pseudocenoceras*
Eutrophoceras berryi Miller, 1947 — *Eutrophoceras*
Aturia (Aturia) berryi Stenzel, 1940 — *Aturia*
N. (Aulaconautilus) bicarinatus Jeannet, 1951 — *Aulaconautilus*
N. bifurcatus Ooster, 1858 — *Cymatoceras*
Deltoidonautilus biygorensis Haas and Miller, 1952 — *Angulithes*
N. blakei Avnimelech, 1947 — *Cimomia*
N. blanfordi Douvillé, 1929 — *Eutrophoceras*
N. bodeni Loesch, 1914 — *Pseudaganides*
N. boissieri Pictet, 1867 — *Eutrophoceras*
N. bouchardianus d'Orbigny, 1840 — *Eutrophoceras*
N. bradfordensis Crick, 1898 — *Cenoceras*
N. brancoi Gemmellaro, 1884 — *Cenoceras*
Aturia (Brazaturia) brazoensis Stenzel, 1935 — *Aturia*
N. breislacki Parona, 1897 — *Cenoceras*
N. broitzemensis Müller and Wollemann, 1906 — *Cymatoceras*
Aturia (Sphenaturia) brüggeni Ihering, 1921 — *Aturia*
N. brunhuberi Loesch, 1914 — *Pseudaganides*
Aturia brunlechneri Frauscher, 1895 — *Aturoidea*
N. bruntrutanae Kuhn, 1936 — *Paracenoceras*
N. bryani Gabb, 1877 — *Eutrophoceras*
Cimomia buccinaeformis Haas and Miller, 1952 — *Cimomia*
N. burkarti Castillo and Aguilera, 1895 — *Eutrophoceras*
N. burtini Galeotti, 1837 — *Cimomia*
N. burtonensis Foord and Crick, 1890 — *Cenoceras*
N. butonensis Martin, 1933 — *Eutrophoceras*
Deltoidonautilus caheni Miller, 1951 — *Angulithes*
N. calloviensis Oppel, 1858 — *Paracenoceras*
N. calvimontensis Bédé, 1948 — *Angulithes*
N. campbelli Meek, 1861 — *Cymatoceras* ?
N. campichei Karakasch, 1907 — *Pseudocenoceras*
N. cantabrigiensis Foord, 1891 — *Cimomia*
N. (Cymatoceras) carlottensis Whiteaves, 1900 — *Cymatoceras*
N. caroliameghinoi Ihering, 1902 — *Aturia*
Eutrophoceras carolinense Kellum, 1926 — *Eutrophoceras*
N. (Hercoglossa) cassinianus Foord and Crick, 1890 — *Angulithes*
N. catonis Gemmellaro, 1886 — *Cenoceras*
N. cenomanensis Schlüter, 1876 — *Cymatoceras*
N. centralis J. Sowerby, 1812 — *Eutrophoceras*
Aturia charlesworthi Foord, 1891 — *Aturia*
N. charpentieri Leymerie, 1851 — *Eutrophoceras*

- N. chilensis* Huppé (in Gay) 1854 — *Cenoceras*
N. chudeaui Douvillé, 1920 — *Angulithes*
Aturia clarkiei Teichert, 1944 — *Aturia*
N. clausus d'Orbigny, 1842 — *Pseudaganides*
N. clementinus d'Orbigny, 1840 — *Eutrephoceras*
Cymatoceras colombiana Durham, 1946 — *Cymatoceras*
N. columbinus Fritsch and Schlönbach, 1872 — *Cimomia*
N. compressus Tavani, 1942 — *Cymatoceras*
N. cookana Whitfield, 1892 — *Eutrephoceras*
N. cossmanni Vredenburg, 1928 — *Cimomia*
Paracenoceras costatum Scott, 1943 — *Procymatoceras*
Aturia ? coxi Miller, 1947 — *Aturia*
N. crassiconcha Vogl, 1908 — *Cimomia*
N. crassisinuatus Crick, 1898 — *Pseudaganides*
N. crassus Schafhäütl, 1863 — *Eutrephoceras*
N. crebricostatus Blanford, 1861 — *Cymatoceras*
N. cubaensis Lea, 1841 — *Aturia*
Aturia curvilineata Miller and Thompson, 1937 — *Aturia*
N. cyclopus Oppel, 1865 — *Eutrephoceras*
N. danicus Schlotheim, 1820 — *Hercoglossa*
Eutrephoceras dartevellei Miller, 1951 — *Eutrephoceras*
N. darupensis Schlüter, 1876 — *Eutrephoceras*
N. decipiens Michelotti, 1861 — *Eutrephoceras*
N. dekayi Morton, 1834 — *Eutrephoceras*
N. deluci d'Archiac 1854 — *Angulithes*
N. demonensis M. Gemmellaro, 1911 — *Cenoceras*
N. depressus Binckhorst, 1861 — *Eutrephoceras*
N. desertorum Quaas, 1902 — *Eutrephoceras*
N. deslongchampsianus d'Orbigny, 1840 — *Cymatoceras*
Aturia dickersoni Schenck, 1931 — *Aturia*
Hercoglossa diderichi Vincent, 1913 — *Hercoglossa*
N. dietrichi Zwierzycki, 1914 — *Eutrephoceras*
N. (Paracenoceras) dilatatus Jeannet, 1951 — *Paracenoceras*
N. dispansus Morris and Lycett, 1850 — *Cenoceras* ?
Aturoidea distans Teichert, 1943 — *Aturoidea*
N. distefanoi Gemmellaro, 1884 — *Cenoceras*
N. divesianus Kuhn, 1936 — *Paracenoceras*
N. domeykus d'Orbigny, 1842 — *Cenoceras*
N. d'orbignyianus Forbes, 1846 — *Cimomia*
N. dorsatus Roemer, 1836 — *Paracenoceras*
N. dorsoexcavatum Parona and Bonarelli, 1897 — *Paracenoceras*
Eutrephoceras douvillei Spath, 1927 — *Eutrephoceras*
N. drepanensis Tagliarini, 1901 — *Pseudaganides*

- N. dubaleni* Peyrot, 1932 — *Eutrephoceras*
N. dubius Zieten, 1830 — *Cenoceras*
N. duilii Gemmellaro, 1886 — *Pseudaganides*
N. dumasi Pictet, 1867 — *Pseudaganides*
N. egregius Pia, 1914 — *Cenoceras*
N. eichwaldi Karakasch, 1907 — *Cymatoceras*
N. elegans J. Sowerby, 1816 — *Cymatoceras*
N. elegantoides d'Orbigny, 1840 — *Cymatoceras*
Deltoidonautilus elliotti Stenzel, 1940 — *Angulithes*
N. ellipticus Schafhäütl, 1852 — *Cimomia*
N. ennianum Daqué, 1905 — *Paracenoceras*
N. ercycinus Tagliarini, 1901 — *Cenoceras*
Heminautilus etheringtoni Durham, 1946 — *Heminautilus*
N. euthymi Pictet, 1867 — *Eutrephoceras*
N. excavatus, J. de C. Sowerby, 1826 — *Cenoceras*
N. exiguus Crick, 1898 — *Cenoceras*
N. expansus J. de C. Sowerby, 1824 — *Eutrephoceras*
N. expletus Zwierzycki, 1914 — *Cimomia*
N. exterebratus Crick, 1898 — *Cenoceras*
Eutrephoceras faxoense Hyatt, 1894 — *Eutrephoceras*
N. felix Chapman, 1915 — *Eutrephoceras*
Aturia (Sphenaturia) felschi Ihering, 1921 — *Aturia*
N. fischeranus Foord and Crick, 1890 — *Cenoceras*
N. fittoni Sharpe, 1853 — *Pseudocenoceras*
N. flammeus Ronchetti, 1947 — *Eutrephoceras*
N. fleuriausianus d'Orbigny, 1840 — *Angulithes*
N. forbesi d'Archiac and Haime, 1854 — *Cimomia*
N. forbesianus Blanford, 1861 — *Hercoglossa* ?
Aturia formae Parona, 1899 — *Aturia*
N. formosus Blanford, 1861 — *Cymatoceras*
N.ourneti Dumortier, 1874 — *Cenoceras*
N. francomontanus Kuhn, 1939 — *Eutrephoceras*
N. franconicus Oppel, 1865 — *Pseudaganides*
N. (Pseudaganides) frickensis Jeannet, 1951 — *Pseudaganides*
N. fuscus Crick, 1898 — *Somalinautilus*
N. gabbi Anderson, 1902 — *Cymatoceras*
N. galea Fritsch and Schlönbach, 1872 — *Angulithes*
N. galicianus Alth, 1850 — *Pseudocenoceras*
Hercoglossa gardnerae Stenzel, 1940 — *Hercoglossa*
Aturia (Brazaturia) garretti Stenzel, 1940 — *Aturia*
N. geelongensis Foord, 1891 — *Eutrephoceras*
N. geinitzi Oppel, 1865 — *Pseudonautilus*
N. geyeri Prinz, 1906 — *Cenoceras*

- N. giganteus* d'Orbigny, 1825 — *Paracenoceras*
N. girardoti de Lorient, 1903 — *Pseudaganides*
N. glaber Foord and Crick, 1890 — *Pseudaganides*
N. gosavicus Redtenbacher, 1873 — *Eutrephoceras*
Aturia grandior Schenck, 1931 — *Aturia*
Aturia (Aturia) grangei Fleming, 1945 — *Aturia*
N. granulatum d'Orbigny, 1843 — *Paracenoceras*
N. gravesianus d'Orbigny, 1843 — *Pseudaganides*
N. guillemi telli Ooster, 1858 — *Cymatoceras*
N. hallidayi Waring, 1914 — *Eutrephoceras* ?
N. hallstattensis Spengler, 1919 — *Cenoceras*
N. haltomi Aldrich, 1931 — *Cimomia*
Eutrephoceras hannai Vokes, 1937 — *Eutrephoceras*
Hercoglossa harrisi Miller and Thompson, 1937 — *Hercoglossa*
N. haughti Olsson, 1928 — *Cimomia*
N. hazaraensis Das-Gupta, 1916 — *Angulithes*
N. heberti Binckhorst, 1861 — *Cimomia*
N. helveticus Loesch, 1914 — *Pseudaganides*
N. (Cymatoceras?) hendersoni Etheridge (1901) — *Eutrephoceras*
N. (Paracenoceras) herznachensis Jeannet, 1951 — *Paracenoceras*
Cimomia hesperia Miller and Downs, 1950 — *Cimomia*
Paracenoceras hexagonoides Spath, 1927 — *Paracenoceras*
N. hexagonus J. de C. Sowerby, 1826 — *Paracenoceras*
N. hilli Shattuck, 1903 — *Cymatoceras*
N. hunstantonensis Foord and Crick, 1890 — *Cymatoceras*
Cimomia hunti Haas and Miller 1952 — *Cimomia*
N. huxleyanus Blanford, 1861 — *Cymatoceras*
N. imbricatus Crick, 1907 — *Cymatoceras*
Bisiphytes (Cenoceras) imlayi Kummel, 1954 — *Cenoceras*
N. impendens Crick, 1898 — *Cenoceras*
N. imperialis J. Sowerby, 1812 — *Cimomia*
N. indicum Spengler, 1910 — *Eutrephoceras*
Hercoglossa innominanda Fleming, 1945 — *Hercoglossa*
N. inornatus d'Orbigny, 1842 — *Cenoceras*
N. intermedius J. Sowerby, 1816 — *Cenoceras*
N. interstriatus Strombeck, 1863 — *Cymatoceras*
N. intumescens Waagen, 1873 — *Procymatoceras* ?
N. (Javanoceras) intuscatenatus Martin, 1932 — *Cimomia*
N. izumoensis Yokoyama, 1913 — *Eutrephoceras*
N. japonicus Shimizu, 1926 — *Eutrephoceras*
N. javanus Martin, 1879 — *Eutrephoceras*
Paracenoceras jeanneti Sanchez Roig, 1951 — *Paracenoceras*
Eutrephoceras johnsoni Miller, 1947 — *Eutrephoceras*

- Eutrephoceras jonesi* Miller and Thompson, 1933 — *Eutrephoceras*
N. jordani Wanner, 1902 — *Cimomia*
N. jourdani Dumortier, 1874 — *Cenoceras*
N. julianus Fucini, 1895 — *Cenoceras*
N. julii d'Orbigny, 1850 — *Cymatonautilus*
N. jumarensis Waagen, 1873 — *Paracenoceras* ?
N. jurensis Quenstedt, 1858 — *Cenoceras*
N. justus Blanford, 1861 — *Eutrephoceras*
Cimomia karkarensis Haas and Miller 1952 — *Cimomia*
N. karpinskyi Karakasch, 1907 — *Paracymatoceras*
N. kayeanus Blanford, 1861 — *Cymatoceras*
Aturia kerniana Anderson and Hanna, 1925 — *Aturia*
N. klebelsbergi Loesch, 1914 — *Pseudaganides*
Aganides kochi Prinz, 1906 — *Pseudaganides*
Aturia koenei Cagel, 1928 — *Aturia*
N. (Cymatoceras) kossmati Spengler, 1910 — *Cymatoceras*
N. krenkeli Jeannet, 1951 — *Pseudaganides*
Cimomia kugleri Miller, 1947 — *Cimomia*
N. kumagunense Waagen, 1873 — *Paracenoceras*
N. kutchensis Waagen, 1873 — *Pseudaganides*
N. labechei d'Archiac and Haime, 1854 — *Eutrephoceras*
N. lallierianus d'Orbigny, 1840 — *Heminautilus*
N. lamarckii Deshayes, 1824 — *Angulithes*
Hercoglossa lamegoi Oliveira, 1953 — *Hercoglossa*
N. landanensis Vincent, 1913 — *Cimomia*
N. largilliertianus d'Orbigny, 1840 — *Pseudocenoceras*
Aturia (Brazaturia) laticlavata Stenzel, 1935 — *Aturia*
N. latifrons Zwierzycki, 1914 — *Paracenoceras*
Eutrephoceras laverdei Durham, 1946 — *Eutrephoceras*
N. ledonicus de Loriol, 1903 — *Pseudaganides*
N. lehardyi Binckhorst, 1861 — *Pseudocenoceras* ?
N. leiotropis Schlüter, 1876 — *Deltocymatoceras*
Deltoidonautilus lemoinei Miller, 1951 — *Angulithes*
N. lentiformis Stoliczka, 1866 — *Eutrephoceras*
N. liconi Negri, 1934 — *Eutrephoceras*
N. leonicensis de Zigno, 1881 — *Cimomia*
N. libanoticus Foord and Crick, 1890 — *Syrionautilus*
N. lineatus J. Sowerby, 1813 — *Cenoceras*
N. lineolatus Foord and Crick, 1890 — *Cenoceras*
Aturia linicentensis Vincent, 1907 — *Aturia* ?
Cymatoceras loeblichii Miller and Harris, 1945 — *Cymatoceras*
N. loricatus Schlüter, 1876 — *Cymatoceras*
Aturia lotzi Böhm, 1913 — *Aturia*

- Aturia luculoensis* Miller, 1938 — *Aturia*
Bisiphytes (Cenoceras) lupheri Kummel, 1954 — *Cenoceras*
N. lutatii Gemmellaro, 1886 — *Cenoceras*
Cimomia macfadyeni Haas and Miller, 1952 — *Cimomia*
Aturia (Brazaturia) mackayi Fleming, 1945 — *Aturia*
N. macrocephalus Schafhäütl, 1863 — *Cimomia*
N. (Cymatoceras) madagascarensis Yabe and Shimizu, 1924 — *Cymatoceras*
Hercoglossa madagascariensis Collignon, 1951 — *Hercoglossa*
N. malbosii Pictet, 1867 — *Pseudonautilus*
N. malherbii Terquem, 1855 — *Cenoceras*
N. manissadjani Gugenberger, 1928 — *Cenoceras*
N. manuanensis Crick, 1907 — *Cymatoceras*
Hercoglossa maracaiboensis Miller and Collinson, 1951 — *Hercoglossa*
N. mariani M. Gemmellaro, 1911 — *Cenoceras*
N. marii Gemmellaro, 1886 — *Cenoceras*
Eutrephoceras marksi Miller, 1947 — *Eutrephoceras*
Paracenoceras marocense Miller and Collinson, 1952 — *Paracenoceras*
N. marucoensis Giovine, 1950 — *Eutrephoceras*
Cimomia marylandensis Miller and Thompson, 1933 — *Cimomia*
Aturia mathewsonii Gabb, 1864 — *Aturoidea*
N. mazzarensis Tagliarini, 1901 — *Cenoceras*
Hercoglossa meglameryae Miller and Thompson, 1933 — *Hercoglossa*
Hercoglossa merriami Dickerson, 1914 — *Hercoglossa*
N. metafleuriausi Douvillé, 1929 — *Eutrephoceras*
N. meyrati Ooster, 1858 — *Cenoceras*
N. mikado Krenkel, 1910 — *Cymatoceras*
Paracymatoceras milleri Humphrey, 1949 — *Paracymatoceras* ?
N. mjatschkowanus Loesch, 1914 — *Paracenoceras*
N. mojsisovici Neumayr, 1870 — *Cymatonautilus*
N. mokattamensis Foord, 1891 — *Cimomia*
N. molli Douvillé, 1920 — *Angulithes*
Eutrephoceras montanensis Kummel, 1954 — *Eutrephoceras*
N. montmollini Pictet and Campiche, 1859 — *Eutrephoceras*
N. moreaui d'Orbigny, 1842 — *Paracenoceras*
Aturia morrissi Michelotti, 1847 — *Aturia*
Paracenoceras mullerriedi Sanchez Roig, 1951 — *Paracenoceras*
N. multiseptatus Foord and Crick, 1890 — *Cenoceras*
N. muniti Choffat, 1886 — *Angulithes*
Aturia myrlae Hanna, 1927 — *Aturia*
Aturia narica Vredenburg, 1925 — *Aturia*
N. nebrascense Meek and Hayden, 1862 — *Cymatoceras*
N. neckerianus Pictet, 1847 — *Cymatoceras*
N. negama Blanford, 1861 — *Cymatoceras*

- N. negritensis* Olsson, 1928 — *Cimomia*
N. neocomiensis d'Orbigny, 1840 — *Cymatoceras*
N. neohispanicum Burekhardt, 1925 — *Cymatoceras*
N. neubergicus Redtenbacher, 1873 — *Eutrephoceras*
N. obesus J. Sowerby, 1816 — *Cenoceras*
N. obstructus Deslongchamps, 1878 — *Cenoceras*
Nautilus (Cymatoceras?) oclusus Crick, 1907 — *Cymatoceras*
Aturoidea olssoni Miller, 1947 — *Aturoidea*
N. oppeli Zittel, 1868 — *Pseudaganides*
N. orbiculatus Tuomey, 1854 — *Hercoglossa*
N. orbigny Prinz, 1906 — *Cenoceras*
Eutrephoceras oregonense Miller, 1947 — *Eutrephoceras*
N. ornatus Foord and Crick, 1890 — *Cenoceras*
N. ornatus var. *atanatensis* Pia, 1914 — *Cenoceras*
Eutrephoceras ovoideum Crick, 1907 — *Eutrephoceras*
Aturia panamensis Miller, 1947 — *Aturia*
N. parabolicus Schafhäütl, 1863 — *Angulithes*
N. parallelus Schafhäütl, 1863 — *Cimomia*
N. paretoi M. Gemmellaro, 1911 — *Cenoceras*
N. parisiensis Deshayes, 1866 — *Eutrephoceras*
N. parkinsoni Edwards, 1849 — *Aturoidea*
Aturia paronai Rovereto, 1900 — *Aturia*
N. patens Kner, 1850 — *Cymatoceras*
N. paucifex Cope, 1866 — *Aturoidea*
N. pavlowi Arkhangelsky, 1904 — *Hercoglossa*
N. pellerensis Vialli, 1937 — *Pseudaganides*
N. perinflatus Foord and Crick, 1890 — *Cenoceras*
N. perlatus Morton, 1834 — *Eutrephoceras*
N. pernambucensis Maury, 1930 — *Cimomia*
N. perornatus Crick, 1894 — *Cenoceras*
N. perstriatus Steuer, 1921 — *Cymatoceras*
N. pertextus Dumortier, 1867 — *Cenoceras*
Aturia peruviana Olsson, 1928 — *Aturia*
Hercoglossa peruviana Berry, 1923 — *Hercoglossa*
N. (Hercoglossa) phosphaticus Bédé, 1933 — *Cimomia*
N. picteti Karakasch, 1907 — *Pseudocenoceras*
N. picteti Oppel 1865 — *Aulaconautilus*
N. piersantii Sergio, 1933 — *Eutrephoceras*
Aturoidea pilsbryi Miller and Thompson, 1935 — *Aturoidea*
N. pisanus Fucini, 1895 — *Cenoceras*
Eutrephoceras planoventer Stephenson, 1941 — *Eutrephoceras*
N. plicatus Fitton, 1835 — *Eucymatoceras*
N. polygonalis J. de C. Sowerby, 1826 — *Cenoceras*
Hercoglossa popenoei Miller and Downs, 1950 — *Hercoglossa*

- N. portlandicus* Foord and Crick, 1890 — *Pseudaganides*
N. postriatus Prinz, 1906 — *Cenoceras*
Aturia praeziczac Oppenheim, 1903 — *Aturia*
Aturia preaturi (Cuvillier) 1935 — *Aturia*
N. profundisiphites Prinz, 1906 — *Cenoceras*
Paracenoceras prohexagonum Spath, 1935 — *Paracenoceras*
N. (Cymatoceras) pseudoatlas Yabe and Shimizu, 1924 — *Cymatoceras*
N. pseudobouchardianus Spengler, 1910 — *Cimomia*
N. pseudoelegans d'Orbigny, 1840 — *Cymatoceras*
N. pseudolineatus Foord and Crick, 1890 — *Cenoceras*
N. (Cymatoceras) pseudonegama Spengler, 1910 — *Cymatoceras*
Cymatoceras pseudoneokomiense Shimizu, 1931 — *Cymatoceras*
N. pseudorugosus Pia, 1914 — *Cenoceras*
N. pseudotruncatus Crick, 1921 — *Cenoceras*
N. (Pseudaganides) pulchellus Jeannel, 1951 — *Pseudaganides*
Obinautilus pulchra Kobayashi, 1954 — *Obinautilus*
Cimomia pusilla Haas and Miller, 1952 — *Cimomia*
N. quadrangularis Pia, 1914 — *Cenoceras*
N. quadrilineatus Favre, 1869 — *Eutrephoceras*
Aturia radiata Bellardi, 1872 — *Aturia*
N. radiatus J. Sowerby, 1822 — *Cymatoceras*
N. rangei Hoppe, 1922 — *Heminautilus*
Eutrephoceras reesidei Stenzel, 1940 — *Eutrephoceras*
N. regalis J. de C. Sowerby, 1843 — *Eutrephoceras*
N. regularis Schafhäütl, 1863 — *Eutrephoceras*
N. restrictus Griepenkerl, 1889 — *Eutrephoceras*
N. resupinatus Redtenbacher, 1873 — *Eutrephoceras*
N. rhodani Roux, 1848 — *Paracenoceras*
Aturia richardsi Miller, 1947 — *Aturia*
N. ricordeanus d'Orbigny, 1847 (in Kilian and Reboul 1915) — *Hercoglossa*?
N. robustus Foord and Crick, 1890 — *Cenoceras*
N. roemeri Loesch, 1914 — *Pseudaganides*
Deltoidonautilus rogeri Miller, 1951 — *Angulithes*
N. rogeri Loesch, 1914 — *Pseudaganides*
N. rollandi Leymerie, 1846 — *Angulithes*
N. rollieri Loesch, 1914 — *Paracenoceras*
N. romeroi Ihering, 1903 — *Cimomia*
N. rota Blanford, 1861 — *Paracymatoceras*
Digonioceras rotundum Hyatt, 1894 — *Cenoceras*
N. rotundus Crick, 1898 — *Cenoceras*
Aturia rovasendiana Parona 1899 — *Aturia*
N. royeri de Loriol, 1872 — *Pseudaganides*
N. rugatus Fritsch and Schlönbach, 1872 — *Deltocymatoceras*
N. rugosus Buvignier, 1852 — *Cenoceras*

- N. sahariensis* Keller, 1932 — *Cimomia*
Cymatoceras sakalavum Collignon, 1949 — *Cymatoceras*
N. sanfilippii Sorrentino, 1932 — *Eutrephoceras*
N. sattleri Krenkel, 1910 — *Paracenoceras*
N. saussureanus Pictet, 1847 — *Cymatoceras*
N. saxbii Morris, 1848 — *Haminautilus*
N. seequirensis Tavani, 1942 — *Cymatoceras*
N. schattenbergi Kuhn, 1936 — *Paracenoceras*
N. schlosseri Loesch, 1914 — *Pseudaganides*
N. schlothemi Loesch, 1914 — *Pseudaganides*
N. schlumbergeri Terquem, 1855 — *Cenoceras*
N. schmidtii Giebel, 1852 — *Cenoceras*
N. schneidi Loesch, 1914 — *Pseudaganides*
N. schusteri Loesch, 1912 — *Paracenoceras*
N. schwalmi Prinz, 1906 — *Cenoceras*
N. schweinfurthi Quaas, 1902 — *Aturoidea*
N. schwertschlagerei Loesch, 1912 — *Pseudaganides*
N. secernendus Pia, 1914 — *Cenoceras*
N. seelandi Penecke, 1884 — *Cimomia*
N. (Cymatoceras) semilobatus Spengler, 1910 — *Cymatoceras*
N. semiornatus Crick, 1898 — *Cenoceras*
N. semistriatus d'Orbigny, 1843 — *Cenoceras*
N. semiundatus Foord, 1891 — *Cymatoceras*
N. semseyi Prinz, 1904 — *Cenoceras*
N. senegalensis Douvillé, 1920 — *Angulithes*
Cimomia septemcastrensis Haas and Miller, 1952 — *Cimomia*
N. serpentinus Blanford, 1861 — *Aturoidea*
N. sexcarinatus Pictet, 1867 — *Aulaconautilus*
N. sharpei Schlüter, 1876 — *Cymatoceras*
N. sicilis Gemmellaro, 1868 — *Paracenoceras*
Hercoglossa simiensis Vokes, 1937 — *Hercoglossa*
Eutrephoceras simile Spath, 1953 — *Eutrephoceras*
N. sinillimus Foord and Crick, 1890 — *Cenoceras*
N. sindiensis Vredenburg, 1928 — *Cimomia*
Daltondonautilus singularis Haas and Miller, 1952 — *Angulithes*
N. sinuaticplicatus Geinitz, 1843 — *Cymatoceras* ?
N. sinuatus Sowerby, 1818 — *Pseudaganides*
N. sinuosus Roemer, 1836 — *Paracenoceras*
Eutrephoceras sloani Reeside, 1924 — *Eutrephoceras*
N. smithi Foord and Crick, 1890 — *Cenoceras*
N. somaliensis Newton, 1925 — *Angulithes*
Aturia somaliensis Haas and Miller, 1952 — *Aturia*
N. sowerbyanus d'Orbigny, 1840 — *Angulithes*
N. sowerbyi Wetherell, 1836 — *Angulithes*

- Deltoidonautilus spathi* Haas and Miller, 1952 — *Angulithes*
N. (Paraturia) spathi Vredenburg, 1928 — *Aturoidea*
N. sphaericus Forbes, 1846 — *Eutrephoceras*
Woodringia splendens Stenzel, 1940 — *Hercoglossa*
N. spreaficoi Parona, 1897 — *Cenoceras*
N. staadti Cossmann, 1902 — *Eutrephoceras*
N. staffelbergensis Kuhn, 1936 — *Paracenoceras*
Vorticoceras stantoni Scott, 1940 — *Heminautilus*
N. steinmanni Möricke, 1894 — *Cenoceras*
N. stephensoni Dickerson, 1914 — *Eutrephoceras*
N. steveni Karakasch, 1907 — *Eucymatoceras*
N. stoppanii Parona, 1897 — *Cenoceras*
N. strambergensis Oppel, 1865 — *Pseudaganides*
N. straticostatus Crick, 1907 — *Cymatoceras*
N. striatus J. Sowerby, 1817 — *Cenoceras*
N. stricteumbilicatus Stchépinsky, 1943 — *Eutrephoceras*
N. stromeri Loesch, 1914 — *Pseudaganides*
N. stschurousskii Milashevitch, 1877 — *Eucymatoceras*
N. sturi Hauer, 1856 — *Cenoceras*
N. subalbensis Sinzow, 1913 — *Anglonautilus*
N. subbiangulatus d'Orbigny, 1850 — *Pseudaganides*
N. subfleuriausianus d'Archiac, 1850 — *Angulithes*
N. (Paracenoceras) subhexagonus Jeannet, 1951 — *Paracenoceras*
Eutrephoceras subinflatus d'Orbigny, 1850 — *Eutrephoceras*
N. sublaevigatus d'Orbigny, 1840 — *Eutrephoceras*
N. subplicatus Philippi (in Sleinmann, 1895) — *Eutrephoceras*
Cimomia subrecta Miller and Thompson, 1933 — *Cimomia*
N. subrotundus Crick, 1898 — *Cenoceras*
N. subsinuatus d'Orbigny, 1850 — *Pseudaganides*
N. subtruncatus Morris and Lycett, 1850 — *Procyamatoceras*
N. subtruncatus Prinz, 1906 — *Cenoceras*
N. suciense Whiteaves, 1879 — *Cymatoceras*
Cimomia sudanensis Miller, 1951 — *Cimomia*
N. szontaghi Vogl, 1910 — *Eutrephoceras*
N. tamulicus Kossmat, 1897 — *Angulithes*
N. tenuicostatus Schlüter, 1876 — *Cymatoceras*
N. terebratus Dumortier, 1874 — *Cenoceras*
Cimomia tessieri Miller, 1951 — *Cimomia*
N. texanum Shumard, 1860 — *Paracyamatoceras*
Eutrephoceras thomi Reeside, 1927 — *Eutrephoceras*
N. thyrrenus Tagliarini, 1901 — *Cenoceras*
N. toarcensis d'Orbigny, 1849 — *Cenoceras*
Deltoidonautilus togoensis Miller, 1951 — *Angulithes*
Aturia tokunagai Shimizu, 1926 — *Aturia*

- N. tourtia* Schlüter, 1876 — *Cymatoceras*
Aturia (*Brazaturia*) *triangulata* Stenzel, 1935 — *Aturia*
N. triangularis Montfort, 1802 — *Angulithes*
N. tricarinatus Vadasz, 1911 — *Cenoceras*
N. trichinopolitensis Blanford, 1861 — *Paracymatoceras*
N. truncatus J. Sowerby, 1816 — *Cenoceras*
N. tsaltsithelensis Rouchadze, 1931 — *Cymatoceras*
Neocymatoceras tsukushiense Kobayashi, 1954 — *Cymatoceras*
N. turingensis Loesch, 1914 — *Pseudaganides*
N. tumescens Fraucher, 1895 — *Eutrophoceras*
Hercoglossa tuomeyi Clark and Martin, 1901 — *Hercoglossa*
N. turcius Krumbeck, 1905 — *Cimomia*
N. turkeryi Gemmellaro, 1886 — *Pseudaganides*
Aturia (*Brazaturia*) *turneri* Stenzel, 1940 — *Aturia*
Platynautilus työsiensis Yabe and Ozaki, 1953 — *Heminautilus*
Eutrophoceras uitehagense Spath, 1930 — *Eutrophoceras*
Enclimatoceras ulrichi White, 1882 — *Hercoglossa*
N. umbilicaris Deshayes, 1835 — *Eutrophoceras*
Cymatoceras undulatifomis Spath, 1927 — *Cymatoceras*
N. undulatus J. Sowerby, 1813 — *Anglonutilus*
N. urbanus J. de C. Sowerby, 1843 — *Eutrophoceras*
N. vaelensis Binckhorst, 1861 — *Epicymatoceras*
Nautilopsis vanuxemi Conrad, 1847 — *Aturia*
N. vastus Kner, 1850 — *Eutrophoceras*
N. voughani Gardner, 1923 — *Cimomia*
N. ventroplicatus Foord, 1891 — *Cymatoceras*
Cimomia vestali Miller and Thompson, 1933 — *Cimomia*
N. vicentinus Oppenheim, 1901 — *Eutrophoceras*
N. victorianus Teichert, 1943 — *Eutrophoceras*
Aturoidea vieirai Miller, 1951 — *Aturoidea*
N. vinassai Venzo, 1937 — *Eutrophoceras*
N. (Cymatoceras) virgatus Spengler, 1910 — *Cymatoceras*
N. volgensis Nikitin, 1888 — *Paracenoceras*
V. waageni Gemmellaro, 1886 — *Cenoceras*
Hercoglossa walteri Miller, 1947 — *Hercoglossa*
N. wandaense Waagen, 1873 — *Paracenoceras*
Hercoglossa waringi Miller, 1947 — *Hercoglossa*
N. westphalicus Schlüter, 1872 — *Angulithes*
N. (Paracenoceras) wilmae Jeannet 1951 — *Paracenoceras*
N. woodsi v. Hoepen, 1921 — *Cymatoceras*
N. wylliei Newton, 1925 — *Cimomia*
Aturia yokoyamai Nagao, 1926 — *Aturia*
N. ziczac J. Sowerby, 1812 — *Aturia*
N. zignoi Gemmellaro, 1886 — *Cenoceras*

N. zitteli Gemmellaro, 1886 — *Cenoceras*

Tithonoceras zitteli Retowski, 1894 — *Tithonoceras*

The following are species for which the available data is insufficient to place them in a generic group with any degree of certainty.

N. astierianus d'Orbigny, 1850

N. delphinus Forbes, 1846

N. fricator Beck, 1835 (nomen nudum)

N. hartmanni Loesch, 1914 (nomen nudum)

N. herbertinus d'Orbigny, 1850

N. inaequalis J. Sowerby, 1813

N. krenkeli Loesch, 1914 (nomen nudum)

N. marcoui d'Orbigny, 1850

N. matheronianus d'Orbigny, 1841

N. naufragus Craigin, 1905

N. nobilis Münster (see Foord, 1891, p. 326) (nomen nudum)

N. normannicus Loesch, 1914 (nomen nudum)

N. pseudoganiticus Loesch, 1914 (nomen nudum)

N. reussii Fritsch and Schlönbach, 1872

N. staffelbergensis Loesch, 1914 (nomen nudum)

N. sumatranus Zwierzycki, 1915

N. tenuiplanatus Dana, 1849

N. valenciennii Hupé (in Gay, 1854)

N. varusensis d'Orbigny, 1850

N. wepferi Loesch, 1914 (nomen nudum)

EVOLUTION

Evolutionary patterns, characterized by almost complete extinction followed by adaptive phases with both eruptive and stable periods, are well displayed in the general history of the Cephalopoda. Few other invertebrate groups display such marked expansion and contraction in their evolution. Within the ammonoids, periods of abrupt contraction, characterized by mass extinction of most evolving lines, occurred in the late Permian and in the late Triassic. Complete extinction of the group came at the end of the Cretaceous. Within the ammonoids each of the two earlier periods of near extinction was followed by an even greater evolutionary radiation. This is well illustrated by the number of genera involved in each of these phases; there are 172 genera of ammonoids of Devonian to Permian age, 370 in the Triassic, and 1228 in the Jurassic and Cretaceous.

There is some parallelism to the ammonoid history in the evolution of the nautiloids; however, in the latter group instead

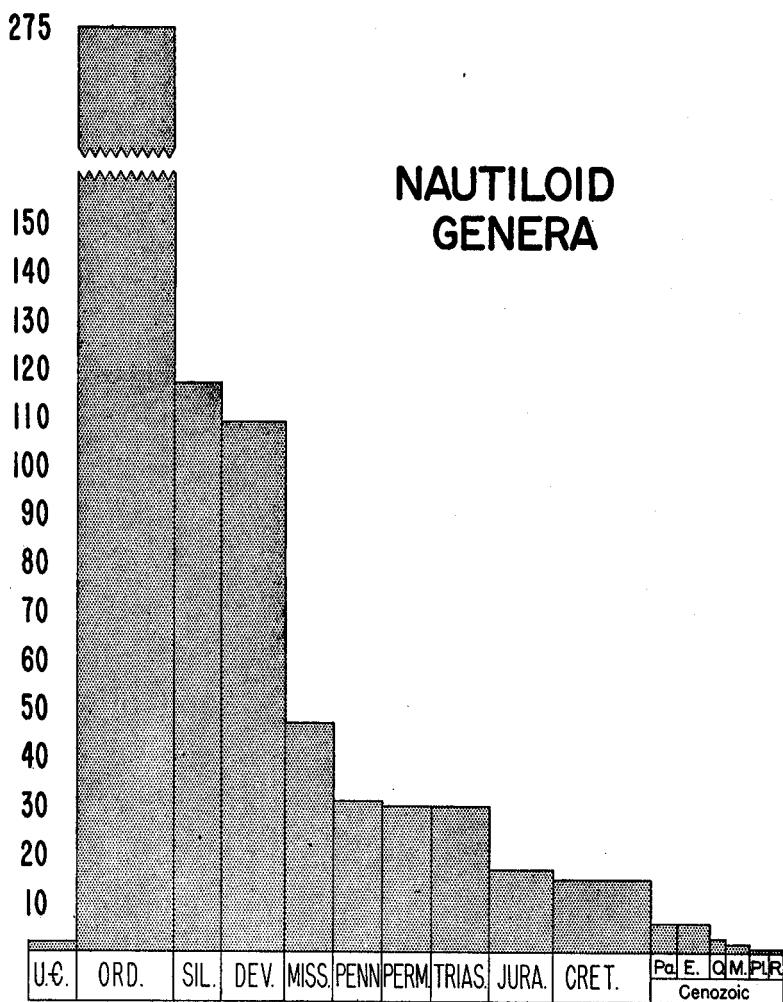


Fig. 1. Bar chart showing number of genera of nautiloid cephalopods present in each period.

of an ever expanding evolutionary complex, the nautiloids experienced their widest radiation in the Ordovician relatively soon after their appearance in the Upper Cambrian. Soon after this period of maximum expansion, there set in a steady, gradual contraction in numbers and diversity of taxonomic units (Fig. 1). There is no wave of extinction toward the end of the Paleozoic; in fact the whole evolutionary pattern of Triassic nautiloids is really a culmination of trends begun back in the Carboniferous (Kummel, 1953c). Thus the evolutionary phases at the transition from the Paleozoic to the Mesozoic are quite different in the ammonoids and the nautiloids. However, toward the end of the Triassic most of the long-persisting Carboniferous to Triassic stocks became extinct. This phase of the evolutionary history of the nautiloids has recently been discussed by Kummel (1953c). There are, in fact, no Rhaetic nautiloids known.

The earliest marine deposits of the Jurassic contain a very homogeneous nautiloid fauna of nearly world-wide distribution. Insofar as nautiloids are concerned, there must have existed at the transition period from the Triassic to the Jurassic an ecologic vacuum. A single stock survived this transition period from the Triassic (Kummel, 1953b), and in the early Jurassic (Lias) an intensified and new evolutionary radiation took place (Fig. 2). The early Jurassic stocks are quite clearly of a single genetic complex, but at the same time show a wide adaptive range in terms of conch shape, size, suture, and shell characters. All these features reflect and express the wide adaptive radiation that took place at this time. Whereas there is very little factual data available as to the adaptive significance of most morphological features it seems only logical to conclude that the various conch shapes, etc., represent adaptations to a specific niche in the marine environment. The repopulation of the early Jurassic seas by nautiloids was uninhibited as far as other nautiloid groups are concerned, and the diversity of conch types is cogent testimony to the adaptation to and occupation of many environmental niches.

Eruptive phases expressed in terms of great plasticity of a group are quite common among the ammonoids. Spath (1934, p. 19) has drawn attention to the "sudden burst of Gephuroceratids in the Upper Devonian of the Domanik, Southern Timan. In that locality there appeared in large numbers depressed and

compressed, smooth and ornamented, evolute and involute, rounded, square, or acute-ventered forms, and even highly

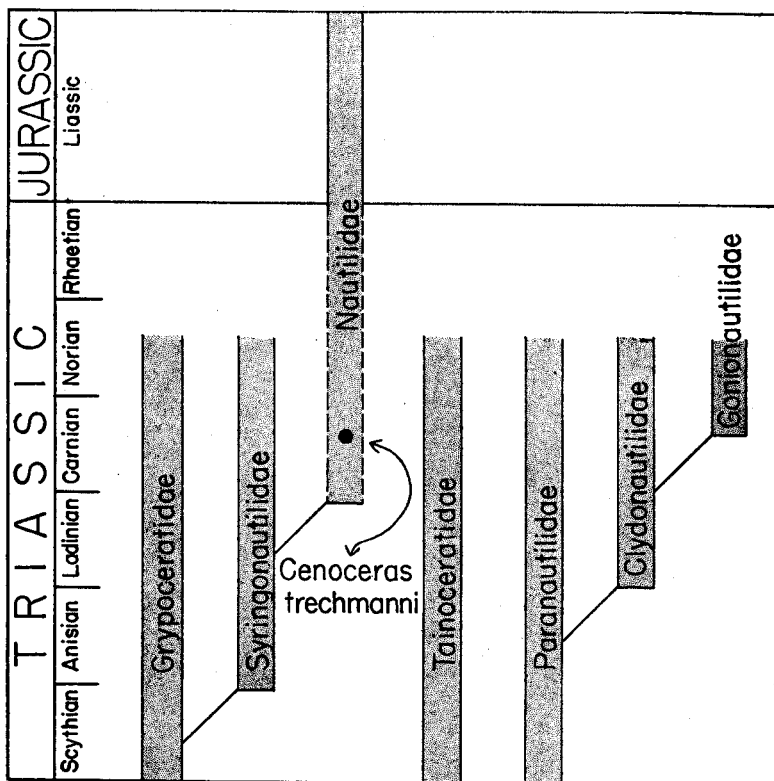


Fig. 2. Phylogenetic diagram illustrating the relationships of the Liassic Nautilidae with the Triassic nautiloid families. The columns representing the Triassic families have been terminated at an arbitrary even line in the Norian. The exact relative extinction dates of these families in the Norian are not known.

specialized oxycones" (See Holzapfel, 1899). A similar situation is found with the early Triassic ophiceratids of the Himalayas (Diener, 1897) and Greenland (Spath, 1930a, 1935a). More examples can be found within the Jurassic and Cretaceous ammonoids.

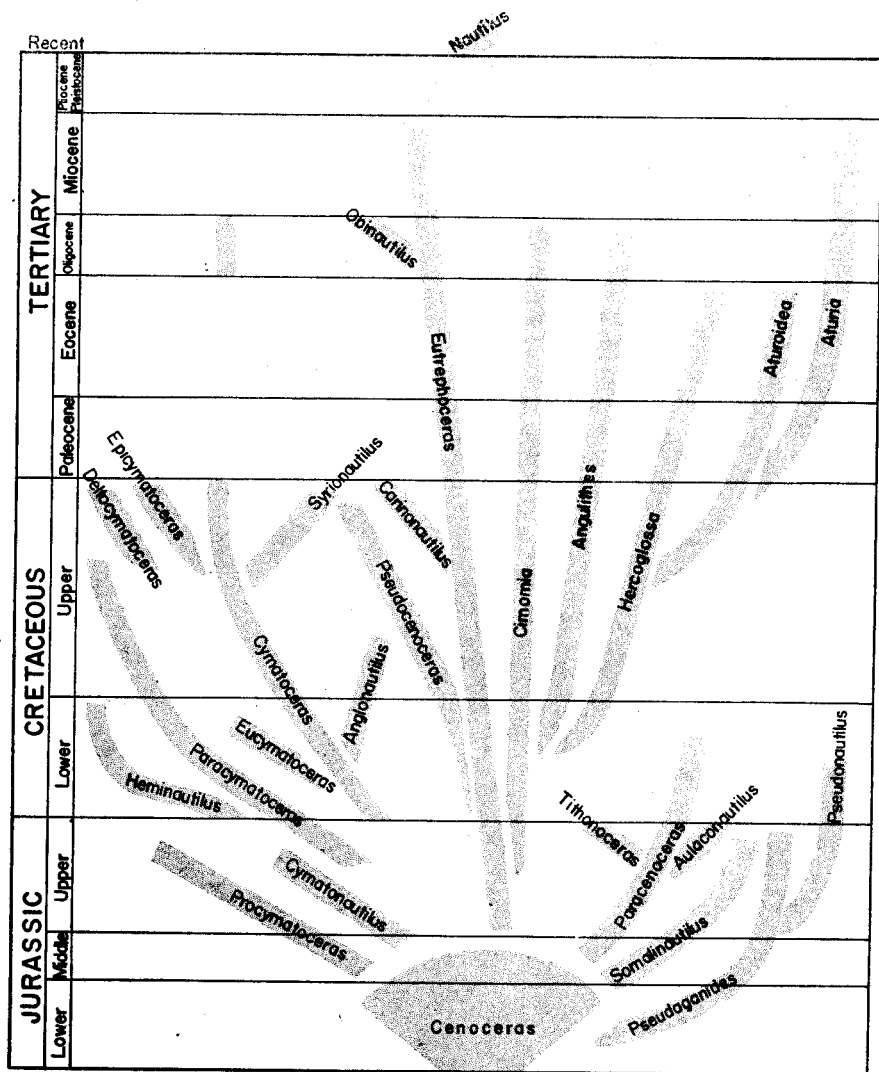


Fig. 3. Diagram showing inferred phylogeny and geologic distribution of post-Triassic nautiloids.

Most early Jurassic nautiloids are here considered species of a single genus, *Cenoceras*. The earliest species of *Cenoceras*, *C. trechmanni*, is from Carnian strata of New Zealand and is derived from the Syringonautilidae (Kummel, 1953b). No species of any other Triassic stock survived into the Jurassic. In the Lias there is thus a world-wide fauna of involute to evolute, strigate to smooth forms with a wide range in whorl shapes — a genetic complex of great plasticity. From this homogeneous but plastic stock there arose from diverse parts of the complex several distinct evolutionary lines built on specialization of one or more morphological features. From this *Cenoceras* complex arose the persisting stable stock (*Eutrephoceras*) which gave rise to other members of the Nautilinae. Likewise the Pseudaganidinae, Paracenoceratinae and most probably the Cymatoceratinae arose directly out of the *Cenoceras* complex (Fig. 3).

The Pseudaganidinae are characterized by their sinuous sutures. In this respect they are adaptive types like the Triassic Clydonautilidae, Gonionautilidae, and Siberionautilidae. They are likewise similar to these Triassic groups in that they show stability in the general form and patterns of the suture and great variability in conch shape. The Pseudaganidinae range from the Liassic into the Lower Cretaceous. There are only two genera involved in this radiation, of which *Pseudaganides* is the main line and *Pseudonautilus* is a specialized offshoot of Upper Jurassic and Lower Cretaceous age. In the evolutionary history of the nautiloids from the Carboniferous to the Recent, adaptive trends expressed in terms of sinuous — “goniatitic” — sutures occurred at four separate times. The first is known through the genus *Permoceras* Miller and Collinson based on *Aganides bitauniense* Haniel from Middle Permian strata of Timor. In my opinion, *Permoceras* is related to the *Grypoceras-Domatoceras* evolving stock and is an aberrant development of this stock. *Grypoceras* (*Plummeroceras*) Kummel (1953c) likewise had a highly sinuous suture with a deep ventral lobe and a deep lateral lobe but it has a very evolute conch. The second radiation repeating this adaptive trend is that in the Upper Triassic including the Clydonautilidae, Gonionautilidae and Siberionautilidae. All of the genera of these families include species with very involute conchs but show great variability in conch shape. The

only other Triassic species with a "goniatitic" suture is *Clymenonautilus ehrlichi* Mojsisovics which in all features but the suture is allied to the Syringonaulitidae. The suture however has a deep, tongue-shaped, narrow, lateral lobe. The Upper Triassic families listed above which include those involute species with highly sinuous sutures, evolved from involute, smooth forms with nearly straight sutures (Paranautilidae).

The third radiation of this series is that of the Pseudaganidinae of Lower Jurassic to Lower Cretaceous age. This group evolved out of some part of the *Cenoceras* complex in the Lias. There is almost perfect homeomorphy between *Permoceras bitauniense* Haniel of the Middle Permian and *Pseudonautilus geinitzi* Oppel of the Upper Jurassic (Miller and Collinson, 1953). Each however represents similar adaptive types from different root stocks and they are not related.

The fourth and last radiation centered on the sinuosity of the suture is that of the Hercoglossinae and Aturinae. The Aturinae with its single genus *Aturia* is a very specialized development out of the Hercoglossinae. The specialization in this case is not so much on a further elaboration of the suture but in the development of the peculiar dorsal siphuncle. Within the Hercoglossinae there is a beautiful developmental series (usually treated as genera) showing gradual increase in sutural complexity. The subfamily has its origin within the stable evolving stock of the Nautilinae represented by *Eutrephoceras* which is characterized by an involute smooth conch with straight or slightly sinuous sutures. *Cimomia* of the Hercoglossinae has a slightly more individualized suture and is gradational with *Eutrephoceras*, as it is also with *Hercoglossa* which has very distinct lobes and saddles. *Angulithes* is merely a sagittate development of these forms. In *Aturoidea* the sutural individuality is carried slightly farther.

The Paracenoceratinae is a small subfamily of mainly Jurassic age with four genera characterized by specialization of the venter. The main stock of this subfamily, *Paracenoceras*, is nearly worldwide in distribution and has by far the largest number of species. The other genera, namely *Somalinautilus*, *Aulaconutilus*, and *Tithonoceras* are more highly specialized forms with few known species. In *Paracenoceras* the whorl section is subtrapezoid, generally with a broad, sulcate venter. *Somalinautilus* has angu-

lar ventral shoulders but a broad arched venter. *Aulaconautilus* has four or more longitudinal ribs. In this respect it is homeomorphous to *Aulametaceras* of the Permian and Triassic. *Tithonoceras* has prominent rounded ventrolateral keels with a sulcate venter. *Paracenoceras* and *Somalinautilus* are undoubtedly derived from distinct elements of the *Cenoceras* complex but *Aulaconautilus* and *Tithonoceras* appear to be specialized developments of *Paracenoceras*.

One of the most successful and diverse groups to stem directly or indirectly from the *Cenoceras* complex is the Cymatoceratinae. This subfamily comprising 10 genera ranging from the Jurassic to the mid-Tertiary is characterized by conchs bearing ribs. This is the only group of post-Triassic nautiloids to have ornamentation, aside from *Aulaconautilus* of the Paracenoceratinae. Radiation within the Cymatoceratinae is reflected in the shape of the conch, suture and ornamentation. The main evolving stock, *Cymatoceras*, has an involute, rounded conch with only a slightly sinuous suture. Most of the other genera of this subfamily are thought to represent various specialized groups derived from *Cymatoceras*. *Paracymatoceras* has a more sinuous suture, in fact much like that of *Hercoglossa*, and on even this feature it is gradational with *Cymatoceras*. Those forms differentiated on the basis of conch shape include *Heminautilus*, *Deltocymatoceras* (n. gen. p. 438), *Epicymatoceras* (n. gen. p. 439) and *Cymatonautilus*. *Herminautilus* has a compressed involute conch with a highly sinuous suture, that has deep ventral and lateral lobes. *Deltocymatoceras* is a homeomorph of *Angulithes* with a sagittate whorl section. *Epicymatoceras* has an evolute, highly compressed conch with a subrectangular whorl section. *Cymatonautilus* has a concave venter and concave lateral areas. Those genera differentiated on the basis of modification of the ribbing pattern include *Eucymatoceras*, *Anglonautilus*, *Procymatoceras*, and *Syrionautilus*. In *Eucymatoceras* the ribs form prominent V-shaped salients on the venter and flanks. In *Anglonautilus* there are coarse folds on the venter whereas *Procymatoceras* has a rapidly expanding robust conch with ribs mainly on the lateral areas. *Syrionautilus* has peculiar shaped ribs with wide interspaces like that of *Proclydonautilus spirolobus* of the Triassic. *Cymatonautilus* and *Procymatoceras* are Jurassic developments, the remaining genera mostly Cre-

taceous. In fact the most widespread and characteristic nautiloids of the Cretaceous are genera of the Cymatoceratinae.

Thinking of the Cymatoceratinae as representing a single genetic unit with its origin within the *Cenoceras* complex, and having as the basic common denominator the ribbing pattern, all of the diverse morphologic types represented by the various genera reflect a broad adaptive radiation which produced numerous homeomorphs of other genera of the Nautilidae.

The most persistent stock evolved from the early Jurassic *Cenoceras* complex is that of *Eutrephoceras*. This genus has a world-wide distribution and ranges in time from the Upper Jurassic to mid-Tertiary. It and *Cymatoceras* are the most common post-Triassic nautiloids. Some 90 so-called species, assigned to this genus, have been described. The genotype has a tightly involute, subglobular, smooth conch with a nearly straight suture. This basic, very simplified, conch pattern became modified either by greater compression, depression or by slightly looser coiling. The variants, however, on the basis of the record available appear to be completely random in their chronologic or geographic distribution. Each such variant has usually been treated as a distinct species. The geologic record thus shows the occurrence of nautiloids with the basic, simplified, globose conch persisting from Upper Jurassic to mid-Tertiary time and with numerous variants of this basic pattern.

Whereas the suture is generally straight or nearly so there are gradational forms to *Cimomia*. Data are not available as to whether there is any particular chronologic or geographic relationship in regard to the sutural variants, which appear to be completely random as is the case with conch form.

The eutrephoceratids are thus a persisting generalized stock which arose from the *Cenoceras* complex, and they show no particular adaptive trends throughout their history. They do show, however, a certain variability in conch shape and suture. The group has the longest range of any of the post-Triassic nautiloids. It is from this persisting generalized form that the remaining more specialized genera and subfamilies arose. The most important offshoots are the genus *Nautilus* and the whole subfamily Hercoglossinae. The nature of the evolutionary pattern from *Eutrephoceras* to *Cimomia* is not easy to decipher. The only significant difference is the degree of sinuosity of the

suture, that in *Eutrephoceras* being straight, or nearly so, and that in *Cimomia* having a distinct lobe and saddle on the lateral areas. There are gradational forms between these two genera. The time range of the two genera is approximately the same, *Cimomia* being slightly younger in origin. It seems quite clear that *Cimomia* arose from *Eutrephoceras* but whether or not there was a single time and point of origin in the late Jurassic, or if

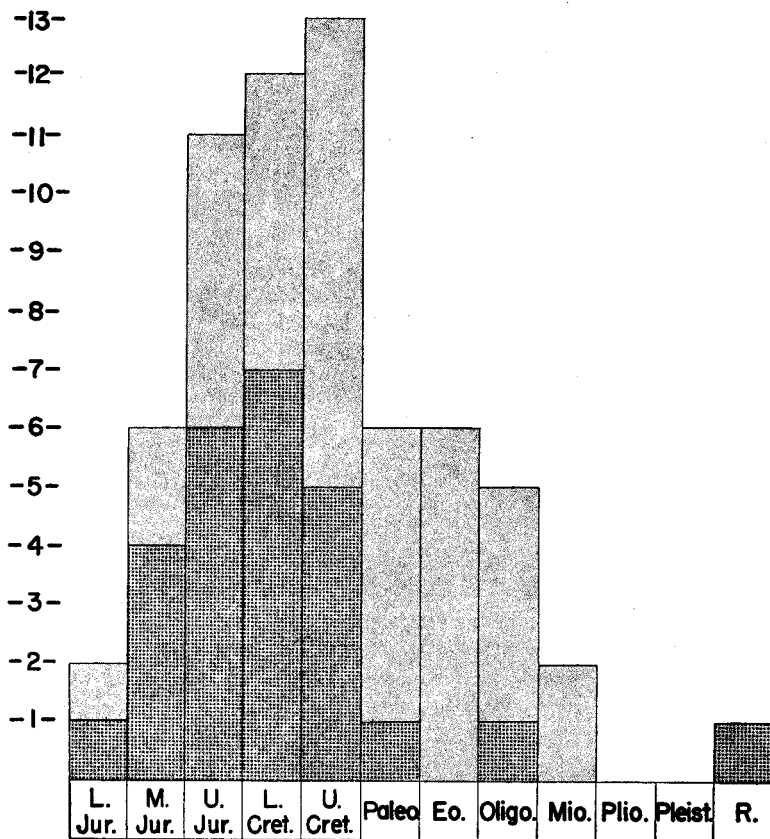


Fig. 4. Bar chart showing total number of genera of nautiloids present in each series of the Mesozoic and Tertiary (light stippling) and number of new genera appearing for the first time in each series (dense stippling).

there were numerous times of origin, throughout the Cretaceous and Tertiary cannot be told from the kind of data available. The alternatives are a parallel evolutionary pattern of the two genera or a consideration of these transitional forms of suture (*Cimomia*) as a form genus including numerous distinct radiations from the eutrephoceratid evolving stock.

Iterative patterns of evolution are recognized within the Carboniferous through Triassic nautiloids. With these nautiloids three main, slowly-evolving, persisting stocks are recognized, namely the *Domatoceras-Grypoceras* line, the *Metacoceras-Mojs-varoceras* line, and the *Liroceras-Paranautilus* line. Each of these stocks has a relatively large number of species (which is merely an indication of relative abundance) and is widespread geographically. Throughout their history they show only relatively minor evolutionary changes. Each of these lines represents a stable, slowly-evolving, but persisting parent stock of their particular family groups. These lines are the evolutionary reservoirs from which other, generally more specialized, groups evolved. The offshoots most often are adaptations accentuating one or more generalized characters of the parent stock. Most of the offshoots are forms with few species and limited geographic range. However, some of these offshoots became in themselves virile, evolving stocks, each with a wide adaptive range and many species (e.g. *Pleuronautilidae* from the *Metacoceras-Mojs-varoceras* line and the *Clydonautilidae* from the *Liroceras-Paranautilus* line).

The *Eutrephoceras* stock gave rise to four other small and aberrant groups, *Pseudocenoceras*, *Obinautilus*, *Carinonautilus*, and *Nautilus*. *Pseudocenoceras* is a compressed form somewhat evolute and with an arched venter, flattened sides and steep umbilical shoulders. *Carinonautilus* is a much compressed form with a prominent rounded keel. It is a monotypic form from Upper Cretaceous strata of South India. *Obinautilus* is another monotypic form recently described by Kobayashi from Oligocene strata of Japan. It is a much compressed involute form with a shallow but distinct furrow on the venter. This genus is still very incompletely known since on the type and only available specimen neither the suture nor position of the siphuncle is preserved.

No fossil species are assigned to the genus *Nautilus*. No *Plio-*

cene or Pleistocene nautiloids are known. Several species of Eocene, Oligocene, and Miocene age have been at times assigned to *Nautilus* but all of these are here considered as having closer affinities to the persisting eutrephoceratid stock than to modern species of *Nautilus*.

TABLE 1

	L. Jur.	M. Jur.	U. Jur.	L. Cret.	U. Cret.	Paleoc.	Eocene	Oligo.	Mio.	Plio.	Recent
Cenoceras	x	x									
Eutrephoceras			x	x	x	x	x	x	x		
Pseudocenoceras				x	x						
Carinonautilus					x						
Obinautilus								x			
Nautilus											x
Pseudaganides	x	x	x								
Pseudonautilus			x	x							
Paracenoceras		x	x	x							
Aulaconautilus			x								
Tithonoceras			x								
Somalinautilus		x	x								
Cymatoceras				x	x			x			
Paracymatoceras			x	x	x						
Proecymatoceras		x	x								
Cymatonautilus		x	x								
Anglonautilus				x	x						
Eucymatoceras				x							
Syrionautilus					x						
Heminautilus				x							
Deltocymatoceras					x						
Epiecymatoceras					x						
Cimomia			x	x	x	x	x	x			
Angulithes				x	x	x	x	x			
Hercoglossa				x	x	x	x				
Aturoidea					x	x	x				
Aturia						x	x	x	x		

The geologic range of the genera of post-Triassic nautiloids is summarized on Table 1, and the bar chart of Figure 4 shows the number of genera and number of new genera per series division of the Jurassic, Cretaceous, and Tertiary. This bar chart clearly brings out the increasing adaptive diversity of the nautiloids in their resurgence after their near extinction in the late Triassic. There is a gradual increase in numbers of new types through the Jurassic. However, of the total of 11 genera in the Upper Jurassic, only 3 (*Eutrephoceras*, *Paracymatoceras* and *Cimomia*) are still destined for a long history. More than half of the total Upper Jurassic fauna (6 genera) do not survive into the Cretaceous and 2 genera (*Pseudonautilus* and *Paracenoceras*) have their main evolutionary play in the Upper Jurassic with only a few species known from Lower Cretaceous. Thus the Jurassic faunas are replaced in the Cretaceous by new phyletic lines, mainly of the Cymatoceratinae, with a much smaller portion from the Nautilinae and Hercoglossinae. By the early Tertiary the cymatoceratid radiation is almost at an end, with a single surviving species in the middle Tertiary. Only one new genetic unit, the Aturinae, comes into the picture in the Paleocene; this became by mid-Tertiary time the most conspicuous element of the fauna. Early Tertiary time was the heyday of the Hercoglossinae; however, the origin of all members of this radiation is well down in the Cretaceous. Wherever early Tertiary faunas are found, members of the Hercoglossinae are the principal elements; the great number of species of this subfamily for the early Tertiary merely reflects the large amount of study concentrated on them in recent years, especially by Miller.

Thus from this summary picture, post-Triassic nautiloid evolution took place in three successive waves, one in the Jurassic, another in the Cretaceous, and the last in the early Tertiary. Each wave introduced new genetic lines which gradually replaced existing or previous lines. The Jurassic and Cretaceous radiations are of approximately equal magnitude; that of the early Tertiary is greatly reduced. Whether or not *Nautilus* should be considered an additional radiation is a moot question. Of the derivations from the eutrephoceratid surviving stock only the Hercoglossinae had an extensive evolutionary history. The other offshoots including *Nautilus* are either monotypic or represented by few species of no great geographic or stratigraphic

range. It seems highly likely that *Nautilus* will follow this same fate.

In most of the principal evolutionary trends of the post-Triassic nautiloids the main evolving stock of each subfamily is repre-

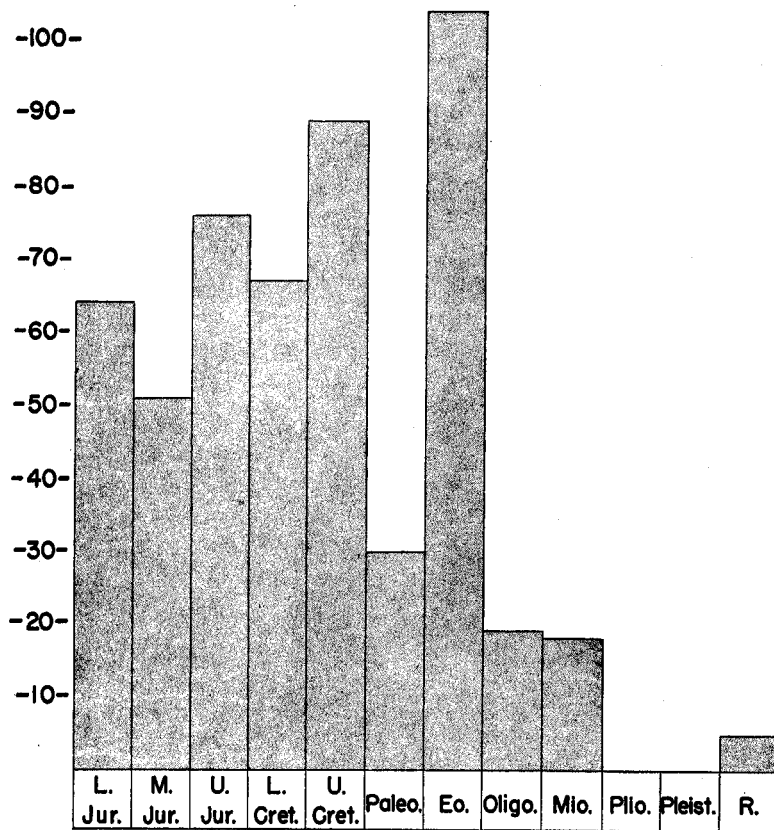


Fig. 5. Bar chart showing total number of species of nautiloids for each series of Mesozoic and Tertiary.

sented by the largest number of species, with the other genera having only a fraction of that amount. Thus of the Nautilinae, *Cenoceras* and *Eutrephoceras* have by far the largest number of species. In the Paracenoceratinae, it is *Paracenoceras*; in the

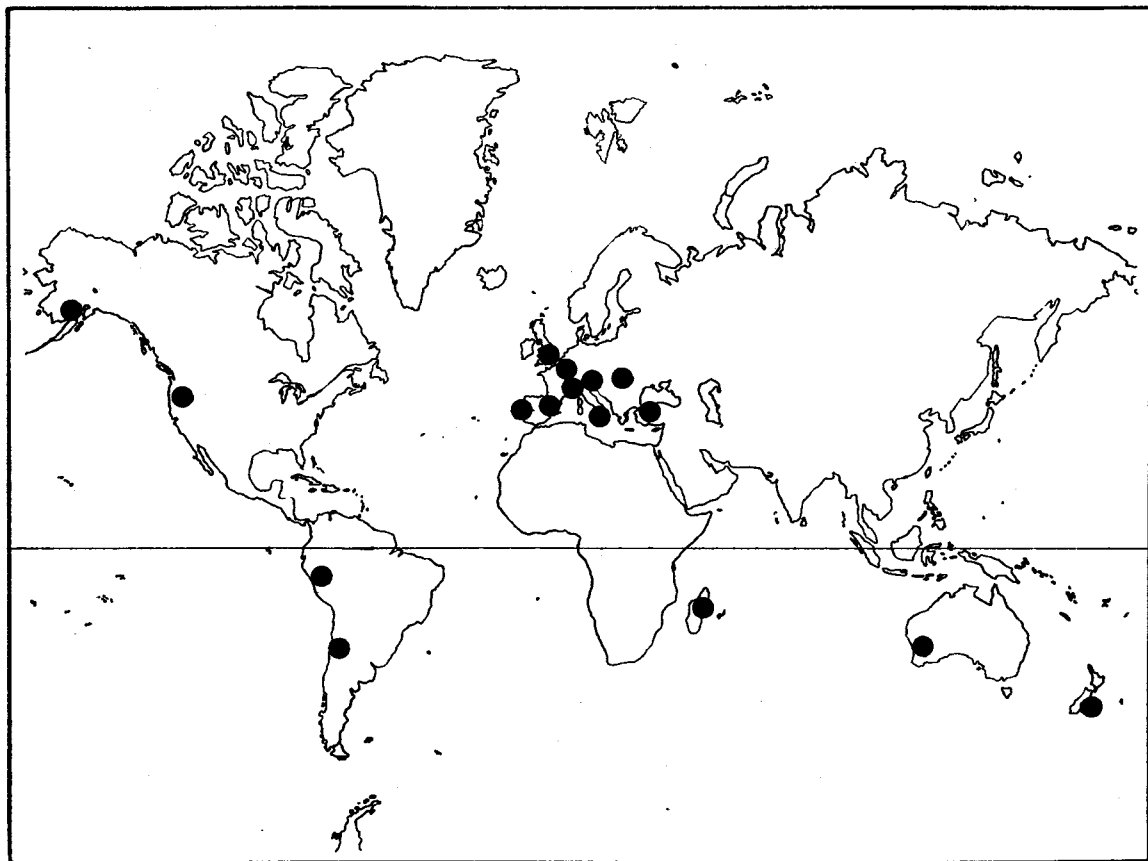


Fig. 6. Geographic distribution of species of the genus *Cenoceras* in formations of Lower and Middle Jurassic age.

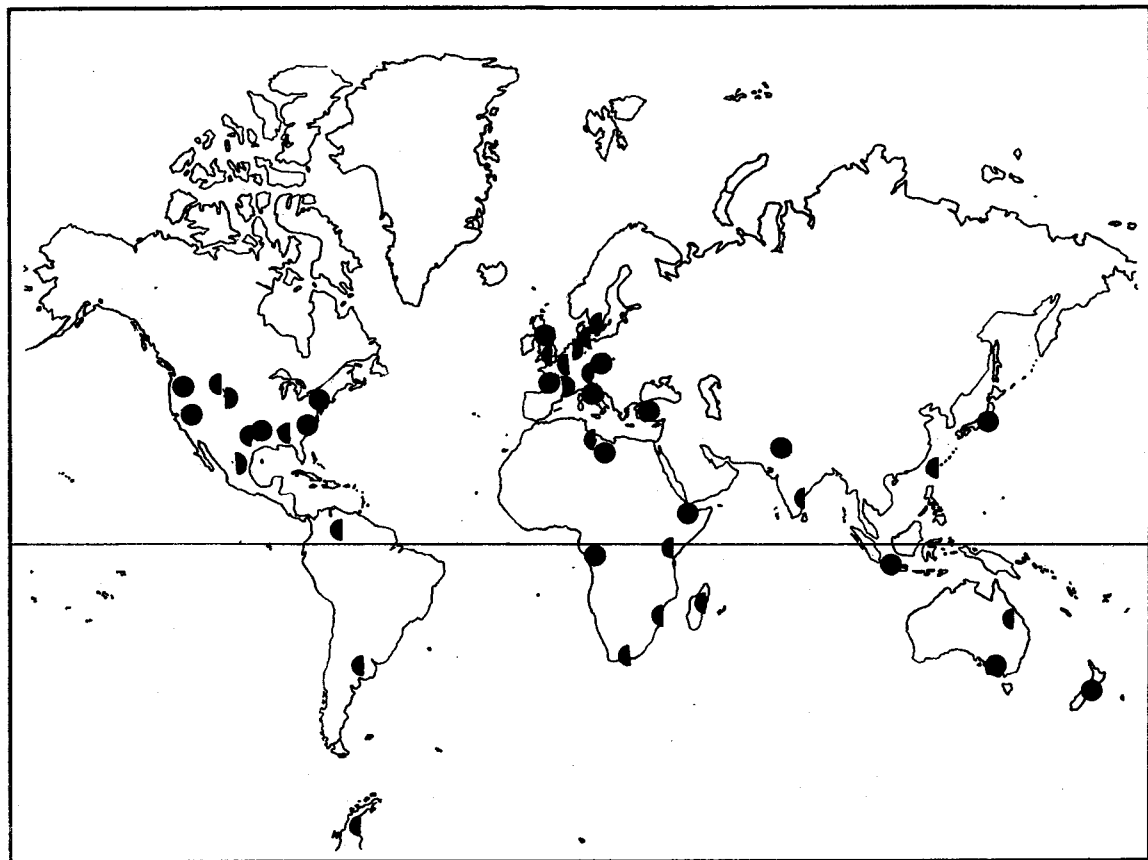


Fig. 7. Geographic distribution of species of the genus *Eutrephoceras* in formations of Upper Jurassic, Cretaceous, and Tertiary age. Circles= Tertiary; left half-circles=Cretaceous; right half-circles=Jurassic.

Cymatoceratinae, it is *Cymatoceras*; in the Pseudaganidinae it is *Pseudaganides*, and in the Hercoglossinae it is *Cimomia* that has the greatest number of species. The Aturinae has only the genus *Aturia*. In spite of the unsatisfactory nature of our understanding of most nautiloid species, these named units do express morphologic diversity, geographic range, and general abundance in nautiloid faunas of these periods. These data likewise tend to substantiate the thesis presented here for persisting, evolving stocks of wide geographic distribution from which more restricted adapted types evolved. On Figure 5 are summarized the number of species per series of the Jurassic, Cretaceous, and Tertiary. Except for the large number of early Tertiary species, interpreted here as a monographic high, this bar chart reflects very well the bar chart on distribution of genera during this time span.

SYSTEMATIC PALEONTOLOGY

Family NAUTILIDAE d'Orbigny, 1840

This family is interpreted here to include all post-Triassic nautiloid genera, which are placed in six subfamilies: Nautilinae d'Orbigny, Pseudaganidinae nov., Paracenoceratinae Spath, Cymatoceratinae Spath, Hercoglossinae Spath, and Aturinae Hyatt. The overall evolutionary pattern of post-Triassic nautiloids with the plastic *Cenoceras* complex of the early Jurassic from which developed directly or indirectly several distinct phyletic trends produced a very homogeneous evolutionary unit. The subfamily units are adaptive trends interpreted for the most part on the basis of single characters — in the Cymatoceratinae it is the presence of ribbing; in the Paracenoceratinae it is elaboration of the periphery; in the Hercoglossinae and Pseudaganidinae it is elaboration of the suture; and in the Aturinae it is the unique dorsal siphuncle and its structure. None of these trends is really a major shift in the evolutionary complex but each is more in the nature of elaboration of genetic potentials in the evolving parent stocks. It thus seems that the taxonomic ranks used here reflect the phylogenetic picture.

Subfamily NAUTILINAE d'Orbigny, 1840

The Nautilinae includes among its genera the earliest forms and the latest and living species of the Nautilidae. Thus in the history of this subfamily we have the origin of the Nautilidae, the persisting stock which gave rise to the remaining subfamily units, and the few living species represented by the relic genus *Nautilus*. The genera included in the Nautilinae are: *Nautilus*, *Cenoceras*, *Eutrophoceras*, *Pseudocenoceras*, *Carinonautilus*, and *Obinautilus*. *Cenoceras* is the plastic evolving complex which survived the great period of extinction at the end of the Triassic and experienced a very intense radiation in the early Jurassic. From the *Cenoceras* complex arose the Pseudaganidinae, Paracenoceratinae, and probably the Cymatoceratinae. *Eutrophoceras* is interpreted as a slowly evolving, long persisting, generalized stock also derived from the *Cenoceras* complex and from which the remaining members of the Nautilinae were derived plus the Hercoglossinae.

Carinonautilus and *Obinautilus* are monotypic; *Pseudocenoceras* has 8 species, and *Nautilus* only 5 species (all Recent). However, *Cenoceras* has 97 species and *Eutrophoceras* 90. This great number of species (or named units) reflects the wide geographic range, morphologic diversity and relative abundance of these two genera. *Cenoceras* is mainly confined to the Lower and Middle Jurassic (with one Upper Triassic [Carnian] species), and *Eutrophoceras* ranges from the Upper Jurassic into the Miocene. Both genera have world-wide distributions (Figs. 6, 7).

Genus CENOCERAS Hyatt, 1883

Cenoceras Hyatt, 1883, pp. 300-301.

Cenoceras Hyatt, 1894, p. 550.

Digonicoceras Hyatt, 1894, pp. 548-549.

Nautilites Prinz, 1906, p. 201.

Cenoceras Spath, 1927a, pp. 20-24.

Ophionautilus Spath, 1927a, pp. 21, 24.

Sphaeronautilus Spath, 1927a, pp. 21, 24.

Cenoceras Flower and Kummel, 1950, p. 615.

Bisiphytes (*Cenoceras*) Kummel, 1954, p. 322.

Type species. *Nautilus intermedius* d'Orbigny non Sowerby = *N. orbignyi* Prinz (1906, p. 213). By original designation. Type illustration reproduced on Plate 1, figs. 1, 2.

The genus *Cenoceras* is here interpreted to include those nautiloid species of the Liassic and Inferior Oolite that are part of the evolving complex which survived the Triassic and which in the great plasticity of the group reflect an extensive adaptive radiation. It is from this very plastic adaptive unit that the more stable, more clearly defined evolutionary lines evolved. The nautiloids nearly became extinct at the end of the Triassic. A single surviving line derived from the Syringonautilidae gave rise to the sole surviving stock (Spath, 1927a, p. 23; Kummel, 1953b). This surviving stock entered an environmental vacuum (insofar as nautiloids are concerned) in the earliest Jurassic. The re-occupation of the diverse ecological niches available for a homogeneous unit stock gave rise to many morphological types, especially in regard to conch form. It is not possible at this time to decipher the individual evolutionary lines within the main complex. There is a complete range of variation and gradation in conch form, suture, position of siphuncle, ornamentation, etc. To bring the taxonomy of these nautiloids to reflect the phylogenetic interpretation, all of the genera previously proposed for aberrant types in the Liassic are placed in synonymy of *Cenoceras*. There is no particular reason for retaining these genera since their included species fit well within the range of variability and evolutionary pattern of the genus *Cenoceras*.

Fig. 8. Cross sections of the conch of species of *Cenoceras*. Redrawn from Pia (1914, pl. 8 [5]). A, *C. araris* (Dumortier) after Dumortier, diameter 210 mm.; B, *C. arariformis* (Pia) after Pia, diameter 190 mm.; C, *C. adneticus* (Pia) after Pia, diameter 137 mm.; D, *C. domeykus* (d'Orbigny) after d'Orbigny, diameter 150 mm.; E, *C. stoppani* (Parona) after Parona, diameter 142 mm.; F, *C. baconicus* (Vadász) after Vadász, diameter 50 mm.; G, *C. altisiphites* (Prinz) after Prinz, diameter 60 mm.; H, *C. julianus* (Fucini) after Fucini, diameter 20 mm.; I, *C. similinus* (Foord and Crick) after Pia, diameter 107 mm.; J, *C. secernendus* (Pia) after Pia, diameter 135 mm.; K, *C. ornatus* (Foord and Crick) var. *atanatensis* (Pia) after Pia, diameter 158 mm.; L, *C. paretoi* (Gemmellaro) after M. Gemmellaro, diameter 17.5 mm.; M, *C. sp. ind. No. 2*, after Prinz, diameter 65 mm.; N, *C. striatus* (Sowerby) after d'Orbigny, diameter 110 mm.; O, *C. striatus* (Sowerby) after Hauer, diameter 80 mm.; P, *C. sturi* (Hauer) after Hauer, diameter 65 mm.; Q, *C. semseyi* (Prinz) after Prinz, diameter 88 mm.; R, *C. robustus* (Foord and Crick) after Foord, diameter 200 mm.; S, *C. geyeri* (Prinz) after Geyer, diameter 80 mm.; T, *C. fourneti* (Dumortier) after Dumortier and Pia, diameter 80 mm.

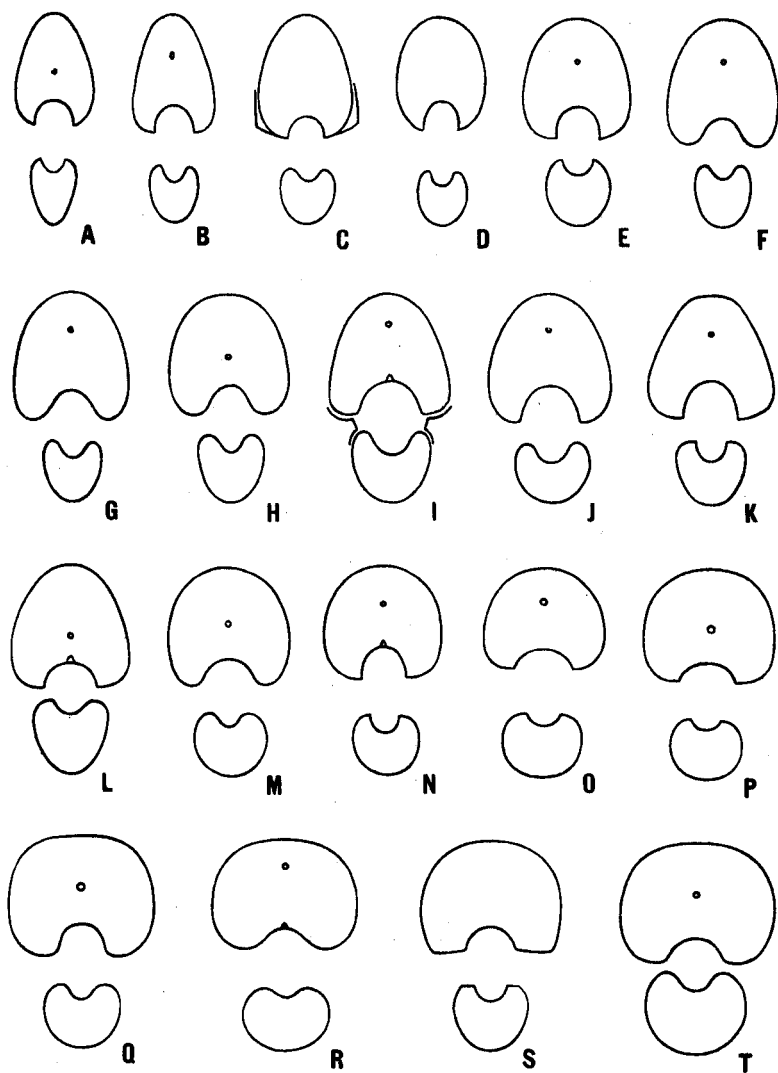


Figure 8

Nomenclature of early Jurassic nautiloids has an involved and ambiguous history. As pointed out by Spath (1927a, p. 20), Hyatt's genus *Cenoceras* (for the group of *Nautilus intermedius* d'Orbigny non Sowerby) has been universally rejected, since Hyatt left in *Nautilus* s.s. other members of the same group, such as *Nautilus striatus*. However, Spath in his 1927 revision of post-Triassic nautiloids accepted *Cenoceras* as a distinct unit on the basis of Hyatt's (1894, p. 550) revised definition limiting *Cenoceras* to forms with a trigonal ananepionic, a subquadrangular metanepionic, and a dorsally sulcate nepionic stage. At the same time Spath readily recognized that the groups of *Nautilus striatus* Sowerby and *Nautilus intermedius* Sowerby could not be differentiated on the shape of the conch and they "agree in ornamentation, position of the siphuncle, presence of an annular lobe, and chiefly in the course of the septal suture" (Spath, 1927a, p. 20).

Now for the group of *Nautilus striatus* Sowerby, Spath revived the genus *Bisiphytes* Montfort (1808). This genus has been discussed to a varied degree by Spath (1927a, pp. 19-24), Miller, Dunbar, and Condra (1933, pp. 42, 43), Teichert (1940, p. 591) and Kummel (1954, pp. 322-323). Montfort listed as type of his genus *Bisiphytes reticulatus* (a then newly proposed species) which came from Sombernon, Burgundy (east-central France), presumably from Jurassic strata. As indicated by the generic name, Montfort thought his specimen had two siphuncles but the

Fig. 9. Cross sections of the conch of species of *Cenoceras*. Redrawn from Pia (1914, pl. 9 [6]). A, *C. toarcensis* (d'Orbigny) after d'Orbigny, diameter 240 mm.; B, *C. jurensis* (Quenstedt) after Quenstedt, diameter 40 mm.; C, *C. sp. ind. No. 6*, after Rosenberg, diameter 50 mm.; D, *C. demonensis* (Gemmellaro) after M. Gemmellaro, diameter 40 mm.; E, *C. austriacus* (Hauer) after Hauer, diameter 230 mm.; F, *C. aratus* (Quenstedt) after Quenstedt, diameter 40 mm.; G, *C. meyrati* (Ooster) after Ooster, diameter 80 mm.; H, *C. terebratus* (Dumortier) after Dumortier, diameter 98 mm.; I, *C. pseudorugosus* (Pia) after Ooster, diameter 90 mm.; J, *C. mariani* (Gemmellaro) after M. Gemmellaro, diameter 46 mm.; K, *C. rugosus* (Buvignier) after Buvignier, diameter 75 mm.; L, *C. astacoides* (Young and Bird) after Dumortier, diameter 112 mm.; M, *C. intermedius* (Sowerby), diameter 200 mm.; N, *C. jourdani* (Dumortier) after Dumortier, diameter 130 mm.; O, *C. inornatus* (d'Orbigny) after d'Orbigny, diameter 85 mm.; P, *C. sp. ind. No. 8*, after Vadász, diameter 66 mm.; Q, *C. truncatus* (Sowerby) after Geyer, diameter 80 mm.

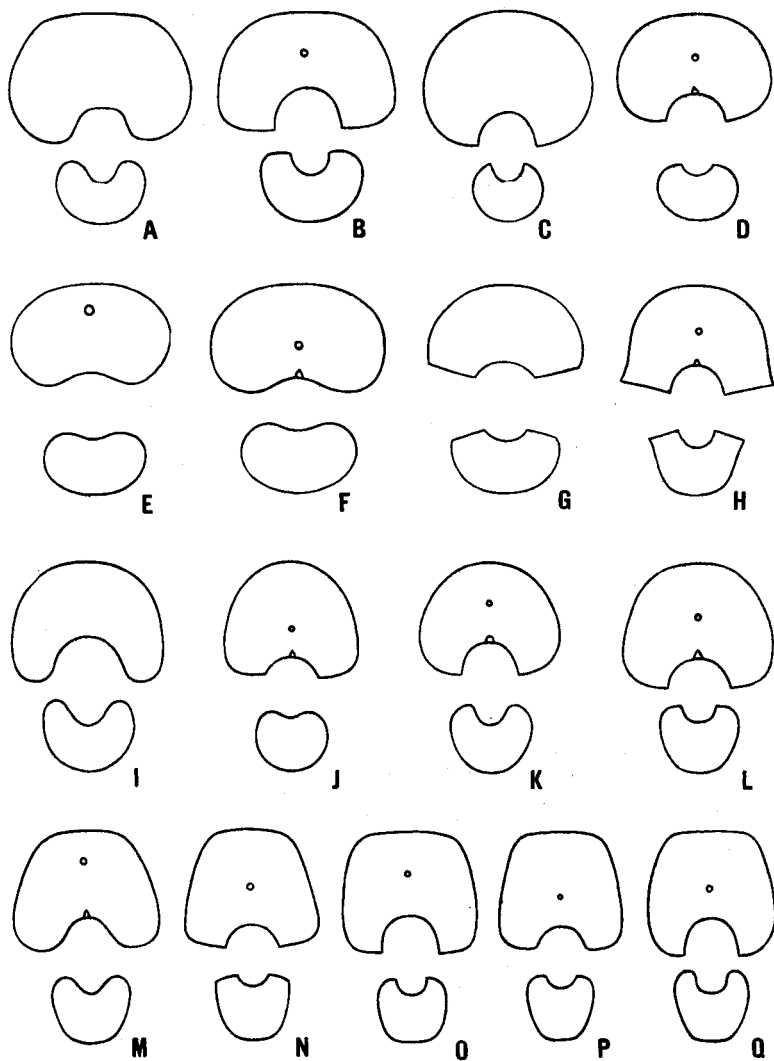


Figure 9

second "siphuncle" is undoubtedly an indentation of the dorsal lobe. The only illustration of *Bisiphytes reticulatus* is a rather crude sketch (reproduced here on Plate 25, fig. 3). It is not possible to recognize the specific features of the genotype of *Bisiphytes* from Montfort's description and/or his illustration; likewise the exact locality and horizon from which the specimen was collected is not known. For these reasons the genus *Bisiphytes* should not be used (a recommendation set forth by Teichert in 1940, p. 591, and in several written communications to the writer). A petition to suppress the generic name *Bisiphytes* is being made to the International Commission on Zoological Nomenclature. Abandonment of *Bisiphytes* leaves available the genus *Cenoceras*—type *Nautilus intermedius* d'Orbigny non Sowerby=*N. orbignyi* Prinz. I am in perfect agreement with Spath that the quadrate whorled *Cenoceras* cannot be separated from the rounder whorled *Bisiphytes*. My previous use of *Cenoceras* as a subgenus of *Bisiphytes* was an attempt to express the homogeneity of these two groups but I am now convinced that Teichert's recommendation to suppress *Bisiphytes*, because of the almost complete ambiguity surrounding the type species, will do much to clarify the taxonomy of these Jurassic nautiloids.

Fig. 10. Cross section of the conch of species of *Cenoceras* and *Pseudaganides*. Redrawn from Pia (1914, pl. 10, [7]). A, *C. quadrangularis* (Pia) after Pia, diameter 103 mm.; B, *C. balsamocrivellii* (Parona), after Parona, diameter 155 mm.; C, *C. distefanoi* (Gemmellaro) after M. Gemmellaro, diameter 52 mm.; D, *D. branconi* (Gemmellaro) after M. Gemmellaro, diameter 60 mm.; E, *C. affinis* (Chapuis and Dewalque) after Chapuis and Dewalque, diameter 101 mm.; F, *C. sp. ind. No. 5*, after Rosenberg, diameter 32 mm.; G, *C. profundisiphites* (Prinz) after Prinz, diameter 82 mm.; H, *C. tricarinatus* (Vadász) after Vadász, diameter 91 mm.; I, *C. anomphalus* (Pia) after d'Orbigny, diameter 90 mm.; J, *C. sp. ind. No. 9*, after Vadász, diameter 36 mm.; K, *C. chilensis* (Huppé) after Möricke, diameter 99 mm.; L, *C. amorettii* (Parona) after Parona, diameter 80 mm.; M, *C. breislacki* (Parona) after Parona, diameter 93 mm.; N, *C. egregius* (Pia) after Pia, diameter 207 mm.; O, *C. semistriatus* (d'Orbigny) after d'Orbigny, diameter 165 mm.; P, *Pseudaganides grave-siana* (d'Orbigny), diameter 240 mm.; Q, *C. schwalmi* (Prinz) after Prinz, diameter 89 mm.; R, *C. fischeranus* (Foord and Crick) after Foord, diameter 180 mm.; S, *C. pertextus* (Dumortier) after Dumortier, diameter 180 mm.; T, *C. spreaficoi* (Parona) after Parona, diameter 58 mm.; U, *C. pisanus* (Fucini) after Fucini, diameter 12 mm.

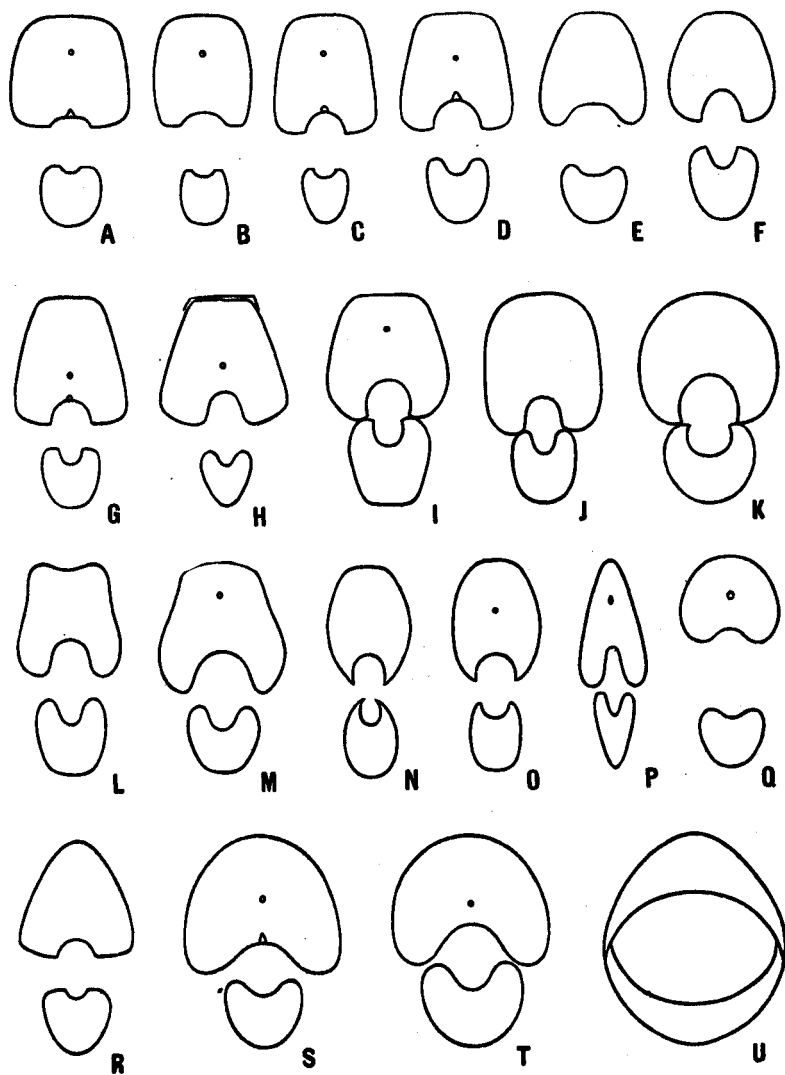


Figure 10

A precise morphological definition of *Cenoceras* is not possible because of the wide variability and range in conch shape and ornamentation. The suture is for the most part quite uniform having only slight ventral and lateral lobes. The variability in conch shape has been most admirably illustrated in a set of text figures by Pia (1914) which are reproduced here as Text Figures 8, 9, 10. Interpreting conch form as an expression of adaptation, these text figures clearly show the range of radiation in the group. The uniformity of the suture and types of ornamental patterns supports the conclusion that all these species are part of a single genetic complex.

Spath (1927a) listed four other genera of Liassic nautiloids, namely: *Sphaeronautilus* Spath, *Digonioceras* Hyatt, *Ophionautilus* Spath, and *Hercoglossoceras* Spath. All these genera are now placed in synonymy of other forms. *Hercoglossoceras* is considered a synonym of *Pseudaganides*. The remaining genera (*Sphaeronautilus*, *Digonioceras*, and *Ophionautilus*) are considered to be synonyms of *Cenoceras*.

The type species of *Digonioceras* Hyatt, 1894, is *Digonioceras rotundum* Hyatt, non Crick, 1898, by original designation and not *Nautilus excavatus* J. de C. Sowerby (1826, pl. 529, fig. 1; Pl. 9, figs. 3-5, of this report) as indicated by Spath (1927a, p. 21). The original description and illustration of *D. rotundum* (Hyatt, 1894, p. 549) leaves much to be desired. The type specimen, which is in the M.C.Z., is a juvenile of one volution and consists only of phragmocone. It measures 34 mm. in diameter; the width and height of the most adoral whorl are 23 mm. and 17.5 mm. respectively. The whorls are depressed and ovoid in cross section. The venter is broadly arched. The whorl sides are convex and grade onto the venter and the umbilical wall with no distinct shoulders to break the even curvature. The venter of the second camera is bluntly angular or fastigate. The rounded

aspect of the venter is apparent on the third camera. Adorally, the whorls become gradually more depressed producing the broad venter and narrowly rounded sides. The umbilicus is perforate, measuring approximately 2 mm. in diameter. The suture has very shallow ventral and lateral lobes, and no annular lobe. The siphuncle is in a subventral position. The shell is smooth except for fine growth lines that form a deep tongue-shaped sinus on the venter.

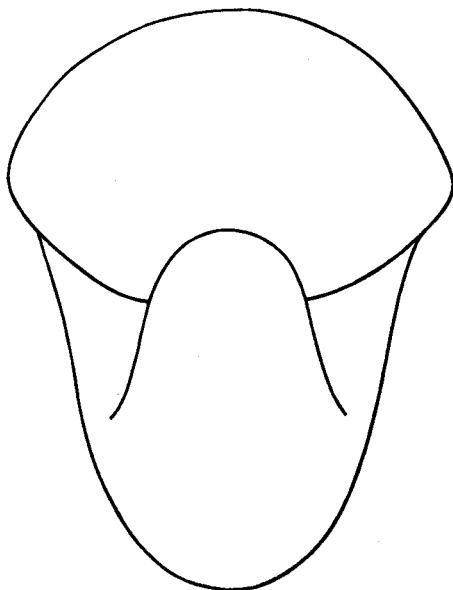


Fig. 11. *Cenoceras excavatus* (Sowerby). Diagrammatic cross-section of holotype represented by figures 1, 2, Plate 7. X 1.

Hyatt (1883, p. 288) included *Nautilus excavatus*, d'Orbigny in *Endolobus* and considered that species to be the latest survivor of that series. However, in 1894 (p. 549) he noted that there were significant differences between the Carboniferous *Endolobus* and the Jurassic species he placed in *Digoniceras*. My own study of Sowerby's type of *Nautilus excavatus* in the B.M.N.H. (figured here on Plate 7 and Text Figure 11) and Hyatt's type

of *Digonioceras rotundum* which is in the M.C.Z. lead me to conclude that it is not possible to tell whether or not these two species are congeneric in Hyatt's sense. *Digonioceras rotundum* is based on a juvenile specimen which is very generalized in its characters. The locality and geologic horizon of *D. rotundum* is not known, but Hyatt (1894, p. 549) writes, "It is obviously from the Oolite but the locality is not known."

The large funnel-shaped umbilicus of *Nautilus excavatus* is the principal character used by Hyatt and later by Spath to set this group aside as a separate generic category under the name *Digonioceras*. Other Middle Jurassic species which appear to be related to *Nautilus excavatus*, at least in the general character of the umbilicus, are *N. smithi* Foord and Crick, 1890, and *N. dispansus* Morris and Lycett, 1850. From the Lias, similar umbilical features are found in *Nautilus meyrati* Ooster (1858) (Fig. 9*G*) and in *N. terebratus* Dumortier (1874) (Fig. 9*H*). The umbilical shoulders of the latter species are flared and angular; the umbilical wall is broad and sloping toward the umbilicus. The group of *Nautilus excavatus* does not appear to have given rise to any later stock of nautiloids and is here interpreted as merely one (of the many) adaptive types produced in the early Jurassic within the *Cenoceras* complex. From an evolutionary viewpoint the group is merely a part or expression of the adaptive radiation or plastic phase found in the early Jurassic, and the group should be taxonomically treated as species of *Cenoceras*.

Ophionautilus Spath (1927), type species *Nautilus burtonensis* Foord and Crick, 1890 (illustrated here on Plate 6, and Text Figure 12), was differentiated on the basis of the very evolute, widely umbilicate conch. The type species is from the Inferior Oolite of England. In addition to the type species, *Nautilus zitteli* Gemmellaro (1886) of the lower Dogger of Sicily, *N. austriacus* Hauer (1856) (Fig. 9*E*) and *N. schwalmi* Prinz (1906) (Fig. 10*Q*) from the Liassic of the Alps and Hungary, respectively, belong to this species group. These species which have been or can be assigned to *Ophionautilus* are interpreted as evolute adaptations of the *Cenoceras* complex. These evolute elements did not give rise to any of the succeeding more stable evolutionary lines. *Nautilus burtonensis* Foord and Crick has an evolute, smooth, rather large conch. The whorl section is

wider than high. The venter is broadly rounded to slightly flattened; the whorl sides are rounded as are the umbilical shoulders. The umbilical wall is convex and steep. The umbilicus is broad and deep, exposing much of the inner whorls. The suture is only slightly sinuous with a shallow ventral and a shallow lateral lobe that includes the whole whorl side. The only markings on the shell are growth lines and they form a deep sinus on the venter. The siphuncle is more or less centrally

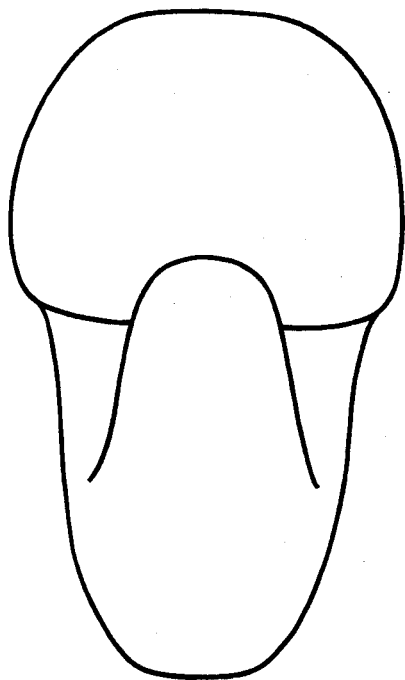


Fig. 12. *Cenoceras burtonensis* (Foord and Crick). Diagrammatic cross section of holotype represented by figures 1, 2, Plate 6, X 1.

located. The group of *Nautilus burtonensis* includes the most evolute adaptation of the *Cenoceras* complex but there is within this complex a nearly complete gradational series in degree of involution.

Whereas the group of *Nautilus burtonensis* includes the most evolute elements of the *Cenoceras* complex, the most involute form is *Nautilus pisanus* Fucini (1895, p. 328, pl. 13, fig. 5) from lower Liassic strata of Italy for which Spath (1927a, p. 21) established the genus *Sphaeronautilus* (Fig. 10U). In its arcestd-like shape *Nautilus pisanus* is indeed an extreme aberrant type. The conch is small and smooth. The suture has only a slight lobe on the ventral and lateral areas. There is not known at present a perfect gradational series from "typical" *Cenoceras* to the extremely involute *Nautilus pisanus*. However, its stratigraphic position and general morphological characters make it logical to consider *Nautilus pisanus* as the extreme involute development of the *Cenoceras* complex and the genus *Sphaeronautilus* is placed in synonymy of *Cenoceras*.

More species have been described for *Cenoceras* than for any other genus of post-Triassic nautiloids. Of the 96 species, two-thirds are Lias in age and the remaining third Middle Jurassic in age. *Cenoceras* is a truly cosmopolitan form being known from nearly all continental areas (Fig. 6). The species belonging to *Cenoceras* with their age and geographic distribution are listed below.

DISTRIBUTION OF SPECIES OF THE GENUS CENOCERAS

Species	Stratigraphic Distribution	Geographic Distribution
<i>C. adneticus</i> (Pia) 1914	Jurassic (Lias)	Austria
<i>C. affinis</i> (Chapuis and Dewalque) 1853	Jurassic (Lias)	Luxembourg
<i>C. altisiphites</i> (Prinz) 1906	Jurassic (Lias)	Hungary
<i>C. amasianus</i> (Gugenberger) 1928	Jurassic (Lias)	Turkey
<i>C. amorettii</i> (Parona) 1897	Jurassic (Lias)	Italy
<i>C. anomphalus</i> (Pia) 1914	Jurassic (Lias)	France
<i>C. arariformis</i> (Pia) 1914	Jurassic (Lias)	Austria
<i>C. araris</i> (Dumortier) 1869	Jurassic (Lias)	Europe

Species	Stratigraphic Distribution	Geographic Distribution
<i>C. aratus</i> (Quenstedt) 1846	Jurassic (Lias)	Germany
<i>C. arthaberi</i> (Gugenberger) 1928	Jurassic (Lias)	Turkey
<i>C. astacoides</i> (Young and Bird) 1828	Jurassic (Lias)	Europe
<i>C. austriacus</i> (Hauer) 1856	Jurassic (Lias)	Alps
<i>C. baconicus</i> (Vadász) 1911	Jurassic (Lias)	Hungary
<i>C. balsamocrivellii</i> (Parona) 1897	Jurassic (Lias)	Italy
<i>C. bradfordensis</i> (Crick) 1898	Jurassic (Bajocian)	England
<i>C. brancoi</i> (Gemmellaro) 1884	Jurassic (Lias)	Italy
<i>C. breislacki</i> (Parona) 1897	Jurassic (Lias)	Italy
<i>C. burtonensis</i> (Foord and Crick) 1890	Jurassic (Bajocian)	England
<i>C. catonis</i> (Gemmellaro) 1886	Jurassic (L. Dogger)	Sicily
<i>C. chilensis</i> (Huppé) 1854	Jurassic (Lias)	Chile
<i>C. demonensis</i> (M. Gemmellaro) 1911	Jurassic (Lias)	Sicily
‡ <i>C. dispansus</i> (Morris and Lycett) 1850	Jurassic (Bathonian)	England
<i>C. distefanoi</i> (Gemmellaro) 1884	Jurassic (Lias)	Italy
<i>C. domeykus</i> (d'Orbigny) 1842	Jurassic (Lias)	Chile
<i>C. egregius</i> (Pia) 1914	Jurassic (Lias)	Austria
<i>C. ercycinus</i> (Tagliarini) 1901	Jurassic (L. Dogger)	Sicily
<i>C. excavatus</i> (J. de C. Sowerby) 1826	Jurassic (Bajocian)	England
<i>C. exiguus</i> (Crick) 1898	Jurassic (Bajocian)	England

Species	Stratigraphic Distribution	Geographic Distribution
<i>C. exterebratus</i> (Crick) 1898	Jurassic (Bajocian)	England
<i>C. fischeranus</i> (Foord and Crick) 1890	Jurassic (Lias)	France
<i>C.ourneti</i> (Dumortier) 1874	Jurassic (Lias)	Europe
<i>C. geyeri</i> (Prinz) 1906	Jurassic (Lias)	Austria
<i>C. hallstattensis</i> (Spengler) 1919	Jurassic (Lias)	Austria
<i>C. imlayi</i> (Kummel) 1954	Jurassic (Bajocian)	Alaska
<i>C. impendens</i> (Crick) 1898	Jurassic (Bajocian)	England
<i>C. inornatus</i> (d'Orbigny) 1842	Jurassic (Lias)	Europe
<i>E. intermedius</i> (J. Sowerby) 1816	Jurassic (Lias)	Europe
<i>C. jourdani</i> (Dumortier) 1874	Jurassic (Lias)	Europe
<i>C. julianus</i> (Fucini) 1895	Jurassic (Lias)	Italy
<i>C. jurensis</i> (Quenstedt) 1858	Jurassic (Lias)	Europe
<i>C. lineatus</i> (J. Sowerby) 1813	Jurassic (Bajocian)	England
<i>C. lineolatus</i> (Foord and Crick) 1890	Jurassic (Lias and Bajocian)	England France
<i>C. lupheri</i> (Kummel) 1954	Jurassic (Bajocian)	Oregon (U.S.A.)
<i>C. lutatii</i> (Gemmellaro) 1886	Jurassic (L. Dogger)	Sicily
<i>C. malherbii</i> (Terquem) 1855	Jurassic (Lias)	Luxembourg
<i>C. manissadjiani</i> (Gugenberger) 1928	Jurassic (Lias)	Turkey
<i>C. mariani</i> (M. Gemmellaro) 1911	Jurassic (Lias)	Sicily
<i>C. marii</i> (Gemmellaro) 1886	Jurassic (L. Dogger)	Sicily

Species	Stratigraphic Distribution	Geographic Distribution
<i>C. mazzarensis</i> (Tagliarini) 1901	Jurassic (L. Dogger)	Sicily
<i>C. meyrati</i> (Ooster) 1858	Jurassic (Lias)	Alps
<i>C. multiseptatus</i> (Foord and Crick) 1890	Jurassic (Bajocian)	England
<i>C. obesus</i> (J. Sowerby) 1816	Jurassic (Bajocian)	England
<i>C. obstructus</i> (Deslongchamps) 1878	Jurassic (Bajocian)	France, England
<i>C. orbignyi</i> (Prinz) 1906	Jurassic (Lias)	Europe
<i>C. ornatus</i> (Foord and Crick) 1890	Jurassic (Bajocian)	England
<i>C. ornatus</i> var. <i>atanatensis</i> (Pia) 1914	Jurassic (Lias)	Austria
<i>C. paretoi</i> (M. Gemmellaro) 1911	Jurassic (Lias)	Sicily
<i>C. perinflatus</i> (Foord and Crick) 1890	Jurassic (Bajocian)	England
<i>C. perornatus</i> (Crick) 1894	Jurassic (Bajocian)	Western Australia
<i>C. pertextus</i> (Dumortier) 1867	Jurassic (Lias)	France Austria
<i>C. pisanus</i> (Fucini) 1895	Jurassic (Lias)	Italy
<i>C. polygonalis</i> (J. de C. Sowerby) 1826	Jurassic (Bajocian)	England
<i>C. postriatus</i> (Prinz) 1906	Jurassic (Lias)	Europe
<i>C. profundisiphytes</i> (Prinz) 1906	Jurassic (Lias)	Austria
<i>C. pseudolineatus</i> (Foord and Crick) 1890	Jurassic (Bajocian)	England
<i>C. pseudorugosus</i> (Pia) 1914	Jurassic (Lias)	Alpine Region
<i>C. pseudotruncatus</i> (Crick) 1921	Jurassic (Lias)	England
<i>C. quadrangularis</i> (Pia) 1914	Jurassic (Lias)	Austria
<i>C. robustus</i> (Foord and Crick) 1890	Jurassic (Lias)	France, Austria

Species	Stratigraphic Distribution	Geographic Distribution
<i>C. rotundum</i> (Hyatt) 1894	Jurassic (Bajocian?)	England
<i>C. rotundum</i> (Crick) 1898	Jurassic (Bajocian)	England
<i>C. rugosus</i> (Buvignier) 1852	Jurassic (Lias)	Europe
<i>C. schlumbergeri</i> (Terquem) 1855	Jurassic (Lias)	Luxembourg
<i>C. schmidtii</i> (Giebel) 1852	Jurassic (Lias)	Germany
<i>C. schwalmi</i> (Prinz) 1906	Jurassic (Lias)	Hungary
<i>C. secernendus</i> (Pia) 1914	Jurassic (Lias)	Austria
<i>C. semiornatus</i> (Crick) 1898	Jurassic (Bajocian)	England
<i>C. semistriatus</i> (d'Orbigny) 1843	Jurassic (Lias)	France
<i>C. semseyi</i> (Prinz) 1904	Jurassic (Lias and L. Dogger)	Hungary
<i>C. simillimus</i> (Foord and Crick) 1890	Jurassic (Lias)	England, Austria
<i>C. smithi</i> (Foord and Crick) 1890	Jurassic (Bajocian)	England
<i>C. spreaficoi</i> (Parona) 1897	Jurassic (Lias)	Italy
<i>C. steinmanni</i> (Möricke) 1894	Jurassic (Middle)	Chile
<i>C. stoppanii</i> (Parona) 1897	Jurassic (Lias)	Italy
<i>C. striatus</i> (J. Sowerby) 1817	Jurassic (Lias)	Europe
<i>C. sturi</i> (Hauer) 1856	Jurassic (Lias)	Alpine Region
<i>C. subrotundus</i> (Crick) 1898	Jurassic (Bajocian)	England
<i>C. subtruncatus</i> (Prinz) 1906	Jurassic (Lias)	France
<i>C. terebratus</i> (Dumortier) 1874	Jurassic (Lias)	France, England

Species	Stratigraphic Distribution	Geographic Distribution
<i>C. thyrrenus</i> (Tagliarini) 1901	Jurassic (L. Dogger)	Sicily
<i>C. toarcensis</i> (d'Orbigny) 1849	Jurassic (Lias)	France, Germany, *
<i>C. tricarinatus</i> (Vadász) 1911	Jurassic (Lias)	Austria
<i>C. truncatus</i> (Sowerby) 1816	Jurassic (Lias)	Europe
<i>C. waageni</i> (Gemmellaro) 1886	Jurassic (L. Dogger)	Sicily
<i>C. zignoi</i> (Gemmellaro) 1886	Jurassic (L. Dogger)	Sicily
<i>C. zitteli</i> (Gemmellaro) 1886	Jurassic (Middle)	Sicily

Genus *EUTREPHOCERAS* Hyatt, 1894

Eutrephoceras Hyatt, 1894, p. 555.

Eutrephoceras Reeside, 1924, p. 2.

Eutrephoceras Reeside, 1927b, pp. 6, 7.

Eutrephoceras Miller and Thompson, 1933, pp. 300-304.

Eutrephoceras Spath, 1927a, pp. 21, 24.

Eutrephoceras Spath, 1927b, pp. 425, 426, 428.

Eutrephoceras Stenzel, 1940, pp. 738-742.

Eutrephoceras Miller, 1947, pp. 26-39.

Eutrephoceras Miller, 1951, pp. 33-36.

The genus *Eutrephoceras* represents the long-lived and persistent stock arising from the lower Jurassic *Cenoceras* complex and is considered to be the root from which most of the remaining Cretaceous and Tertiary nautiloids, excepting the Cymatoceratinae, are derived. It is most similar to *Cimomia* and *Nautilus*. *Cimomia* arose from *Eutrephoceras* in the Upper Jurassic or Cretaceous and is in itself the root stock of the Hercoglossinae. *Cimomia* differs from *Eutrephoceras* in the greater sinuosity of the suture, but many intermediate forms are known.

Thus the interpretation of *Eutrephoceras* presented here visualizes a persisting, slowly evolving stock consisting of generally involute, smooth forms with straight or nearly straight sutures, and a conch that is generally subglobular but can be quite compressed or depressed. The rather wide variation in the shape of the conch is illustrated in Text Figure 13.

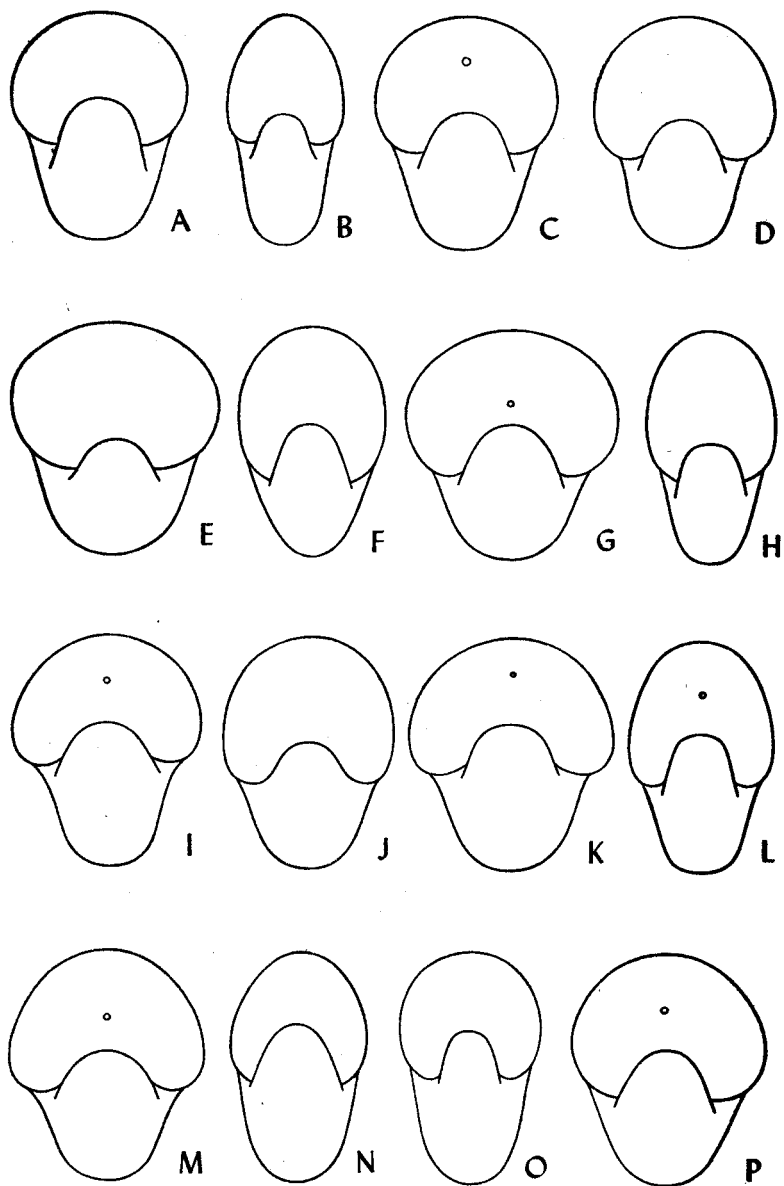


Figure 13

Probably the commonest and most widespread genus of post-Triassic nautiloids is *Eutrephoceras*. To date, approximately 89 species are recognized ranging in age from the Jurassic to the Miocene; of these, 6 species are Jurassic in age, 39 Cretaceous and 44 from the Tertiary.

Miller has recently described the American Tertiary species of *Eutrephoceras* and his comprehensive diagnosis of the genus is quoted here (1947, p. 27): "Conch nautiliconic and typically subglobular; whorls reniform in cross section, broadly rounded ventrally and laterally, and moderately deeply impressed dorsally. Aperture marked ventrally by a broad shallow rounded hyponomic sinus. Umbilicus small and inconspicuous; umbilical shoulders low and rounded. Surface of conch smooth or essentially so. Septa moderately convex apicad; sutures of typical forms slightly sinuous, but at least the external sutures of some forms are essentially straight. An annular lobe is present in some forms but not in the genotype. Siphuncle small, circular in cross section, and orthochoanitic in structure; its position varies considerably in the different species, but in no case is it marginal."

The large number of species of *Eutrephoceras* reflects their general abundance and widespread distribution geographically and stratigraphically. The wide variability in conch shape, degree of involution, and inflection of the suture suggest a wide adaptive range for this genetic stock. Probably in no other

Fig. 13. Cross sections of the conch of A, *Eutrephoceras cyclotus* (Opel) from Zittel 1868, pl. 3, fig. 2a, diameter 117 mm.; B, *E. boissieri* (Pictet) 1867, pl. 8, fig. 4b, diameter 63 mm.; C, *E. subinflatus* (d'Orbigny) 1850, from d'Orbigny 1840, pl. 37, fig. 2, diameter 88 mm.; D, *E. jonesi* Miller and Thompson, from Stenzel 1940, fig. 115, diameter 225 mm.; E, *E. piersantii* (Sergio) 1933, pl. 2, fig. 4b, diameter 144 mm.; F, *E. justus* (Blanford), from Stoliczka 1866, pl. 93, fig. 2a, diameter 64 mm.; G, *E. dekayi* (Morton), from Stenzel 1940, fig. 115, diameter 46 mm.; H, *E. victorianum* Teichert 1947, fig. 5, diameter 102 mm.; I, *E. reesidei* Stenzel 1940, fig. 115, diameter 14.6 mm.; J, *E. neubergicus* (Redtenbacher) from Schlüter 1876, pl. 48, fig. 4, diameter 90 mm.; K, *E. dekayi* (Morton) from Stenzel 1940, fig. 115, diameter 85 mm.; L, *E. sloani* Reeside from Stenzel 1940, fig. 115, diameter 120 mm.; M, *E. carolinense* Kellum, from Stenzel 1940, fig. 115, diameter 20.7 mm.; N, *E. lentiformis* (Stoliczka) 1866, pl. 93, fig. 1a, diameter 74 mm.; O, *E. cookanum* (Whitfield), Stenzel 1940, fig. 115, diameter 220 mm.; P, *E. laverdei* Durham 1946, pl. 63, fig. 4, diameter 61 mm.

generic group are the recognized species so gradational in character and generally lacking in objectivity. Variability studies of large populations would be extremely helpful in assessing the many species groups.

Since *Eutrophoceras* is interpreted as the basic persisting stock derived from the *Cenoceras* complex, its relationships to the other genetic groups are discussed in detail under each of these derived groups and need not be repeated here.

A similar long-persisting, smooth, involute, generalized stock is represented in the Permo-Carboniferous and Triassic by the *Liroceras-Paranautilus* trend. From this particular trend was derived the Upper Triassic Clydonautilidae which is a stock adapted for sinuosity of the suture; a homeomorphous development of the Hercoglossinae.

Eutrophoceras is world-wide in distribution and ranges in age from the Upper Jurassic into the Miocene.

DISTRIBUTION OF SPECIES OF THE GENUS EUTROPHOCERAS

Species	Stratigraphic Distribution	Geographic Distribution
<i>E. ahltenensis</i> (Schlüter) 1876	Cretaceous (Upper)	Germany
<i>E. alcesense</i> Reeside, 1927	Cretaceous (Upper)	Montana (U.S.A.)
<i>E. allani</i> (Fleming) 1945	Oligocene ?	New Zealand
<i>E. allioni</i> (Michelotti) 1840	Miocene	Italy, Malta
<i>E. altifrons</i> (Chapman) 1915	Miocene	Australia
<i>E. archiacianus</i> d'Orbigny 1840	Cretaceous	France
<i>E. balcombensis</i> (Chapman) 1915	Miocene	Australia
<i>E. bellerophon</i> (Lundgren) 1867	Cretaceous (Danian)	Sweden
<i>E. berryi</i> Miller, 1947	Eocene	North Carolina (U.S.A.)
<i>E. blanfordi</i> (Douvillé) 1929	Eocene	Pakistan
<i>E. boissieri</i> (Pictet) 1867	Cretaceous (Lower)	Switzerland, Algeria
<i>E. bouchardianus</i> (d'Orbigny) 1840	Cretaceous (Albian)	France
<i>E. bryani</i> (Gabb) 1877	Eocene	New Jersey (U.S.A.)

Species	Stratigraphic Distribution	Geographic Distribution
<i>E. burkarti</i> (Castillo and Aguilera) 1895	Jurassic (Tithonian)	Mexico
<i>E. butonensis</i> (Martin) 1933	Oligocene	East Indies
<i>E. carolinense</i> Kellum, 1926	Eocene	North Carolina (U.S.A.)
<i>E. centralis</i> (J. Sowerby) 1812	Eocene	England, Germany
<i>E. charpentieri</i> (Leymerie) 1851	Cretaceous (Upper)	France
<i>E. clementinus</i> (d'Orbigny) 1840	Cretaceous (Albian)	England France
<i>E. cookanum</i> (Whitfield) 1892	Eocene	New Jersey (U.S.A.)
<i>E. crassus</i> (Schafhäütl) 1863	Eocene	Bavaria
<i>E. cyclotus</i> (Oppel) 1865	Jurassic (Tithonian)	Moravia
<i>E. dartevellei</i> Miller 1951	Eocene	Landana, West Africa
<i>E. darupensis</i> (Schlüter) 1876	Cretaceous (Senonian)	Germany
<i>E. decipiens</i> (Michelotti) 1861	Miocene	Italy
<i>E. dekayi</i> (Morton) 1834	Cretaceous (Upper)	U.S.A.
<i>E. depressus</i> (Binckhorst) 1861	Cretaceous (Maestrichtian)	Belgium
<i>E. dersertorum</i> (Quaas) 1902	Cretaceous (Danian)	Libya
<i>E. dietrichi</i> (Zwierzycycki) 1914	Cretaceous (Neocomian)	East Africa
<i>E. douvillei</i> Spath, 1927	Jurassic (Oxfordian)	Egypt
<i>E. dubaleni</i> (Peyrot) 1932	Miocene	France
<i>E. euthymi</i> (Pictet) 1867	Cretaceous (Lower)	France, Switzerland
<i>E. expansum</i> (J. de C. Sowerby) 1824	Cretaceous (Cenomanian)	England
<i>E. faxoense</i> Hyatt, 1894	Cretaceous (Danian)	Denmark
<i>E. felix</i> (Chapman) 1915	Miocene	Australia

Species	Stratigraphic Distribution	Geographic Distribution
<i>E. flammeus</i> (Ronchetti) 1947	Cretaceous (Maestrichtian)	Tripolitania
<i>E. francomontanus</i> (Kuhn) 1939	Jurassic (Upper)	Germany
<i>E. geelongensis</i> (Foord) 1891	Miocene	Australia
<i>E. gosavicus</i> (Redtenbacher) 1873	Cretaceous (Upper)	Austria
<i>E. hannai</i> Vokes, 1937	Eocene	California (U.S.A.)
<i>E. ? hallidayi</i> (Waring) 1914	Paleocene	California (U.S.A.)
<i>E. hendersoni</i> (Etheridge) 1901	Cretaceous (Lower)	Queensland, Australia
<i>E. indicum</i> (Spengler) 1910	Cretaceous (Upper)	India
<i>E. izumoensis</i> Yokoyama, 1913	Tertiary	Japan
<i>E. japonicus</i> (Shimizu) 1926	Eocene	Japan
<i>E. javanus</i> (Martin) 1879	Tertiary	Java
<i>E. johnsoni</i> Miller, 1947	Paleocene ?	Alabama (U.S.A.)
<i>E. jonesi</i> Miller and Thompson, 1933	Paleocene	Alabama (U.S.A.)
<i>E. labechi</i> (d'Archiac and Haime) 1854	Eocene	Pakistan
<i>E. laverdei</i> Durham, 1946	Cretaceous (Aptian)	Colombia
<i>E. leonei</i> (Negri) 1934	Eocene	Libya
<i>E. marksii</i> Miller, 1947	Eocene	California (U.S.A.)
<i>E. marucoensis</i> (Giovine) 1950	Cretaceous (Hauterivian)	Argentina
<i>E. metafleuriensis</i> (Douvillé) 1929	Cretaceous (Upper)	N. Africa
<i>E. montanensi</i> Kummel, 1954	L. Tertiary Jurassic (Callovian)	Pakistan Montana (U.S.A.)
<i>E. montmollini</i> (Pietet and Campiche) 1859	Cretaceous (Albian)	Switzerland
<i>E. neubergicus</i> (Redtenbacher) 1873	Cretaceous (Upper)	France Austria
<i>E. oregonense</i> Miller, 1947	Eocene	Oregon (U.S.A.)

Species	Stratigraphic Distribution	Geographic Distribution
<i>E. ovoideum</i> Crick, 1907	Cretaceous	Zululand
<i>E. parisiensis</i> (Deshayes) 1866	Eocene	France
<i>E. perlatus</i> (Morton) 1834	Cretaceous (Upper)	Alabama (U.S.A.)
<i>E. piersantii</i> (Sergio) 1933	Oligocene	Italy
<i>E. planoverter</i> Stephenson, 1941	Cretaceous (Upper)	Tennessee, Texas (U.S.A.)
<i>E. quadrilineatus</i> (Favre) 1869	Cretaceous (Upper)	Germany
<i>E. reesidei</i> Stengel, 1940	Eocene	Texas (U.S.A.)
<i>E. regalis</i> (J. de C. Sowerby) 1843	Eocene	England
<i>E. regularis</i> (Schafhäütl) 1863	Eocene	Bavaria
<i>E. restrictus</i> (Griepenkerl) 1889	Cretaceous (Senonian)	Germany
<i>E. resupinatus</i> (Redtenbacher) 1873	Cretaceous (Upper)	Austria
<i>E. sanfilippoi</i> (Sorrentino) 1932	Cretaceous (Maestrichtian)	Tripolitania
<i>E. simile</i> Spath, 1953	Cretaceous (Upper)	Graham Land
<i>E. sloani</i> Reeside, 1924	Eocene	South Carolina (U.S.A.)
<i>E. sphaericum</i> (Forbes) 1846	Cretaceous	India
<i>E. staadti</i> (Cossmann) 1902	Eocene	France
<i>E. stephensoni</i> (Dickerson) 1914	Paleocene	California (U.S.A.)
<i>E. stricteumbilicatus</i> (Stchépinsky) 1943	Oligocene	Turkey
<i>E. subinflatus</i> (d'Orbigny) 1850	Jurassic (Kimmeridgian)	France
<i>E. sublaevigatum</i> (d'Orbigny) 1840	Cretaceous (Upper)	England, India, Madagascar, Libya
<i>E. subplicatum</i> (Philippi) 1895	Cretaceous (Upper)	Argentina, Chile
<i>E. szontaghi</i> (Vogl) 1910	Eocene	Hungary
<i>E. thomi</i> Reeside, 1927	Cretaceous (Upper)	Montana (U.S.A.)
<i>E. tumescens</i> (Frauscher) 1895	Eocene	Austria

Species	Stratigraphic Distribution	Geographic Distribution
<i>E. witenhagensen</i> Spath, 1930	Cretaceous (Valanginian)	South Africa
<i>E. umbilicaris</i> (Deshayes) 1835	Eocene	France
<i>E. urbanus</i> (Sowerby) 1843	Eocene	England
<i>E. vastus</i> (Kner) 1850	Cretaceous (Upper)	Poland
<i>E. vicentinus</i> (Oppenheim) 1901	Tertiary (Lower)	Italy
<i>E. victorianum</i> (Teichert) 1943	Eocene	Australia
<i>E. vinassai</i> (Venzo) 1937	Oligocene	Italy

Genus *PSEUDOCENOCERAS* Spath, 1927

Type species. *Nautilus largilliertianus* d'Orbigny, 1840, pl. 18 (by original designation). Plesiotype illustrated on Plate 10, figs. 3, 4.

This genus can be diagnosed as follows: Conch involute, compressed, smooth. Whorl section subrectangular, venter broad, flattened, ventral shoulders rounded. Whorl sides flattened, subparallel. Umbilical shoulders rounded, umbilical wall nearly vertical. The suture is only slightly sinuous, essentially straight across the venter and with a broad, generally shallow, lateral lobe. The siphuncle is subcentral in position, that is, closer to the dorsum.

As stated by Spath (1927a, p. 24), "*Pseudocenoceras* is easily distinguished from its Cretaceous contemporaries by its steep umbilical edge, truncated whorl-shape, entomarginal siphuncle and reclined septal edges."

The Cretaceous contemporaries of *Pseudocenoceras* include members of the Cymatoceratinae, the Hercoglossinae, *Eutrephoceras*, and *Carinonautilus*. The smooth conch and simple suture would ally *Eutrephoceras* and *Pseudocenoceras*; all of the other generic groups are specialized forms trending on quite different patterns.

There are only 8 species of Cretaceous nautiloids that can be assigned to *Pseudocenoceras*, and all are for the most part very similar. The type species is a common form in Cretaceous strata of England and France. *Nautilus berriasensis* Pictet (1867) from Lower Cretaceous strata of France appears to be closely allied to *Nautilus largilliertianus* but has a more central siphuncle. *Nautilus lehardyi* Binckhorst (1861) is a quite aberrant

form with subangular ventral shoulders and a concave venter. It is placed in *Pseudocenoceras* with question.

Pseudocenoceras is a fairly common form in Cretaceous rocks of Europe from England to the Crimea. One species, *Nautilus applanatus* Wanner (1902), is from the Upper Cretaceous of Libya. A list of the species of *Pseudocenoceras*, their age, and geographic distribution is given below.

DISTRIBUTION OF SPECIES OF THE
GENUS PSEUDOCENOCERAS

Species	Stratigraphic Distribution	Geographic Distribution
<i>P. applanatus</i> (Wanner) 1902	Cretaceous (Upper)	Libya
<i>P. berriasensis</i> (Pictet) 1867	Cretaceous (Lower)	France
<i>P. campichei</i> (Karakasch) 1907	Cretaceous (Lower)	Crimea
<i>P. fittoni</i> (Sharpe) 1853	Cretaceous (Upper)	Europe
<i>P. galicianus</i> (Alth) 1850	Cretaceous	Poland
<i>P. largilliertianus</i> (d'Orbigny) 1840	Cretaceous (Cenomanian)	Europe
<i>P. ? lehardyi</i> (Binckhorst) 1861	Cretaceous (Maestrichtian)	Belgium
<i>P. picteti</i> (Karakasch) 1907	Cretaceous (Lower)	Crimea

Genus CARINONAUTILUS Spengler, 1910

Type species. *Carinonutilus ariyalurensis* Spengler, 1910, p. 149, pl. 14, figs. 1 a c (monotypic). Illustrated here on Plate 11.

The only data available on this monotypic genus are the description and illustration of the type species. However, from this source the following diagnosis is made. The conch is very involute, compressed, and much higher than wide. The umbilicus is small and shallow. The whorl sides are broadly rounded and converge toward the venter. A distinct furrow aligns the ventral shoulder. The venter has a prominent rounded keel that on the adoral part of the living chamber is much broader and is divided by a median furrow. The umbilical shoulders are broadly rounded. The widest part of the whorl section is just ventral of the umbilical shoulders. The suture is only slightly convex.

The only markings on the shell are growth lines which form a deep sinus over the venter. The position of the siphuncle is not known.

At a diameter of 1.5 cm. the venter is not yet keeled but merely sharply rounded. At 3 cm. the single prominent keel is present, and at 6 cm. diameter the median furrow is well developed on the widened keel.

The measurements of the type species are as follows (Spengler, 1910, p. 149):

Diameter	93 mm.
Height of last whorl	54 mm.
Width of umbilicus	5.5 mm.
Width of last whorl	32 mm.

Spengler (1910, p. 149) recognized the uniqueness of this species and suggested that it was derived from *Nautilus angustus* Blanford (= *Cimomia*) by sharpening of the ventral area. Contemporaneous forms include members of the Cymatoceratinae, Hercoglossinae, *Eutrephoceras* and *Pseudocenoceras*. I am in essential agreement with Spengler on the phylogenetic position of *Carinonautilus* but would derive them from *Eutrephoceras*, which is here considered the persistent evolving stock. There is slight difference between the eutrephoceratid stock and the cimomids. The eutrephoceratids show great variability in their smooth, involute conchs and appear to be the only evolutionary reservoir available to give rise to *Carinonautilus*.

This monotypic genus is known only from the Ariyalur group (Campanian) of the Trichinopoly district of southeast India.

Genus OBINAUTILUS Kobayashi, 1954

Type species. Obinautilus pulchra Kobayashi, 1954b. Type illustration reproduced on Plate 9, figs. 1, 2.

Kobayashi's description of his new monotypic species and genus is quoted below. The specimen is 78 mm. in diameter; last whorl 25 mm. in width, 46 mm. in height and 35 mm. in median height.

"Shell discoidal, compressed laterally, rapidly coiling and quite involute; umbilicus almost closed, if not completely; flanks a little convex, but nearly parallel in the inner half and inclined abruptly near the umbilicus; ventral sinus shallow but fairly

broad and provided with an obtuse peripheral carina on each side which is subangulated inside but outwardly merges with the flank.

"Radial ribs narrow, flattopped, separated by narrow and shallow grooves and frequently branching distally by insertion of fine grooves. These ribs and grooves distinctly bent forward from the umbilicus, nearly straight or even slightly concave backward in the broad flank, swing back a little near the venter and moderately sinuated behind on the venter. The curvature of these ribs is very similar to the growth lines of living *Nautilus*."

Kobayashi based the above description on a single well-preserved specimen. The shell is very well preserved and he (Kobayashi) notes "its deep and light brown shades must be the original colour pattern." Unfortunately, neither the suture nor position of the siphuncle was observed. The ribbing described by Kobayashi appears to be accentuated growth lines rather than the type of ribbing that is characteristic of the Cymatoceratinae.

The most characteristic feature of *Obinautilus* is the shallow but distinct ventral furrow. Because of this modification of the periphery, Kobayashi rightly pointed to possible affinities with the Paracenoceratidae. However, I agree completely with Kobayashi that *Obinautilus* should be considered a development of the Nautilinae rather than derived from any member of the Paracenoceratinae. Since the suture and position of the siphuncle are not known, this interpretation will have to remain tentative until more data become available.

Obinautilus pulchra is known from one specimen collected at a cutting between Aburatsu and Obi towns in the Province of Hyuga (Miyazaki Pref.), Japan, on the occasion of the highway operation. The locality is situated in the pre-Miocene terrain where the Nichinan formation containing the Oligocene Ashiya fauna lies unconformably beneath the Miocene Aburatsu formation (Kobayashi, 1954b, p. 183).

Genus NAUTILUS Linné, 1758

Type species. Nautilus pompilius Linné.

The interpretation of the scope of the genus *Nautilus* has changed considerably since its formal introduction by Linné.

In the early period of paleontological research on this group of tetrabranchiate cephalopods nearly all species were placed in the single genus *Nautilus*. Gradually as more and more genera were proposed, *Nautilus* became a waste-basket genus for unassigned forms. The greater amount of attention paid to Paleozoic nautiloids soon pre-empted the use of the genus *Nautilus* for species of that age. The genus has persisted for most species of Mesozoic and Tertiary nautiloids until rather recently. At the present, for instance, Miller (1951, p. 32) restricts *Nautilus* to only the Recent species and all of the Tertiary forms previously assigned to *Nautilus* are placed in *Eutrephoceras* or *Cimomia*. In this interpretation I am in full agreement. *Eutrephoceras* is the persisting stock out of the *Cenoceras* complex in Upper Jurassic time that shows no particular evolutionary trends from its time of origin to the time of its apparent extinction in the late Tertiary. It is the longest-lived single genetic stock of post-Triassic nautiloids, and was ancestral to several other aberrant groups, namely *Pseudocenoceras*, *Carinonautilus*, and *Obinautilus*. It is also ancestral to *Cimomia* of the Hercoglossinae which developed into an extremely abundant and diverse evolutionary complex. There appear to be no records of any Pliocene or Pleistocene nautiloids. Aside from *Aturia*, all other species of nautiloids seem to be more closely related to the eutrephoceratid evolving stock than to modern *Nautilus*. The number of species and specimens of Miocene nautiloids is still very few. However, with the above interpretation *Nautilus* is thought to arise from the eutrephoceratid stock at some time in the mid or late Tertiary.

The biology and ecology of modern *Nautilus* has been very ably summarized by Stenzel (1948, 1952). Similar comprehensive discussions of the morphology, etc., can be found in Miller (1947). The extensive literature on modern *Nautilus* is covered in the bibliographies of Stenzel's and Miller's papers.

Three species of living *Nautilus* are generally recognized, namely *N. pompilius* (with the umbilicus practically obliterated by the deposition of callus) *N. macromphalus* (with an open imperforate umbilicus), and *N. umbilicatus* (with an open finely perforate umbilicus) (Miller 1947, p. 13). Several "varieties" of *N. pompilius* are recognized but their significance and relationships are poorly known. To the above three species, Iredale

(1944) has added two new species, namely *N. alumnus*, from off Queensland and New South Wales, and *N. repertus* from off Western Australia.

Living *Nautilus* is restricted to the southwest Pacific from South Australia to the southern Philippines and eastward to the Fiji Islands. Stenzel (1948, p. 84) gives a good summary of the known records for live specimens of *Nautilus*.

Subfamily PSEUDAGANIDINAE nov.

This new subfamily is established for two genera of mainly Jurassic age that include adaptive types characterized by great sinuosity of the suture. These genera are *Pseudaganides* Spath, and *Pseudonautilus* Meek which Spath (1927) had previously included in his family Hercoglossidae. As is discussed in more detail below, *Pseudaganides* is considered to be a direct radiation from the *Cenoceras* complex in the Lower Jurassic; by the Upper Jurassic it was a widely distributed form in the European geosynclinal areas and showed a wide variation in conch form and suture. The group did not survive into the Cretaceous. Sometime during the Upper Jurassic an offshoot from *Pseudaganides* developed, characterized mainly by greater elaboration of the suture, that is, the formation of a deeper ventral lobe and angular lateral lobes. Species of this genus range into the Lower Cretaceous.

In the Carboniferous to Recent history of the nautiloids there were four distinct adaptive trends built around elaboration of the suture. As would be expected, there are many homeomorphous forms between these adaptive trends. Each of these trends had its origin in long-persisting, smooth, generalized stocks with very simple, nearly straight sutures. The duration of each of these trends is likewise somewhat limited. The Permian trend is known only through a single species of the genus *Permoceras* from Middle Permian strata of Timor. The Triassic radiation is mainly Upper Triassic (Carnian-Norian) in age. The Jurassic trend, represented by Pseudaganidinae, is Lower Jurassic to Lower Cretaceous in age with the principal radiation in the Upper Jurassic. The last such trend, that of the Hercoglossinae and Aturinae, is Upper Cretaceous to mid-Tertiary in range with the principal radiation in the Lower Tertiary.

Genus *PSEUDAGANIDES* Spath, 1927

Pseudaganides Spath, 1927a, pp. 22, 25.

Hercoglossoceras Spath, 1927a, pp. 22, 26.

Nautilus (*Pseudaganides*) Jeannet, 1951, pp. 17-21.

Type species. *Nautilus kutchensis* Waagen, 1873, pl. 3, fig. 4 (Plate 28, figures 3, 4 of this report). Type by original designation.

When Spath (1927a, p. 22) established this genus the only remark he made as to its characters was the following statement: "*Pseudaganides*, which comprises the early 'aganitici', like *Somalinutilus*, has its origin in '*Cenoceras*' and includes, for example, the large *subsINUATUS* group of the Inferior Oolite, as already mentioned." In his discussion of the type species, *Pseudaganides kutchensis* (Waagen), Spath (1927a, pp. 34-35) mentions the following species as belonging to this genus: *N. aganiticus* Schlotheim, *N. schlotheimi* Loesch (= *Nautilus* (*Hercoglossa*) *aganiticus* Foord and Crick, 1890b, p. 394, fig. 1), and *N. ammoni* Loesch; he also included with question *N. girardoti* de Loriol and *N. subbiangulatus* d'Orbigny (= *Nautilus biangulatus* d'Orbigny, 1845, pl. 34, figs. 1-3).

There are approximately 40 species of Jurassic nautiloids with "goniatitic" sutures. Besides the "aganitici" included by Spath in *Pseudaganides*, he established the genus *Hercoglossoceras* [type species—*Hercoglossa* ('*gravesiana* (d'Orbigny) var.') *kochi* (Prinz)], a highly compressed form. *Pseudonautilus* was established by Meek for *Nautilus geinitzi* Oppel (in Zittel, 1868), and is characterized by a pointed lateral lobe and a very deep ventral lobe. A number of species from the Upper Jurassic (recently discussed by Loesch, 1914), Spath tentatively assigns to *Hercoglossa* (principally an Upper Cretaceous-Eocene development) though he does mention that they probably represent an independent development.

My own studies lead me to conclude that all of the Jurassic nautiloids with "goniatitic" sutures are part of a single evolutionary line developed from some compressed elements of "*Cenoceras*" and this line is quite independent of the later hercoglossid development.

The type species of *Pseudaganides*—*N. kutchensis*—comes from the Middle Chari group (*anceps* zone) of Kachh (Cutch) Pakistan. The type measures 47 mm. in diameter, 28 mm. for

length of whorl, 27 mm. as width of the whorl, and the umbilicus is 5 mm. across. Waagen's illustration is reproduced here on Plate 28, figures 3, 4. The form of the shell is involute with a somewhat rectangular whorl section with flattened sides and venter. The greatest width of the whorl is near the umbilicus. The suture has a prominent lateral lobe and a saddle next to the umbilicus. The suture is projected toward the venter and has a shallow lobe on the venter. The shell has fine longitudinal strigation and growth lines. The strigations disappear towards the aperture.

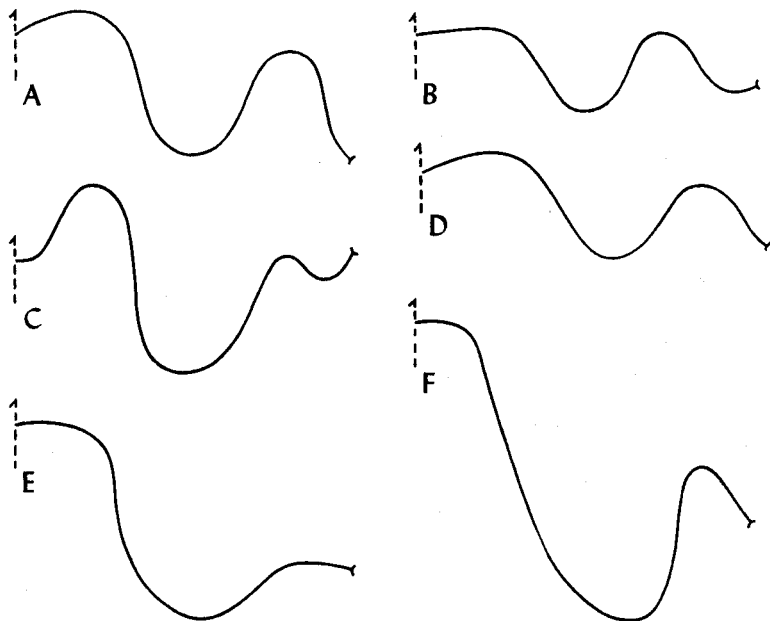


Fig. 14. Diagrammatic representation of sutures of *A*, *Pseudaganides brunhuberi* (Loesch) 1914, fig. 5c; *B*, *P. franconicus* (Oppel) from Loesch 1914, fig. 1a; *C*, *P. subbiangulatus* (d'Orbigny) 1843, from d'Orbigny 1850, pl. 34, fig. 3; *D*, *P. rogeri* (Loesch) 1914, fig. 3a; *E*, *P. pellerensis* (Vialli) 1937, fig. 1a; *F*, *P. sinuatus* (Sowerby), from Vialli, 1937, fig. 1a. All figures greatly reduced.

From the Carboniferous to the Tertiary, evolutionary trends, formulated on a complication of the suture, have occurred re-

peatedly. In most cases it can be established that such evolutionary lines arose from ancestors with essentially uncomplicated (nearly straight) sutures. Many of these evolutionary lines are represented by a single or very few species. However, some groups as the Triassic Clydonautilidae have large numbers of species. In genera such as *Clydonautilus* and *Proclydonautilus* there is a constancy in the pattern of the suture with, of course, a degree of modification in shape and depth of the lobes, etc.; there is, however, a very striking difference or range of variation in the shape of the conch (see Kummel, 1953c, figs. 38, 40, 41). This suggests that the genetic complex governing the nature of the suture is less adaptive than the shape of the conch. Among the Jurassic "aganitici" there is a certain homogeneity in the suture, mainly in the pronounced lateral lobe, and in the projected ventral saddle with its shallow lobe. The differences encountered are more a matter of degree, with some element of the suture being larger, deeper, or of slightly different shape (Fig. 14). The scope of variation is similar to that found in species of the Clydonautilidae.

The early "aganitici" such as "*Hercoglossa*" *kochi* (Prinz) of the Lias, *Nautilus subsinuatus* d'Orbigny of the Inferior Oolite, *N. crassisinuatus* Crick also of the Inferior Oolite, *N. pellerensis* Vialli of the Bajocian of north Italy, and *N. duilii* Gem-

Fig. 15. Cross sections of the conch of A, *Pseudaganides pulchellus* (Jeannet) 1951, fig. 45, diameter 44 mm.; B, *P. krenkeli* (Jeannet) 1951, fig. 37, diameter 50 mm.; C, *P. oppeli* (Zittel) 1868, pl. 4, fig. 1b, diameter 100 mm.; D, *P. subbiangulatus* (d'Orbigny) 1850, from d'Orbigny, 1843, pl. 34, fig. 2, diameter 92 mm.; E, *P. rogeri* (Loesch) 1914, fig. 3b, height 50 mm.; F, *P. schneidi* (Loesch) 1914, fig. 2a, height 35 mm.; G, *P. aganiticus* (Schlotheim) from Jeannet, 1951, fig. 42, height 25 mm.; H, *P. kochi* (Prinz) 1906, fig. 5, height 77 mm.; I, *P. frickensis* (Jeannet) 1951, fig. 36, diameter 46 mm.; J, *P. strambergensis* (Oppel) 1865, pl. 2, fig. 8a, diameter 98 mm.; K, *P. brunhuberi* (Loesch) 1914, fig. 5b, height 50 mm.; living chamber; L, *P. brunhuberi* (Loesch) 1914, fig. 5a, height 39 mm.; phragmocone; M, *P. sinuatus* (Sowerby) from d'Orbigny, 1843, pl. 32, diameter 188 mm.; N, *P. gravesianus* (d'Orbigny) 1843, pl. 38, diameter 270 mm.; O, *Pseudonautilus atwioides* (Pictet) 1867, pl. 11, fig. 1c, diameter 60 mm.; P, *P. malbosii* (Pictet) 1867, pl. 9, fig. 2b, diameter 100 mm.; Q, *Pseudaganides dumasi* (Pictet) 1867, pl. 10, fig. 2b, diameter 69 mm.

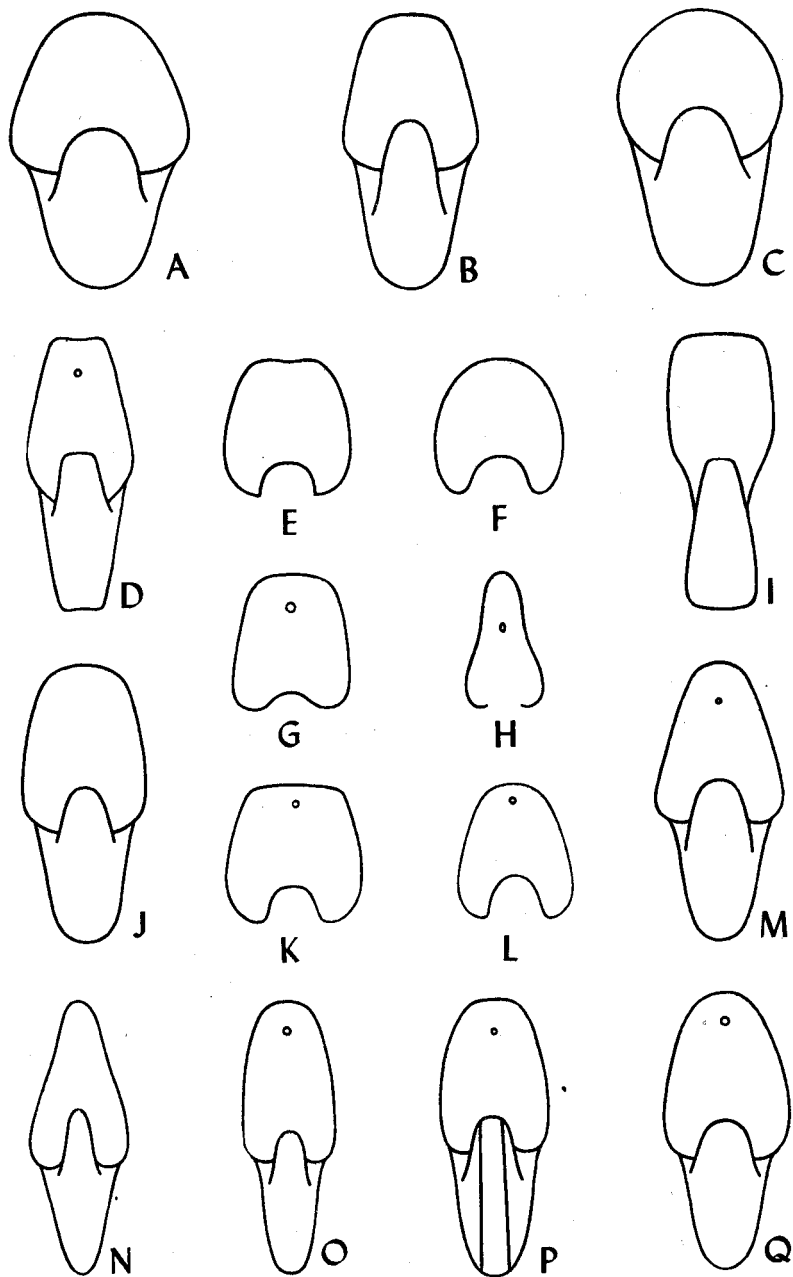


Figure 15

mellaro are all compressed, involute forms with the whorls higher than wide. The sutures have pronounced lateral lobes and are strongly projected towards the venter which they cross in nearly a straight line. In nearly all other species of *Pseudaganides* there is a slight lobe on the peripheral area. The lateral saddle in the above early "aganitici" is quite variable. It is very pronounced in *N. subsinuatus* and *N. crassisinuatus* but very low in *N. pellerensis* and *N. duilii*. In each of these latter two species the umbilical seam passes through about the middle of the lateral saddle.

The sutures in most of the remaining "aganitici" of the Jurassic have a shallow lobe on the venter. This small ventral lobe appears to persist in forms like *N. ammoni* Loesch, *N. rogeri* Loesch, *N. schneidi* Loesch, etc., but in *N. schlosseri*, after the ventral lobe having been present, it disappears in the last few sutures and is nearly straight or only slightly arched across the venter (see Loesch, 1914, p. 115, fig. 8).

There is a rather large degree of variation in the shape of the conch in the species here assigned to *Pseudaganides* (Fig. 15). All of the species have nautiliconic conchs but vary in the character of the ventral shoulders and in the width to height proportions of the whorl section. In the type species, *N. kutchensis*, the whorl section is subrectangular with subangular ventral shoulders, an arched venter, and flattened convergent flanks. Subangular to acutely rounded ventral shoulders are present in *N. argoviensis* Loesch, *N. ammoni* Loesch, *N. klebelsbergi* Loesch, *N. aganiticus* Schlotheim, *N. tuingensis* Loesch, *N. helveticus* Loesch, *N. brunhuberi* Loesch, *N. frickensis* Jeanet, and *N. subbiangulatus* d'Orbigny. Well rounded ventral shoulders and arched venters are found in *N. pulchellus* Jeanet, *N. schneidi* Loesch, *N. strambergensis* Oppel, *N. franconicus* Oppel and *N. oppeli* Zittel. Some species have slightly concave venters, as in *N. subbiangulatus* d'Orbigny and *N. rogeri* Loesch. In *N. ammoni* and *N. schlosseri* the venter becomes slightly concave on the living chamber, but is arched on the phragmocone. The width and height measurements of the whorl section in *N. kutchensis* are approximately equal. This same ratio is present in many other species of *Pseudaganides* (e.g. *N. pulchellus* Jeanet, *N. rogeri* Loesch, *N. brunhuberi* Loesch, *N. schneidi* Loesch, *N. ammoni* Loesch, etc.). More compressed species include *N.*

subbiangulatus d'Orbigny, *N. frickensis* Jeannet, *N. strambergensis* Oppel, etc. *Nautilus kochi* has a highly compressed conch with convergent whorl sides and a rather narrow rounded venter. It appears to be merely an extreme form of *Pseudaganides* and does not warrant separation as a distinct genus. *Hercoglossoceras* established by Spath for *N. kochi* is here considered a synonym of *Pseudaganides*. Whereas the degree of convergence of the whorl sides is greatest in *N. kochi* the degree of compression of the conch is found in several other species.

Loesch (1914) has described several species of Upper Jurassic nautiloids which are very similar in conch shape and suture to typical *Hercoglossa* of the late Cretaceous and early Tertiary. That is, these species have well rounded ventral shoulders and arched venters. Spath (1927a) included them tentatively in *Hercoglossa* but also expressed the opinion that they "probably form an independent development." These Upper Jurassic "hercoglossids" include among others: *N. franconicus* Oppel, *N. schneidi* Loesch, *N. rogeri* Loesch, *N. brunhuberi* Loesch, *N. roemeri* Loesch, *N. schwertschlageri* Loesch, *N. schlosseri* Loesch, *N. stromeri* Loesch, *N. oppeli* Zittel, and *N. strambergensis* Oppel. In all of these species, however, there is a shallow ventral lobe which is not found in the Upper Cretaceous-Tertiary *Hercoglossa*. The great similarity of these two groups is thought to be a case of homeomorphy. The true *Hercoglossa* develop from Cretaceous *Cimomia* whereas the Jurassic "aganitici" are derived from Liassic *Cenoceras*.

Pseudaganides is widely distributed in Jurassic strata throughout Europe, and in Pakistan. Of a total of 37 species listed below, 1 is from the Lias, 9 are from Middle Jurassic strata, and 28 are known from Upper Jurassic formations.

DISTRIBUTION OF SPECIES OF THE GENUS PSEUDAGANIDES

Species	Stratigraphic Distribution	Geographic Distribution
<i>P. aganiticus</i> (Schlotheim) 1820	Jurassic (Oxfordian)	France
<i>P. ammoni</i> (Loesch) 1914	Jurassic (Upper)	Europe
<i>P. argoviensis</i> (Loesch) 1912	Jurassic (Oxfordian)	Switzerland

Species	Stratigraphic Distribution	Geographic Distribution
<i>P. bodeni</i> (Loesch) 1914	Jurassic (Oxfordian)	France
<i>P. brunhuberi</i> (Loesch) 1914	Jurassic (Upper)	Europe
<i>P. clausus</i> (d'Orbigny) 1842	Jurassic (Bajocian)	France
<i>P. crassisinuatus</i> (Crick) 1898	Jurassic (Bajocian)	England
<i>P. drepanensis</i> (Tagliarini) 1901	Jurassic (Middle)	Sicily
<i>P. duilii</i> (Gemmellaro) 1886	Jurassic (Middle)	Sicily
<i>P. franconicus</i> (Oppel) 1865	Jurassic (Tithonian)	Europe
<i>P. frickensis</i> (Jeannet) 1951	Jurassic (Calloviaian)	Switzerland
<i>P. girardoti</i> (de Loriol) 1903	Jurassic (Oxfordian)	Switzerland
<i>P. glaber</i> (Foord and Crick) 1890	Jurassic	England, France
<i>P. gravesianus</i> (d'Orbigny) 1843	Jurassic	France
<i>P. helveticus</i> (Loesch) 1914	Jurassic (Upper)	Switzerland
<i>P. klebelsbergi</i> (Loesch) 1914	Jurassic (Tithonian)	Czecho- slovakia
<i>P. kochi</i> (Prinz) 1906	Jurassic (Lias)	Austria, Hungary
<i>P. krenkeli</i> (Jeannet) 1951	Jurassic (Upper)	Switzerland
<i>P. kutchensis</i> (Waagen) 1873	Jurassic (Upper)	Pakistan
<i>P. ledonicus</i> (de Loriol) 1903	Jurassic (Oxfordian)	France
<i>P. oppeli</i> (Zittel) 1868	Jurassic (Upper)	Europe
<i>P. pellerensis</i> (Vialli) 1937	Jurassic (Middle)	North Italy
<i>P. portlandicus</i> (Foord and Crick) 1890	Jurassic (Upper)	England
<i>P. pulchellus</i> (Jeannet) 1951	Jurassic (Oxfordian)	Switzerland

Species	Stratigraphic Distribution	Geographic Distribution
<i>P. roemeri</i> (Loesch) 1914	Jurassic (Upper)	East Europe
<i>P. rogeri</i> (Loesch) 1914	Jurassic (Upper)	East Europe
<i>P. royeri</i> (de Loriol) 1872	Jurassic (Upper)	France
<i>P. schlosseri</i> (Loesch) 1914	Jurassic (Tithonian)	East Europe
<i>P. schlotheimi</i> (Loesch) 1914	Jurassic (Middle)	Lorraine
<i>P. schneidi</i> (Loesch) 1914	Jurassic (Tithonian)	Europe
<i>P. schwertschlagerei</i> (Loesch) 1912	Jurassic (Upper)	Europe
<i>P. strambergensis</i> (Oppel) 1865	Jurassic (Tithonian)	Czecho- slovakia
<i>P. stromeri</i> (Loesch) 1914	Jurassic (Tithonian)	Czecho- slovakia
<i>P. subbiangulatus</i> (d'Orbigny) 1850	Jurassic (Bathonian)	France
<i>P. subsinuatus</i> (d'Orbigny) 1850	Jurassic (Middle)	England
<i>P. turingensis</i> (Loesch) 1914	Jurassic (Upper)	Germany
<i>P. turkeryi</i> (Gemmellaro) 1886	Jurassic (Middle)	Sicily

Genus PSEUDONAUTILUS Meek, 1876

Pseudonautilus Meek, 1876, p. 491.

Pseudonautilus Spath, 1927a, pp. 20, 22, 26.

Pseudonautilus Miller and Collinson, 1953, pp. 293-295.

Type species. *Nautilus geinitzi* Oppel, in Zittel, 1868, p. 45, pl. 2, figs. 1-7 (Plate 12, figures 1, 2 and Text-Figure 16 of this report).

This genus is well characterized by the extreme "goniatitic" development of its suture. Only four species are assignable to the genus and the following diagnosis has been compiled from specimens in the M.C.Z. and the description and illustrations of these species.

Conch involute, compressed, and smooth. Whorl sides flattened, venter low and broadly arched. The ventral and umbilical shoulders are rounded. The whorl section is higher than wide.

The umbilicus is very small and deep. The suture has a deep narrow ventral lobe, a large V-shaped lateral lobe followed by a rounded saddle with a small second lateral lobe just above the umbilical seam. There is a deep pointed dorsal lobe. The siphuncle is in a subventral position.

The most diagnostic character of *Pseudonautilus* is the sinuous suture with the deep V-shaped ventral lobe. The four species assignable to *Pseudonautilus* are: *P. geinitzi* Oppel, the type species; *N. aturioides* Pictet (1867); *N. dumasi* Pictet (1867); and *N. malbosi* Pictet (1867). Loesch (1914, p. 130-131) discussed in some detail various aspects of *N. geinitzi* and *N. aturioides*. *Nautilus geinitzi* is from the Upper Jurassic (Tithonian) of Moravia, Silesia, and France, and has also been recorded from the Berriasian of Tunisia by Arnould-Saget (1953). *Nautilus aturioides* is from the zone of *Hoplites boissieri*, lowest Valanginian (Loesch, 1914, p. 131). *Nautilus malbosi* Pictet has more angular ventral shoulders than in the type species and likewise the ventral and lateral lobes are rounded rather than pointed. In respect to the suture, *N. malbosi* and *N. dumasi* are more or less intermediate forms between typical *Pseudaganides* and *N. geinitzi*, the type species of *Pseudonautilus*. The assignment of these two species to *Pseudonautilus* is open to question. *Nautilus malbosi* has been recorded from Lower Cretaceous formations in central Europe (Pictet, 1867), Algeria (Pomel, 1889), and from the Crimea (Karakasch, 1907).

One of the most remarkable cases of homeomorphy among post-Carboniferous nautiloids is the similarity of *Nautilus* (*Aganides*) *bitauniensis* Haniel from the Permian Bitauni beds (Leonardian) of Timor and *Pseudonautilus geinitzi* Oppel (Fig. 16.) Miller and Collinson (1953) have recently discussed this problem and erected the genus *Permoceras* and the family Permoceratidae for Haniel's species. They likewise recognized the homeomorphous relationship of these two nautiloids. Among Triassic nautiloids sinuous sutures are found in the Clydonautilidae, Gonionautilidae Siberionautilidae, and in the genus *Clymenonautilus* of the Syringonautilidae. Sinuous sutures are, however, not common in Permian nautiloids. Among the forms comprising the Grypoceratidae, *Grypoceras* (*Plummeroceras*) *plummeri* (Kummel, 1953c) — a compressed evolute, quadrate whorled form — has a suture with a deep ventral lobe and a broad

deep lateral lobe. The general shape of the conch except for the degree of involution is rather similar in *G.* (*Plummeroceras*) and *Permoceras*. Within the complex of Permian nautiloids now known it seems more logical to consider *Permoceras* an offshoot of the *Domatoceras-Grypoceras* evolving stock and thus a member of the Grypoceratidae.

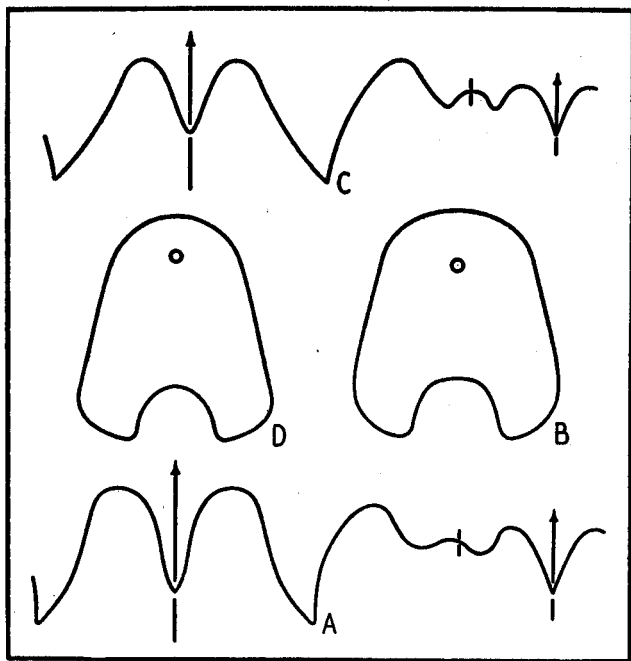


Fig. 16. Diagrammatic representation of sutures and cross sections of *Permoceras bitaeniense* (Haniel) A, B, and *Pseudonautilus geinitzi* (Oppel) C, D, all X 1. From Miller and Collinson, 1953, fig. 1.

Subfamily PARACENOCERATINAE Spath, 1927

When Spath established this taxonomic unit (originally as a family) he included in it *Paracenoceras* Spath, *Tithonoceras* Retowski, *Somalinautilus* Spath, *Aulaconautilus* Spath, *Carinonautilus* Spengler and with question *Heminautilus* Spath. Ex-

amination of topotypes of *Heminautilus etheringtoni* Durham and the descriptions and illustrations of *H. lallierianus* d'Orbigny (especially in Douvillé, 1916, pl. 17) lead me to conclude that these species belong more properly in the Cymatoceratinae. They have the characteristic ribbing, even though in some specimens the ribbing is very weak or absent, and a hercoglossid suture, more sinuous than the suture in most species of the Paracenoceratinae. However, on the basis of the ornament alone this genus should not be left in the Paracenoceratinae.

Carinonautilus is a monotypic form known only from the Upper Cretaceous of south India. The paracenoceratids are primarily a Jurassic radiation from the *Cenoceras* complex and it is difficult to visualize a derivation of *Carinonautilus* from this source. It is here allied to the Nautilinae and considered a derivative of *Eutrephoceras* which is the long-persisting, slowly-evolving stock ranging from the Upper Jurassic to the middle Tertiary. Of the remaining genera, only *Paracenoceras* is widespread and fairly common as far as Mesozoic nautiloids go. It has by far the largest number of species; of a total of 42 species in this family 35 belong in *Paracenoceras*. *Tithonoceras* is monotypic, *Somalinautilus* and *Aulaconutilus* have three or less species each.

Whereas Spath did not diagnose this family at length, he did state that it was "characterized by differentiation of the periphery, generally associated with increase of the sinuosity of the suture line, and a ventral lobe" (Spath, 1927a, p. 25). *Paracenoceras* has a broad, generally sulcate periphery. *Tithonoceras* has a broad flattened periphery with a median furrow and the ventrolateral area projected into a prominent blunt keel aligned by furrows. *Somalinautilus* has an arched venter with angular ventral shoulders. *Aulaconutilus* has longitudinal ribs on the peripheral area.

Both *Paracenoceras* and *Somalinautilus* are interpreted as offshoots from the *Cenoceras* complex. Both of these genera first appear in the Middle Jurassic and it seems likely that they stem from separate sources within *Cenoceras*. *Aulaconutilus* and *Tithonoceras* are more specialized developments stemming from *Paracenoceras*. The subfamily is largely confined to the eastern hemisphere, being known from England, Europe, east and north Africa, Arabia, and Pakistan. The only occurrence of a member

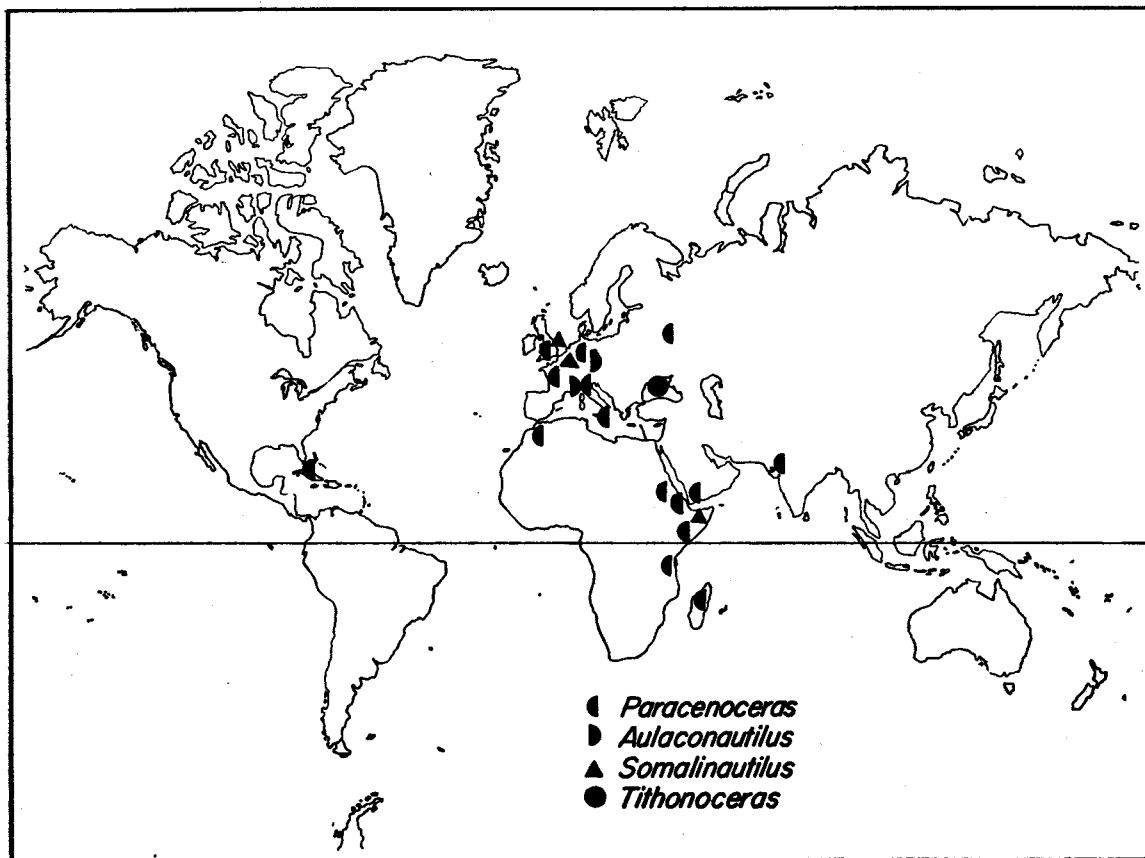


Fig. 17. Geographic distribution of species of the subfamily Paraceno-
ceratinae in formations of Jurassic and early Cretaceous age.

of this subfamily in the western hemisphere is *Paracenoceras* in Cuba. As is so characteristic of post-Triassic nautiloids the main stock of a subfamily is generally a highly variable form with many described species and a wide geographic distribution. This is well illustrated in the distribution of species of this subfamily (Fig. 17).

Genus *PARACENOCERAS* Spath, 1927

Paracenoceras Spath, 1927a, pp. 22, 25.

Paracenoceras Spath, 1935b, pp. 224-225.

Paracenoceras Scott, 1943, pp. 88, 89.

Nautilus (*Paracenoceras*) Jeannet, 1951, pp. 10-17.

Paracenoceras Miller and Collinson, 1952, pp. 626-628.

Type species. *Nautilus hexagonus* J. de C. Sowerby, 1826, pl. 529, fig. 2 (illustrated here on Plate 8, fig. 1, and Plate 13, figs. 1, 2; Text Fig. 18). Type by original designation.

Paracenoceras is the only genus of the Paracenoceratinae that is nearly world wide in distribution and includes a relatively large number of species. Of the remaining genera of this subfamily one is monotypic and the remaining two genera contain no more than three species apiece. The type species — *Nautilus hexagonus* J. de C. Sowerby — was previously only known through the rather unsatisfactory description and woodcut illustration (J. de C. Sowerby, 1826, pl. 529, fig. 2). Sowerby's type is illustrated on Plate 13, figures 1, 2, and Plate 8, figure 1 and Text Figure 18.

The genus can be diagnosed as follows: Conch robust, involute, smooth. Whorl section subtrapezoidal in outline. Whorl sides flattened, convergent towards a broad venter that may be flattened or truncate to distinctly sulcate. Ventral shoulders well rounded. Umbilicus generally small, umbilical shoulders rounded, umbilical walls steep. The shell is smooth except for sinuous growth lines which form a deep sinus on the broad venter. The suture is only slightly sinuous but with a distinct ventral and lateral lobe and a small saddle at the umbilical shoulder and wall. The position of the siphuncle is quite variable but never in an extreme ventral or dorsal position. The polished median section of Sowerby's type specimen shows that the siphuncle is beaded and with short funnels (Plate 8, fig. 1). Similar beaded siphuncles have been also noted by Spath (1927a,

p. 23) in species of "*Bisiphytes*," "*Digonioceras*," and *Cymatoceras*.

Approximately 35 species of *Paracenoceras* have been recorded most of which are from Upper Jurassic strata. Spath (1935b, p. 224) has described *Paracenoceras prohexagonum* from strata of

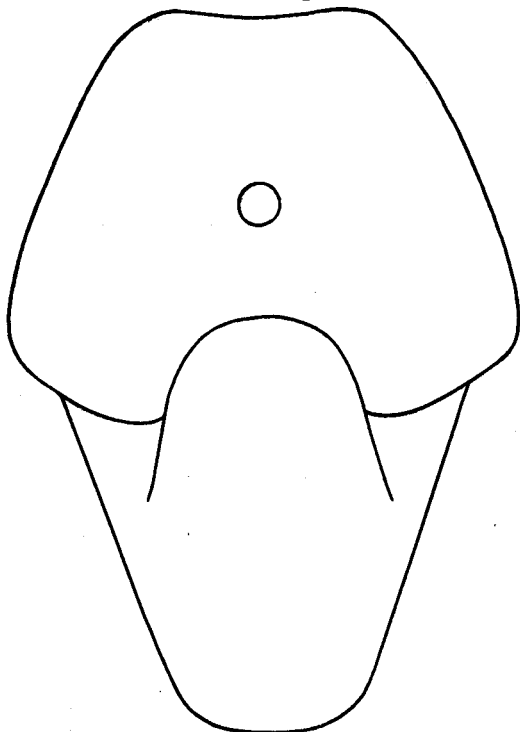


Fig. 18. *Paracenoceras hexagonum* (Sowerby). Diagrammatic cross section of holotype represented by figures 1, 2, Plate 13, and figure 1, Plate 8, X 1.

Bathonian? age. This is the oldest species known, and the youngest species of *Paracenoceras* appears to be *P. rhodani* (Roux) from the Albien of Switzerland.

Sowerby's type of *Nautilus hexagonus*, refigured here on Plate 13, figures 1, 2 and Text Figure 18, is a large phragmocone measuring 95 mm. in diameter, 54 mm. in height of last whorl, and 67 mm. in width of the last whorl. The whorl sides are only slightly convex and converge towards a broad sulcate venter.

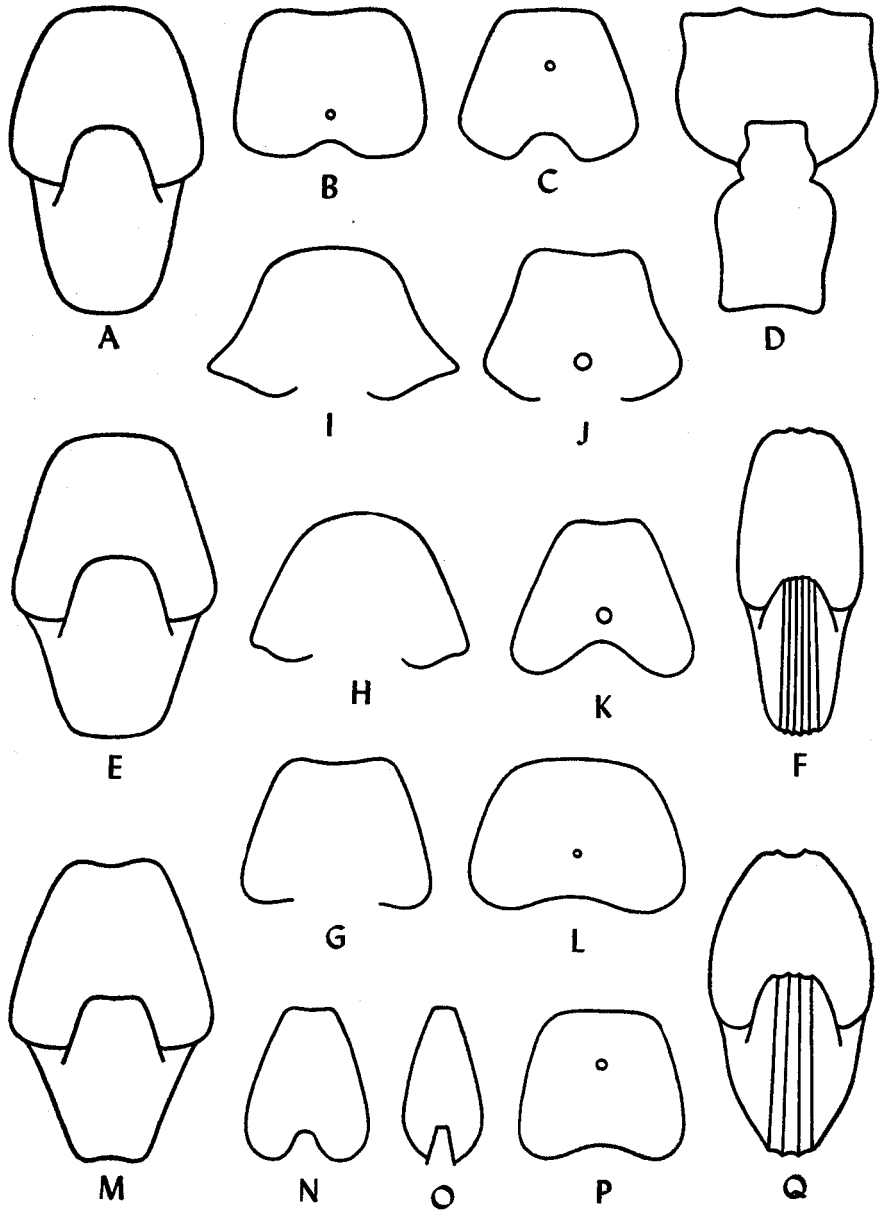


Figure 19

The umbilical and ventral shoulders are well rounded. The umbilicus is fairly large, deep, and funnel shaped. The umbilical walls are very steep. The large siphuncle is subcentral in position.

There is much variation in shape of the whorl section among the various species of *Paracenoceras*. The cross sections of 12 species are illustrated in Figure 19 to show the degree of variation. Sulcation of the venter of the adoral volution as on the type species, is not present on several of the species which have merely truncated venters or ventral areas slightly arched. *Paracenoceras marocense* Miller and Collinson (1952) has a broad sulcate venter at early maturity but the venter becomes arched with increasing size (Text Figure 19 G-I). The whorl sides also show some variation from being slightly concave as in *P. hexagonum* and *P. marocense*, to flattened or slightly convex in most of the remaining species. Variations in suture are mostly a matter of degree. Sutures of several species of *Paracenoceras* are illustrated in Figure 20 for comparison.

Paracenoceras costatum Scott (1943, p. 88, pl. 24, figs. 1, 3), with prominent sigmoidal costae on the whorl sides, belongs in the genus *Procymatoceras*. Scott (1943, p. 89) compared "*Paracenoceras*" *costatum* with *P. jumarensis* (Waagen, 1873, p. 21, pl. 4, figs. 1a, b) which has sigmoidal ribs only on the whorl sides, that terminate in large tubercles at the ventrolateral shoulder. However, Spath (1927a, p. 32) questions the accuracy of

Fig. 19. Cross sections of the conch of A, *Paracenoceras calloviensis* (Oppel), from Waagen 1873, pl. 3, fig. 2b, diameter 65 mm.; B, *P. subhexagonum* Jeannet 1951, fig. 19, height 42 mm.; C, *P. rollieri* (Loesch) from Jeannet 1951, fig. 29, height 27 mm.; D, *Aulaconautilus bicarinatus* Jeannet 1951, fig. 32, diameter 41 mm.; E, *Paracenoceras wandaensis* (Waagen) 1873, pl. 4, fig. 3b, diameter 85 mm.; F, *Aulaconautilus seccarinatus* (Pictet) 1867, pl. 10, fig. 1b, diameter 107 mm., the genotype of *Aulaconautilus*; G, H, I, *Paracenoceras marocense* Miller and Collinson, 1952, fig. 1 (G, height 28 mm.; H, height 48 mm.; I, height, 72 mm.); J, *P. prohexagonum* Spath 1935, fig. 46, height 44 mm.; K, *P. hexagonum* (Sowerby) from Spath 1935, fig. 4d, height 56 mm., the genotype of *Paracenoceras*; L, *P. dilatatus* Jeannet 1951, fig. 8, height 140 mm.; M, *P. kumagunensis* (Waagen) 1873, pl. 3, fig. 1b, diameter 72 mm.; N, *P. herznachensis* Jeannet 1951, fig. 14, height 100 mm.; O, *P. enniatum* (Dacqué), from Scott 1940, pl. 24, fig. 2, height 70 mm.; P, *P. arduennensis* (Loesch, 1914) from Jeannet 1951, fig. 26, height 19 mm.; Q, *Aulaconautilus picteti* (Oppel), from Zittel 1868, pl. 3, fig. 36, diameter 95 mm.

Waagen's illustration and points out that the specimens are badly weathered. Spath quite rightly maintains that the affinities of *P. jumarensis* are very doubtful and the species can be retained in *Paracenoceras* with question.

A list of the species assigned to *Paracenoceras* with their generalized geologic and geographic data is given below. Most of the species are from the Jurassic Tethyan geosynclinal area and adjoining epicontinental seas of Europe. Several occurrences

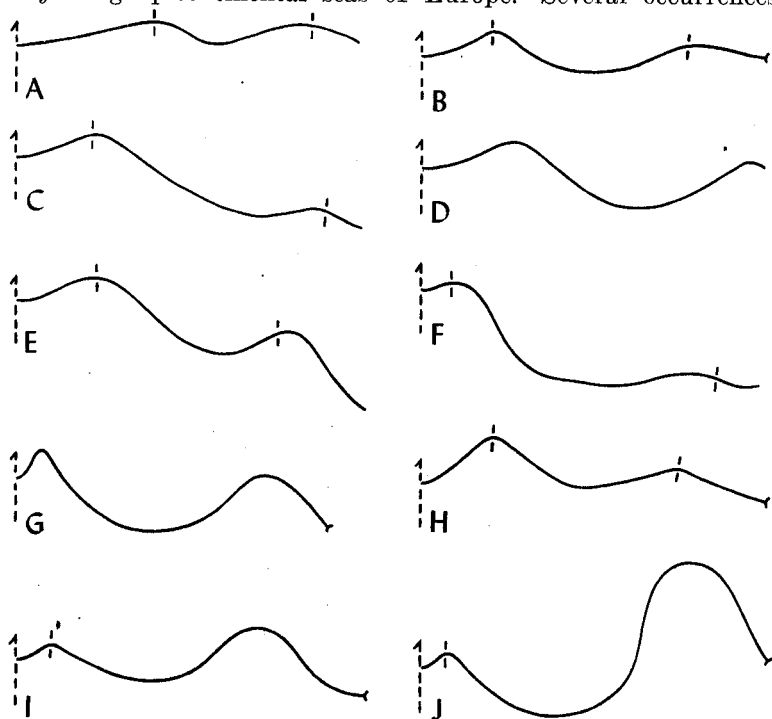


Fig. 20. Diagrammatic representation of sutures of A, *Paracenoceras dilatatus* Jeannet 1951, fig. 8; B, *P. hexagonum* (Sowerby), from Spath 1935, fig. 4e, the genotype of *Paracenoceras*; C, *P. acklini* Jeannet 1951, fig. 25; D, *P. marocense* Miller and Collinson 1952, fig. 1A; E, *P. rollieri* (Loesch, 1914) from Jeannet 1951, fig. 29; F, *P. herznachensis* Jeannet 1951, fig. 14; G, *Heminautilus stantoni* Scott 1940, fig. 179; H, *Paracenoceras prohexagonum* Spath 1935, fig. 4c; I, *Heminautilus etheringtoni* Durham 1946, fig. 3C; J, *Heminautilus lallierianus* (d'Orbigny) from Durham, 1946, fig. 3A. All figures greatly reduced.

in eastern Africa, Madagascar, Arabia, and in Pakistan form an eastern extension of the European faunal distribution. The only occurrence known in the Western Hemisphere is in Cuba (Sánchez Roig, 1951). As noted above, most of the species of *Paracenoceras* are Upper Jurassic in age.

DISTRIBUTION OF SPECIES OF THE GENUS PARACENOCERAS

Species	Stratigraphic Distribution	Geographic Distribution
<i>P. acklini</i> (Jeannet) 1951	Jurassic (Callovian)	Switzerland
<i>P. arduennensis</i> (Loesch) 1914	Jurassic (Oxfordian)	France
<i>P. bruntrutanae</i> (Kuhn) 1936	Jurassic (Upper)	Germany
<i>P. calloviensis</i> (Oppel) 1858	Jurassic (Callovian)	Europe
<i>P. dilatatus</i> (Jeannet) 1951	Jurassic (Callovian)	Switzerland
<i>P. divesianus</i> (Kuhn) 1936	Jurassic (Upper)	France
<i>P. dorsatus</i> (Roemer) 1836	Jurassic (Upper)	Germany
<i>P. dorsoexcavatum</i> (Parona and Bonarelli) 1897	Jurassic (Callovian)	France
<i>P. ennianum</i> (Dacqué) 1905	Jurassic (Upper)	Somaliland
<i>P. giganteus</i> (d'Orbigny) 1825	Jurassic (Upper)	France
<i>P. granulosum</i> (d'Orbigny) 1843	Jurassic (Upper)	France
<i>P. herznachensis</i> Jeannet, 1951	Jurassic (Callovian)	Switzerland
<i>P. hexagonoides</i> Spath, 1927	Jurassic (Tithonian)	Pakistan
<i>P. hexagonum</i> (J. de Sowerby) 1826	Jurassic (Upper)	Europe
<i>P. jeanneti</i> Sanchez Roig, 1951	Jurassic (Oxfordian)	Cuba
<i>P. ? jumarense</i> (Waagen) 1873	Jurassic (Bathonian)	Pakistan

Species	Stratigraphic Distribution	Geographic Distribution
<i>P. kumagunense</i> (Waagen) 1873	Jurassic (Callovian)	Pakistan
<i>P. latifrons</i> (Zwierzycki) 1914	Jurassic (Upper)	Tanganyika
<i>P. marocense</i> Miller and Collinson, 1952	Jurassic (Upper) ?	Morocco
<i>P. mjatschkowanus</i> (Loesch) 1914	Jurassic (Upper)	Russia
<i>P. moreaui</i> (d'Orbigny) 1842	Jurassic (Kimmeridgian)	France
<i>P. mullerriedi</i> Sanchez Roig, 1951	Jurassic (Oxfordian)	Cuba
<i>P. prohexagonum</i> Spath, 1935	Jurassic (Bathonian?)	British Somaliland
<i>P. rhodani</i> (Roux) 1848	Cretaceous (Albian)	Switzerland
<i>P. rollieri</i> (Loesch) 1914	Jurassic (Oxfordian)	Switzerland
<i>P. sattleri</i> (Krenkel) 1910	Jurassic (Kimmeridgian)	Tanganyika
<i>P. schattenbergi</i> (Kuhn) 1936	Jurassic (Upper)	Germany
<i>P. schusteri</i> (Loesch) 1912	Jurassic (Kimmeridgian)	France
<i>P. siculus</i> (Gemmellaro) 1868	Jurassic (Upper)	Sicily
<i>P. sinuosus</i> (Roemer) 1836	Jurassic (Upper)	Germany
<i>P. staffelbergensis</i> (Kuhn) 1936	Jurassic (Upper)	Germany
<i>P. subhexagonus</i> (Jeannet) 1951	Jurassic (Callovian)	Switzerland
<i>P. volgensis</i> (Nikitin) 1888	Jurassic	Russia
<i>P. wandaense</i> (Waagen) 1873	Jurassic (Upper)	Pakistan
<i>P. wilmae</i> (Jeannet) 1951	Jurassic (Callovian)	Switzerland

Genus AULACONAUTILUS Spath, 1927

Aulaconautilus Spath, 1927a, pp. 22, 25.

Nautilus (*Aulaconautilus*) Jeannet, 1951, p. 17.

Type species. *Nautilus sexcarinatus* Pictet, 1867, Pl. 10, figs. 1a-c (reproduced here as Plate 14, figs. 1, 2). Type by original designation.

The following diagnosis is made from study of the descriptions and illustrations of the three species that can be assigned to this genus. No specimens were available for study. Conch involute, generally compressed, with greatest width of the whorls just below the umbilical shoulders. Whorl sides smooth, convex and converging. Ventral shoulders rounded, venter broad, low, and with longitudinal ribs. Umbilicus very small, umbilical shoulders rounded. Suture sinuous with a shallow ventral lobe, a broad deep lateral lobe with a saddle at the umbilical shoulder. Position of the siphuncle not known.

Only three species can be placed in *Aulaconautilus*; these are *A. sexcarinatus* (Pictet) the type species, *A. picteti* (Oppel), and *A. bicarinatus* (Jeannet). There is variability in the conch shape, suture, and ornamentation. The type species, *A. sexcarinatus*, has eight longitudinal ribs on the venter (Plate 14, figs. 1, 2 and Text Figure 19F), divided by shallow furrows. The median furrow is the most prominent. The ribs at the ventrolateral edge are the weakest of the ribs on the venter. *Aulaconautilus picteti* has only four longitudinal ribs all of equal prominence; the median furrow is the widest and deepest of the furrows between these ribs. This species likewise is much more inflated than the type species (Text Fig. 19Q). *Aulaconautilus bicarinatus* has a more depressed, subquadratic whorl section with a broad flattened venter. There are four widely spaced longitudinal ribs on the venter (Text Fig. 19D). The ornamentational pattern of longitudinal ribs on the venter, which characterizes *Aulaconautilus*, is unique for post-Triassic nautiloids. A homeomorphous development is the Permian and Triassic genus *Aulametacoceras* Miller and Unklesbay. The type of this genus is Middle Permian in age (from Arizona). The only other species assigned to it is *Nautilus rectangularis* Hauer of Upper Triassic age. *Aulametacoceras* is considered a radiation from the stable evolving *Metacoceras* complex (Kummel, 1953c).

The sutures of species of this genus, especially those of the

type species, are very similar in plan and degree of sinuosity to those of *Pseudaganides*. The other groups of the Paracenoceratinae have sutures with very shallow lobes and saddles.

The three known species of *Aulaconautilus* come from Upper Jurassic strata of Europe.

Genus TITHONOCERAS Retowski, 1894

Tithonoceras Retowski, 1894, p. 223.

Tithonoceras Crick, 1908, p. 14.

Tithonoceras Spath, 1927a, pp. 20, 22, 25.

Type species. *Tithonoceras zitteli* Retowski, 1894, p. 223, pl. 13, figs. 2a, b, c (refigured here on Plate 15, figs. 1, 2).

This is another of the numerous monotypic Mesozoic nautiloid genera. The type species is from Tithonian (Upper Jurassic) strata of the Crimea. The conch is evolute, compressed, and smooth. The whorls are subrectangular in outline, being higher than wide. The venter is broad, flattened, and with a shallow median furrow. The ventral shoulders are inflated and form a smooth keel-like ridge that is aligned on the venter and the whorl sides by a furrow. The ventral furrow aligning the ventrolateral keel is rather narrow but very distinct. The furrow on the whorl sides adjoining the ventrolateral keel is concave and broad occupying nearly half of the whorl side. The dorsal half of the whorl side is convex passing onto a broadly rounded umbilical shoulder. The umbilicus is large, measuring one-eighth the diameter of the conch. The shell is smooth except for sinuous growth lines which are deeply concave on the venter. The suture is very sinuous with ventral and lateral lobes. The position of the siphuncle is not known.

Proper evaluation of monotypic forms is not entirely satisfactory. Little can be said of *Tithonoceras* except that it appears to be a specialized offshoot of *Paracenoceras*. The general conch form is unique among Carboniferous to Recent nautiloids. There are no homeomorphous types of other ages known to me. In its derivation from *Paracenoceras* there was merely greater compression of the conch and further elaboration of the ventral area.

The type and only known species of *Tithonoceras* came from Tithonian strata (Upper Jurassic) of the Crimea, Russia.

Genus *SOMALINAUTILUS* Spath, 1927

Type species. Nautilus antiquus Dacqué, 1910 (= *N. bisulcatus* Dacqué, 1905, p. 144, pl. 16, figs. 3a, b). Type by original designation. Type figure reproduced here on Plate 14, figs. 3, 4.

The Paracenoceratinae are derived from Liassic cenoceratids and are characterized by modified venters. The earliest species of this subfamily are included in the genus *Somalinautilus*. At this date only three species of *Somalinautilus* have been recorded. The type species is from Upper Jurassic (Kimmeridgian) strata of Somaliland. The other species definitely assigned to this genus are *Nautilus fuscus* Crick (1898, p. 122) and *N. clausus* in Foord and Crick (1890b, p. 284) *non* d'Orbigny (1842, p. 158, pl. 33).

From the description and illustration of the type species and study of several specimens of *Nautilus fuscus* in the British Museum (Natural History), the following diagnosis is made. Conch involute, depressed, rapidly expanding, whorls wider than high. Venter slightly arched with subangular ventral shoulders, with a distinct furrow on venter adjoining the ventral shoulder. The whorl sides are concave adjacent to the ventral shoulders and convex towards the umbilicus. Umbilical shoulders are sharply rounded and the umbilical wall very steep. Umbilicus measures less than one-quarter the diameter of the conch. Surface of the conch with sinuous growth lines and may or may not have longitudinal striae. Suture forms shallow ventral lobe, generally an angular saddle at the ventral shoulder followed by a broad, shallow, lateral lobe, with a low saddle on the umbilical wall. The position of the siphuncle in the type species is not known but in *Nautilus fuscus* it is slightly below the center.

Each of the generic groups of the Paracenoceratinae is very distinct and *Somalinautilus* with its subangular ventral shoulders and low arched venter is readily differentiated from the other genera. *Somalinautilus* most probably arose directly out of the *Cenoceras* complex and not from *Paracenoceras*. There are several quadrate whorled forms of *Cenoceras* which could have given rise to those Middle and Upper Jurassic species placed in *Somalinautilus*. Species of this genus are known from England, France, and Somaliland.

Subfamily CYMATOCERATINAE Spath, 1927

This subfamily now comprises 10 genera of post-Triassic nautiloids which have variable conch shapes and degree of sinuosity of the suture but have in common an ornamental pattern consisting of ribs. Ornamentation is relatively rare in post-Triassic nautiloids, excepting those forms within the Cymatoceratinae. There are no species with nodose ornamentation known. Within this subfamily there is displayed a wide range of adaptive radiation as seen in the extent of variation in conch shape and suture. The genus *Cymatoceras* is the basic adaptive type; it has an involute, rounded conch with only a slightly sinuous suture. *Paracymatoceras* is like *Cymatoceras* in conch form but has a more sinuous suture with distinct lobes and saddles. *Syrionautilus*, *Anglonautilus*, and *Eucymatoceras* are differentiated on modifications of the ribbing plan. *Cymatonautilus*, *Heminautilus*, *Epicymatoceras* (n. gen., p. 439), and *Deltocymatoceras* (n. gen. p. 438) are differentiated by their modified conch shapes. *Heminautilus* and *Epicymatoceras* have highly compressed conchs and flattened venters. The former is very involute and the whorl section more convergent in plan. The latter is more evolute and with a simple, only slightly sinuous, suture. *Deltocymatoceras* has a subtriangular whorl section and *Cymatonautilus* has an evolute conch with a concave venter and whorl sides.

The only common and geographically-widely-distributed genus is *Cymatoceras*. This fact is clearly expressed in the number of species belonging to each group.

<i>Cymatoceras</i>	64 species
<i>Paracymatoceras</i>	6 species
<i>Heminautilus</i>	5 species
<i>Procymatoceras</i>	4 species
<i>Eucymatoceras</i>	3 species
<i>Anglonautilus</i>	3 species
<i>Cymatonautilus</i>	2 species
<i>Syrionautilus</i>	1 species
<i>Epicymatoceras</i>	1 species
<i>Deltocymatoceras</i>	1 species

Cymatoceras has a truly world-wide distribution. The other genera are largely confined to Europe in the epicontinental seas

adjoining the Tethyan geosyncline (Text-Figs. 21, 22). *Eucymatoceras*, *Anglonautilus*, *Syrionautilus*, *Cymatonautilus*, *Epicymatoceras*, and *Deltocymatoceras* are known only from a belt extending from England to the Crimea or Caucasus Mountains in Russia in sediments of the Jurassic and Cretaceous epicontinental seas of and adjoining the Tethys proper. *Procymatoceras* is known from England, Pakistan, and Ethiopia; *Heminautilus* and *Paracymatoceras* are known outside the European Tethyan belt from North and South America, Ethiopia, and Japan.

The known distribution of fossil nautiloids is so dependent on factors of preservation and concentration of field collecting that it is probably dangerous to make any too-sweeping conclusions. However, the number of species does at least reflect the relative abundance of the various genera. If we think of the Tethys as an ancient circum-equatorial sea the Cymatoceratinae are found to be largely confined to the borders of this seaway. Many genera (e.g. *Eucymatoceras*, *Syrionautilus*, *Cymatonautilus*, *Epicymatoceras*, and *Deltocymatoceras*) are confined entirely to the European-Middle East portions of this circum-equatorial sea.

Analysis of the distribution of the Cymatoceratinae on a time basis throws some light on the general problem of their evolution. *Procymatoceras* and *Cymatonautilus* are known only from Middle and Upper Jurassic strata. The species of these genera are confined to the marginal seaways of the Tethys from England to India. Whereas, to the best of my knowledge, the species of these two genera have never been found in a single stratum and locality, their geographic and time ranges do overlap.

In the Cretaceous, the genus *Cymatoceras* is widely distributed throughout the period. *Anglonautilus*, *Eucymatoceras*, and *Heminautilus* are confined to the Lower Cretaceous. *Anglonautilus* and *Eucymatoceras* have approximately the same geographic range from England to the Black Sea. Whereas *Heminautilus* also occurs in this European-Mediterranean-belt it is likewise known from Ethiopia, Arkansas (U.S.A.), and Colombia. The Upper Cretaceous genera *Epicymatoceras* and *Deltocymatoceras* occur together in the type Maestrichtian area of Belgium, and *Syrionautilus* is confined to the Middle East.

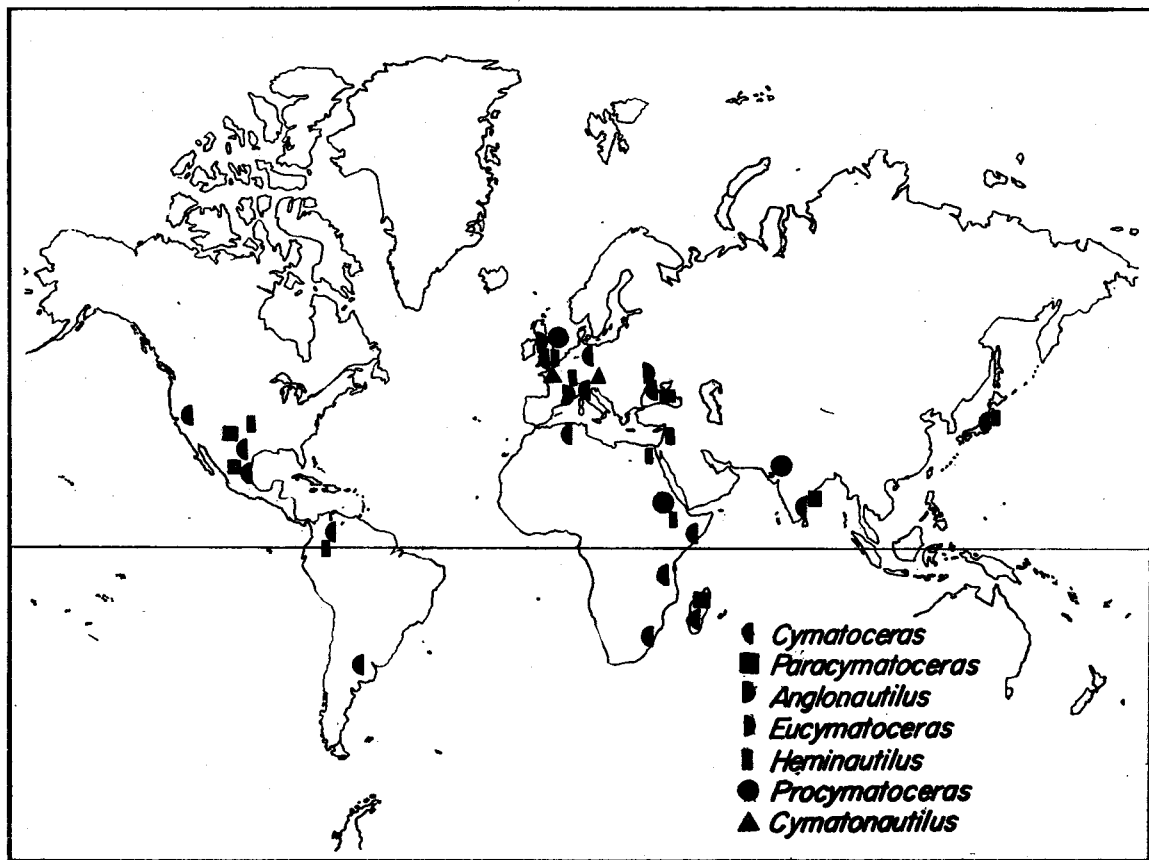


Fig. 21. Geographic distribution of species of the subfamily Cymatoecratinae in formations of Lower Cretaceous age.

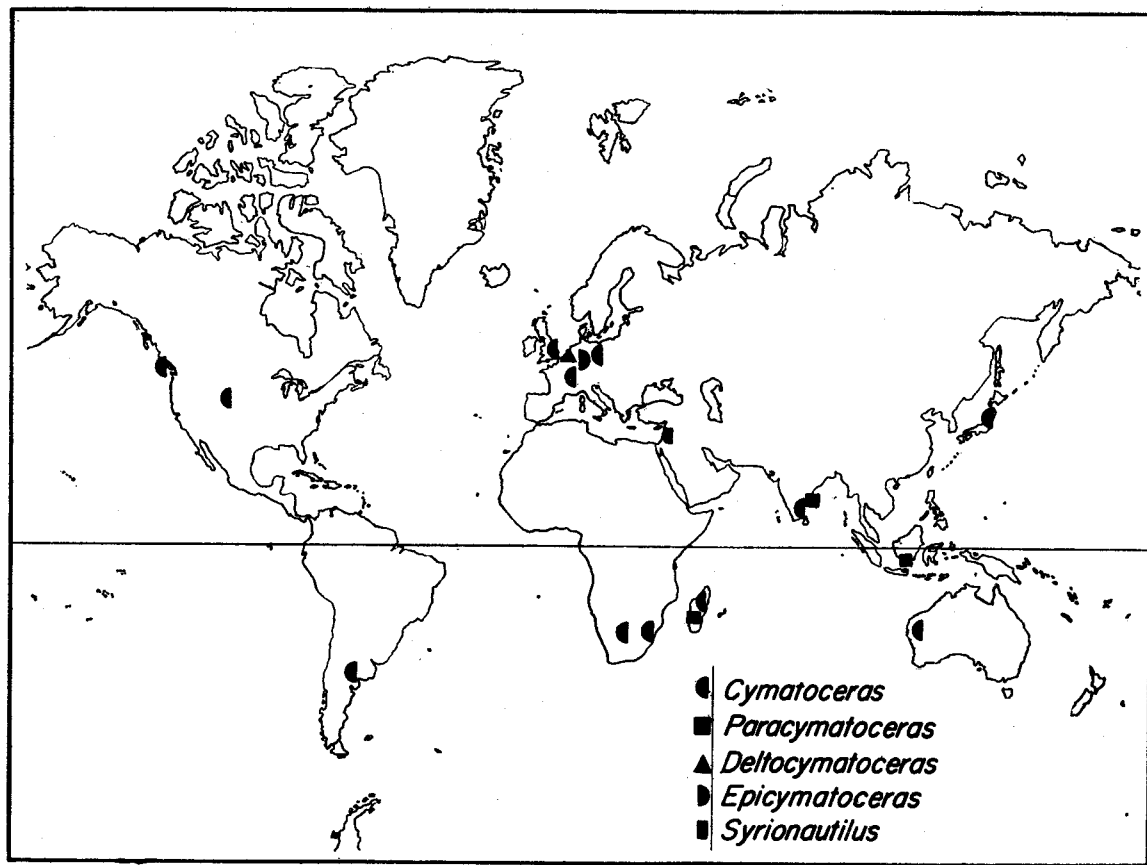


Fig. 22. Geographic distribution of species of the subfamily Cymatoceratinae in formations of Upper Cretaceous age.

The wide range in variation of conch shape and suture within the Cymatoceratinae produced many homeomorphs to other members of the Nautilidae. The presence of the characteristic ribbing makes differentiation easy. The conch shape and suture of *Deltocymatoceras* are closely similar to that of *Angulithes* of the Hercoglossinae. The conch shape and suture of many species of *Cymatoceras* and *Eucymatoceras* are nearly the same as that found in many species of *Eutrephoceras* and *Cimomia*. The suture of *Paracymatoceras* is identical in plan with that found in *Hercoglossa*.

This great variability in conch shape and suture leads me to believe that the Cymatoceratinae form a phyletic group which has as its main genetic base the ribbing character. Once established, this genetic line had its own adaptive radiation which is expressed in the many conch shapes, rib patterns, and sutures as it is in any other group of Mesozoic nautiloids. This subfamily is the dominant group of Cretaceous nautiloids. Ribbing, on a pattern somewhat like that in the Cymatoceratinae, occurred only once before, and that was in a single species of Upper Triassic nautiloid-*Proclydonautilus spirolobus* (Dittmar). The ribbing in this species is very fine and like that in *Syrionautilus*, whereas in most other genera and species of the Cymatoceratinae the ribbing is coarser. It is important to note that *Proclydonautilus spirolobus* belongs to a family that characteristically has smooth conchs except for a few forms with nodes developed during some stage of their ontogeny (*Cosmonautilus* Hyatt and Smith, 1905, and *Callaionautilus* Kieslinger, 1924). The ribbing patterns found in species of *Pleuronautilus* are quite different from those of the Cymatoceratinae.

Data are insufficient to decipher precisely the evolutionary lines within the Cymatoceratinae. The evidence available seems to point to *Cymatoceras* as the parent stock which gave rise to most of the remaining adaptive types. The origin of the subfamily must be directly or indirectly among the cenoceratid complex of the Lower and Middle Jurassic. Even though *Cymatonautilus* and *Procymatoceras* are the oldest forms known, they are both rather specialized and probably not ancestral to *Cymatoceras*, which as far as we now know first appears in the Cretaceous.

Neocymatoceras Kobayashi (1954) was established for a single

specimen from the Oligocene of Kyushu, Japan. *Neocymatoceras tsukushiense*, the type species, is a typical cymatoceratid in conch shape and rib pattern but has a strongly projected suture which forms a rounded ventral saddle, a broad sweeping lobe occupying nearly the whole whorl side, and with what appears to be the beginning of a saddle on the umbilical area. Cymatoceratids with sinuous sutures characterize *Paracymatoceras*. However, in that genus the saddles and lobes are well defined; that is, there is always a well-defined saddle on or near the umbilical shoulder. It is also true though that *Paracymatoceras* is gradational with *Cymatoceras* in regard to sutures. Those cymatoceratids with more sinuous sutures show the sutures to be more strongly projected on the ventral area and in this way give the sinuosity; the lateral saddle at the umbilical area is usually very weak. *Cymatoceras pseudonegama* Spengler (Fig. 24 C) and *C. semilobatus* Spengler (Fig. 24 D) have such strongly projected sutures on the umbilical area but not quite to the extent found in the Japanese Oligocene species. Similar strongly projected sutures in very small juvenile specimens of *Cymatoceras* have been described and figured by Kummel (1953a) from Lower Cretaceous formations of Texas. However, the suture of *Neocymatoceras tsukushiense* appears to me to lie within the range of variation of the suture of *Cymatoceras*, and the lack of any lateral saddle in the umbilical area disallows any affinity with *Paracymatoceras*. The distinctness of the suture in *Neocymatoceras tsukushiense* is only in the marked projection on the peripheral area, a modification present in several Cretaceous species. This interpretation places the Japanese species in the genus *Cymatoceras*, and *Neocymatoceras* is considered a synonym of *Cymatoceras*. It should be emphasized that *C. tsukushiense* is the only Tertiary Cymatoceratinae known.

Genus CYMATOCERAS Hyatt, 1884

Cymatoceras Hyatt, 1884, p. 301.

Cymatoceras Hyatt, 1894, p. 553.

Nautilus (Cymatoceras) Spengler, 1910, p. 127.

Cymatoceras Spath, 1927a, pp. 21, 25.

Cymatoceras Miller and Harris, 1945, p. 2.

Cymatoceras Durham, 1946, p. 429.

Neocymatoceras Kobayashi, 1954a, pp. 18-20.

Type species. *Nautilus pseudoelegans* d'Orbigny, 1840, p. 70, pl. 8 (by original designation).

Species of *Cymatoceras* are the most common and widely distributed nautiloids of the Cretaceous. The characteristic pattern of ribbing and the slightly sinuous septa make identification of the genus easy. A cast of the type specimen (which is in the Museum of Natural History, Paris) is illustrated on Plate 16, figures 1, 2. This same specimen has previously been illustrated by Foord and Crick (1890a, p. 551, figs. 3a, b), and this same figure was reproduced in Foord's second Catalogue of the Fossil Cephalopoda in the British Museum (Foord, 1891, p. 255, fig. 59 a, b). Foord and Crick (1890a, p. 552) quote a letter from Dr. Paul Fischer expressing doubt as to the identity of d'Orbigny's type specimen. Fischer states: "The type of *Nautilus pseudoelegans* is difficult to recognize. According to the dimensions given in the original diagnosis (diameter 240 millimètres, thickness 160 mm. Paléont. Franc. p. 60) our specimens, No. 4834D, which were sent to you are typical. [Foord and Crick, page 552, state that two specimens were sent, both numbered 4834 D; the larger one is represented by their figure 3.] Moreover, they come from the neighborhood of Vandœuvre

Fig. 23. Cross sections of the conch of *A*, *Cymatoceras elegans* (J. Sowerby) from d'Orbigny, 1840, pl. 19, fig. 2, diameter 190 mm.; *B*, *C. sharpei* (Schlüter) 1876; pl. 46, fig. 6, diameter 168 mm.; *C*, *C. tourtiaie* (Schlüter) 1876, pl. 46, fig. 2, diameter 88 mm.; *D*, *C. cenomanensis* (Schlüter), 1876, pl. 45, fig. 2, diameter 115 mm.; *E*, *Procyamatoceras subtruncatus* (Morris and Lycett) 1850, pl. 1, fig. 22, diameter 72 mm., the genotype of *Procyamatoceras*; *F*, *Procyamatoceras baberi* (Morris and Lycett) 1850, pl. 1, fig. 1a, diameter 82 mm.; *G*, *Paracymatoceras asper* (Oppel) from Zittel, 1868, pl. 3, fig. 1a, diameter 83 mm., the genotype of *Paracymatoceras*; *H*, *Procyamatoceras? intumescens* (Waagen) 1873, pl. 3, fig. 3, diameter 90 mm.; *I*, *C. radiatus* (Sowerby) from d'Orbigny, 1840, pl. 14, fig. 2, diameter 188 mm.; *J*, *C. neocomiensis* (d'Orbigny) 1840, pl. 11, fig. 2, diameter 192 mm.; *K*, *C. deslongchampsianum* (d'Orbigny) 1840, pl. 20, fig. 2, diameter 65 mm.; *L*, *Eucymatoceras requienianus* (d'Orbigny) 1840, pl. 10, fig. 2, diameter 280 mm. (= *N. plicatus* Fitton, 1835); *M*, *Cymatoceras neckerianus* Pictet, 1859, pl. 16, fig. 1b, diameter 93 mm.; *N*, *Deltocymatoceras rugatus* (Fritsch and Schlönbach) 1872, pl. 15, fig. 2, height 80 mm.; *O*, *Epicymatoceras vaelsensis* Binckhorst, 1861, pl. 5c, fig. 2b, diameter 105 mm.; *P*, *Cymatoceras albensis* (d'Orbigny) from Pictet, 1859, pl. 17, fig. 1b, diameter 95 mm.

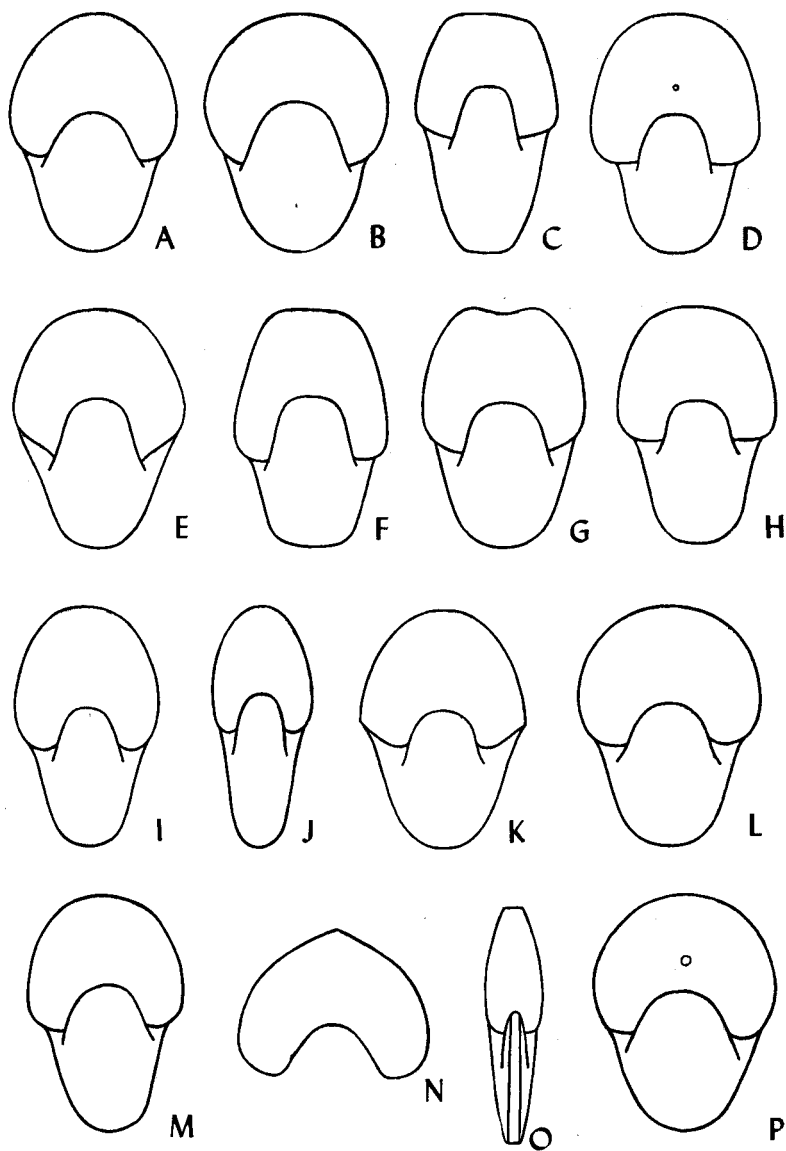


Figure 23

(Département de l'Aube), where the species was found.

"But the drawing given by d'Orbigny is faulty; first its dimensions do not agree with the description; then the drawing being reduced to one-third the natural size, the specimen which it represents should have been at least 360 mm. in diameter; besides, the ornaments are wanting in the drawing on a great part of the last whorl. . . .

"Consider then the figure by d'Orbigny as only approximate. D'Orbigny has restored a great many of his plates, for which, in my opinion, he is very much to blame. . . .

"In the d'Orbigny collection no specimen is specially marked as the type. But d'Archiac (Hist. du progrès de la géologie, vol. iv, p. 295) quotes *N. pseudoelegans*, and he has given to the Museum a specimen marked *type*. This specimen is small (greatest diameter 150 mm.), and agrees neither with the figure nor with the dimensions given in d'Orbigny's original description.

"Perhaps the true type was contained in the collection of the geologist Clément Mullet, who showed d'Orbigny over the locality where *N. pseudoelegans* abounds?" In accordance with the above statement Foord and Crick (1890a, p. 551) in the legend of their figure 3, state that the drawing is from a specimen in the d'Orbigny Collection in the Museum of Natural History, Paris. However, Foord (1891, p. 255, fig. 59 a, b) labelled the same figure as drawn from d'Orbigny's type specimen.

The type specimen is a much inflated conch, very involute and with a small umbilicus. The whorl section is wider than high with a broadly rounded venter. Whorl sides are also broadly rounded. The test bears prominent ribs that are sigmoidal on the whorl sides and form a sinus on the venter. The suture is only slightly sinuous with shallow ventral and lateral lobes. The siphuncle lies below the center of the septa.

There are approximately 64 species of *Cymatoceras* recorded to date. All of these are characterized by the ribbing and the slightly sinuous septa. The shape of the whorl section is quite variable in this genus (Fig. 23). The type species, *C. pseudoelegans*, has a depressed, globular conch; one of the most compressed conchs is that of *C. neocomiensis* (d'Orbigny) (Fig. 23 J). Between these two extremes there are all gradations of

conch patterns with well rounded venters. Whereas most of the species are very involute, as in the type, there is a wide range of variation to rather evolute species as *C. patens* (Kner, 1850) and *C. tsaltsithelensis* (Rouchadzé, 1931). Some of the species develop sharply rounded to subangular shoulders. *Cymatoceras tourtiaie* (Schlüter) has a subquadrate whorl section with subangular ventral and umbilical shoulders; the venter is low and arched (Fig. 23C). The juvenile volutions, however, have broadly arched venter with well rounded ventral shoulders (Schlüter, 1876, pl. 46, fig. 4). *Cymatoceras deslongchampsianum* (d'Orbigny) has an arched venter with rounded ventral shoulders but subangular umbilical shoulders with a sloping, slightly arched umbilical wall (Fig. 23K). *Nautilus vaelsensis* Binckhorst (1861, p. 15, and Schlüter 1876, p. 57) is one of the most aberrant cymatoceratids known to me and is made the type of a new genus (p. 439). The conch is very compressed and evolute. The whorl sides are slightly convex with broadly rounded umbilical shoulders and angular ventral shoulders; the venter is flattened. The test bears the typical cymatoceratid ribbing. The characters of the ventral area, that is, the flattened venter and the angular ventral shoulders, are also found in *Heminautilus*. This latter genus, however, is very involute and the whorl sides are generally slightly inflated near the umbilical shoulders. *Cymatoceras tourtiaie* also has the flattened venter and angular shoulders, but the conch is inflated, involute and the whorl section subquadrate.

The position of the siphuncle in the type species (*C. pseudo-elegans*) is below the center — that is, closer to the dorsum than the venter (d'Orbigny, 1840, pls. 8, 9; Foord, 1891, p. 256). It appears that this condition prevails in a majority of the species of *Cymatoceras* (e.g. *C. neocomiensis*, *C. radiatus*, *C. gabbi*, *C. colombiana*, *C. elegans*, *C. kayeanus*, *C. kossmati*, and *C. cenomanensis*). The siphuncle lies above the center, that is closer to the venter than the dorsum in *C. atlas*, *C. tenuicostatus*, and *C. hunstantonensis*. A specimen of *C. loricatus* (Schlüter) figured by Griepenkerl (1889) has a near marginal (ventral) siphuncle.

The suture of *C. pseudo-elegans* is only slightly sinuous with shallow ventral and lateral lobes. *Paracymatoceras* differs from *Cymatoceras* essentially only in the greater sinuosity of its suture (Fig. 24). As noted by Miller and Harris (1945, p. 10) these two genera are more or less gradational in respect to the

suture. Those specimens with more sinuous sutures, and thus transitional to *Paracymatoceras*, include *C. colombiana* (Fig.

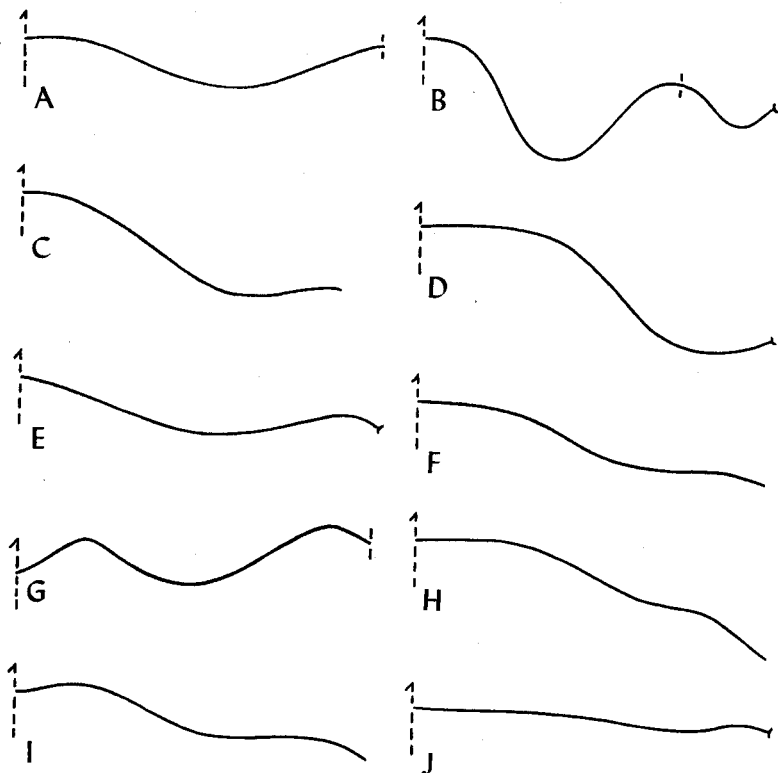


Fig. 24. Diagrammatic representation of sutures of *A*, *Cymatoceras colombiana* Durham 1946, fig. 3G; *B*, *Paracymatoceras texanum* (Shumard) 1860, from Miller and Harris 1945, fig. 3A; *C*, *Cymatoceras pseudonegama* (Spengler) 1910, pl. 12, fig. 7d; *D*, *C. semilobatus* (Spengler) 1910, pl. 11, fig. 4b; *E*, *C. hilli* (Shattuck) from Miller and Harris 1945, fig. 2A; *F*, *C. kayeanum* (Blanford), from Spengler, 1910, pl. 12, fig. 72; *G*, *C. tsaltsithelensis* (Rouchadzé) 1931, fig. 6; *H*, *C. kossmati* (Spengler) 1910, fig. 7b; *I*, *C. virgatum* (Spengler) 1910, fig. 7c; *J*, *C. loeblichii* Miller and Harris 1945, fig. 2C. All figures greatly reduced.

24A), *C. cenomanensis*, *C. tourtiaie*, *C. patens*, *C. semilobatus* (Fig. 24 D), *C. kossmati* (Fig. 24 H), and *C. virgatum* (Fig. 24 I). The type species does not have an annular lobe, which appears to be the case in the majority of species of *Cymatoceras*. However annular lobes in the center of the dorsal lobe are present in *C. radiatus*, *C. loeblichii*, *C. colombiana*, and *C. tourtiaie*. Most species of *Cymatoceras* have broad ventral saddles but some as *C. virgatum* (Spengler) and *C. tsakalsithelensis* (Rouchadzé) have very pronounced ventral lobes.

Cymatoceras is the most common, and has a larger number of species than any of the other genera of the Cymatoceratinae. All members of this subfamily have in common the characteristic ribbing. The other genera are differentiated on the basis of specialization of the ribbing, shape of conch, or suture. *Procymatoceras* has a depressed, rapidly expanding conch, with whorl sides and venter flattened. *Eucymatoceras* has the inflated rounded conch as in *Cymatoceras pseudoelegans* but the ribs form V-shaped patterns on the venter and on the whorl sides. *Paracymatoceras* is like *Cymatoceras* except for the greater sinuosity of the suture which has a well developed lateral lobe and a saddle at the umbilical suture. *Cymatonautilus* has a depressed evolute conch with concave lateral and ventral areas. *Syrionautilus* has acute, widely spaced, and nearly straight ribs. *Anglonautilus* has a depressed whorl section with large transverse undulations on the venter. *Heminautilus* has a much compressed conch, with a flattened venter, and a very sinuous suture. *Epicymatoceras* has a compressed, evolute conch with subquadrate whorl section. *Deltocymatoceras* has a subtriangular whorl section.

As stated above in the discussion of the subfamily Cymatoceratinae, *Neocymatoceras* Kobayashi (1954a) is thought to fall within the range of variation of *Cymatoceras* and is placed in synonymy of that genus.

Cymatoceras is characteristic of the Cretaceous. Steuer (1921) has described *Cymatoceras perstriatus* (Steuer) from very late Jurassic and earliest Cretaceous strata of Argentina. *Cymatoceras tsukushiense* (Kobayashi, 1954a) comes from Oligocene strata of Japan. These two are the only non-Cretaceous species of *Cymatoceras* known to the writer. *Cymatoceras* is worldwide in distribution (Figs. 21, 22).

DISTRIBUTION OF SPECIES OF THE GENUS CYMATOCERAS

Species	Stratigraphic Distribution	Geographic Distribution
<i>C. albensis</i> (d'Orbigny) 1850	Cretaceous	England, France
<i>C. altavensis</i> (Pomel) 1889	Cretaceous (Neocomian)	Algeria
<i>C. andranofotsyense</i> Collignon, 1951	Cretaceous (Albian)	Madagascar
<i>C. anguliferous</i> (Schlüter) 1876	Cretaceous (Cenomanian)	Germany
<i>C. articulatus</i> (Pulteney) 1813	Cretaceous	England
<i>C. atlas</i> (Whiteaves) 1876	Cretaceous (Upper)	England, France
<i>C.? averilli</i> (Anderson) 1938	Cretaceous (Lower)	California (U.S.A.)
<i>C. bayfieldi</i> (Foord and Crick) 1890	Cretaceous (Senonian)	England
<i>C. bifurcatum</i> (Ooster) 1858	Cretaceous	Switzerland
<i>C. broitzemensis</i> (Müller and Wollemaun) 1906	Cretaceous (Senonian)	Germany
<i>C.? campbelli</i> (Meek) 1861	Cretaceous	Vancouver Island, B.C.
<i>C. carlottensis</i> (Whiteaves) 1900	Cretaceous (Upper)	Maple Island, B.C.
<i>C. cenomanensis</i> (Schlüter) 1876	Cretaceous (Cenomanian)	Europe
<i>C. colombiana</i> Durham, 1946	Cretaceous (Aptian)	Colombia
<i>C. compressus</i> (Tavani) 1942	Cretaceous (Albian)	Somaliland
<i>C. crebricostatus</i> (Blanford) 1861	Cretaceous (Albian)	India
<i>C. deslongchampsianum</i> (d'Orbigny) 1840	Cretaceous (Neocomian- Cenomanian)	Europe
<i>C. eichwaldi</i> (Karakasch) 1907	Cretaceous (Lower)	Crimea
<i>C. elegans</i> (J. Sowerby) 1816	Cretaceous (Cenomanian)	England
<i>C. elegantoides</i> (d'Orbigny) 1840	Cretaceous (Cenomanian)	England, France

Species	Stratigraphic Distribution	Geographic Distribution
<i>C. formosus</i> (Blanford) 1861	Cretaceous (Senonian)	India, Madagascar
<i>G. gabbi</i> (Anderson) 1902	Cretaceous (Lower)	California (U.S.A.)
<i>C. guilielmi telli</i> (Ooster) 1858	Cretaceous	Switzerland
<i>C. hilli</i> (Shattuck) 1903	Cretaceous (Lower)	Texas (U.S.A.)
<i>C. hunstantonensis</i> (Foord and Crick) 1890	Cretaceous (Cenomanian)	England
<i>C. huxleyanus</i> (Blanford) 1861	Cretaceous (Turonian)	South India, Madagascar
<i>C. imbricatus</i> (Crick) 1907	Cretaceous	Natal, Africa
<i>C. interstriatus</i> (Strombeck) 1863	Cretaceous (Upper)	Germany
<i>C. kayeanus</i> (Blanford) 1861	Cretaceous (Albian- Cenomanian- Turonian)	India, Madagascar
<i>C. kossmati</i> (Spengler) 1910	Cretaceous (Albian)	India
<i>C. loeblichii</i> (Miller and Harris) 1945	Cretaceous (Lower)	Texas (U.S.A.)
<i>C. loricatus</i> (Schlüter) 1876	Cretaceous (Senonian)	Germany
<i>C. madagascarensis</i> (Yabe and Shimizu) 1924	Cretaceous (Upper)	Madagascar
<i>C. manuanensis</i> (Crick) 1907	Cretaceous (Albian)	Natal, Africa
<i>C. mikado</i> (Krenkel) 1910	Cretaceous (Neocomian)	Tanganyika
<i>C. nebrascense</i> (Meek and Hayden) 1862	Cretaceous (Upper)	Montana (U.S.A.)
<i>C. neckerianus</i> (Pictet) 1847	Cretaceous (Aptian, Albian)	Europe
<i>C. negama</i> (Blanford) 1861	Cretaceous (Albian)	India
<i>C. neocomiensis</i> (d'Orbigny) 1840	Cretaceous (Lower)	Europe, Crimea
<i>C. neohispanicum</i> (Burekhardt) 1925	Cretaceous (Aptian)	Mexico

Species	Stratigraphic Distribution	Geographic Distribution
<i>C. oculus</i> Crick, 1907	Cretaceous	Zululand
<i>C. patens</i> (Kner) 1850	Cretaceous (Senonian)	Poland, Germany
<i>C. perstriatus</i> (Steuer) 1921	Jurassic (Upper) Cretaceous (Lower)	Argentina
<i>C. pseudoatlas</i> (Yabe and Shimizu) 1924	Cretaceous (Upper)	Japan
<i>C. pseudoelegans</i> (d'Orbigny) 1840	Cretaceous	Europe
<i>C. pseudonegama</i> Spengler, 1910	Cretaceous (Albian)	India
<i>C. pseudoneokomiense</i> Shimizu, 1931	Cretaceous (Aptian)	Japan
<i>C. radiatus</i> (J. Sowerby) 1822	Cretaceous	Europe
<i>C. sakalavum</i> Collignon, 1949	Cretaceous (Albian)	Madagascar
<i>C. saussureanus</i> (Pictet) 1847	Cretaceous (Albian)	Switzerland
<i>C. scecequirensis</i> (Tavani) 1942	Cretaceous (Albian)	Somaliland
<i>C. semilobatus</i> Spengler, 1910	Cretaceous (Albian)	India
<i>C. semiundatus</i> (Foord) 1891	Cretaceous (Cenomanian)	England
<i>C. sharpei</i> (Schlüter) 1876	Cretaceous (Cenomanian)	Germany
<i>C. ? sinuatoaplicatus</i> (Geinitz) 1843	Cretaceous (Upper)	Germany
<i>C. straticostatus</i> (Crick) 1907	Cretaceous	Natal, Africa
<i>C. suciense</i> (Whiteaves) 1879	Cretaceous (Upper)	Sucia Island (Group, B. C.)
<i>C. tenuicostatus</i> (Schlüter) 1876	Cretaceous (Cenomanian)	Germany
<i>C. tourtia</i> (Schlüter) 1876	Cretaceous (Cenomanian)	Germany
<i>C. tsaltsithelensis</i> (Rouchadzé) 1931	Cretaceous (Aptian)	Russia
<i>C. tsukushiense</i> (Kobayashi) 1954	Oligocene	Japan
<i>C. undulatifomis</i> Spath, 1927	Cretaceous (Neocomian)	Tanganyika

Species	Stratigraphic Distribution	Geographic Distribution
<i>C. ventroplicatus</i> (Foord) 1891	Cretaceous (Cenomanian)	England
<i>C. virgatus</i> (Spengler) 1910	Cretaceous (Albian)	India
<i>C. woodsi</i> (v. Hoepen) 1921	Cretaceous (Upper)	South Africa

Genus *PARACYMATOCERAS* Spath, 1927

Paracymatoceras Spath, 1927a, pp. 21, 25.

Paracymatoceras Miller and Harris, 1945, p. 9.

Paracymatoceras Kummel, 1953a, p. 4.

Type species. *Nautilus asper* (Oppel) Zittel, 1868, pl. 3, fig. 1 (by original designation). Illustrated on Plate 19, figures 1, 2 and Text Figure 23G, of this report.

Most of the other genera of the Cymatoceratinae are distinguished from *Cymatoceras* on differentiations of the conch form or sculpture. *Paracymatoceras* differs from *Cymatoceras* essentially only in the greater elaboration of the suture. It is also generally agreed that in respect to the suture *Cymatoceras* and *Paracymatoceras* intergrade (Fig. 24). The conch form, degree of involution, and shell sculpture agree perfectly with *Cymatoceras*. The type species — *P. asper* — which is of Upper Jurassic age, has a rounded ventral groove on the most adoral part of the living chamber (Fig. 23G). This feature is not present in any of the five Cretaceous species of *Paracymatoceras* known to date. Aside from the ventral groove in the type species, the conch form in the other species assignable to *Paracymatoceras* are completely similar to or within the range of variation of *Cymatoceras*.

Six species can be assigned to this genus ranging in age from Upper Jurassic through the Cretaceous. Four of the species are Lower Cretaceous in age. The genus does not appear to be a common element in nautiloid faunas but it has been recorded from India, Europe, Texas, and Mexico (Figs. 21, 22). Some juvenile forms from the Lower Cretaceous Pawpaw formation of Texas with perfectly smooth conchs have been recorded by Kummel (1953a). These specimens are of interest in emphasizing the difficulties in identifying weakly-ribbed *Paracymatoceras* and differentiating these from *Hercoglossa*.

DISTRIBUTION OF SPECIES OF THE GENUS PARACYMATOCERAS

Species	Stratigraphic Distribution	Geographic Distribution
<i>P. asper</i> (Oppel) 1865	Jurassic (Upper)	Europe
<i>P. karpinskyi</i> (Karakasch) 1907	Cretaceous (Lower)	Crimea
<i>P. ? milleri</i> Humphrey, 1949	Cretaceous (Aptian)	Durango, Mexico
<i>P. rota</i> (Blanford) 1861	Cretaceous (Albian, Maestrichtian)	South India, Madagascar
<i>P. texanum</i> (Shumard) 1860	Cretaceous (Lower)	Texas (U.S.A.)
<i>P. trichinopolitensis</i> (Blanford) 1861	Cretaceous (Senonian)	South India; East Indies?

Genus PROCYMATOCERAS Spath, 1927

Procymatoceras Spath, 1927a, pp. 21, 25.

Procymatoceras Miller and Harris, 1945, p. 11.

Type species. *Nautilus subtruncatus* Morris and Lycett, 1850, pl. 1, fig. 2
(by original designation).

The genotype described and figured by Morris and Lycett does not seem to be available. Several topotype specimens are in the collections of the British Museum (Natural History) one of which is illustrated on Plate 17 and the cross section of the same specimen in Text Figure 25. From a study of topotype specimens and the original description of the type species the following diagnosis of *Procymatoceras* can be made.

The conch is robust, rapidly expanding, very involute to ocluded. Whorl section generally wider than high. On the living chamber the venter and whorl sides are flattened. The ventral and umbilical shoulders are well rounded. The whorl sides converge towards the venter. The earlier volutions are more rounded in outline. The surface of the conch bears sinuous ribs that form a broad sinus on the venter. The ribs appear to be fasciculate growth lines and may not be homologous with those of typical *Cymatoceras*. The ribbing is most distinct on the living chamber. The sutures are only slightly sinuous with shallow ventral and dorsal lobes.

When Spath (1927a) first established *Procymatoceras* he included only the type species and *P. baberi* (Morris and Lycett) both from the Middle Jurassic of Great Britain. The topotype specimen of *P. subtruncatus* illustrated on Plate 17, and on Text

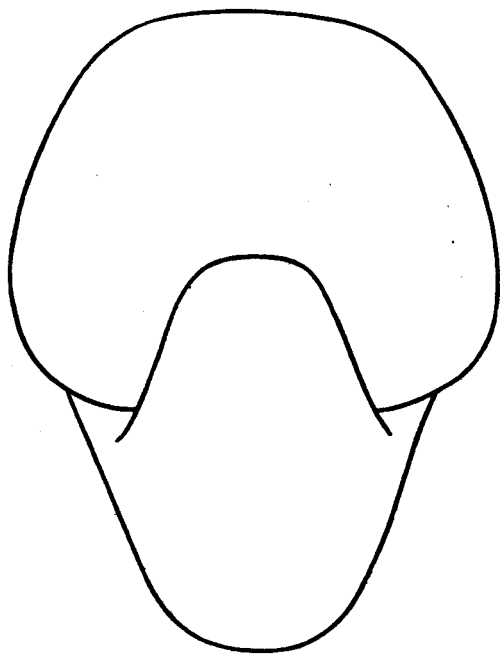


Fig. 25. *Procymatoceras subtruncatus* (Morris and Lycett). Diagrammatic cross section of topotype represented by figures 1, 2, Plate 17, X 0.50.

Figure 25, clearly shows the robust involute character of the conch and the subtrapezoidal outline of the whorl section. Neither the suture nor the siphuncle are visible. *Nautilus intumescens* Waagen has been referred with question to *Procymatoceras*. I agree with Spath (1927a, p. 33) that it is doubtful whether Noetling's (1896) specimens from Baluchistan assigned to *N. intumescens* Waagen are correctly identified. The only

other species that appears to belong to this genus is *Paracenoceras costatum* Scott (1943).

Genus CYMATONAUTILUS Spath, 1927

Cymatonautilus Spath, 1927a, p. 21.

Cymatonautilus Miller and Harris, 1945, p. 9.

Type species. *Nautilus julii* (Baugier MS) d'Orbigny, 1850, p. 328 (by original designation).

The type species of this unusual Jurassic cymatoceratid was originally briefly diagnosed but not illustrated by d'Orbigny (1850, p. 328) who gave Baugier the credit as author of this species. However, Baugier's name apparently was only a manuscript name, and was never published by him. The first complete description and illustration of *Nautilus julii* was published by Guéranger (1865, p. 189, pl. 3). Guéranger's figures are reproduced here on Plate 18, figures 1-4.

This genus can be diagnosed as follows: Conch widely umbilicate, robust, whorls subquadratic, being slightly wider than high. The whorl sides are flattened and with a broad lateral groove. The venter is likewise flattened and with a median groove. The conch bears sinuous ribs that obliquely cross the suture and form a deep ventral sinus. The suture forms a shallow ventral lobe and a broad concave lateral lobe. The siphuncle is subcentral in position, being closer to the dorsum than the venter. The type specimen came from strata of Callovian age in France. Petittclerc (1926) has described and illustrated a specimen of the same species from strata of Bathonian age in France. *Nautilus mojsisovicsi* Neumayr (1870) from Upper Jurassic strata of Austria most probably also belongs in *Cymatonautilus*.

The most distinctive features of this genus are the wide umbilicus and the grooved venter and whorl sides. Most species of the Cymatoceratinae are involute forms.

Genus ANGLONAUTILUS Spath, 1927

Anglonautilus Spath, 1927a, pp. 21, 25.

Anglonautilus Miller and Harris, 1945, p. 8.

Type species. *Nautilus undulatus* J. Sowerby, 1813, pl. 40, upper figure (by original designation).

Sowerby's type specimen does not appear to be in the British Museum, but the specimen referred to by Foord (1891, p. 245) labelled "*Nautilus undulatus*, M. C. 182" in Sowerby's handwriting is figured here, Plate 20, figures 1, 2, and Text Figure 26. This specimen is also numbered B.M.N.H. 66336. Dr. L. F. Spath kindly informs me that this specimen is unlocalized, but

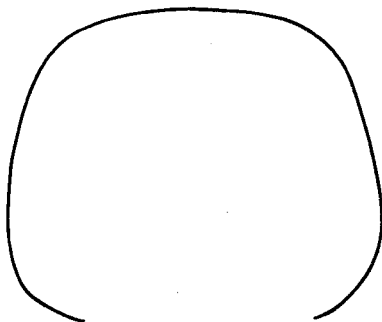


Fig. 26. *Anglonautilus undulatus* (Sowerby). Diagrammatic cross section of adoral part of living chamber of topotype represented by figures 1, 2, Plate 20, X 1.

undoubtedly is a topotype from Nutfield, Surrey. This specimen is incomplete consisting only of two camerae of phragmocone and one-third whorl of living chamber. However, it shows clearly the most diagnostic feature of the genus, that is the large, fold-like undulations which are most prominent on the venter and decrease rapidly on the flanks. The suture forms a very shallow ventral lobe and a broad shallow lateral lobe. The siphuncle is subcentral in position being nearer the dorsum than the venter.

In addition to the type species which is known from Aptian to Cenomanian strata in England and various localities in Europe (*vide* Foord, 1891, p. 244), *Nautilus subalbensis* Sinzow (1913) and *N. begudensis* Kilian and Reboul (1915) should be included in *Anglonautilus*. The former species is from Albian strata in the Crimea and the latter from Hauterivian strata in southern France.

Genus EUCYMATOCERAS Spath, 1927

Eucymatoceras Spath, 1927a, pp. 21, 22, 25.

Eucymatoceras Miller and Harris, 1945, p. 9.

Type species. *Nautilus plicatus* Fitton, 1835, p. 129 (by original designation).

The type specimen was not available for study but several conspecific forms are in the British Museum. One of these specimens from the Lower Greensand, Atherfield, Isle of Wight (B.M.N.H. C335) is illustrated on Plate 21, and the cross section

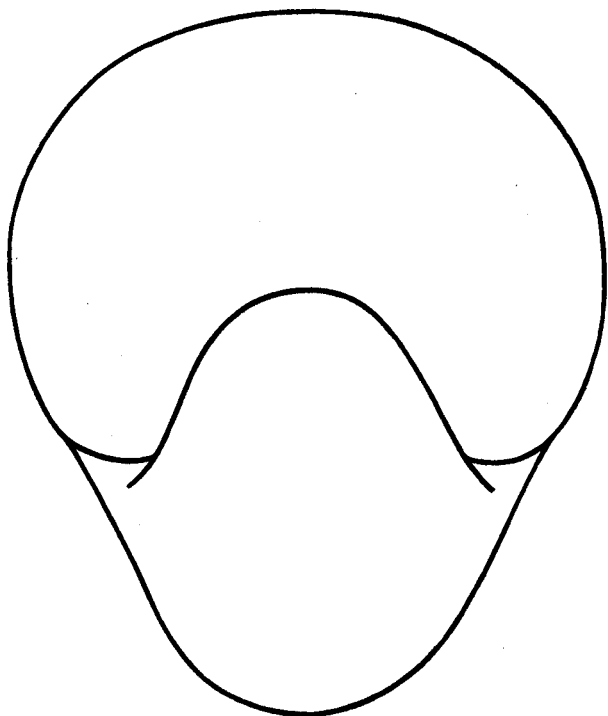


Fig. 27. *Eucymatoceras plicatus* (Fitton). Diagrammatic cross section of plesiotype represented by figures 1, 2, Plate 21, X 1.

in Text Figure 27. The only previous illustrations of the type specimen are the original woodcut in Fitton (1835, p. 129) and figures in d'Orbigny (1840, pl. 10; *Nautilus requienianus* d'Orbigny 1840 = *N. plicatus* Fitton 1835) and in Uhlig (1883, pl. 3).

The genus can be diagnosed as follows: Conch subglobular, involute, umbilicus closed, whorl section rounded, broader than high. Suture only slightly sinuous. The siphuncle is small and subcentral. Surface of conch with prominent ribs that form a deep angular V-shaped ventral sinus and on the whorl sides a similar but asymmetrical salient.

The most diagnostic feature is the V-shaped pattern of the ribs by which it can easily be distinguished from any other genus of the Cymatoceratinae. At present only three species of *Eucymatoceras* have been recorded, namely *N. plicatus* Fitton, the type species, and *N. steveni* Karakasch (1907, p. 30, pl. 2, fig. 13; pl. 8, fig. 12) from Lower Cretaceous formations of the Crimea; and *N. stschurousskii* Milashevitch, (1877, p. 125, pl. 1, figs. 11, 11a) from the Lower Cretaceous of Russia. All of these species have the depressed, subglobular, rounded conchs. From the great variability in conch form in *Cymatoceras* it is doubtful if the conch form in the known species of *Eucymatoceras* can be considered a diagnostic character.

Genus SYRIONAUTILUS Spath, 1927

Syrionautilus Spath, 1927a, pp. 21, 25.

Syrionautilus Miller and Harris, 1945, p. 11.

Syrionautilus Avnimelech, 1946, pp. 523-528; 1947a, p. 690.

Type species. *Nautilus libanoticus* Foord and Crick, 1890, p. 404, fig. 6 (by original designation).

All the specimens of *Nautilus libanoticus* in the British Museum (Natural History) upon which Spath established his genus *Syrionautilus* are more or less crushed and distorted. One of the syntypes with an attached mandible is figured here on Plate 7, figure 3 (previously figured by Foord, 1891, p. 371, fig. 82.). The general form of the conch is like that of *Cymatoceras* but the character of the ribbing is quite distinct. In *Syrionautilus* the ribs are acute and separated by interspaces rather exceeding their own width. The type of ribbing is very similar to that of *Prochlydonautilus spirolobus* of the Upper Triassic. The form and spacing of the ribs in *Syrionautilus* are the distinguishing characters that serve to separate it from allied genera of the Cymatoceratinae. The position of the siphuncle and nature of the suture are not known. The type and only

species so far referable to this genus comes from Senonian formation of Syria.

Recently Avnimelech (1946, 1947a) has published two short notes on additional specimens of *Syrionautilus libanoticus* from Palestine. As with the types, this new material is also incomplete and generally crushed. However, the best and nearly complete specimen was figured by Avnimelech (1947a, pl. 15). Even though this figured specimen is also compressed it clearly shows *Syrionautilus* to have an involute, compressed conch and arched venter. In other words, it has a typical cymatoceratid conch but differs in the character of the ribs.

Genus *HEMINAUTILUS* Spath, 1927

Heminautilus Spath, 1927a, pp. 22, 25.

Vorticoceras Scott, 1940, pp. 1074, 1075.

Heminautilus Scott 1943, p. 89.

Heminautilus Durham, 1946, p. 432.

Platynautilus Yabe and Ozaki, 1953, pp. 55-61.

Type species. *Nautilus saxbii* Morris, 1848, p. 106 (woodcut); Pl. 10, figs. 1, 2 of this report (by original designation).

When Spath established this genus he designated *Nautilus saxbii* Morris (1848, p. 106, woodcut) as genotype and thought this species was the same as *N. lallierianus* d'Orbigny (1841). The latter species was first very briefly diagnosed but not illustrated by d'Orbigny in 1941 in the *Revue Cuvierienne* (p. 318), and was listed the same year in his *Paléontologie Française, Terrains Crétacés* (p. 620). *Nautilus lallierianus* was again cited by d'Orbigny in his *Prodrome* (1850, t. 2, p. 112), and *N. saxbii* was listed as a synonym. In none of these publications is there an illustration and only the first (1841, p. 318) has a very brief diagnosis. *N. lallierianus* was next described and illustrated from Switzerland by Pictet and Campiche (1859). Douvillé (1916) gave a very complete description with several figures of specimens of *N. lallierianus* from Aptian strata east of Suez. Douvillé likewise placed *N. saxbii* in synonymy of *N. lallierianus*. Foord (1891) recognized both of these species.

The type specimen of *Nautilus saxbii* is illustrated on Plate 10, figures 1, 2, and the cross section in Text Figure 28. The only previous illustrations of this specimen are the woodcuts in Morris (1848, p. 106) and Foord (1891, p. 311, fig. 68). Since

d'Orbigny's *N. lallierianus* has not been illustrated, and the description is very brief, it is impossible to tell whether it is conspecific with *N. saxbii*. *Nautilus lallierianus*, Douvillé (1916) is sufficiently distinct from *N. saxbii* Morris in the form of the septa and ornamentation of the conch to keep these two species separate. The plaster casts of the specimen of *N. lallierianus* figured by Pictet and Campiche (1859, pl. 19, figs. 6a, 6c) are in the Museum of Comparative Zoology. These show no surface ornamentation whatsoever. The tricarinate character of the venter is not as well preserved as the figures by Pictet and Campiche would lead one to believe.

The genus *Heminautilus* can be diagnosed as follows: Conch involute, very compressed, whorls much higher than wide. Whorl sides flattened and strongly converge towards a narrow, flattened or slightly concave venter. The ventral shoulders are angular. The venter on the earlier volutions is rounded. The umbilical shoulders are broadly rounded. Greatest width of the conch is just ventral of the umbilical shoulders. The suture is rather sinuous with a ventral lobe, a subangular saddle on the ventral shoulder, broad deep lateral lobe and a narrowly rounded saddle on the umbilical shoulder. The siphuncle is subcentral in position lying closer to the dorsum than the venter. The conch bears sinuous ribs that curve strongly aborally over the ventral half of the whorl side. The ribbing may be very weak and in fact is absent on the type of *Nautilus saxbii* (which is probably a juvenile).

Spath originally placed *Heminautilus* in his Paracenoceratidae with question and made note of the possibility that it more properly belonged in his Cymatoceratidae. The Paracenoceratinae are characterized by differentiation of the periphery, generally associated with increase in sinuosity of the suture line, and a ventral lobe (Spath, 1927a, p. 25). However, the sutures of *Heminautilus* are much more sinuous (Fig. 20). The Paracenoceratinae have smooth shells, devoid of ribbing. *Tithonoceras*, and *Aulaconautilus* have longitudinal ribs or carinae on the ventral area but no sculpture on the flanks. Sinuous cymatoceratid-like ribbing is characteristic of *Heminautilus*. The ribbing is well preserved on the specimens of *H. lallierianus* figured by Douvillé (1916, pl. 17, figures 2-6) and on *H. rangei* Hoppe (1922, pl. 4, figures 2, 3). Among the specimens illus-

trated by Douvillé there is some variability in the strength and patterns of the ribs. On the earlier volutions the ribs are low, broad, and rounded and decrease towards the venter. The mature specimen of Douvillé's (1916) figure 5, plate 17, has a smooth outer volution, whereas the larger specimen of figure 6a, b, shows prominent ribs that are very broad and separated by narrow concave interspaces. In *Heminautilus etheringtoni* Durham (1946) the ribs are most prominent on the living chamber

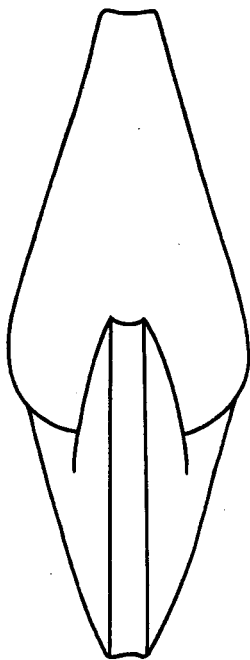


Fig. 28. *Heminautilus saxbii* (Morris). Diagrammatic cross section of holotype represented by figures 1, 2, Plate 10, X 1.

which is about one-third of a volution in length. Topotype specimens of *Heminautilus etheringtoni* kindly loaned to me by J. Wyatt Durham show rather distinct ribbing on early volutions, with a single large topotype smooth except for prominent growth

lines. A crushed and weathered specimen, not referred to by Durham (1946), from near the top of the basal Velez Sandstone measures approximately 145 mm. in diameter and has very prominent "cymatoceratid" ribs. The ventral area likewise appears to have a median longitudinal rib. With the material available it cannot be determined whether or not this specimen is conspecific with *H. etheringtoni*. They do not come from the same horizon within the Aptian. No data are available on the degree and extent of variation in the sculpture of this or most species of nautiloids. It is very rare that really representative populations can be collected.

Heminautilus tyôsiensis (Yabe and Ozaki) 1953, shows prominent growth lines on the venter that form a deep V-shaped pattern. On the lateral whorl sides low radial folds with broader intervals are present on the type (and only) specimen of this species. These authors proposed a new genus — *Platynautilus* — for their new species, but it is clearly a representative of *Heminautilus* and thus *Platynautilus* is placed in synonymy.

Heminautilus stantoni (Scott) has broad, low, rounded and widely spaced ribs reaching their greatest prominence on the middle of the flanks. *Heminautilus saxbii*, the type specimen which is figured here on Plate 10, figures 1, 2, is perfectly smooth but is probably not a mature specimen.

The suture in most species of the Cymatoceratinae are only very slightly sinuous. *Paracymatoceras* has a well-developed, deep, lateral lobe followed by a saddle on the umbilical shoulder. The suture across the venter generally develops a ventral saddle, not a lobe. *Cymatonautilus julii* has a deep ventral lobe, and a broad lateral lobe with the beginnings of a saddle on the umbilical region. "*Nautilus*" *vaelsensis* (Binckhorst, 1861) is a very compressed form with a subrectangular whorl section and a wide, shallow umbilicus. The truncate venter and compressed conch are very reminiscent of *Heminautilus* except in the difference of involution. The suture of "*Nautilus*" *vaelsensis* has a very shallow ventral lobe and a broad, shallow, lateral lobe.

The six known species of *Heminautilus* are from Lower Cretaceous formations in Arkansas, England, France, Switzerland, Egypt, Palestine, Colombia, and Japan.

DISTRIBUTION OF SPECIES OF THE GENUS *HEMINAUTILUS*

Species	Stratigraphic Distribution	Geographic Distribution
<i>H. etheringtoni</i> Durham, 1946	Cretaceous (Aptian)	Colombia
<i>H. lallierianus</i> (d'Orbigny) 1840	Cretaceous (Neocomian)	Europe, Egypt, Ethiopia
<i>H. rangei</i> (Hoppe) 1922	Cretaceous (Albian)	Palestine
<i>H. saxbii</i> (Morris) 1848	Cretaceous (Aptian)	England, France
<i>H. stantoni</i> (Scott) 1940	Cretaceous (Aptian)	Arkansas (U.S.A.)
<i>H. tyôsiensis</i> (Yabe and Ozaki) 1953	Cretaceous (Aptian?)	Japan

Genus *DELTOCYMATOCERAS* n. gen.

Type species. *Nautilus leiotropis* Schlüter, 1876, p. 175, pl. 48, figs. 1, 2 (Plate 22, figures 1, 2 of this paper).

The adaptive radiation within the Cymatoceratinae is expressed in patterns that are homeomorphous with evolutionary trends in other phyletic lines within the Nautilidae. Modification of rib patterns, conch shape, and suture are the more obvious characters which express evolution within the subfamily. The present genus is established for those cymatoceratids with a more or less triangular outline of the whorl section. The type species — *Nautilus leiotropis*, and *N. rugatus* (Fritsch and Schlönbach) are the only species known to date that can be placed in this genus. The triangular outline of the whorl section serves readily to differentiate this genus from all others within the Cymatoceratinae.

The type species has a large, inflated, involute conch with broadly arched and strongly convergent whorl sides. The venter is marked by a slight rounded, smooth, keel-like ridge. There are no distinct ventral shoulders, the ventral region grading evenly onto the flanks. The flanks have prominent cymatoceratid ribs that bifurcate near the middle of the whorl sides. The ribs do not cross the keel-like ridge on the venter. The suture forms a narrow, somewhat pointed, ventral saddle, a broad,

rather shallow lateral lobe, and a prominent saddle on the umbilical shoulder. The position of the siphuncle is not known.

The distinctive subtriangular whorl section with the smooth keel-like ridge on the venter set *Deltocymatoceras leiotropis* apart from all other cymatoceratids. In conch form and suture pattern *Deltocymatoceras* is homeomorphous with *Angulithes* of the Hercoglossinae, being distinguished by its ribbing. *Angulithes* is most probably a development of *Cimomia*, a form with a more rounded whorl shape. *Deltocymatoceras* is best visualized as a sagittate derivative of *Cymatoceras* which shows much variation in conch shape.

The type species of *Deltocymatoceras* comes from Upper Cretaceous (Emscher-Mergel) of Germany. The original is in the Museum of the University of Bonn (*vide* Schlüter, 1876, p. 175). *Deltocymatoceras rugatus* comes from Upper Cretaceous strata of Bohemia.

Genus EPICYMATOCERAS n. gen.

Type species. Nautilus vaelsensis Binckhorst, 1861, p. 15, pl. 5c, figs. 2a, b, c.

This new genus is established for a species of Upper Cretaceous nautiloid that has a most unusual conch shape for post-Triassic nautiloids. The species has been described and figured by Binckhorst (1861, p. 15, pl. 5c, figs. 2a, b, c) and Schlüter (1876, p. 177, pl. 51, figs. 3-4). Schlüter's figure is reproduced here on Plate 23, figs. 1, 2.

Nautilus vaelsensis has an evolute and greatly compressed conch. The umbilical diameter is approximately 25 per cent of the diameter of the conch. The whorl section is subquadrate, being nearly twice as high as wide. The ventral shoulders are angular, the venter narrow and flattened. The lateral flanks are only slightly inflated. The umbilical shoulders are broadly arched. The suture inscribes a very shallow ventral lobe and a shallow lateral lobe. The position of the siphuncle is not known. The conch bears fine sinuous ribs that curve backwards toward the ventral shoulder and form a slight sinus on the venter.

Epicymatoceras is distinguished from all other genera of the Cymatoceratinae by its compressed, evolute conch and flattened venter. It is the ribbing which attaches this genus to the Cyma-

toceratinae. Among the Cymatoceratinae the only group somewhat similar is *Heminautilus* which is likewise compressed in conch form and with a flattened venter. However, in *Heminautilus* the whorl section is much more inflated near the umbilical shoulders and the flanks more convergent. Likewise this genus is very involute and with a more sinuous suture. Most of the remaining genera and species of the Cymatoceratinae have more involute and inflated conchs.

The presence of cymatoceratid ribbing readily differentiates *Epicymatoceras* from other subfamilies of the Nautilidae. There is some similarity in conch shape of *Epicymatoceras* with that of *Pseudocenoceras* of the Nautilinae. However, in that genus the smooth conch has a well rounded ventral area, steep umbilical shoulders, and is more involute.

The type and only species of this genus has been identified from Upper Cretaceous (Maestrichtian) strata at Vaels near Aachen (Germany) and at Limbourg (Belgium) just south of Aachen.

Subfamily HERCOGLOSSINAE Spath, 1927

Spath (1927a) originally erected this family to include the following genera: *Pseudaganides* Spath of the Jurassic and lowermost Cretaceous; *Hercoglossa* Conrad, Upper Cretaceous to Eocene; *Hercoglossoceras* Spath, Liassic; *Pseudonautilus* Meek, Upper Jurassic; *Paraturia* Spath (= *Aturoidea* Vredenburg), Cretaceous to Eocene; and *Deltoidonautilus* Spath, Eocene. Later he (Spath 1927b) included *Cimomia* Conrad, and Stenzel (1940) added his genus *Woodringia*. Restudy of this group alters the above interpretation in many important details. The Jurassic hercoglossids, namely *Pseudaganides* and *Pseudonautilus* are interpreted as a distinct phyletic line from the Cretaceous-Eocene trend involving *Hercoglossa* itself (see page 389). *Hercoglossoceras* is considered to be a synonym of *Pseudaganides*. It is merely an early, highly compressed "aganitici" and is part of the radiation from the cenoceratid complex which went in for highly modified sutures (*Pseudaganitinae*). Adaptation towards modified (highly sinuous) sutures is a trend that has occurred many times in the evolutionary history of the nautiloids. Within the Upper Paleozoic few nautiloids are known with

highly sinuous sutures. The most extreme development is that found in *Permoceras bitauniensis* (Haniel) from strata of Leonard age in Timor. *Grypoceras* (*Plummeroceras*) *plummeri* Kummel (1953c) of the Grypoceratidae from beds of Leonard age in Texas has a deep ventral lobe and lateral lobe. When Miller and Collinson (1953) established the genus *Permoceras* they also erected the family Permoceratidae for their monotypic genus. It appears more likely that *Permoceras* is an aberrant development from the *Domatoceras-Grypoceras* evolutionary line and should be included in the Grypoceratidae.

In the Triassic, the first large-scale adaptation towards highly modified sutures appears in the Clydonautilidae, Gonionautilidae, and Siberionautilidae all of the Upper Triassic. The sutural patterns seen in these groups are closely similar to those of the *Pseudaganides-Pseudonutilus* trend of Jurassic age and to the *Hercoglossa-Aturoidea* trend of Cretaceous-Eocene age. The details have been discussed previously (p. 389) and the evidence seems quite strong that in the Mesozoic there were three separate radiations built largely around modification of the suture, the first in the Triassic, the second in the Jurassic, and the third in the Cretaceous. A similar adaptive trend also took place in the Cymatoceratinae. Since the basic sutural type must surely be an adaptive character it is no more than to be expected that repetition of similar forms will be produced. For the above reasons *Pseudaganides* and *Pseudonutilus* are considered a separate phyletic development and placed in the subfamily Pseudaganidinae.

Deltoidonutilus Spath is considered to be a synonym of *Angulithes* Montfort (Kummel 1953a). Spath placed *Angulithes* in the Nautilidae but it is here considered part of the Hercoglossinae. *Woodringia* Stenzel (1940) is placed as a synonym of *Hercoglossa* since the character upon which it was distinguished—a slight ventral lobe in the ventral saddle—is of no more than specific importance in other genera of this subfamily.

Thus, as now interpreted, the Hercoglossinae include the following genera: *Hercoglossa* Conrad, *Cimomia* Conrad, *Angulithes* Montfort, and *Aturoidea* Vredenburg. These genera are all characterized by involute, smooth, conchs with modified sutures. As has been shown by Miller (1947, 1949) on several occasions this group of genera appears to form a linear series

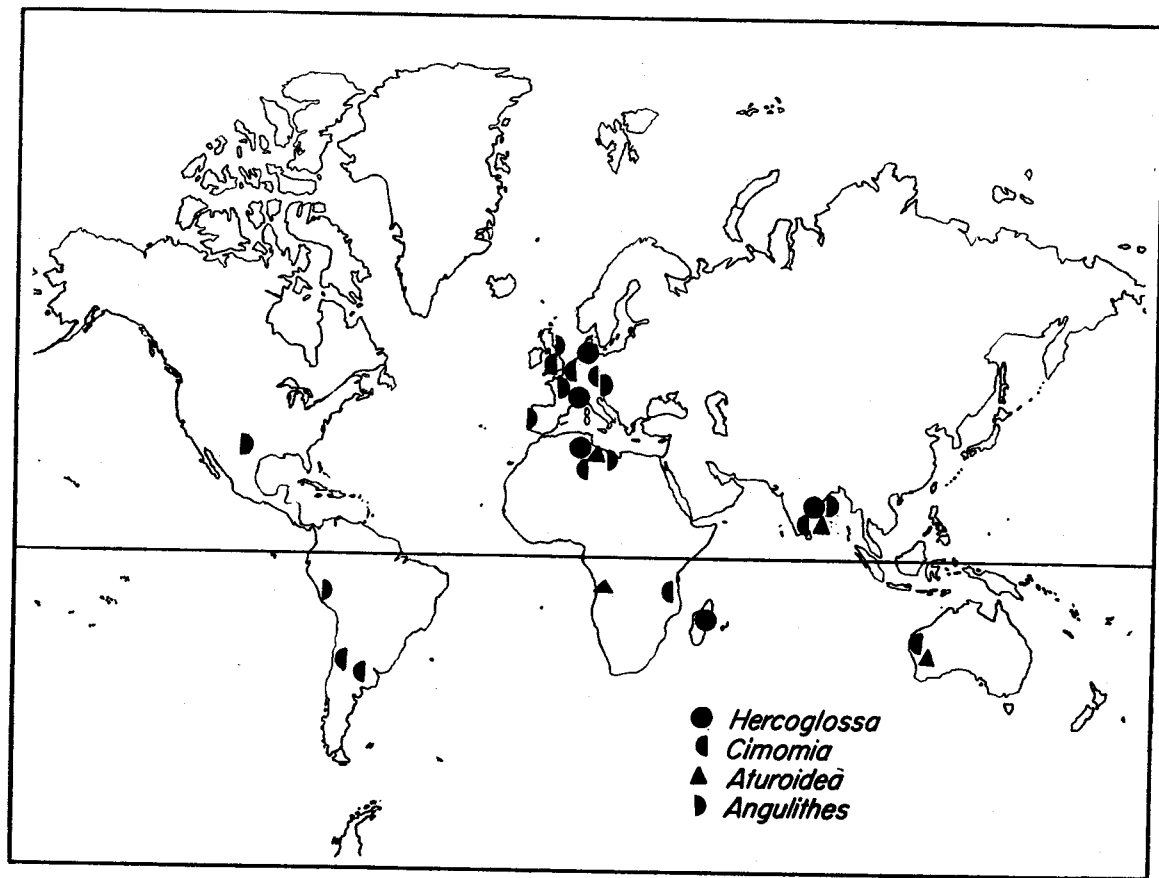


Fig. 29. Geographic distribution of species of the subfamily Hercoglossinae in formations of Cretaceous age.

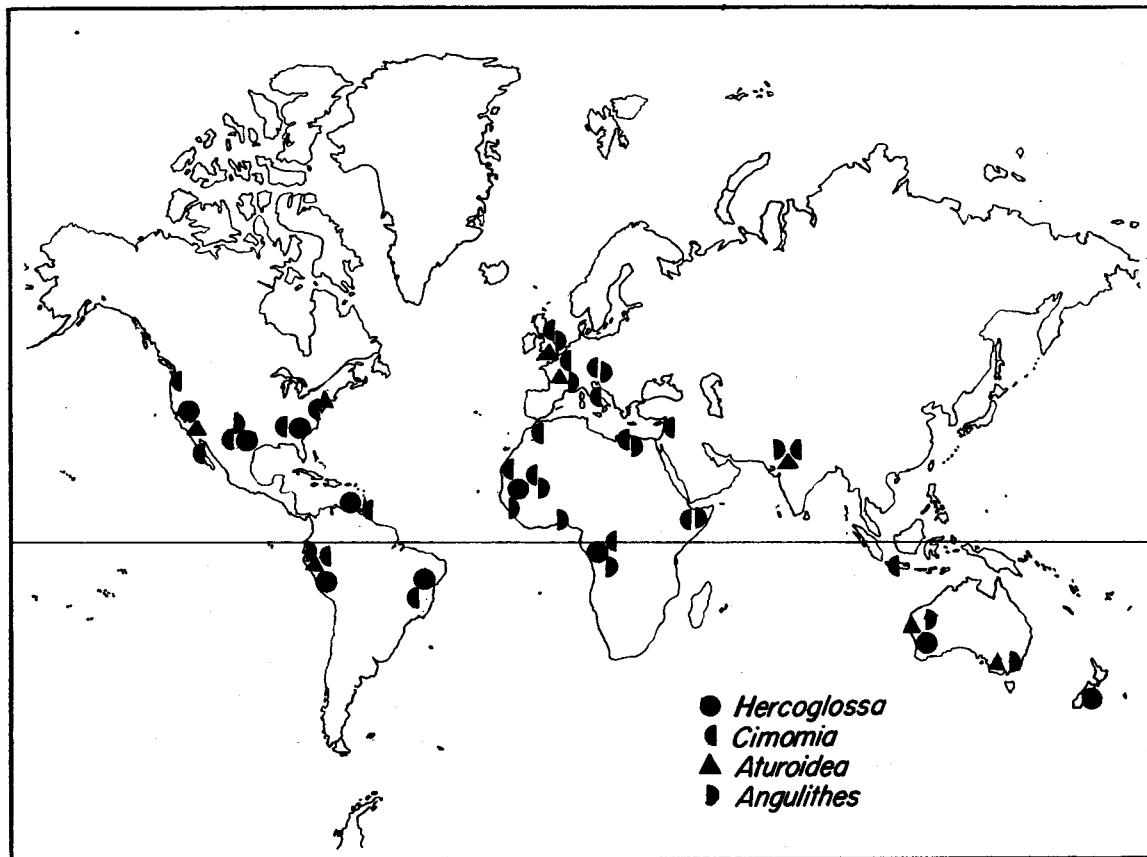


Fig. 30. Geographic distribution of species of the subfamily Hercoglossinae in formations of Paleocene, Eocene, and Oligocene age.

of increasing sinuosity in the suture ranging from *Cimomia* to *Hercoglossa* to *Aturoidea*. *Angulithes* is probably a special development out of *Cimomia* maintaining an approximate cimomid type of suture but modifying the whorl section to a subtriangular shape rather than rounded. *Cimomia* is readily derived from *Eutrephoceras* with which it is more or less gradational. Since the genera of this subfamily (with the exception of *Angulithes*) are separated on the basis of increasing sinuosity of the suture, it is understandable that there should be gradational forms. These gradational forms are found especially between *Eutrephoceras* and *Cimomia* and between *Cimomia* and *Hercoglossa*. It has been generally assumed that each of these units had a single time of origin and thereafter were distinct genetic stocks (Miller, 1949). An alternative interpretation is, however, possible; that is, that there were several times in the Cretaceous and Tertiary when radiations towards sinuosity of the suture occurred and what is normally included in the genus *Cimomia* is a group of transitional species and not part of a single linear trend. The kind and nature of the data available, however, is not sufficient to test this suggestion. The eutrephoceratid-evolving stock is the parent stock of several radiations (generic groups) of rather diverse morphology. The fact that the genetic potential of the group shows variability in conch shape and suture, is no reason why any number of these variants in suture could not become in themselves genetically distinct, to become part of the species complex included in *Cimomia*.

All four of these genera occur in the Cretaceous and range into the Eocene or Oligocene. *Cimomia* probably includes some Upper Jurassic species. In numbers of species, *Hercoglossa* has 21, *Cimomia* 44, *Angulithes* 32, and *Aturoidea* 11. The relatively large number of species is largely due to "monographic" highs, especially in Tertiary faunas.

Geographically, species of this subfamily are very widespread. The distribution of the Cretaceous species of the subfamily is illustrated on Figure 29, those of the Tertiary on Figure 30. The maps show very well the general overlap in range of all of the genera. None of the forms is sufficiently common at any of the localities indicated so that collections could be made for detailed population studies.

Genus *CIMOMIA* Conrad, 1866

Cimomia Conrad, 1866a, p. 102.

Cymomia Conrad, 1866b, p. 19.

Cymmomea Conrad, 1868, p. 732.

Cymomia Conrad, 1868, p. 732.

Cimomia Spath, 1927b, pp. 424-428.

Nautilus (*Javanoceras*) Martin, 1932, pp. 1, 2.

Cimomia Miller and Thompson, 1933, pp. 305-313.

Cimomia Stenzel, 1940, pp. 751-753.

Cimomia Miller, 1947, pp. 39-49.

Cimomia Miller, 1951, pp. 38-47.

Cimomia Haas and Miller, 1952, pp. 329-338.

Type species. *Nautilus burtini* Galeotti, 1837, from Eocene of Belgium, by original designation. Figured here on Plate 24.

Most of the species of this genus are Tertiary in age (Paleocene — Lower Oligocene) and the Tertiary species have in recent years been thoroughly discussed by Miller and Thompson (1933), Stenzel (1940), Miller (1947), Miller (1951), and Haas and Miller (1952). The very able diagnosis of the genus by Miller (1947, pp. 39-40) is quoted here: "Conch subglobular to subdiscoidal in shape and nautiliconic in its mode of growth. Whorls broadly rounded laterally, rounded ventrally, and impressed dorsally. Umbilicus small; umbilical shoulders low and broadly rounded. Surface of conch marked by growth lines but does not bear ribs or nodes. Septa numerous and each suture forms a broad very shallow broadly rounded or slightly retuse ventral saddle, a broad shallow broadly rounded lateral lobe, a narrower higher rounded lateral saddle (located near the umbilical shoulder), a broad rounded lobe on the umbilical wall, and a fairly prominent internal lateral saddle that extends to a broad rounded dorsal lobe. Siphuncle small, circular in cross section, and orthochoanitic in structure; its position varies considerably in different species, but in no case is it marginal."

Cimomia is in a sense a morphological transitional form, especially in its suture, between *Eutrephoceras* and *Hercoglossa*. In *Eutrephoceras* the suture is essentially straight, or only slightly sinuous; in *Hercoglossa* the suture has well defined lobes and saddles. In both of these genera there are transitional forms to *Cimomia*, reflected especially by the suture. That is, in *Cimomia* there is great variation in the intensity of the lateral

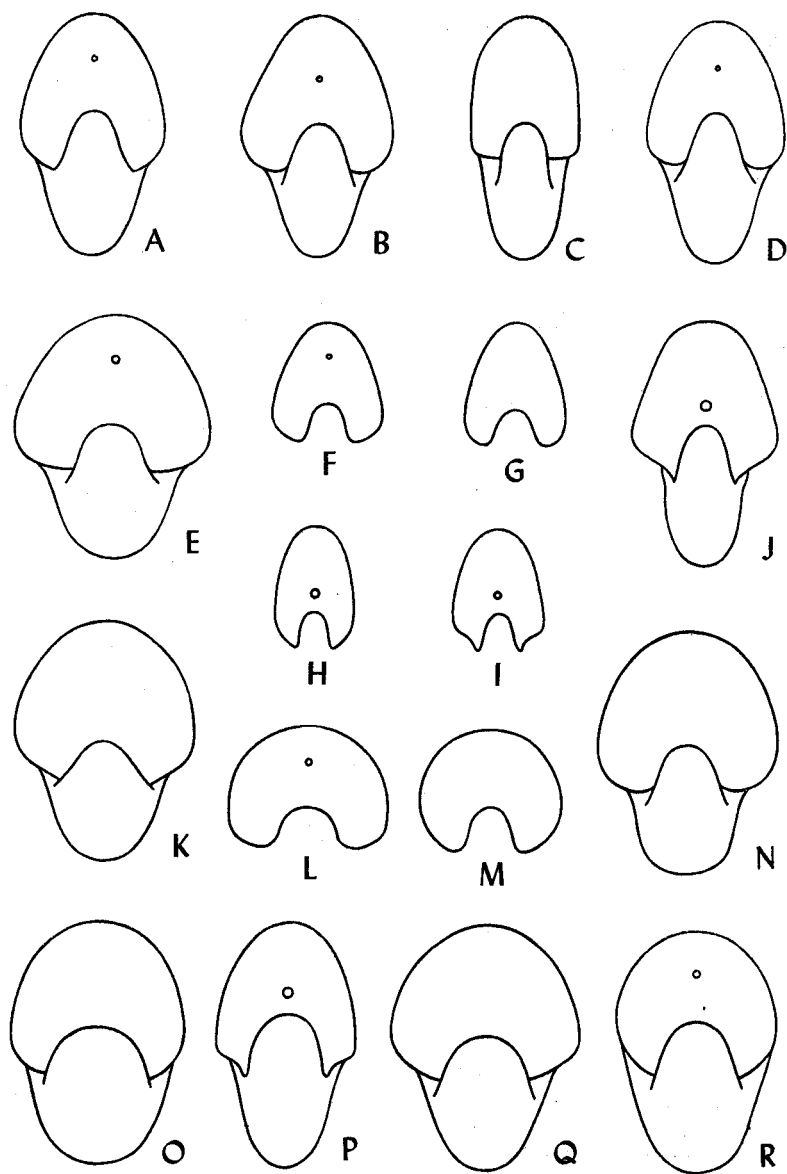


Figure 31

lobe and saddle (Fig. 32). There is likewise much variation in the shape of the conch (Fig. 31). I agree heartily with Miller (1947, p. 41) that *C. kugleri* and *C. vaughani* which have slight lobes in the ventral saddle should be retained in *Cimomia* and not separated from *Hercoglossa*, as *Woodringia* was, solely on this character. In both these species the median lobe is not developed until full maturity.

Most previous authors who have discussed this genus were mainly concerned with the species which occur in Tertiary formations. There are in addition to these, several species of Cretaceous and possibly Upper Jurassic age that should be assigned to this genus. There is first of all *Nautilus romeroi* Ihering (1903, pp. 195-196, fig. 1) of the "Étage Rocanéen" (Upper Cretaceous?) of the territory of Rio Negro in central Argentina, previously mentioned by Miller and Thompson (1935, p. 570) and Miller (1947, p. 41). Recently Miller (1951) has recorded poorly preserved specimens which most surely belong to *Cimomia* from Maestrichtian formation of Senegal. These specimens are too poorly preserved to accurately identify specifically, but there is no doubt as to their generic affinities. From Libya, in

Fig. 31. Cross sections of the conch of A, *Hercoglossa harrisi* Miller and Thompson, from Stenzel 1940, fig. 116, diameter 100 mm. $\pm$; B, *H. ulrichi* (White) from Stenzel 1940, fig. 116, diameter 170 mm.; C, *H.?* *forbesianus* Blanford 1861, pl. 13, fig. 2, diameter 75 mm.; D, *H. gardnerae* Stenzel 1940, fig. 116, diameter 145 mm.; E, *H. splendens* Stenzel 1940, fig. 120, diameter 73 mm.; F, *Hercoglossa orbiculata* (Tuomey) from Miller 1947, fig. 12, height 174 mm.; G, *H. meglameryae* Miller and Thompson, from Miller and Collinson 1951, fig. 1B, height 100 mm.; H, *Aturoidea vieirai* Miller 1951, fig. 16B, height 130 mm.; I, *A. parkinsoni* (Edwards) from Miller 1951, fig. 15A, height 180 mm., the genotype of *Aturoidea*; J, *A. paucifer* (Cope), from Miller 1947, fig. 18, diameter 228 mm.; K, *Cimomia vestali* Miller and Thompson, from Stenzel 1940, fig. 118, diameter 126 mm.; L, *C. haltomi* (Aldrich) from Miller 1947, fig. 8, height 104 mm.; M, *C. buccinaeformis* Haas and Miller 1952, fig. 2, height 29 mm.; N, *C. vaughani* (Gardner) from Stenzel 1940, fig. 118, diameter 59 mm.; O, *C. turcicus* (Krumbeck) 1905, pl. 7, fig. 6b, diameter 120 mm.; P, *C. haughti* (Olsson) from Miller 1947, fig. 9, diameter 60 mm.; Q, *C. subrecta* Miller and Thompson, from Stenzel 1940, fig. 118, diameter 120 mm.; R, *C. angustus* (Blanford), from Stoliczka 1866, pl. 93, fig. 42, diameter 40 mm.

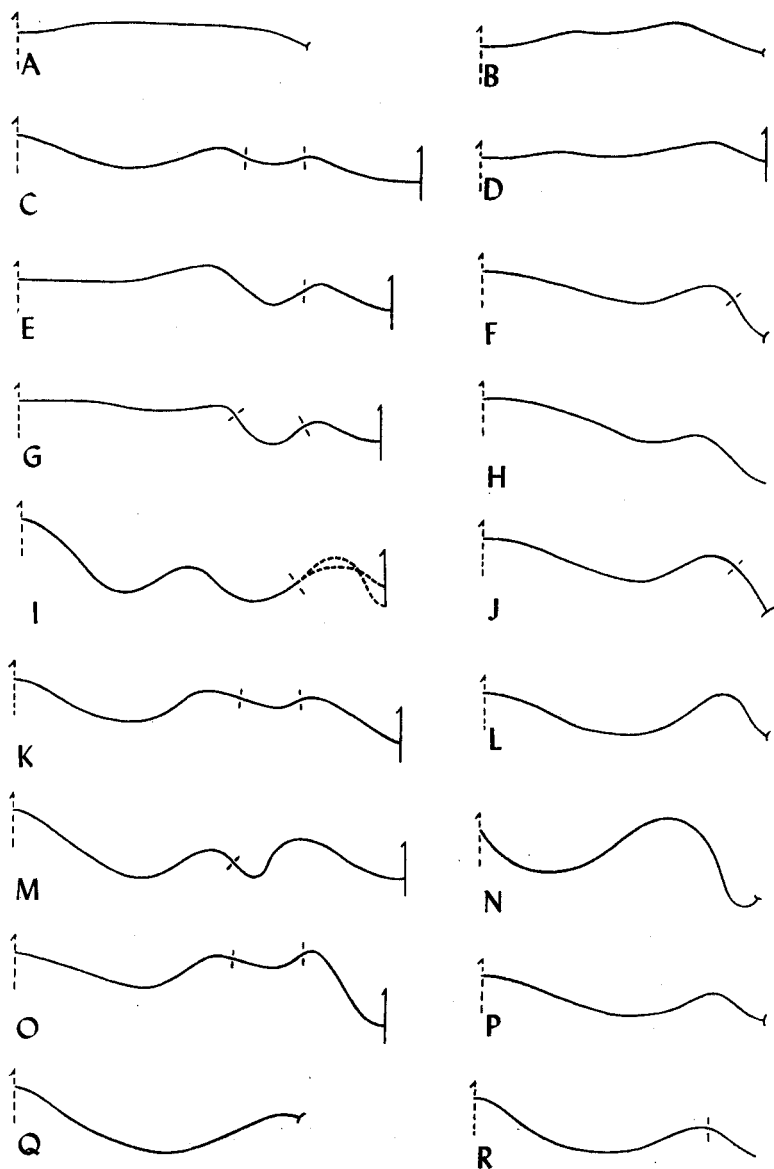


Figure 32

North Africa, Wanner (1902, p. 143) has described *Nautilus jordani*, from formations of Danian age, which is clearly a species of *Cimomia*. Alberici (1940, p. 187) lists the range of this species as Campanian to Danian. The lateral saddle next to the umbilical shoulder in both *C. romeroi* and *C. jordani* is well developed and more distinct than in many lower Tertiary species such as *C. septemcastrensis* Haas and Miller from Lower Eocene of British Somaliland and *C. sahariensis* (Keller) from Eocene? of French Sudan. Another Cretaceous species which should be placed in *Cimomia* is *N. angustus* Blanford (1861, p. 27, pl. 14, figs. 1, 2) from the Ootatoor group (Cenomanian) of south India. Stoliczka (1866, p. 209) records an additional specimen of this species from the Ariyalur group (upper Senonian) of south India. The type specimen of *N. angustus* is a much compressed form with a narrowly rounded venter, and is the most compressed species of *Cimomia* of which a record is available. Stoliczka's specimen (1866, pl. 93, fig. 4, 4a) is a more inflated form and more typical of most species of *Cimomia*. Spengler (1910, p. 145) expressed doubt as to whether Stoliczka's specimen is conspecific with that illustrated by Blanford. Even if these two specimens are not conspecific, they both belong in *Cimomia*. In both specimens the suture has the characteristic pattern found in *Cimomia*.

Fig. 32. Diagrammatic representation of sutures of *A*, *Eutrephoceras victorianum* (Teichert) 1947, fig. 7; *B*, *E. dekayi* (Morton) from Reeside, 1924, fig. 1d.; *C*, *Cimomia wylliei* (Newton) from Haas and Miller, 1952, fig. 5; *D*, *Eutrephoceras sloani* Reeside from Miller, 1947, fig. 6; *E*, *Cimomia landanensis* (Vincent) from Miller, 1947, fig. 7A; *F*, *Cimomia subrecta* Miller and Thompson, 1933, from Stenzel, 1940, fig. 119 (2); *G*, *Cimomia haltomi* (Aldrich) from Stenzel, 1940, fig. 119 (1); *H*, *Cimomia pseudobouchardianum* (Spengler) 1910, from Blanford, 1861, pl. 5, fig. 6; *I*, *Angulithes sowerbyi* (Wetherell) from Stenzel, 1940, fig. 124 (1); *J*, *Cimomia vestali* Miller and Thompson, 1933, from Stenzel, 1940, fig. 119 (4); *K*, *Angulithes molli* (Douvillé), from Miller, 1951, fig. 12A; *L*, *Cimomia macfadyeni* (Haas and Miller) 1952, fig. 4A; *M*, *Angulithes elliotti* (Stenzel) 1940, fig. 124 (2); *N*, *A. bakeri* (Teichert) 1947, fig. 3; *O*, *A. spathi* (Haas and Miller) 1952, fig. 7; *P*, *A. biyogorensis* (Haas and Miller) 1952, fig. 6; *Q*, *A. chudeaui* (Douvillé) from Miller, 1951, fig. 10B; *R*, *A. sp.* from Haas and Miller, 1952, fig. 8B. All figures greatly reduced.

The oldest species of *Cimomia* is thought to be *Nautilus turcicus* Krumbeck (1905, p. 137, pl. 14, fig. 6 a, b) from Upper Jurassic Glandarienkalkes of Libya. This species has an inflated, subglobular, smooth conch and a suture that is slightly sinuous with a rather weak lateral lobe followed by a broad very shallow saddle. As was pointed out above, gradational forms between *Eutrephoceras* and *Cimomia* are known; *N. turcicus* can surely be considered such a form. The shallow, but very distinct lateral saddle lying above the umbilical shoulder shows a clear pattern like that found in *Cimomia*, even though it is only weakly developed.

The distribution and age of the species of *Cimomia* are given below. In addition to these it should be noted that Teichert and Glenister (1952, p. 737) record the presence of undescribed species of *Cimomia* in beds of Upper Campanian to Lower Maestrichtian age from the northwest basin of Western Australia.

DISTRIBUTION OF SPECIES OF THE GENUS CIMOMIA

Species	Stratigraphic Distribution	Geographic Distribution
<i>C. angustus</i> (Blanford) 1861	Cretaceous (Upper)	south India
<i>C. blakei</i> (Avnimelech) 1947	Oligocene	Palestine
<i>C. buccinaeformis</i> Haas and Miller, 1952	Eocene	British Somaliland
<i>C. burtini</i> (Galeotti) 1837	Eocene	Belgium
<i>C. cantabrigiensis</i> (Foord) 1891	Cretaceous (Cenomanian)	England
<i>C. columbinus</i> (Fritsch and Schlönbach) 1872	Cretaceous (Cenomanian)	Bohemia
<i>C. cossmanni</i> (Vredenburg) 1928	Tertiary (Lower)	Pakistan
<i>C. crassiconcha</i> (Vogl) 1908	Eocene	Hungary
<i>C. d'orbignyianus</i> (Forbes) 1846	Cretaceous	Chile
<i>C. ellipticus</i> (Schafhäutl) 1852	Eocene	Bavaria
<i>C. expletus</i> (Zwierzycki) 1914	Cretaceous (Neocomian)	East Africa
<i>C. forbesi</i> (D'Archiac and Haime) 1854	Eocene	Pakistan
<i>C. haltomi</i> (Aldrich) 1931	Paleocene	Alabama (U.S.A.)

Species	Stratigraphic Distribution	Geographic Distribution
<i>C. heberti</i> (Binckhorst) 1861	Cretaceous (Maestrichtian)	Belgium
<i>C. hesperia</i> Miller and Downes, 1950	Eocene	Washington (U.S.A.)
<i>C. hunti</i> Haas and Miller, 1952	Eocene	British Somaliland
<i>C. intuscatenatus</i> (Martin) 1932	Eocene	Java
<i>C. imperialis</i> (J. Sowerby) 1812	Eocene	England
<i>C. jordani</i> (Wanner) 1902	Cretaceous (Campanian- Danian)	Libya
<i>C. karkarensis</i> Haas and Miller 1952	Eocene	British Somaliland
<i>C. kugleri</i> Miller, 1947	Paleocene	Trinidad
<i>C. landanensis</i> (Vincent) 1913	Paleocene	Cabinda, Africa
<i>C. leonicensis</i> (de Zigno) 1881	Eocene	Italy
<i>C. macfadyeni</i> Haas and Miller 1952	Eocene	British Somaliland
<i>C. macrocephalus</i> (Schafhäütl) 1863	Eocene	Bavaria
<i>C. marylandensis</i> Miller and Thompson, 1933	Eocene	Maryland (U.S.A.)
<i>C. mokattamensis</i> (Foord) 1891	Eocene	Egypt
<i>C. negritensis</i> (Olsson) 1928	Eocene	Peru
<i>C. parallelus</i> (Schafhäütl) 1863	Eocene	Bavaria
<i>C. pernambucensis</i> (Maury) 1930	Paleocene?	Brazil
<i>C. phosphaticus</i> (Bédé) 1933	Eocene	Morocco
<i>C. pseudobouchardianum</i> (Spengler) 1910	Cretaceous (Upper)	India
<i>C. pusilla</i> Haas and Miller, 1952	Eocene	British Somaliland
<i>C. romeroi</i> (Ihering) 1903	Cretaceous (Upper)?	Argentina
<i>C. sahariensis</i> (Keller) 1932	Eocene ?	French Sudan
<i>C. seelandi</i> (Penecke) 1884	Eocene	Austria
<i>C. septemcastrensis</i> Haas and Miller, 1952	Eocene	British Somaliland
<i>C. sindiensis</i> (Vredenburg) 1928	Tertiary (Lower)	Pakistan

Species	Stratigraphic Distribution	Geographic Distribution
<i>C. subrecta</i> Miller and Thompson, 1933	Paleocene	Mississippi (U.S.A.), Trinidad
<i>C. sudanensis</i> Miller, 1951	Paleocene	French Sudan
<i>C. tessieri</i> Miller, 1951	Paleocene	Senegal, Africa
<i>C. turcicus</i> (Krumbeck) 1905	Jurassic (Upper)	Libya
<i>C. vauhani</i> (Gardner) 1923	Paleocene	Texas, Alabama (U.S.A.)
<i>C. vestali</i> Miller and Thompson, 1933	Paleocene	Mississippi (U.S.A.)
<i>C. wylliei</i> (Newton) 1925	Eocene	Somaliland

Genus *ANGULITHES* Montfort, 1808

Angulithes Montfort, 1808, p. 7.

Angulithes Spath, 1927a, pp. 21, 24.

Deltoidonautilus Spath, 1927a, pp. 22, 26.

Deltoidonautilus Spath, 1927b, pp. 427, 428.

Deltoidonautilus Stenzel 1940, p. 759.

Deltoidonautilus Teichert, 1947b.

Deltoidonautilus, Miller, 1947, pp. 64-67.

Deltoidonautilus Miller, 1951, p. 51

Deltoidonautilus Haas and Miller, 1952, pp. 338-344.

Angulithes Kummel, 1953a, p. 8.

Type species. *Nautilus triangularis* Montfort, 1802 (by original designation in Montfort, 1808, p. 7).

The generic name *Angulithes* remained unused by paleontologists until Spath (1927a) revived it and placed the genus in the family Nautilidae. Spath (1927a, p. 21) listed as genolectotype '*Nautilites*' *triangularis*, Montfort, in d'Orbigny, 1840, plate 12. However, Montfort (1808, p. 7) specifically designated as type of his genus '*Nautilite triangulaire du Havre*' (Histoire des Mollusques, Buffon, édition de Sonnini, tom. 4, pag. 292, planche 49, 1802). Montfort's illustration of the type of *Angulithes triangularis* (1802, pl. 49) is reproduced here on Plate 25, figure 2. His 1808 illustration of this species is reproduced on Plate 25, figure 1. Both of these illustrations clearly show the triangular outline of the whorl section, the degree of involution,

and the subcentral position of the siphuncle. The sutures on the type illustration (Pl. 25, fig. 2) are undoubtedly oversimplified and wrong. Many specimens of this species from France have been illustrated and recorded; they all have a sinuous suture with a wide lateral lobe and a small saddle near the umbilicus. D'Orbigny (1840, p. 79) described and illustrated *Nautilus triangularis* Montfort including in the synonymy both of Montfort's 1802 and 1808 citations. He likewise listed numerous localities where *N. triangularis* had been found. It is not known whether or not d'Orbigny had access to Montfort's type.

The name combination of *Angulithes triangularis* Montfort (1808) has been validly introduced. There may be a question as to whether the species could be recognized from Montfort's text and illustrations. Even though the suture line as represented on Montfort's (1802) illustration of *Angulithes triangularis* is undoubtedly oversimplified I believe that the species is recognizable.

At the same time that Spath (1927a) revived the name *Angulithes*, he established a new genus *Deltoiconautilus*, type species, *Nautilus sowerbyi* Wetherell, 1836, in J. de C. Sowerby, 1843, p. 35, pl. 627, figs. 1-3. *Angulithes* was thought to be confined to the Cretaceous and *Deltoiconautilus* to the Cenozoic. While Spath (1927a, p. 26) did not diagnose his new genus, he made the following comment: "*Deltoiconautilus* in whorl shape resembles the Cretaceous *Angulithes*, and d'Archiac, and Foord (1891, p. 327) had compared *Deltoiconautilus deluci* (d'Archiac) with *Angulithes triangularis*. The latter, however, with its less sinuous suture line, is more closely allied, via *Ang. fleuriausianus* (d'Orbigny) with the regular Nautilid stock that produced *Pseudocnoceras* in the Cretaceous, as it had given rise before to the less specialized *Paracenceras* of the *calloviensis* type." The degree of variability in conch shape and sinuosity of the suture are such that the two groups cannot be distinguished (Figs. 32, 33). There is almost a continuous series of species, through the Cretaceous to the Eocene, of involute nautiloids with narrowly rounded to angular venters. *Deltoiconautilus* is placed as a synonym of *Angulithes* (Kummel, 1953a).

Angulithes can be diagnosed as follows: Conch very involute, generally compressed, whorl sides slightly convex, strongly convergent, venter narrowly rounded to angular. Suture moder-

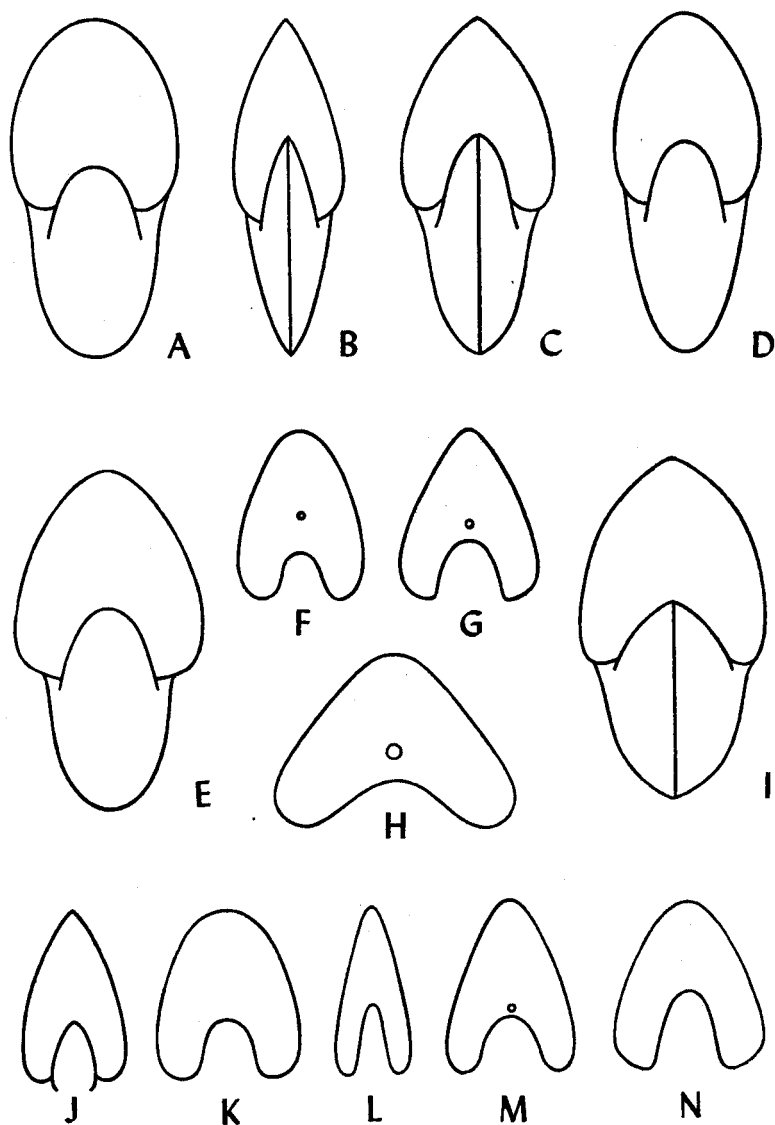


Figure 33

ately sinuous with a narrowly rounded ventral saddle, a broad lateral lobe, a narrow, rounded saddle, and a small lobe on the umbilical shoulder. Siphuncle small and located near the dorsum.

Foord (1891, p. 267) has noted that in the type species—*A. triangularis*—the periphery can be alternately rounded and sharply angular. *Angulithes senegalensis* (Douvillé) has a sub-angular periphery on the earlier growth stages but at maturity the venter is rounded (Miller, 1951, fig. 14).

Angulithes is in many respects transitional to both *Cimomia* and *Hercoglossa*, differing mainly in its subtriangular whorl section. It is open to question whether this generic group represents a continuous genetic line or trend or whether it may be composed of numerous adaptive trends with this conch shape stemming at several times from either *Cimomia* or *Hercoglossa*. The oldest species of *Angulithes* known to date are *A. arcuatus* (Deshayes) from the Albian of France and England and *A. munieri* (Choffat) from Cenomanian (Cretaceous) of Portugal (Choffat, 1886) and Peru (Schlagintweit, 1912). Kummel (1953a) has recorded an indeterminate species of *Angulithes* from the Pawpaw formation, Tarrant County, Texas. The youngest species is *A. bakeri* (Teichert, 1947, 1952) from Oligocene strata of Australia. There are seven species of *Angulithes* recorded from the Cretaceous (Fig. 29). Most of these are known

Fig. 33. Cross sections of the conch of *A. Angulithes sowerbyanus* (d'Orbigny) 1840, pl. 16, fig. 2, diameter 270 mm.; *B. A. deluci* (d'Archiac) from Miller, 1951, fig. 11A, diameter 128 mm.; *C. A. triangularis* Montfort, from d'Orbigny, 1840, pl. 12, fig. 2, diameter 200 mm., the genotype of *Angulithes*; *D. A. fleuriausianus* (d'Orbigny) 1840, pl. 15, fig. 2, diameter 192 mm.; *E. A. fleuriausianus* (d'Orbigny) from Stoliczka, 1866, pl. 94, fig. 1a, diameter 100 mm.; *F. A. fleuriausianus* (d'Orbigny) 1840, pl. 15, fig. 3, height 64 mm.; *G. A. sowerbyi* (Wetherell) from Miller 1947, fig. 13A, height 81 mm.; *H. A. sp.* (Haas and Miller) 1952, fig. 8B, height 38 mm.; *I. A. westphalicus* (Schlüter) 1876, pl. 47, fig. 2, diameter 369 mm.; *J. A. tamulicus* (Kossmat) 1897, pl. 6, fig. 6, height 84 mm.; *K. A. ellioti* (Stenzel) from Miller 1947, fig. 13B, height 110 mm.; *L. A. chudeaui* (Douvillé), from Miller 1951, fig. 10A, height 56 mm.; *M. A. rogeri* (Miller) 1951, fig. 13, height 100 mm.; *N. A. molli* (Douvillé), from Miller 1951, fig. 12B, height 72 mm.

from Upper Cretaceous formations of Europe. Species are also known from south India, Peru and Texas (U.S.A.). Tertiary species of *Angulithes* are very widely distributed, being known from North and South America, Europe, Africa, Pakistan, and Australia. Most of the Tertiary species are Eocene in age (Fig. 30).

DISTRIBUTION OF SPECIES OF THE GENUS ANGULITHES

Species	Stratigraphic Distribution	Geographic Distribution
<i>A. aegyptiacus</i> (Foord) 1891	Eocene	Egypt
<i>A. arcuatus</i> (Deshayes) in Leymerie, 1842	Albian	France, England
<i>A. bakeri</i> (Teichert) 1947	Oligocene	Australia
<i>A. biyogorensis</i> (Haas and Miller) 1952	Eocene	British Somaliland
<i>A. caheni</i> (Miller) 1951	Eocene	Landana, West Africa
<i>A. calvimontensis</i> (Bédé) 1948	Eocene	France
<i>A. cassinianus</i> (Foord and Crick) 1890	Eocene	England
<i>A. chudeaui</i> (Douvillé) 1920	Eocene	French Sudan
<i>A. delucii</i> (d'Archiac) 1854	Tertiary (Lower)	Pakistan
<i>A. ellioti</i> (Stenzel) 1940	Eocene	Texas (U.S.A.)
<i>A. fleuriansianus</i> (d'Orbigny) 1840	Cretaceous	Europe
<i>A. galea</i> (Fritsch and Schlönbach) 1872	Cretaceous (Upper)	Bohemia
<i>A. haughti</i> (Olsson) 1928	Eocene	Peru
<i>A. hazaraensis</i> (Das-Gupta) 1916	Tertiary (Lower)	Pakistan
<i>A. lamarckii</i> (Deshayes) 1824	Eocene	France
<i>A. lemoinei</i> (Miller) 1951	Eocene	French Sudan
<i>A. molli</i> (Douvillé) 1920	Eocene	French West Africa
<i>A. munieri</i> (Choffat) 1886	Cretaceous (Cenomanian)	Portugal, Peru
<i>A. parabolicus</i> (Schafhäütl) 1863	Eocene	Bavaria

Species	Stratigraphic Distribution	Geographic Distribution
<i>A. rogeri</i> (Miller) 1951	Paleocene	Senegal
<i>A. rollandi</i> (Leymerie) 1846	Eocene	France
<i>A. senegalensis</i> (Douvill�) 1920	Eocene	Senegal
<i>A. singularis</i> (Haas and Miller) 1952	Eocene	British Somaliland
<i>A. somaliensis</i> (Newton) 1925	Eocene	British Somaliland
<i>A. sowerbyanus</i> (d'Orbigny) 1840	Cretaceous (Upper)	France
<i>A. sowerbyi</i> (Wetherell) 1836	Eocene	England
<i>A. spathi</i> (Haas and Miller) 1952	Eocene	British Somaliland
<i>A. subfleuriausianus</i> (d'Archiac) 1850	Tertiary (Lower)	Pakistan
<i>A. tamulicus</i> (Kossmat) 1897	Danian	India
<i>A. togoensis</i> (Miller) 1951	Eocene	Togo
<i>A. triangularis</i> Montfort, 1802	Cretaceous (Upper)	France, England
<i>A. westphalicus</i> (Schl�ter) 1872	Cretaceous (Senonian)	Germany

Genus HERCOGLOSSA Conrad, 1866

Hercoglossa Conrad, 1866a, p. 101.

Hercoglossa Hyatt, 1883, pp. 270-271.

Enclimatoceras Hyatt, 1883, p. 270.

Hercoglossa Spath, 1927a, pp. 22, 25, 26.

Hercoglossa Miller and Thompson, 1933, pp. 313-324.

Hercoglossa Stenzel, 1940, p. 743.

Woodringia Stenzel, 1940, pp. 753-759.

Hercoglossa Miller, 1947, pp. 49-64.

Woodringia Miller, 1947, pp. 67-69.

Hercoglossa Miller, 1951, pp. 47-51.

Type species. *Nautilus orbiculatus* Tuomey, 1854, from Paleocene of Alabama, designated by Hyatt (1883), neotype designated by Miller and Thompson (1933). Neotype refigured here on Plate 27, figs. 1, 2.

The most recent and comprehensive study of this genus is that by Miller and his diagnosis is quoted here (Miller, 1947, p. 50):

"Conch nautiliconic in its mode of growth and subglobular to subdiscoidal in form. Whorls more or less flattened (but typically very broadly rounded) laterally, rather narrowly

rounded ventrally, and deeply impressed dorsally. Umbilicus small; umbilical shoulders rounded. Surface of the test smooth. Septa fairly numerous, and each suture forms a broad very broadly rounded ventral saddle, a deep rounded lateral lobe, a

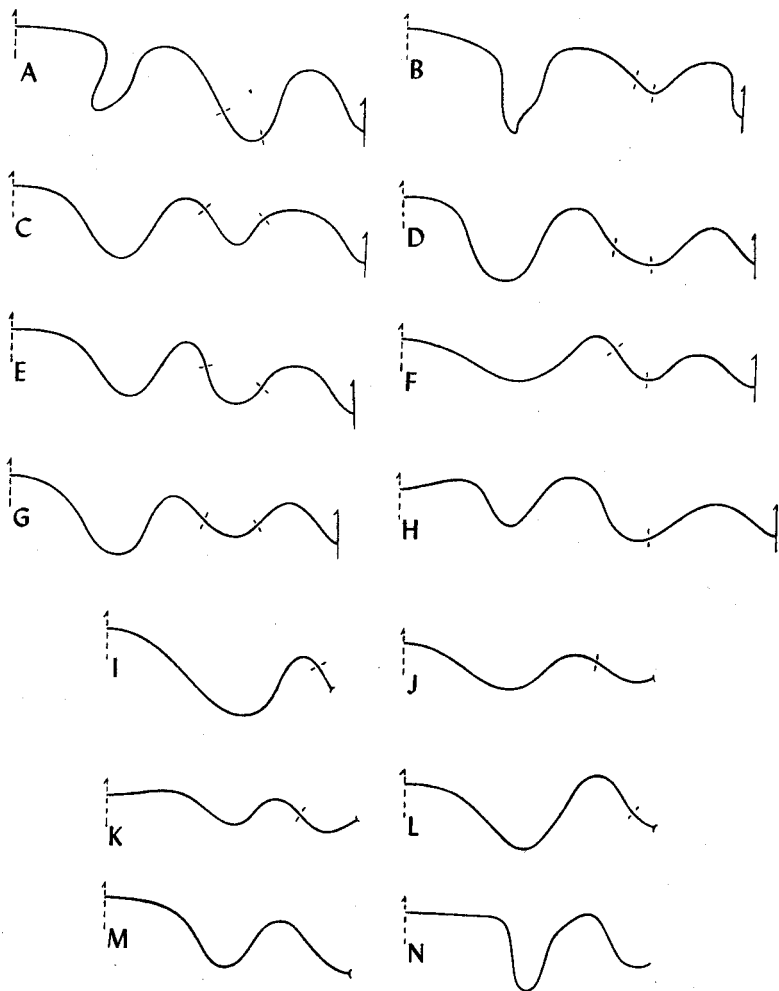


Figure 34

similar lateral saddle, a shallower rather broad rounded lobe on or near the umbilical wall, and a broad rounded internal lateral saddle that extends to a deep rather narrowly rounded dorsal lobe. Siphuncle small and orthochoanitic in structure; its position varies considerably in the different species but in no case is it marginal."

Hercoglossa is closely related to *Cimomia* from which it differs in shape of the suture, to *Angulithes* from which it differs in shape of the whorl section and from *Aturoidea* from which it differs in shape of suture and position of the siphuncle (Figs. 31, 32, 33, 34). *Hercoglossa* is derived from *Cimomia* and incorporates a more advanced or sinuous suture.

The genus *Woodringia* was established by Stenzel for *W. splendens* Stenzel and *W. simiensis* (Vokes) which have a cimomid type of conch in being subglobular, and a hercoglossid type of suture except for a shallow lobe on the venter (Fig. 34). Stenzel differentiates *Woodringia* on the depressed aspect of the whorl section and the presence of a ventral lobe; he considered *Woodringia* to be an independent offshoot from some hercoglossid ancestor. Whereas hercoglossids have in general more compressed conchs than cimomids, there is much variation in the shape of the whorl section (Figure 31). I do not consider the shape of the conch in this particular case to be of any diagnostic value. As to the suture, the presence of the ventral lobe in the ventral saddle is a modification that has occurred in other stocks and has been held to be of not more than specific value. Among species of *Cimomia*, for example, the ventral sad-

Fig. 34. Diagrammatic representation of sutures of A, *Aturoidea paucifex* (Cope) from Miller and Thompson, 1935, pl. 65, fig. 2; B, *A. vieirai* Miller, 1951, fig. 16-A; C, *Hercoglossa gardnerae* Stenzel, 1940, fig. 117 (1); D, *H. diderrichi* Vincent, from Miller, 1951, fig. 9; E, *H. diderrichi* Vincent, from Stenzel, 1939, fig. 117 (2); F, *H. harrisi* Miller and Thompson, 1937, from Stenzel, 1940, fig. 117 (8); G, *H. orbiculata* (Tuomey) from Stenzel, 1940, fig. 117 (3); H, *H. splendens* (Stenzel) 1940, fig. 121 (1); I, *H. meglameryae* Miller and Thompson, 1933, fig. 2D; J, *H. maracaiboensis* Miller and Collinson, 1951, fig. 2A; K, *H. simiensis* Vokes, 1937, from Stenzel, 1940, fig. 121 (2); L, *H. popenoei* Miller and Downs, 1950, fig. 1; M, *H. danicus* (Schlotheim) from Blanford, 1861, pl. 13, fig. 4. All figures greatly reduced.

dle is normally well rounded, but in *C. kugleri* Miller and *C. vaughani* (Gardner) a slight median lobe appears at late maturity. Likewise two species of *Aturia* have ventral lobes whereas the "normal" state is a rounded ventral saddle. In *Aturia berryi* Stenzel (1940, p. 764-770, pl. 40, figs. 1-3, text figs. 125 (7) and 126 (2)) the suture is "slightly wavy across the venter so that there is a very shallow ventral lobe in the center flanked on either side by a shallow ventral saddle." However, Miller (1947, p. 88) suggested that the slight ventral lobe may be adventitious in that he could not discern this lobe in any of the other sutures. However, there is another species of *Aturia*, *A. coxi* Miller, 1947 (= *A. narica* Cox 1927, non Vredenburg) from Lower Miocene of Pemba Island in the Zanzibar Protectorate. In this species there is a distinct, rather deep, ventral lobe. I have had the opportunity of examining this specimen in the British Museum and agree with Cox that it belongs in *Aturia*, and I agree with Miller that it is a distinct species. In each of the above cases we are dealing with merely local aberrant species.

Another generic group that displays the same type of variation in the ventral suture is *Pseudaganides*. In this genus the "normal" condition is to have a slight lobe on the venter; however, a few Upper Jurassic species as *P. schlosseri* (Loesch, 1914, pp. 114-118, fig. 8) develop a rounded ventral saddle on the last mature sutures where previously a shallow lobe appeared.

Two species of early Cretaceous nautiloids with sinuous "hercoglossid" sutures are very difficult to evaluate. These are *Nautilus ricordeanus* d'Orbigny and *N. forbesianus* Blanford. The former species (*N. ricordeanus* d'Orbigny) was never illustrated by its author and only very briefly diagnosed. Subsequently Kilian (1915, pp. 17, 18) described and illustrated a specimen from Aptian (Lower Cretaceous) formations of southeastern France which he assigned to *N. ricordeanus*. The specimen is small (44 mm. diameter), involute, compressed, with rounded venter, and flattened sides. The suture is broadly arched over the venter and forms a narrowly rounded V-shaped lobe on the lateral sides. The remaining portion of the suture is not visible in Kilian's illustration. *Nautilus forbesianus* is from Albian strata of south India (Blanford, 1861) and is likewise

an involute, compressed form with an arched venter and the suture has a broad, nearly straight course across the venter and a V-shaped lateral lobe. The character of the suture of these two species suggests affinity to *Aturoidea* more than to *Hercoglossa*. However, the position of the siphuncle is nearer the venter rather than nearer the dorsum as in *Aturoidea*. Cretaceous species of *Hercoglossa* and *Aturoidea* are indeed very rare and any interpretation of these two species can only be tentative pending discovery of new material. It seems that in spite of the apparent specialization of the lateral lobe it would be best to ally these two species, with question, in *Hercoglossa*. The derivation of *Aturoidea* from *Hercoglossa* has been a long-accepted, and to me, a correct interpretation. The oldest species of *Aturoidea* is *A. serpentinus* (Blanford) from Senonian strata of south India. *Nautilus ricordeanus* and *N. forbesianus* are thus here considered as part of the earliest radiation from *Cimomia* but perhaps are not part of the main evolutionary line but still congeneric with the principal group.

The species assigned to *Hercoglossa* with their time and geographic range are listed below. The geographic distribution is noted on the maps of Figures 29, 30. Teichert and Glenister (1952, p. 737) record the presence of an undescribed new carinate species of *Hercoglossa* from Eocene strata from the north-west basin of Western Australia.

DISTRIBUTION OF SPECIES OF THE GENUS HERCOGLOSSA

Species	Stratigraphic Distribution	Geographic Distribution
<i>H. danicus</i> (Schlotheim) 1820	Danian	Europe, Asia, Africa
<i>H. diderichi</i> Vincent, 1913	Paleocene	Senegal
<i>H. ? forbesianus</i> (Blanford) 1861	Cretaceous (Albian)	South India
<i>H. gardnerae</i> Stenzel, 1940	Paleocene	Texas (U.S.A.)
<i>H. harrisi</i> Miller and Thompson, 1937	Paleocene	Trinidad
<i>H. innominanda</i> Fleming, 1945	Eocene	New Zealand
<i>H. lamegoi</i> Oliveira, 1953	Paleocene	Brazil
<i>H. madagascariensis</i> Collignon, 1951	Cretaceous (Upper)	Madagascar

Species	Stratigraphic Geographic	
	Distribution	Distribution
<i>H. mcglameryae</i> Miller and Thompson, 1933	Paleocene	Alabama (U.S.A.)
<i>H. merriami</i> Dickerson, 1914	Paleocene	California (U.S.A.)
<i>H. orbiculata</i> (Tuomey) 1854	Paleocene	Alabama (U.S.A.)
<i>H. pavlowi</i> (Arkhanguelsky) 1904	Paleocene	Russia
<i>H. peruviana</i> Berry, 1923	Eocene	Peru
<i>H. popenoei</i> Miller and Downs, 1950	Paleocene	Baja, California (U.S.A.)
<i>H. ? ricordeanus</i> (d'Orbigny) 1847	Cretaceous (Aptian)	France
<i>H. simiensis</i> Vokes, 1937	Paleocene	California (U.S.A.)
<i>H. splendens</i> (Stenzel) 1940	Paleocene	Texas (U.S.A.)
<i>H. tuomeyi</i> Clark and Martin, 1901	Eocene	Maryland, Virginia (U.S.A.)
<i>H. ulrichi</i> (White) 1882	Paleocene	Ark., Tenn., Ala., Miss., Texas (U.S.A.)
<i>H. walteri</i> Miller, 1947	Paleocene	Alabama (U.S.A.)
<i>H. waringi</i> Miller, 1947	Eocene	Trinidad

Genus ATUROIDEA Vredenburg, 1925

Aturoidea Vredenburg, 1925, p. 9.

Paraturia Spath, 1927a, pp. 22, 26.

Paraturia Spath, 1927b, p. 428.

Aturoidea Vredenburg and Cotter, 1928, p. 18.

Aturoidea Schenck, 1931, p. 450.

Aturoidea Miller and Thompson, 1935, pp. 563-571.

Aturoidea Teichert, 1943, pp. 258-261.

Aturoidea Haas, 1947, pp. 243, 244.

Aturoidea Miller, 1947, pp. 69-77.

Aturoidea Miller, 1951, p. 68.

Type species. *Nautilus parkinsoni* Edwards (subsequent designation by Miller and Thompson 1935, p. 563). Figured here on Plate 28, figures 1, 2.

Miller (1947) has recently thoroughly reviewed the available data on this interesting genus and I find myself in essential agreement with most of his conclusions. His diagnosis of *Aturoidea* is quoted here (Miller 1947, p. 70):

"Conch sublenticular in shape and nautiliconic in its mode of growth; all known forms are large. Whorls compressed, flattened laterally, rounded ventrally, impressed dorsally. Umbilicus closed; umbilical shoulders rounded. Septa asymmetrically sigmoidal; each mature suture forms a very broad high blunt ventral saddle, and on either side of it a deep narrow asymmetrical narrowly rounded lateral lobe, a broad high broadly rounded asymmetrical lateral saddle, a broad rounded lobe with its center near the umbilical seam, and a broad rounded saddle located on the side of the impressed zone and extending to the large rounded V-shaped dorsal lobe. Siphuncle subcentral or subdorsal in position (being nearer the dorsum than the venter, but not in contact with the dorsum), and orthochoanitic in structure — the siphuncular segments are essentially cylindrical in shape and the septal necks are relatively long, being only slightly shorter than the connecting rings."

Only 11 species of *Aturoidea* have been recorded to date and each species is known by one or very few specimens only, a fact unfortunately applicable to most post-Triassic nautiloids. As pointed out by Miller on various occasions *Aturoidea* is very closely related to *Hercoglossa* and *Aturia*; in fact, it is more or less intermediate between them. It differs from *Hercoglossa* in the position of the siphuncle and in the character of the suture. In *Aturia* the dorsal (marginal) position of the siphuncle and the infundibular flexures of the septa are distinctive. The main variations in the suture are in the width and shape of the lateral lobe.

In *A. serpentinus* and *A. schweinfurthi*, both of Upper Cretaceous age, the lobe is well rounded and rather broad. However, in *A. vieirai* from strata of questionable Upper Cretaceous age the ventral flank of the lateral lobe has a distinctive flexure in the lower part making the tip of the lobe narrowly rounded. This same type of modification of the lateral lobe is present in *A. mathewsonii* of Paleocene? age, in *A. paucifex* of Eocene age, in *A. pilsbryi* of Eocene age, and in *A. parkinsoni*, of

Eocene age. The lateral lobe is very narrow and pointed in *A. distans* from the Eocene of Australia.

There are too few specimens or species of *Aturoidea* known to recognize any distinct evolutionary patterns within the group. Species of *Aturoidea* are known from formations of Cretaceous, Paleocene, and Eocene age and have been recorded from England, Austria, India, Africa, Australia, Peru, California, and New Jersey (U.S.A.) (Figs. 29, 30). Teichert and Glenister (1952) report undescribed specimens of *Aturoidea* from Upper Maestrichtian age from western Australia.

DISTRIBUTION OF SPECIES OF THE GENUS ATUROIDEA

Species	Stratigraphic Distribution	Geographic Distribution
<i>A. brunlechneri</i> (Frauscher) 1895	Eocene	Austria
<i>A. distans</i> Teichert, 1943	Eocene	Australia
<i>A. matthewsonii</i> (Gabb) 1864	Paleocene	California (U.S.A.)
<i>A. olssoni</i> Miller, 1947	Eocene	Peru
<i>A. parkinsoni</i> (Edwards) 1849	Eocene	England
<i>A. paucifex</i> (Cope) 1866	Eocene	New Jersey (U.S.A.)
<i>A. pilsbryi</i> Miller and Thompson, 1935	Eocene	New Jersey (U.S.A.)
<i>A. schweinfurthi</i> (Quaas) 1902	Cretaceous (Campanian-Maest.)	Libya
<i>A. serpentinus</i> (Blanford)	Cretaceous (Senonian)	India
<i>A. spathi</i> (Vredenburg) 1928	Eocene	India
<i>A. vieirai</i> Miller, 1951	Cretaceous (Upper?)	Angola

Subfamily ATURINAE Hyatt, 1894

Genus ATURIA Bronn, 1838

Type species. *Nautilus aturi* Basterot, by subsequent designation, Herrmannsen, 1846, and by virtual tautonymy.

The genus *Aturia*, the sole member of the Aturinae, has received more intensive study than any other group of post-Trias-

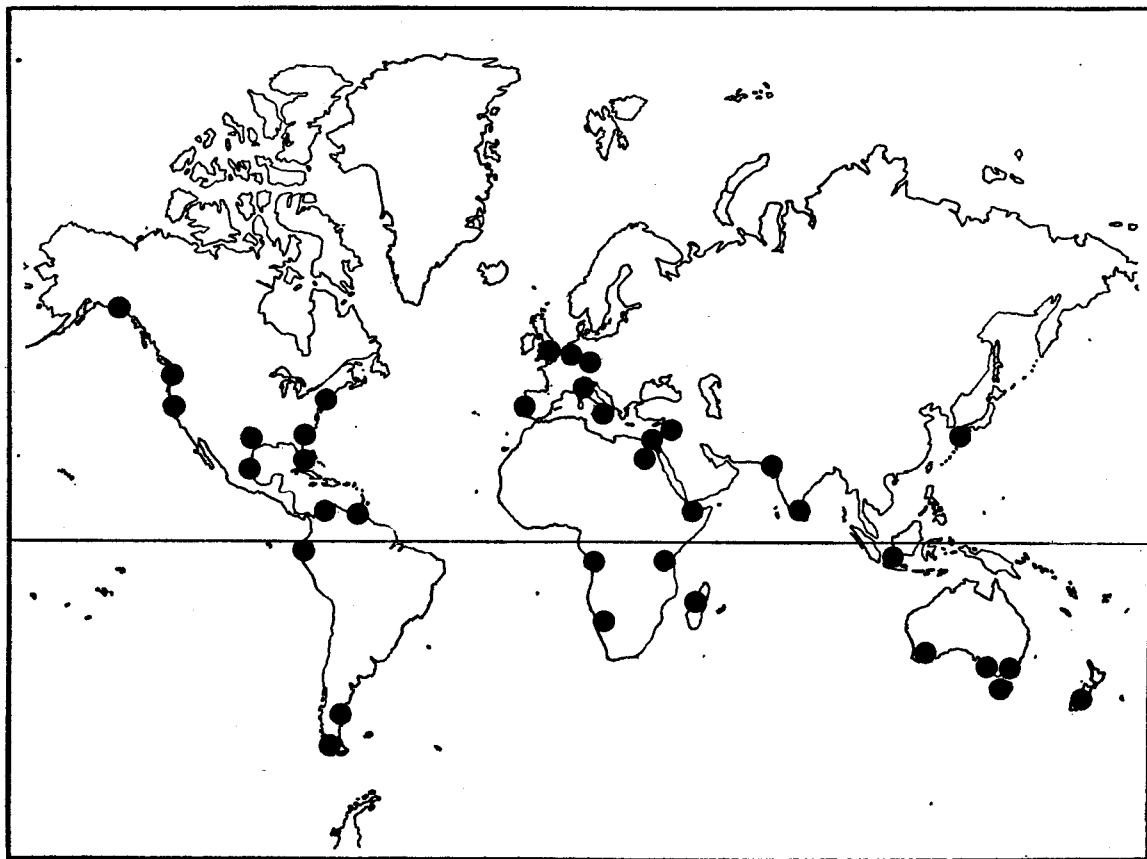


Fig. 35. Geographic distribution of species of the genus *Aturia* in formations of Paleocene, Eocene, Oligocene, and Miocene age.

sic nautiloids. The most comprehensive discussion is that of Schenck (1931), and recently Miller (1947) has described the specimens of *Aturia* known from the Americas. Schenck (1931, pp. 448, 449) gives a complete synonymy of the genus and this need not be repeated here. Since Schenck's paper, Stenzel (1935, pp. 553-556) has proposed two new subgenera, *A. (Nilaturia)* and *A. (Brazaturia)*; however, I agree with Miller (1947, p. 81) that these subgeneric categories should not be used. Previously Ihering (1921, p. 76) had proposed the subgenus *Aturia* (*Sphenaturia*) but this name is also suppressed (Schenck, 1931, p. 450; Miller, 1947, p. 81).

This genus is characterized mainly by the infundibular adapical flexure of the septa around the dorsal marginal siphuncle. The conch is usually more compressed and the suture more advanced than in other Tertiary nautiloids. There is very good ontogenetic evidence of the origin of *Aturia* from *Hercoglossa* through *Aturoidea* (Miller 1947, pp. 78, 79). The genus has been so thoroughly discussed by Schenck (1931) and Miller (1947) that I have nothing of significance to add.

Aturia is truly a cosmopolitan genus, nearly world-wide in distribution and ranges in age from lowest Paleocene (possibly Upper Cretaceous) well into the Miocene (Fig. 35). The named units, "species," of *Aturia* recorded so far are listed below.

DISTRIBUTION OF SPECIES OF THE GENUS ATURIA

Species	Stratigraphic Distribution	Geographic Distribution
<i>A. alabamensis</i> (Morton) 1834	Eocene	Atlantic and Gulf Coastal Plain; Mexico
<i>A. alaskensis</i> Schenck, 1931	Oligocene	Gulf of Alaska
<i>A. angustata</i> (Conrad) 1849	Oligocene- Miocene	Calif.; Wash.; Oregon (U.S.A.)
<i>A. aturi</i> (Basterot) 1825	Miocene	France, Java

Species	Stratigraphic Distribution	Geographic Distribution
<i>A. australis</i> McCoy, 1867	Miocene	Southeast Australia
<i>A. basteroti</i> Benoist, 1888	Oligocene	France
<i>A. berryi</i> Stenzel, 1940	Oligocene	Mississippi (U.S.A.)
<i>A. brazoensis</i> Stenzel, 1935	Eocene	Texas (U.S.A.)
<i>A. brüggeni</i> Ihering, 1921	Eocene ?	Chile (Tierra del Fuego)
<i>A. caroliameghinai</i> (Ihering) 1902	Eocene ?	Argentina
<i>A. charlesworthi</i> Foord, 1891	Eocene	England
<i>A. clarkei</i> Teichert, 1944	Miocene	Western Australia
<i>A. coxi</i> Miller, 1947	Miocene	Pemba Island, Zanzibar
<i>A. cubaensis</i> (Lea) 1841	Oligocene ?	Cuba
<i>A. curvilineata</i> Miller and Thompson, 1937	Miocene	Florida (U.S.A.), Trinidad, Venezuela, Ecuador
<i>A. dickersoni</i> Schenck, 1931	Paleocene ?	California (U.S.A.)
<i>A. felschi</i> Ihering, 1921	Eocene ?	Chile
<i>A. formae</i> Parona, 1899	Eocene	Italy
<i>A. garretti</i> Stenzel, 1940	Eocene	Louisiana (U.S.A.)
<i>A. grandior</i> Schenck, 1931	Eocene	Washington (U.S.A.)
<i>A. grangei</i> Fleming, 1945	Oligocene	New Zealand
<i>A. kerniana</i> Anderson and Hanna, 1925	Miocene	California (U.S.A.)
<i>A. koenei</i> Gagel, 1928	Eocene	Germany
<i>A. laticlavata</i> Stenzel, 1935	Eocene	Texas (U.S.A.)
<i>A. ? linicentensis</i> Vincent, 1907	Eocene	Belgium
<i>Aturia lotzi</i> Böhm, 1913	Miocene ?	S. Africa
<i>A. luculoensis</i> Miller, 1938	Miocene	Angola

Species	Stratigraphic Distribution	Geographic Distribution
<i>A. mackayi</i> Fleming, 1945	Eocene	New Zealand
<i>A. morrissi</i> Michelotti, 1847	Miocene	Italy
<i>A. myrlae</i> Hanna, 1927	Eocene	California (U.S.A.)
<i>A. narica</i> Vredenburg, 1925	Oligocene	Pakistan
<i>A. panamensis</i> Miller, 1947	Eocene	Panama
<i>A. paronai</i> Rovereto, 1900	Oligocene	Italy
<i>A. peruviana</i> Olsson, 1928	Eocene, Oligocene	Peru, Ecuador, Colombia, Venezuela
<i>A. praeziczac</i> Oppenheim, 1903	Paleocene	Egypt
<i>A. preaturi</i> (Cuvillier) 1935	Eocene	Egypt
<i>A. radiata</i> Bellardi, 1872	Miocene	Italy
<i>A. richardsi</i> Miller, 1947	Oligocene	Mississippi (U.S.A.)
<i>A. rovasendiana</i> Parona, 1899	Eocene	Italy, Hungary, Egypt, Palestine
<i>A. somaliensis</i> Haas and Miller, 1952	Eocene	Somaliland
<i>A. tokunagai</i> Shimizu, 1926	Miocene	Japan
<i>A. triangula</i> Stenzel, 1935	Eocene	Texas (U.S.A.)
<i>A. turneri</i> Stenzel, 1940	Eocene	Texas (U.S.A.)
<i>A. vanuxemi</i> (Conrad) 1847	Eocene	New Jersey (U.S.A.)
<i>A. yokoyamai</i> Nagao, 1926	Eocene	Japan
<i>A. ziczac</i> (Sowerby) 1812	Eocene	England

ADDENDUM

The very stimulating monograph by Benavides (1956, Cretaceous System in northern Peru. Am. Mus. Nat. Hist., Bull. 108, pp. 357-493, pls. 31-66) was published when this paper was in page proof. The new genus of nautiloid proposed by Benavides, *Lissoniceras* (type, *Nautilus mermeti* Coquand) is clearly a synonym of *Angulithes* as interpreted in this report.

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PLATES

PLATE 1. CENOCERAS ORBIGNYI

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1, 2	<i>Cenoceras orbigny</i> (Prinz)	361
	Two views of type species of the genus <i>Cenoceras</i> (= <i>Nautilus intermedius</i> d'Orbigny — non Sowerby). From d'Orbigny. X 1.	

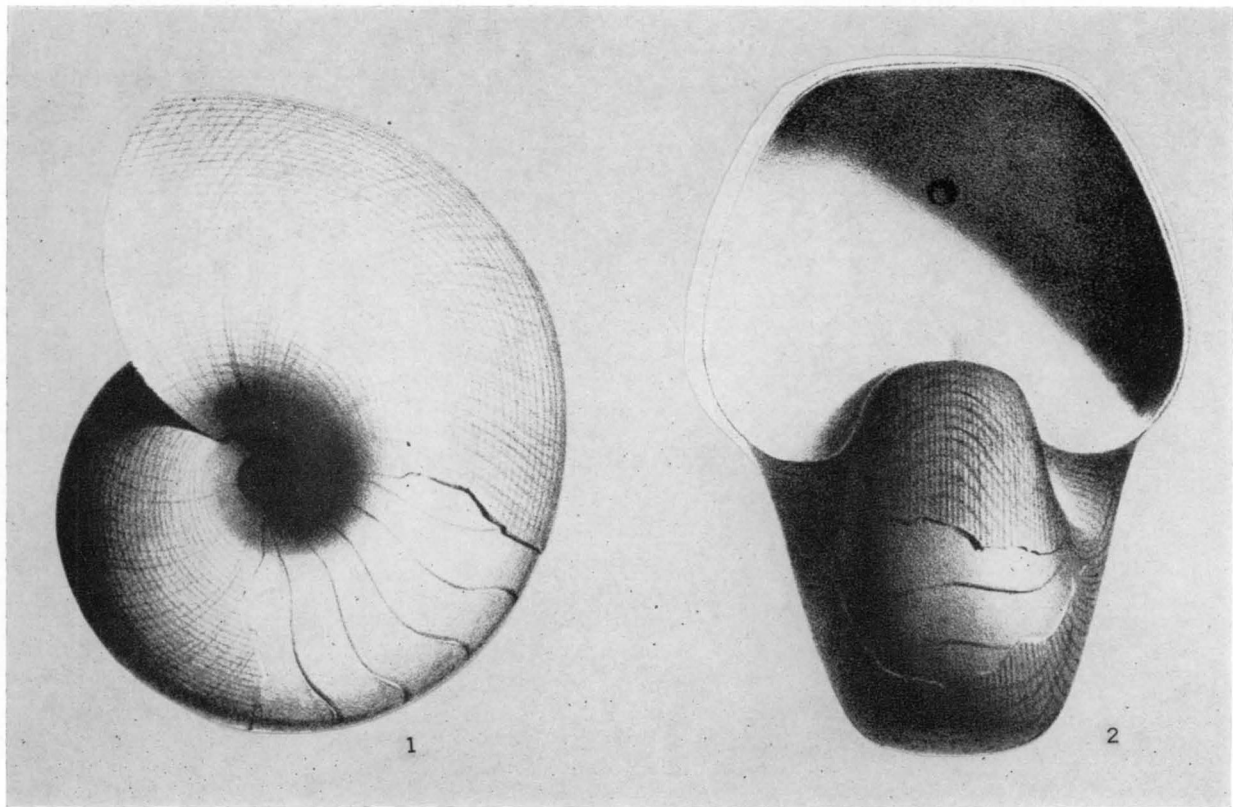


PLATE 2. CENOCERAS TRECHMANNI

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	Three views of holotype from Upper Triassic, Carnian, Bed C, Otomita, Hokonin Hills, New Zealand. B.M.N.H. C21947. X 1.	

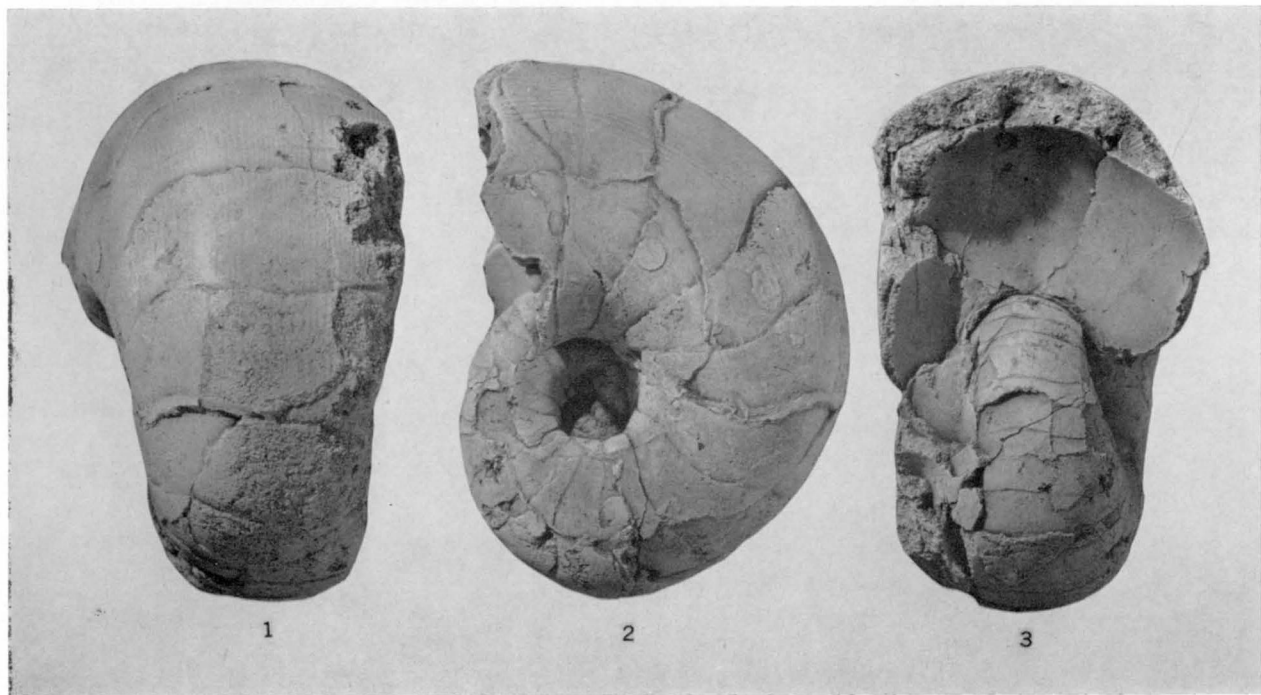
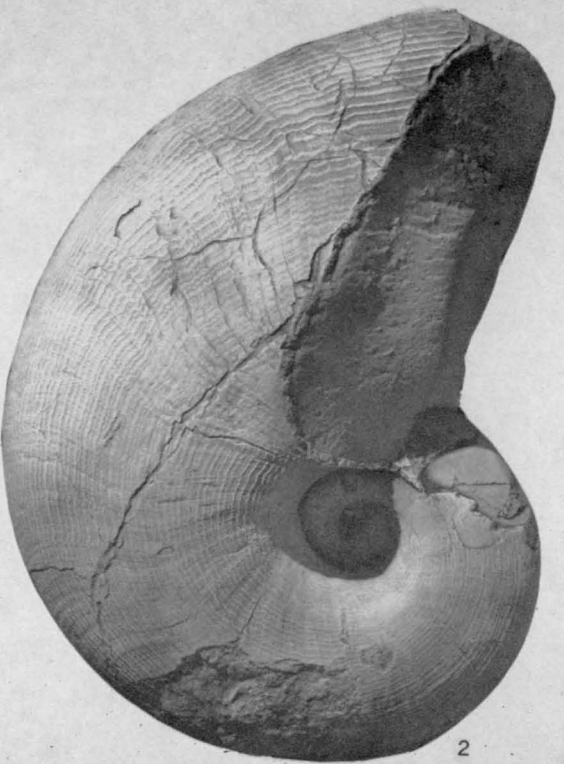


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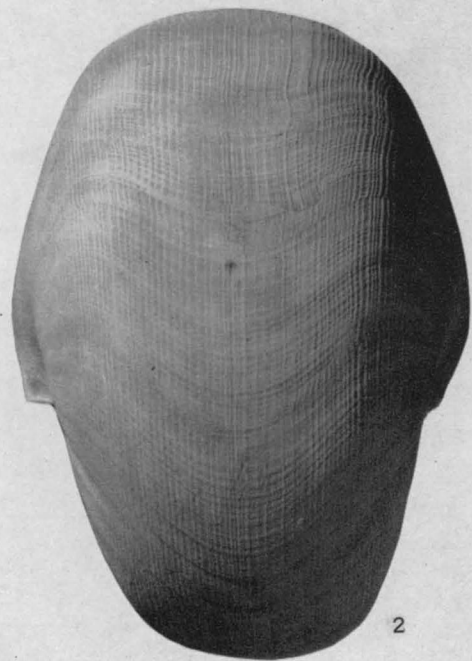
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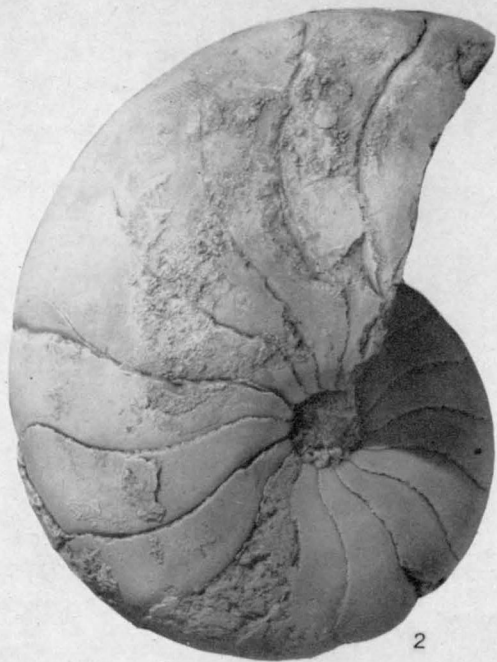
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PLATE 6

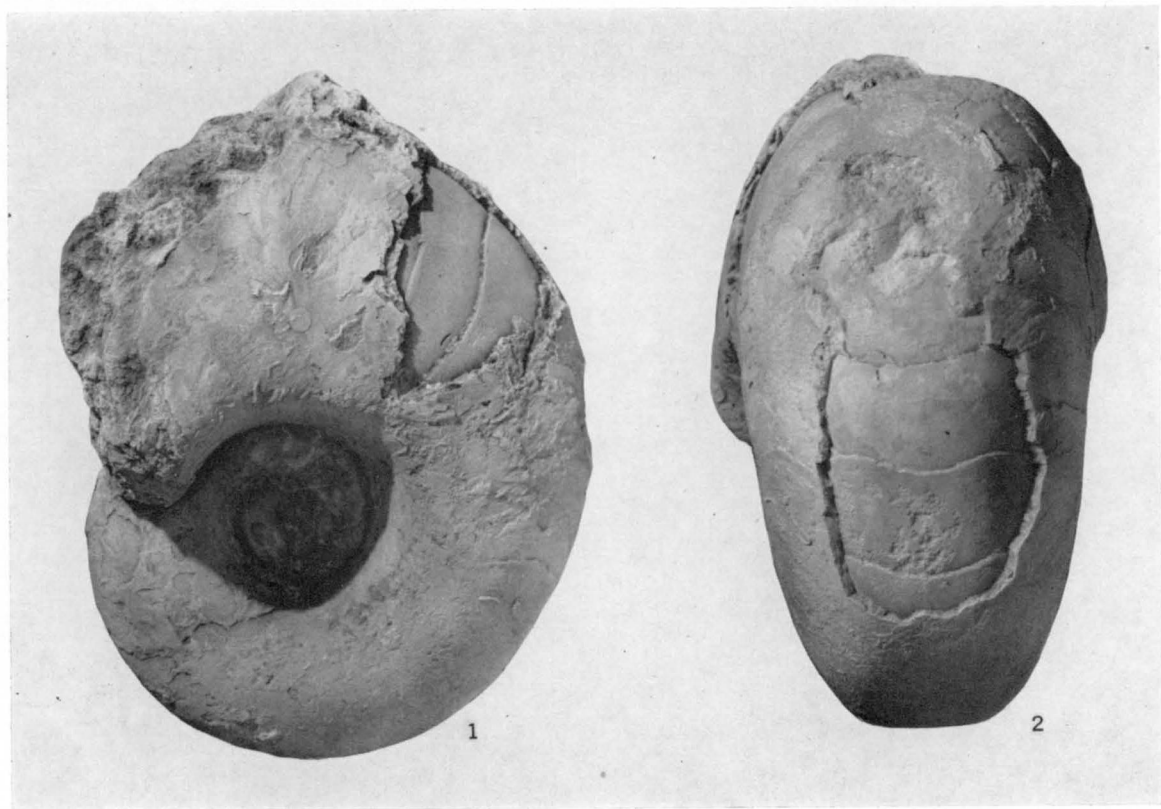
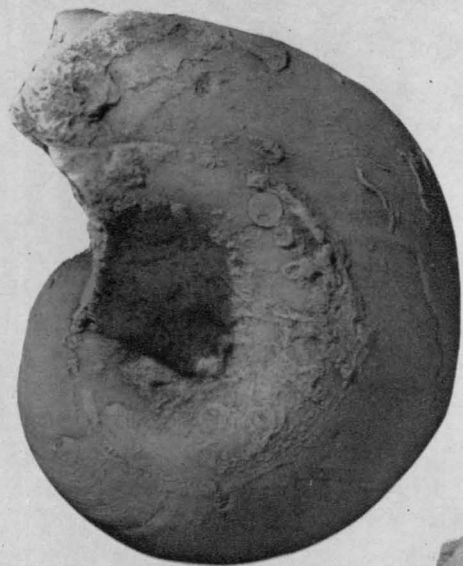
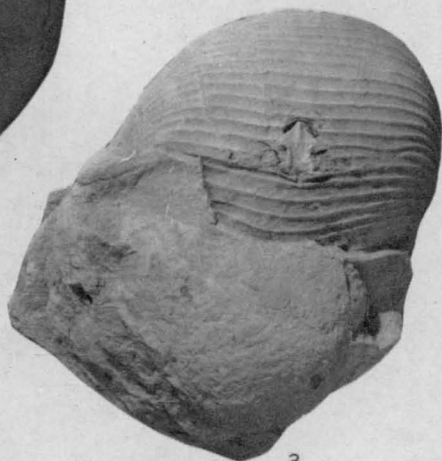


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3	<i>Syrionautilus libanoticus</i> (Foord and Crick) Ventral view of syntype, X 1, with mandible on surface, from Upper Cretaceous, Sahil Alma, Lebanon, Syria. B.M.N.H. 83663 (Lewis Collection). Previously figured in Cat. Foss. Ceph., B.M., Pt. 2, p. 371, fig. 82; mandible figured, Ann. Mag. Nat. Hist. [6], vol. 5 (1890), p. 405, fig. 6c; and Cat. Foss. Ceph. B.M., Pt. 2, p. 305, fig. 67c.	433



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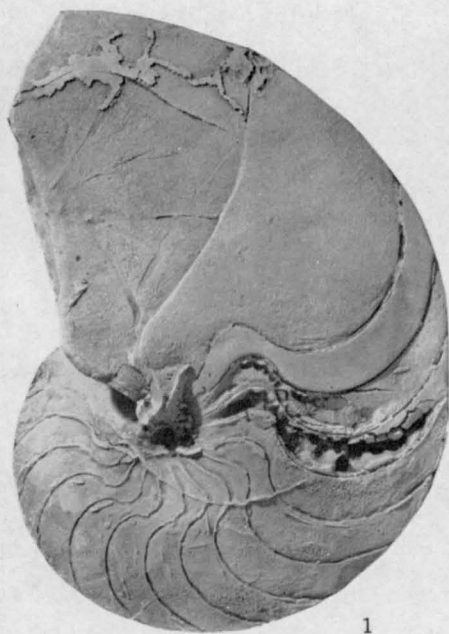
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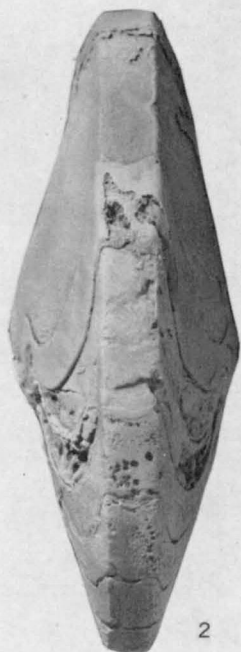
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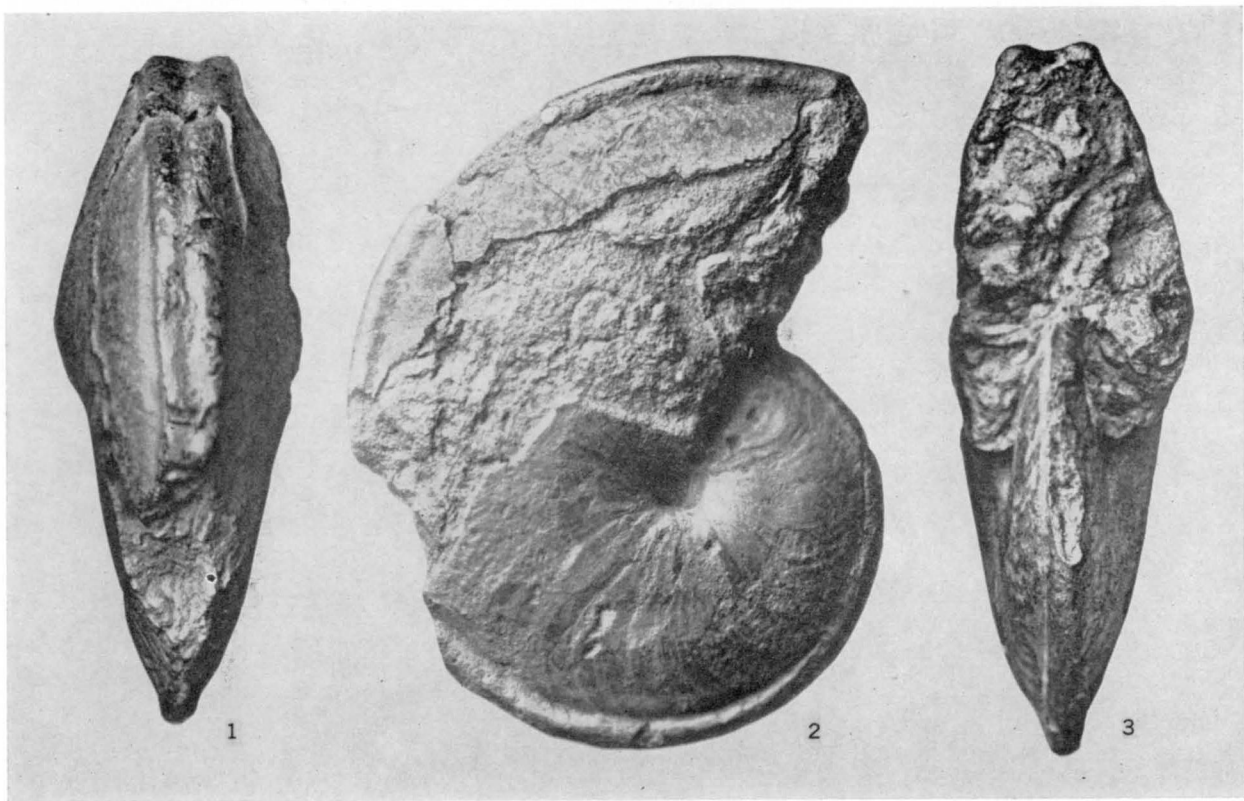
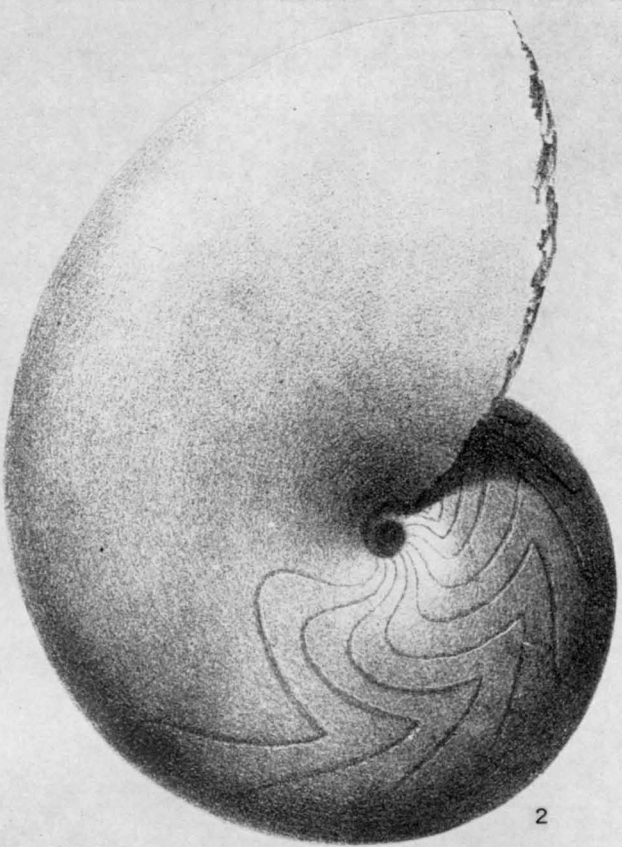


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Figures

1, 2

Paracenoceras hexagonum (Sowerby)
 Two views of holotype, X 1, from Corallian Oolite, locality
 unknown. B.M.N.H. 43856 (Sowerby Collection, MC
 529-f2).

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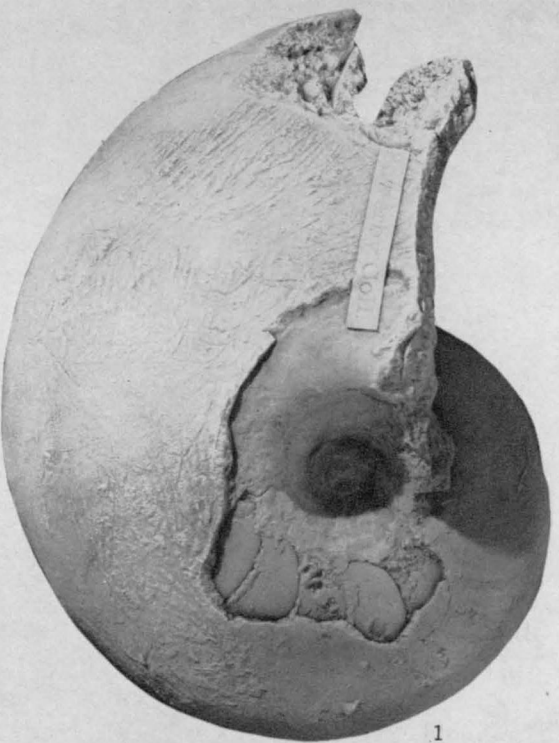
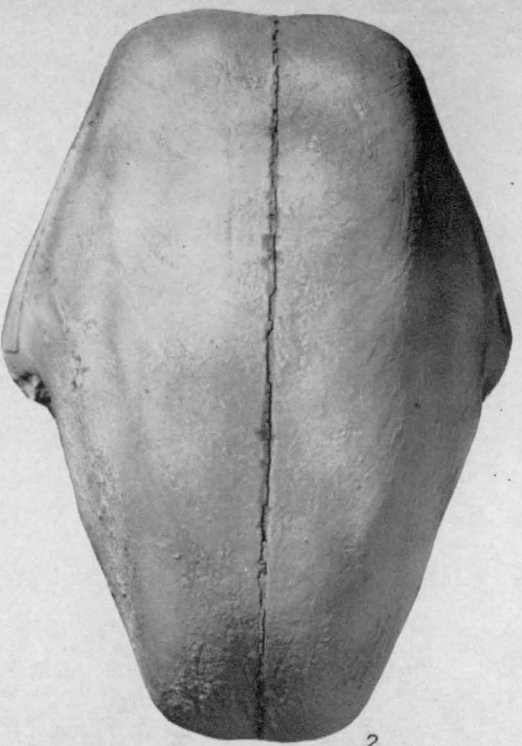


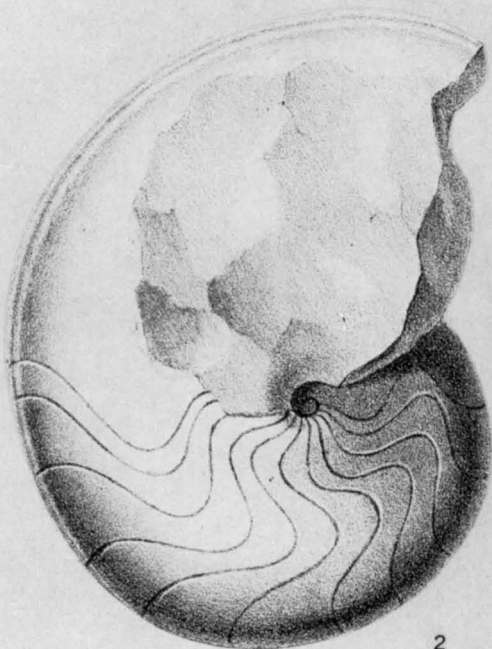
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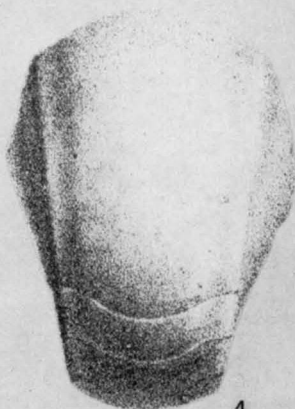
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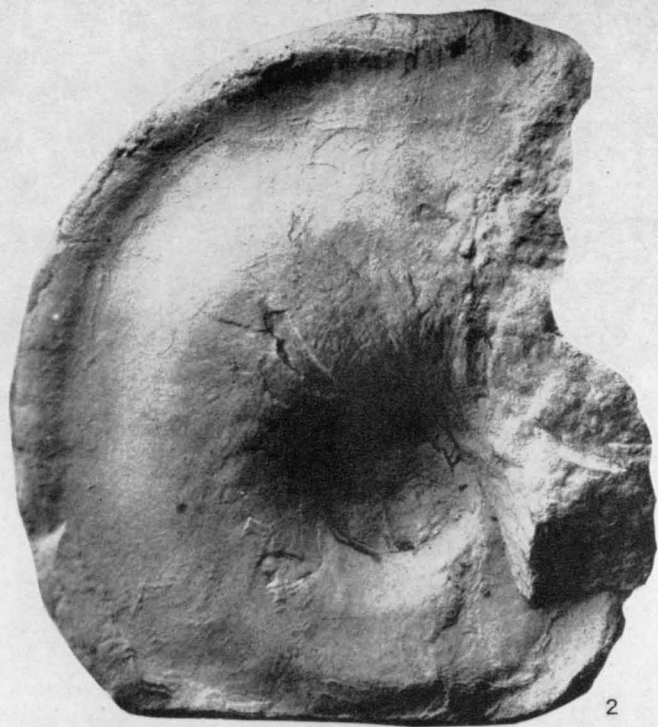
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Figures

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 Two views of cast of holotype ? (see text page 418) in
 Museum of Natural History, Paris. X 0.5. B.M.N.H.
 C5266.

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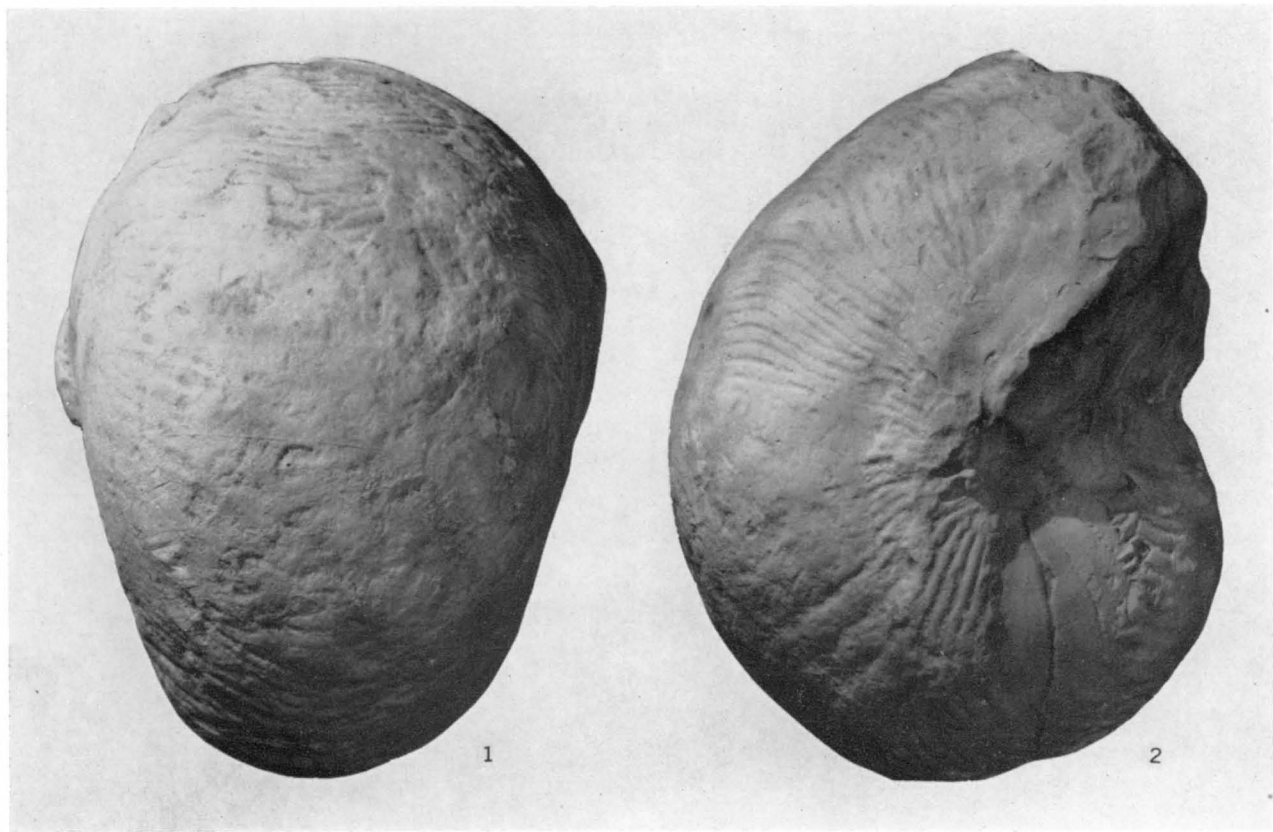


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Figures

- 1, 2 *Procymatoceras subtruncatus* (Morris and Lycett).....
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chinhampton, Gloucestershire, England. B.M.N.H. 21275.

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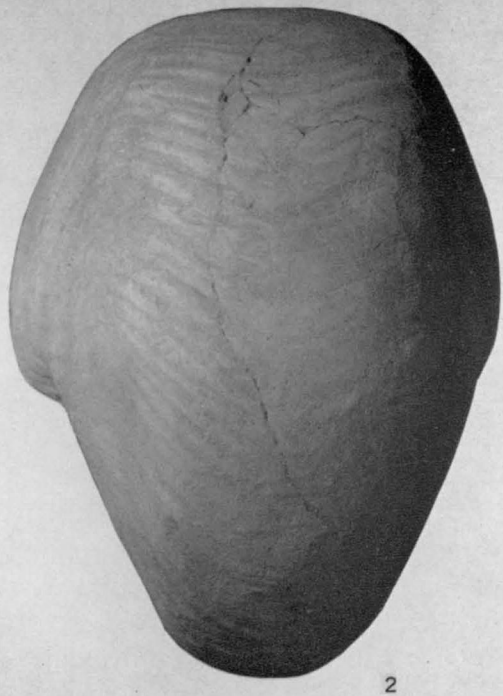


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Figures

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Four views of type species from strata of Callovian age
near Montreuil-Bellay and Chauffour, France. From
Guéranger.

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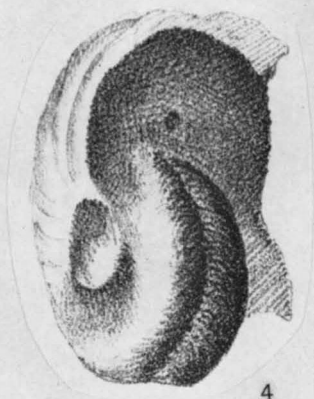


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	Two views of holotype, X 1, from the Stramberger beds (Upper Jurassic) of Stramberg, Moravia. From Zittel.	

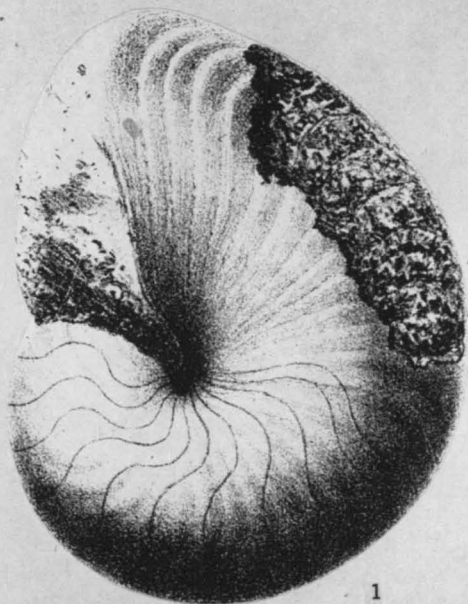


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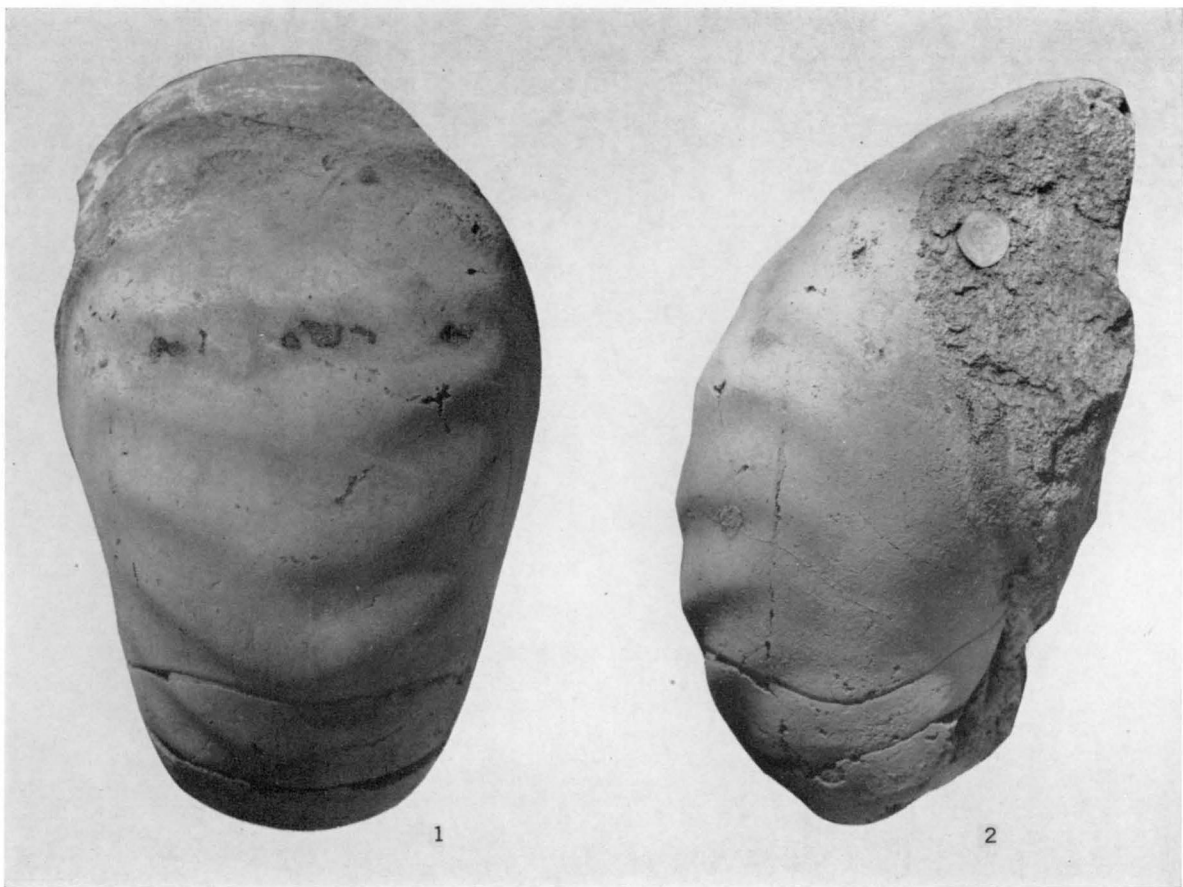


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1, 2	<i>Eucymatoceras plicatus</i> (Fitton)	431
	Two views of plesiotype, X 0.73, from Lower Greensand, Atherfield, Isle of Wight. B.M.N.H. C335.	

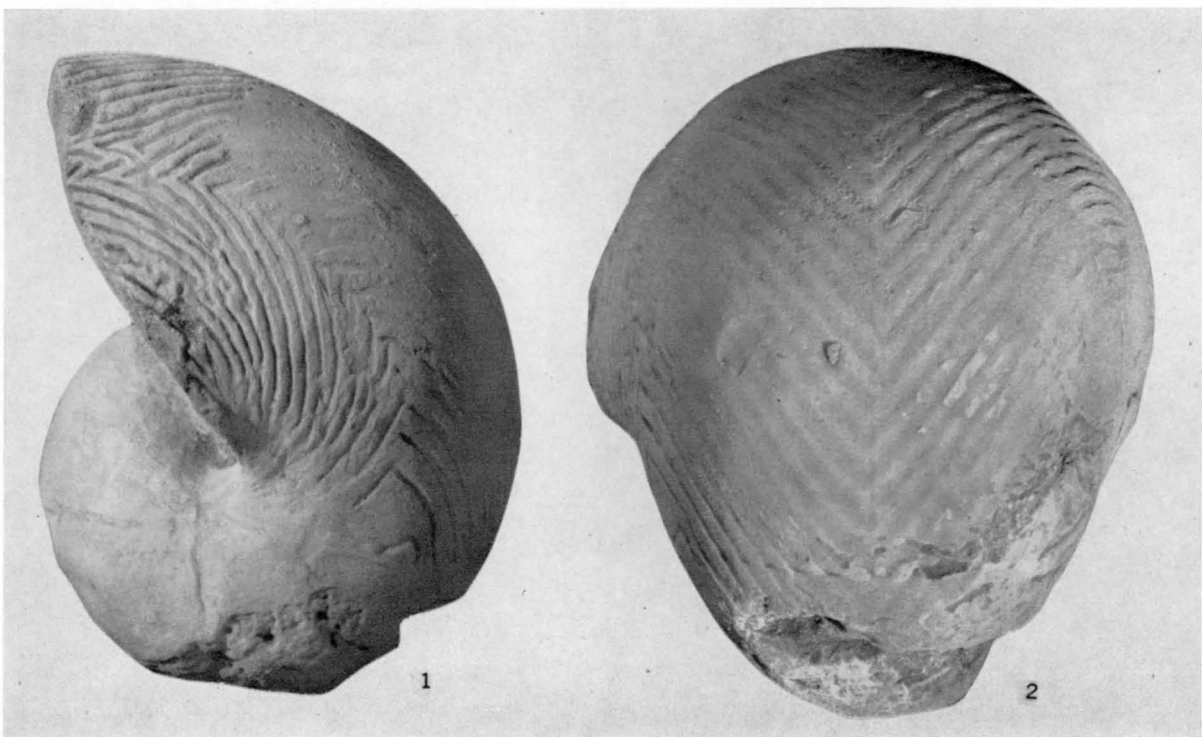


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PLATE 22. DELTOCYMATOCERAS LEIOTROPIS

Figures

- 1, 2 *Deltocymatoceras leiotropis* (Schlüter)
 Two views of type specimen, X 0.4, from Upper Cre-
 taceous formation of Essen, Germany. From Schlüter,
 1876.

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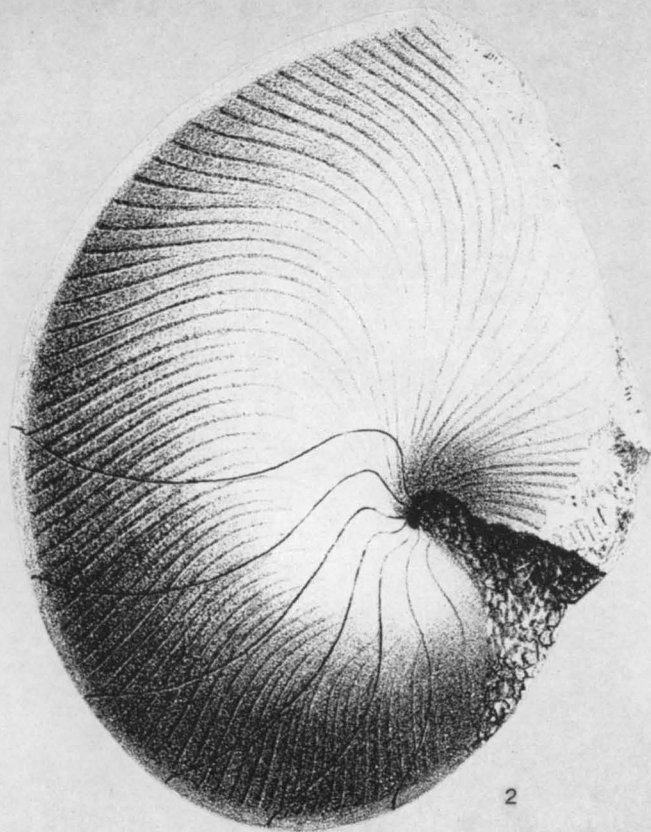
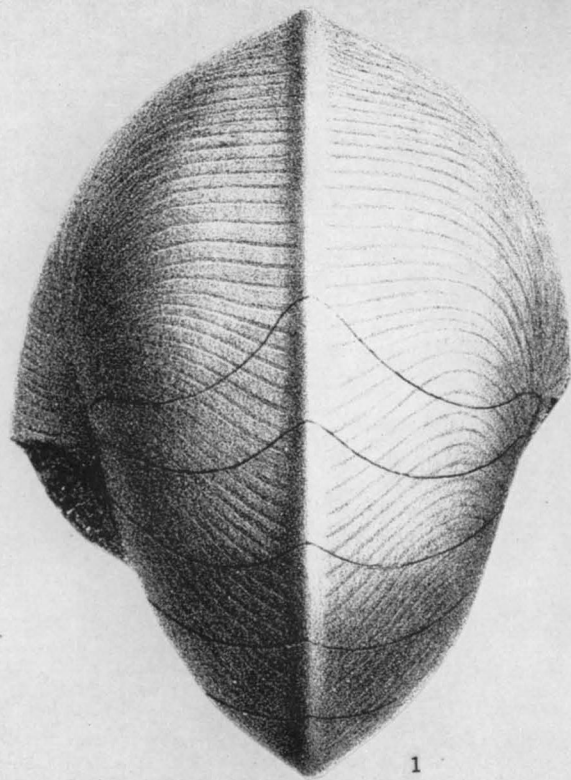


PLATE 23. EPICYMATOCERAS VAELSENSIS

Figures

1, 2

Epicymatoceras vaelensis (Binckhorst)
Two views of type species, X 1, from Upper Cretaceous
(Maestrichtian) formation at Limbourg, Belgium. From
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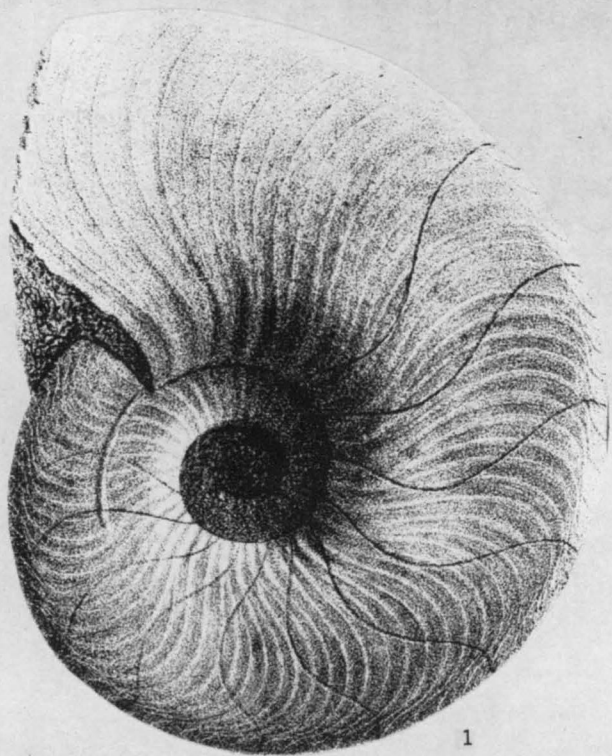


PLATE 23

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Figure

1

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 Reproduction of original illustration of holotype, from the
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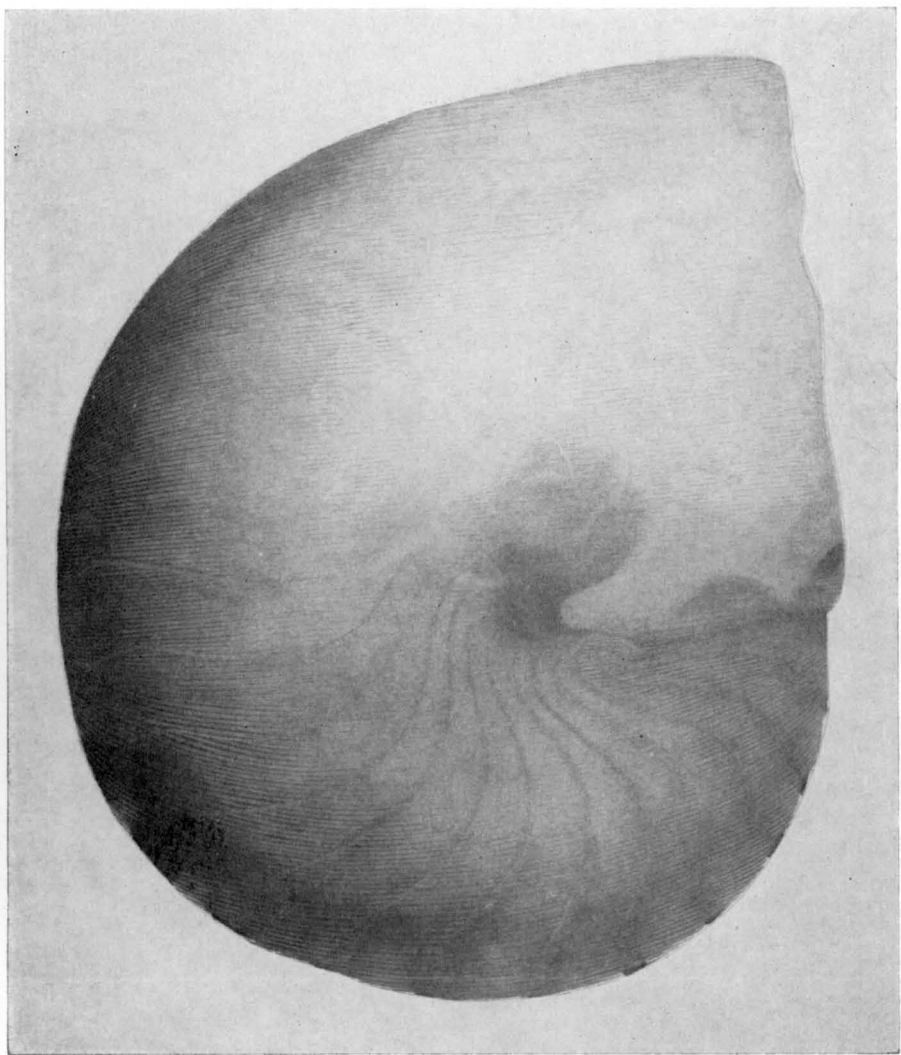
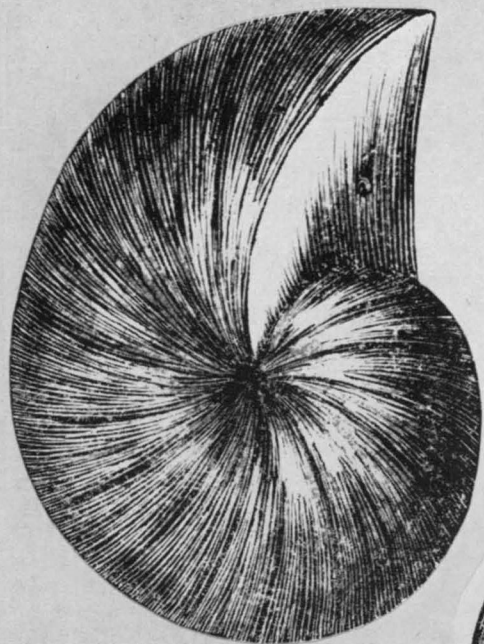


PLATE 24

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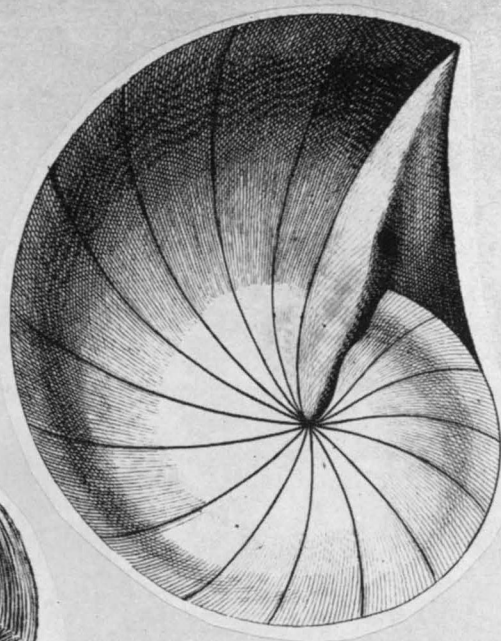
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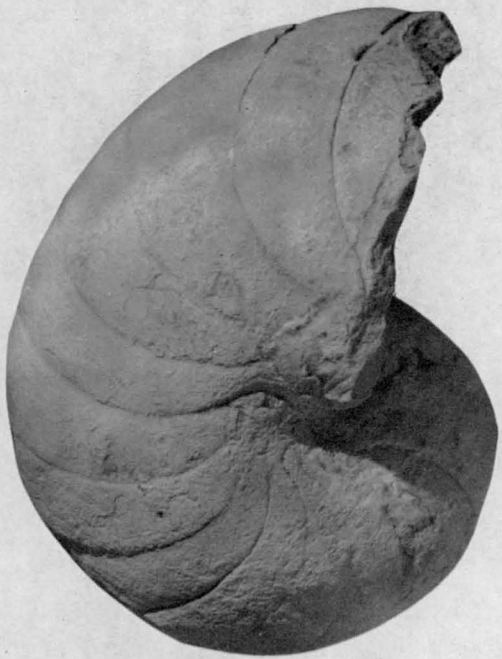
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Figures

- 1, 2 *Angulithes triangularis* (Montfort)
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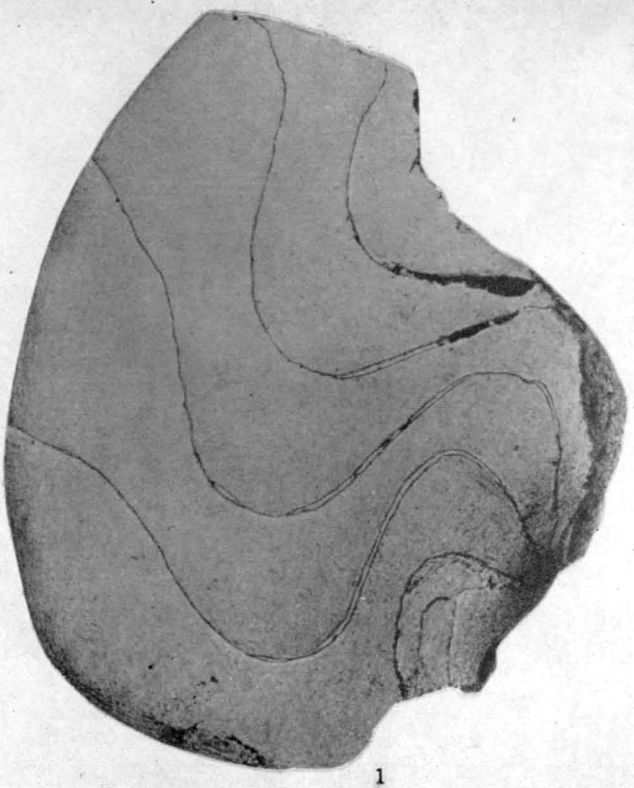
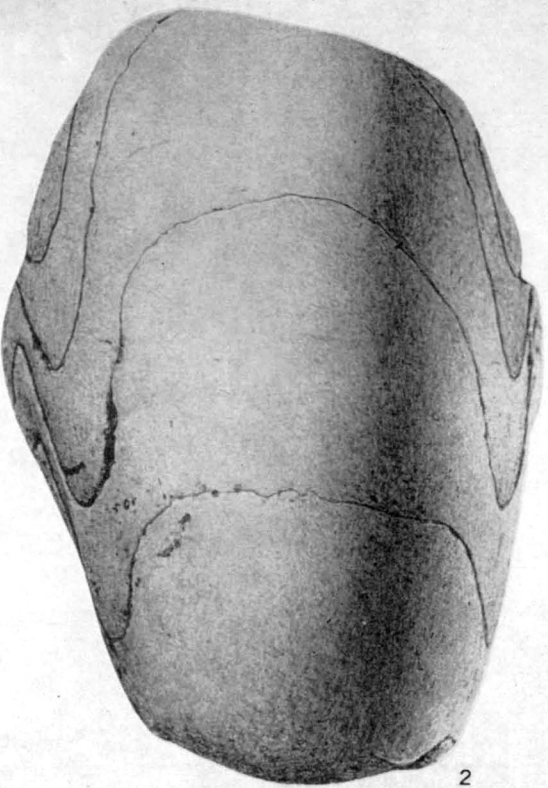


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