American Triassic Coiled Nautiloids

GEOLOGICAL SURVEY PROFESSIONAL PAPER 250

DEPARTMENT OF THE INTERIOR
March 3, 1849

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By BERNHARD KUMMEL

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A study of the classification and evolution of late
Paleozoic and early Mesozoic cephalopods,
and description of new species

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AMERICAN TRIASSIC COILED NAUTILOIDS

By BERNHARD KUMMEL

ABSTRACT

The relationships of late Paleozoic and Triassic nautiloids are studied. Of the nine families of late Paleozoic nautiloids three are directly involved in the ancestry of Triassic nautiloids. Two of these "Paleozoic" families include Triassic genera. Only three families of nautiloids are confined to the Triassic. Pennsylvanian, Permian, and Triassic nautiloids are very closely related and show no big breaks in their history. There is a large change in the evolutionary pattern of nautiloids between the Triassic and the Jurassic but only a very minor one at the Permian-Triassic boundary. Evolution of the nautiloids in the Triassic is mostly one of culminating patterns and modes started in the late Paleozoic.

The late Paleozoic and Triassic nautiloid families discussed are: (1) the Tainoceratidae, which includes *Temnocheilus, Foordiceras, Metacoceras, M.* (*Mojsvaroceras*), *Parametacoceras, Tainoceras, Aulametacoceras, Cooperoceras, Tirolonautilus, Tainionautilus, Germanonautilus, Pleuronautilus, Pl.* (*Encoiloceras*), *Pl.* (*Enoploceras*), *Pl.* (*Anoploceras*), *Pl.* (*Trachynautilus*), *Pl.* (*Holconautilus*), *Phloioceras;* (2) the Grypoceratidae, which includes *Grypoceras, G.* (*Domatoceras*), *G.* (*Plummeroceras*), n. subgen., *Stearoceras, Titanoceras, Stenopoceras, Pselioceras, Menuthionautilus, Gryponautilus;* (3) the Syringonautilidae, which includes *Syringonautilus, Syringoceras, Juvavionautilus, Oxynautilus, Clymenonautilus;* (4) the Liroceratidae, which includes *Liroceras, Condraoceras, Acanthonautilus, Coelogasteroceras,* and *Peripetoceras;* (5) the Paranautilidae, which includes *Paranautilus, Sybillonautilus,* and *Indonautilus;* (6) the Clydonautilidae, which includes *Styrionautilus, Proclydonautilus, Clydonautilus, Cosmonautilus,* and *Callaionautilus;* (7) the Gonionautilidae, which includes *Gonionautilus.*

Triassic nautiloids are not nearly as common in North America as they are in the region of the Tethyian geosyncline. About 30 species are known from North America, including 12 new ones.

INTRODUCTION AND ACKNOWLEDGMENTS

Studies in American Triassic paleontology have been almost completely neglected since the days of Alpheus Hyatt and J. P. Smith. The several large monographs by these pioneers were mainly on the ammonitic cephalopods. The nautiloids were only briefly treated. There is not a single American publication devoted solely to Triassic nautiloids. The writer has for the past ten years been studying the stratigraphy and paleontology of the Triassic formations in the Middle Rockies. Some of the rarest fossils in these Triassic formations are the nautiloid cephalopods. Interest in this particular group of invertebrates was greatly stimulated by Dr. A. K. Miller of the University of Iowa. Identification of the few dozen specimens collected from the Thaynes formation in southeastern Idaho was a relatively easy task. However, study of the great monographs by Triassic scholars such as Mojsisovics, Hauer, Hyatt, Arthaber, Diener, Kieslinger, etc., revealed a surprising lack of discussion or speculation as to the relationships of Triassic genera with the late Paleozoic forms. The same observation holds true for published monographs on late Paleozoic nautiloids by Miller, Kruglov, Hyatt, and others.

The present study is an attempt to review the status and phylogenetic relationships of late Paleozoic and Triassic nautiloids. The orthoceraconic nautiloids are not included in this report; only the coiled forms are discussed. Of the late Paleozoic families only those which were involved directly or indirectly in the ancestry of Triassic nautiloids are discussed. The ranges and geographic distribution of species in each genus are listed at the end of each generic discussion. The relationships of the genera have been established from all their characters. The value of certain morphological features in classification differs in the various phyletic units. One feature found to be of significance was the shape of the conch in cross section. Cross sections of many species are figured to show their relationships, and degrees of variability within genera. Most of the cross section drawings were obtained from the literature and reproduced at one size to facilitate comparison.

The taxonomic part of the text includes a discussion and description of all North American species of Triassic nautiloids. The collections available were those of the U. S. Geological Survey and the author's collections from southeastern Idaho. Late Paleozoic nautiloids are treated only as to families and genera, with the exception of one new subgenus and species. The original descriptions of most genera are included because many are to be found only in rare publications. It is hoped that this study, which systematically treats an invertebrate group on both sides of the Paleozoic-Mesozoic boundary, will be of value to those interested in the biological significance of the great systematic boundaries.

The author is greatly indebted to Dr. J. B. Reeside Jr., who kindly arranged the loan of the specimens and devoted much time to the tedious task of checking speci-

men data. Many stimulating discussions on nautiloid taxonomy and evolution were held with N. D. Newell, A. K. Miller, R. H. Flower, and H. B. Stenzel, and analysis of the evolution of late Paleozoic and Triassic nautiloids was greatly facilitated by the splendid monographs on late Paleozoic nautiloids by A. K. Miller. Finally, the author is grateful to the Graduate School of the University of Illinois, which furnished the working facilities, equipment, and all the funds for preparation of the plates and figures.

OCCURRENCE

Triassic nautiloids are very rare in North America. Only 28 species distributed in 17 genera have been recorded in contrast to myriads of ammonites in many zones in the Triassic of western North America. About two tons of material collected in southeastern Idaho from the Lower Triassic ammonite-rich limestone containing *Meekoceras* yielded only one fragmentary specimen of an orthoceraconic nautiloid. In contrast to this scarcity of nautiloids, however, the Hosselkus limestone of Late Triassic age of California seems to contain abundant nautiloid remains. It has long been recognized that the nautiloids, after their almost explosive introduction in the Ordovician, declined steadily to the present. Nautiloid shells are not generally common throughout the late Paleozoic and Triassic. Part of this seeming scarcity is due to lack of interest in this group and lack of thorough collecting. Most of the collections available were made by field parties whose main objectives were not stratigraphic or paleontologic. The quality of some recent collections, especially those from Mexico, Nevada, and Alaska indicates that future collecting should be very profitable in these areas.

The occurrence of Triassic nautiloids is discussed below by regions. The distribution outside North America is not listed here but the geographic and geologic range of all species are listed in the discussion of each genus, in the systematic part of this paper.

MIDDLE ROCKY MOUNTAINS REGION

No nautiloids have been described from the Lower Triassic formations of the Middle Rocky Mountains region. The Dinwoody formation in Slight Canyon, west of Bear Lake, southeastern Idaho has yielded one specimen, *Grypoceras* (*Grypoceras*) *milleri*, n. sp., and a very large fragment of the living chamber of a nautiloid that must have measured at least a foot in diameter came from pre-*Meekoceras* beds (Dinwoody formation) in Montpelier Canyon, southeastern Idaho.

The limestone with *Meekoceras*, of the Thaynes formation, which contains myriads of ammonites throughout southeastern Idaho is practically barren of nautiloids. Only one fragmentary "Orthoceras" has been found in this very fossiliferous bed. The black shale with black limestone concretions about 500 ft above the limestone with *Meekoceras*, and referred to as the *Columbites* shale by Kummel (1943) has yielded a small but well-preserved nautiloid fauna. In four field seasons the author visited several outcrops in southeastern Idaho, and was able to collect about 40 specimens. The *Columbites* shale contains the following species:

Metacoceras (*Mojsvaroceras*) *frenchi*, n. sp.
Germanonautilus montpelierensis, n. sp.
Pleuronautilus (*Enoploceras*) *newelli*, n. sp.
Pleuronautilus (*Pleuronautilus*) *idahoensis*, n. sp.

The *Tirolites* zone, which lies between the *Meekoceras* and *Columbites* beds of the Thaynes formation, in Paris Canyon, southeastern Idaho has yielded one specimen, described here as *Pleuronautilus* sp.

The Lower Triassic rocks of Montana are not as fossiliferous as those in southeastern Idaho. Only one specimen, described here as *Pleuronautilus* sp., from the Thaynes formation, is available for study.

No nautiloids have been reported from the Lower Triassic of Utah.

NEVADA

Few nautiloid specimens are available from Triassic formations of the Hawthorne and Tonopah Quadrangles, Nevada. From the Luning formation *Germanonautilus* sp. and *Paranautilus* sp. are recognized. The Gabbs formation has yielded *Sibyllonautilus fergusoni*, n. sp. Muller and Ferguson (1939) list *Grypoceras* cf. *G. brahmanicum* (Griesbach) from the Candelaria formation, *Cosmonautilus* cf. *C. pacificus* Smith from the Luning formation, and from the Gabbs formation, *Proclydonautilus spirolobus* and *Gonionautilus securis*.

The Middle Triassic series of the Humboldt Range has yielded a fair number of nautiloids, including:

Orthoceras campanile Mojsisovics
Orthoceras blakei Gabb
Paranautilus smithi n. sp.
Paranautilus multicameratus (Gabb)
Germanonautilus furlongi Smith
Grypoceras (*Grypoceras*) *whitneyi* (Gabb)

At New Pass, Desatoya Mountains the *Daonella* zone has yielded the following species:

Germanonautilus johnstoni, n. sp.
Germanonautilus furlongi Smith
Grypoceras (*Grypoceras*) *whitneyi* (Gabb)
Orthoceras blakei Gabb
Paranautilus sp.
Styrionautilus sp.

From the upper part of the Star Peak formation, West Humboldt Range, in shales carrying *Pseudomonotis subcircularis*, Smith (1927) has described *Syringoceras spurri* Smith.

CALIFORNIA

The largest and most varied Triassic nautiloid fauna of North America occurs in the Upper Triassic series of California. The *Tropites subbullatus* zone of the Hosselkus limestone, Brock Mountain, Shasta County, California, has yielded the following fauna:

Orthoceras shastense Hyatt and Smith
Proclydonautilus hessi (Smith)
Proclydonautilus squawensis n. sp.
Proclydonautilus spirolobus (Dittmar)
Proclydonautilus stantoni Smith
Proclydonautilus triadicus Mojsisovics
Proclydonautilus ursensis Smith
Oxynautilus acutus (Hauer)
Gryponautilus cooperi Smith
Metacoceras (*Mojsvaroceras*) *turneri* Hyatt and Smith
Cosmonautilus dilleri Hyatt and Smith
Cosmonautilus hersheyi Smith
Cosmonautilus pacificus Smith
Cosmonautilus shastensis Smith

The zone of *Parapopanoceras* (Anisian), Inyo County, California, has yielded *Orthoceras* sp. indet. (Smith 1914, p. 6).

CANADA

Only two species of Triassic nautiloids have been described from the extensive Triassic sequence of Western Canada: *Sibyllonautilus liardensis* (Whiteaves) from the Liard formation, Liard River, northeastern British Columbia (see McLearn 1947, p. 10) and *Proclydonautilus natosini* McLearn and *Proclydonautilus* sp. from Norian beds, Sikanni Chief River Basin, British Columbia (McLearn 1946, pp. 2, 3). *Proclydonautilus natosini* also occurs in the Pardonet beds, Pardonet Hills, Peace River foothills, British Columbia. From beds containing the *Nathorstites* fauna McLearn (1947) reports "*Nautilus*" sp. at Hage Creek, Sikanni Chief Valley and from outcrops a little west of mile post 386 on the Alaskan Highway. The Toad formation has only yielded "*Nautilus*" sp. and *Orthoceras* sp. (McLearn 1946, 1948). No nautiloids are known from the Lower Triassic formations of British Columbia (McLearn 1945).

ALASKA

The extensive Upper Triassic formations of Alaska have yielded relatively few nautiloids. The best summary of the known Triassic invertebrates in Alaska is by Martin (1916, 1926). The Chitistone limestone of the Chitina Valley contains *Orthoceras* cf. *O. shastense* Hyatt and Smith, *Orthoceras* sp. (Martin, 1926, p. 15) and *Pleuronautilus alaskensis,* n. sp. The Upper Triassic rocks on Gravina Island contain *Cosmonautilus*? (Martin 1926, p. 71). *Mojsvaroceras*? has been reported from Upper Triassic limestones 7 miles southeast of Kake, on Kupreanof Island. The Upper Triassic limestone near Nation River, Yukon Valley contains *Germanonautilus brooksi* Smith, *Germanonautilus* sp. and *Orthoceras* sp. The collections under study contain a specimen of *Germanonautilus* sp. from Cape Kekurnoi, between Gold and Alinchak Bays, Alaska Peninsula. The Upper Triassic rocks exposed at Herring Bay, Admiralty Island, Alaska have yielded a fragmentary but very well preserved specimen of *Phloioceras* sp.

MEXICO

The Upper Triassic Barranca formation of Sonora, Mexico, has yielded a few nautiloids (see Keller, 1928, and King, 1939). At the Mina el Antimonio, in beds containing a rich Karnian fauna, the following species have been recognized:

Proclydonautilus triadicus (Mojsisovics)
Cosmonautilus pacificus Smith
Orthoceratoids

The collections of the U. S. Geological Survey include three specimens, and a plaster cast of a specimen in the Instituto Geologico de Mexico, that are referable to *Cosmonautilus dilleri* Hyatt and Smith. These specimens also came from the locality of Mina el Antimonio.

SOUTH AMERICA

Triassic cephalopods are indeed rare in South America. The only Triassic nautiloid known to the author is one he collected in the upper Triassic Utcubamba formation in Suta Valley, a tributary of the Utcubamba River, northern Peru (Kummel, 1950). The specimen is immature and silicified. It consists of only one-third volution with a rounded whorl section and a subcentral siphuncle. The specimen can be identified only as *Syringonautilus*?.

CLASSIFICATION OF LATE PALEOZOIC AND TRIASSIC NAUTILOIDS

During the past three decades active interest in nautiloid cephalopods has been revived by Flower, Foerste, Miller, Kieslinger, Kruglov, Schindewolf, Spath, Stenzel, Strand, Teichert, Troedsson, and others. Only Kieslinger concerned himself with Triassic nautiloids, the others concentrating on Palezoic and post-Triassic nautiloids. Fine monographs on late Paleozoic nautiloids of North America have been published in the last two decades by Miller and various coworkers. As pointed out by Miller and Youngquist (1949, p. 15)

> * * * the classification of the nautiloid cephalopods is not in as satisfactory condition as is that of the ammonoids and most other major groups of fossil invertebrates, and the best existing systematic arrangement seems to be that which Hyatt published in 1900 in the Zittel-Eastman *Text-book of paleontology.*

These authors further emphasize the tentative nature of this system and are cognizant of its many weaknesses. Flower and Kummel (1950) proposed a completely revised classification of the Nautiloidea placing the 75 families of nautiloids into 14 orders.

Hyatt (1900) placed the Triassic nautiloid genera known at that time in four families, the Grypoceratidae, Clydonautilidae, Rhineceratidae, and Pleuronautilidae. Mojsisovics two years later published the first comprehensive taxonomic treatment of Triassic nautiloids and accepted only one of Hyatt's families. He (Mojsisovics) also classified the twenty genera of Triassic nautiloids known at that time into four families, the Clydonautilidae, Syringonautilidae, Gryponautilidae, and the Temnocheilidae, using the presence or absence of an annular lobe as a primary character in his classification. Temnocheilidae (Mojsisovics) is synonymous with Tainoceratidae of Hyatt. They include essentially the same Paleozoic genera, but Mojsisovics included several Triassic genera. Diener (1919) took exception to Mojsisovics' classification because he had overemphasized the importance of the annular lobe. Diener combined the genera that Mojsisovics had included in the Clydonautilidae and Gryponautilidae into one family, the Grypoceratidae. Diener retained the Temnocheilidae and Syringonautilidae as proposed by Mojsisovics. This taxonomic scheme was also followed by Kieslinger (1924). Since Kieslinger's publication there has been no publication devoted solely to Triassic nautiloids, although nautiloids have been included in numerous general faunal studies.

A marked handicap in most taxonomic studies of Triassic nautiloids has been an insufficient understanding of late Paleozoic nautiloids and their relationships with the Triassic forms. Fortunately, owing to the work of Miller and others our knowledge of Pennsylvanian and Permian nautiloids has increased greatly in the past twenty years. In preparation of this report, data on the geologic and geographic distribution of most late Paleozoic nautiloids have been assembled. The writer was impressed by the general lack of statements as to the evolutionary status of the various taxonomic groups, but in the early papers such speculation was impossible or unwise owing to incomplete knowledge. Restudy of all late Paleozoic genera with the aim of presenting a reasonable phylogeny in accordance with our present state of knowledge was undertaken to determine the probable phylogenetic lines from which the Triassic nautiloids developed.

The most significant fact brought out in this study is the close genetic relationship of many Triassic and late Paleozoic genera. Several well-known Triassic genera are considered as direct evolutionary descendants that replaced the Paleozoic genera. In this report the Triassic nautiloids are placed in the Tainoceratidae Hyatt (Temnocheilidae Mojsisovics), Syringonautilidae Mojsisovics, Grypoceratidae Hyatt, Paranautilidae Kummel, Clydonautilidae Hyatt, and Gonionautilidae Kummel. The Tainoceratidae, Grypoceratidae, and Paranautilidae include both late Paleozoic and Triassic genera.

The interpretation of phylogenetic relationships presented here is not radically different from the conclusions of earlier workers; however, there are significant differences. All genera of families involved in the evolution of late Paleozoic-Triassic nautiloids, and their inferred position in nautiloid evolution are discussed in the taxonomic part of this report.

The system presented here can be only tentative. Frequently the data available are so meager that one can only make the most logical proposal possible and wait for additional information. A study like this is always open to criticism from many sides. However, to those who feel our knowledge has as yet not attained a sufficient level the only answer possible is that we probably never will know all the answers within the limits of paleontological research. It is felt that if such studies stimulate action as well as reaction they have been at least partly successful.

The classification used in this report is as follows:

Family Tainoceratidae Hyatt, 1883
    Genus *Temnocheilus* M'Coy, 1844
        Genotype: *Nautilus* (*Temnocheilus*) *coronatus* M'Coy
    Genus *Foordiceras* Hyatt, 1893
        Genotype: *Nautilus goliathus* Waagen
    Genus *Metacoceras* Hyatt, 1883
        Genotype: *Nautilus* (*Discus*) *sangamonensis* Meek and Worthen
      Subgenus *Mojsvaroceras* Hyatt, 1883
        Subgenotype: *Temnocheilus neumayri* Mojsisovics
    Genus *Parametacoceras* Miller and Owen, 1934
        Genotype: *Parametacoceras bellatulum* Miller and Owen
    Genus *Tainoceras* Hyatt, 1883
        Genotype: *Nautilus quadrangulus* McChesney
    Genus *Cooperoceras* Miller, 1945
        Genotype: *Cooperoceras texanum* Miller
    Genus *Tainionautilus* Mojsisovics, 1902
        Genotype: *Nautilus transitorius* Waagen
    Genus *Tirolonautilus* Mojsisovics, 1902
        Lectotype: *Nautilus crux* Stache
    Genus *Aulametacoceras* Miller and Unklesbay, 1942
        Genotype: *Aulametacoceras mckeei* Miller and Unklesbay
    Genus *Germanonautilus* Mojsisovics, 1902
        Genotype: *Nautilus bidorsatus* Schlotheim
    Genus *Thuringionautilus* Mojsisovics, 1902
        Genotype: *Trematodiscus jugatonodosus* Zimmermann
    Genus *Pleuronautilus* Mojsisovics, 1882
        Genotype: *Pleuronautilus trinodosus* Mojsisovics
      Subgenus *Enoploceras* Hyatt, 1900
        Subgenotype: *Nautilus wulfeni* Mojsisovics
      Subgenus *Holconautilus* Mojsisovics, 1902
        Subgenotype: *Nautilus semicostatus* Beyrich

- Family Tainoceratidae, Hyatt, 1883—Continued
    - Genus *Pleuronautilus* Mojsosovics, 1882—Continued
        - Subgenus *Anoploceras* Hyatt, 1900
            - Subgenotype: *Nautilus ampezzanus* Loretz
        - Subgenus *Encoiloceras* Hyatt, 1900
            - Subgenotype: *Nautilus superbus* Mojsisovics
        - Subgenus *Trachynautilus* Mojsisovics, 1902
            - Subgenotype: *Pleuronautilus subgemmatus* Mojsisovics
    - Genus *Phloioceras* Hyatt, 1883
        - Genotype: *Nautilus gemmatus* Mojsisovics
- Family *Grypoceratidae* Hyatt, 1900
    - Genus *Grypoceras* Hyatt, 1883
        - Genotype: *Nautilus mesodiscus* Hauer
        - Subgenus *Domatoceras* Hyatt, 1891
            - Subgenotype: *Domatoceras umbilicatum* Hyatt
        - Subgenus *Plummeroceras* n. subgen.
            - Subgenotype: *Plummeroceras plummeri*, n. sp.
    - Genus *Gryponautilus* Mojsisovics, 1902
        - Genotype: *Nautilus galeatus* Mojsisovics
    - Genus *Menuthionautilus* Collignon, 1933
        - Genotype: *Nautilus (Menuthionautilus) kieslingeri* Collignon
    - Genus *Stenopoceras* Hyatt, 1893
        - Genotype: *Phacoceras dumblei* Hyatt
    - Genus *Stearoceras* Hyatt, 1893
        - Genotype: *Endolobus gibbosus* Hyatt
    - Genus *Pselioceras* Hyatt, 1883
        - Genotype: *Nautilus ophioneus* Waagen
    - Genus *Titanoceras* Hyatt, 1884
        - Genotype: *Nautilus ponderosus* White
- Family Syringonautilidae Mojsisovics, 1902
    - Genus *Syringonautilus* Mojsisovics, 1902
        - Genotype: *Nautilus lilianus* Mojsisovics, 1882
    - Genus *Syringoceras* Hyatt, 1894
        - Genotype: *Nautilus granulosostriatus* Klipstein
    - Genus *Juvavionautilus* Mojsisovics, 1902
        - Genotype: *Nautilus heterophyllus* Hauer
    - Genus *Oxynautilus* Mojsisovics, 1902
        - Genotype: *Nautilus acutus* Hauer
    - Genus *Clymenonautilus* Hyatt, 1900
        - Genotype: *Nautilus ehrlichi* Mojsisovics
- Family Paranautilidae Kummel, 1950
    - Genus *Paranautilus* Mojsisovics, 1902
        - Genotype: *Nautilus simonyi* Hauer
    - Genus *Indonautilus* Mojsisovics, 1902
        - Genotype: *Nautilus kraffti* Mojsisovics
    - Genus *Sibyllonautilus* Diener, 1915
        - Genotype: *Nautilus sibyllae* Mojsisovics
- Family Clydonautilidae Hyatt, 1900
    - Genus *Styrionautilus* Mojsisovics, 1902
        - Genotype: *Nautilus styriacus* Mojsisovics
    - Genus *Proclydonautilus* Mojsisovics, 1902
        - Genotype: *Nautilus griesbachi* Mojsisovics
    - Genus *Cosmonautilus* Hyatt and Smith, 1905
        - Genotype: *Cosmonautilus dilleri* Hyatt and Smith
    - Genus *Callaionautilus* Kieslinger, 1924
        - Genotype: *Callaionautilus turgidus* Kieslinger
    - Genus *Clydonautilus* Mojsisovics, 1882
        - Genotype: *Nautilus noricus* Mojsisovics
- Family Gonionautilidae Kummel, 1950
    - Genus *Gonionautilus* Mojsisovics, 1902
        - Genotype: *Nautilus securis* Dittmar

GEOLOGIC HISTORY

The nautiloids with their long geologic history make an excellent group for evolutionary studies. The approximately 630 genera of nautiloids represent a complex evolution extending from the Late Cambrian to the Recent epoch. From the Pliocene to the Recent epoch only one genus, *Nautilus,* is left of what was once an important and abundant invertebrate group. The nautiloids illustrate a peculiar evolutionary pattern in that they attain a peak of diversity soon after their introduction into the fossil record. Figure 1 is a bar chart of the number of genera per period. The data upon which this chart was made were kindly furnished by Dr. Curt Teichert. The earliest nautiloids, those of the Ordovician, are represented by far the most genera; in fact, there are more than twice as many nautiloid genera in the Ordovician as in the Silurian. This great discrepancy would, of course, be decreased if the graph were plotted in terms of the number of genera per million years. Miller (1949, p. 231) suggests the Silurian as the "heyday of the nautiloids, insofar as both numbers and kinds are concerned." The number of Ordovician and Silurian species of nautiloids is not known, but the number of genera is much larger for the Ordovician.

By the end of the Ordovician most of the major stocks of nautiloids were well established. One stock, the "Orthochoanites," was destined to give rise to the modern *Nautilus.* Most of the other stocks were short lived. The holochoanitids and mixochoanitids died out in the Silurian, the cyrtochoanitids lived through the Paleozoic era.

It has been known generally that there was a steady and progressive decline in the nautiloids from the Ordovician onward. This fact is well illustrated in figure 1. The large breaks in the distribution come between the Ordovician and the Silurian, between the Devonian and the Carboniferous and to a lesser degree between the Triassic and Jurassic periods. Although the number of genera of post-Devonian nautiloids was never great for any one period, there were times of great expansion in numbers of individuals and species. Miller (1949) has shown that early Cenozoic nautiloids were very abundant in many widely scattered places in the world. Kieslinger (1925) has noted a secondary peak of development during the Late Triassic. This aspect of nautiloid history will be the concern of this paper.

There are about 250 established species of Triassic nautiloids placed in 30 genera (no species identified as cf. or aff. with recognized species are included in this number). The distribution of species per epoch is illustrated in figure 2. Early Triassic (Scythian)

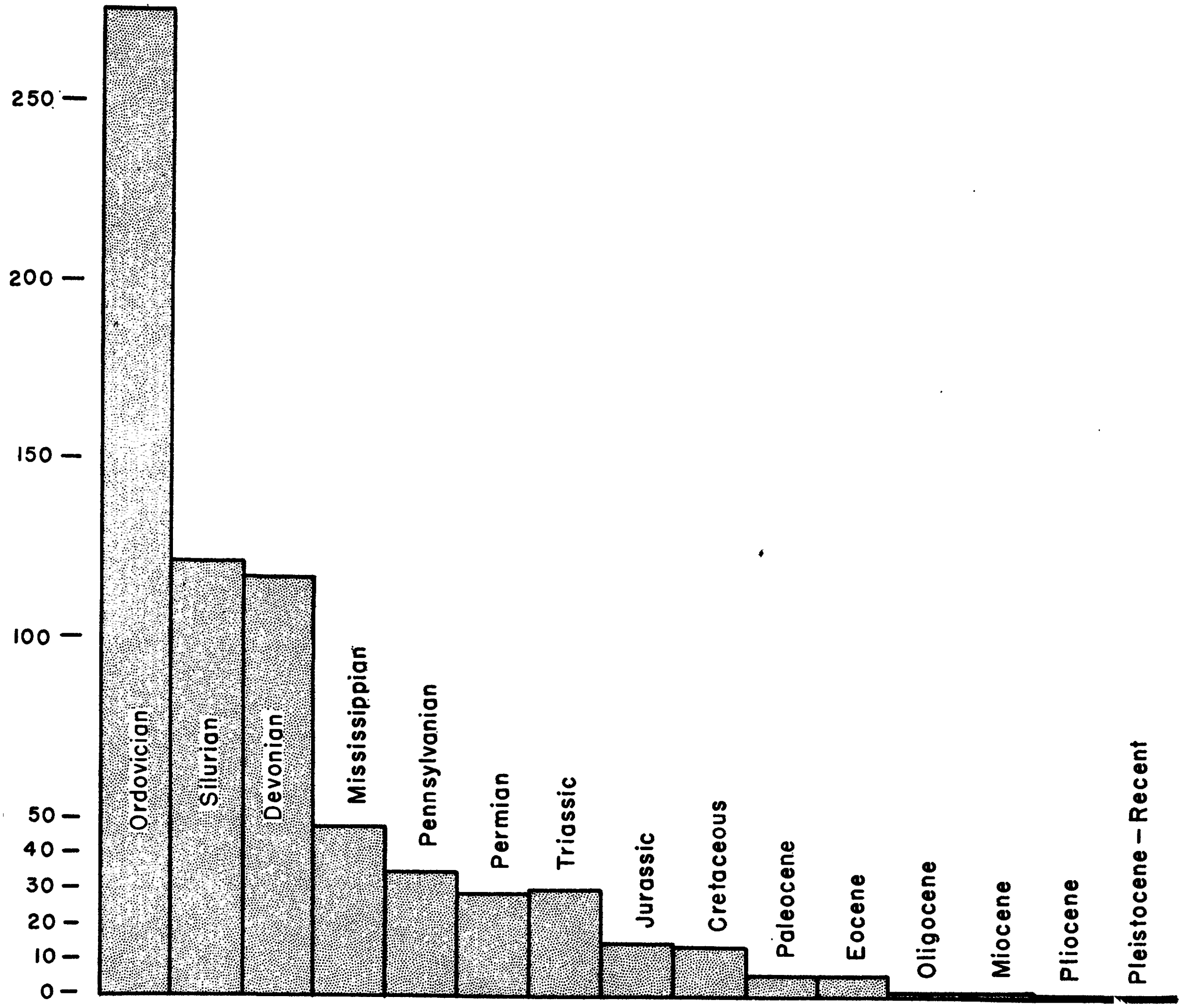

FIGURE 1.—Bar chart showing number of genera of nautiloid cephalopods present in each period. (Data from C. Teichert, personal communication.)

nautiloids are relatively rare as to numbers of species and individuals. By the Anisian the nautiloids became very widespread and most of the important genera had become established. The decline in numbers of species in the Ladinian is difficult to explain. How much of this decline is only apparent, and due to lack of a paleontological record is not known. The evolution of the genera and families shows no significant break in the Ladinian. About 90 species occur in the Karnian, and less than half that number (about 35) in the Norian.

The distribution of the genera of Triassic nautiloids is illustrated in figure 3. In the Scythian the nautiloids are represented by members of 2 late Paleozoic families: *Grypoceras* and *Menuthionautilus* (Grypoceratidae), and *Pleuronautilus*, *Enoploceras*, *Tainionautilus*, *Mojsvaroceras*, and *Germanonautilus* (Tainoceratidae). *Grypoceras* and *Mojsvaroceras* are considered direct evolutionary offshoots of the basic evolving stock of their respective families. *Tainionautilus* and *Menuthionautilus* are not present in younger Triassic rocks. In the Anisian, 8 new genera are introduced and the actual evolutionary radiation of Triassic nautiloids begins. The oldest species of the Syringonautilidae and Clydonautilidae are found in the Anisian. The genera having their first Triassic species in the Anisian are *Paranautilus*, *Sibyllonautilus*, *Styrionautilus*, *Syringoceras*, *Syringonautilus*, *Trachynautilus*, *Anoploceras*, and *Holconautilus*. *Paranautilus* is believed to include 2 possible Permian species; however, no Scythian species are known. The radiation of the pleuronautilids is well established during the Anisian. There may be justification in placing all these forms in the family Pleuro-

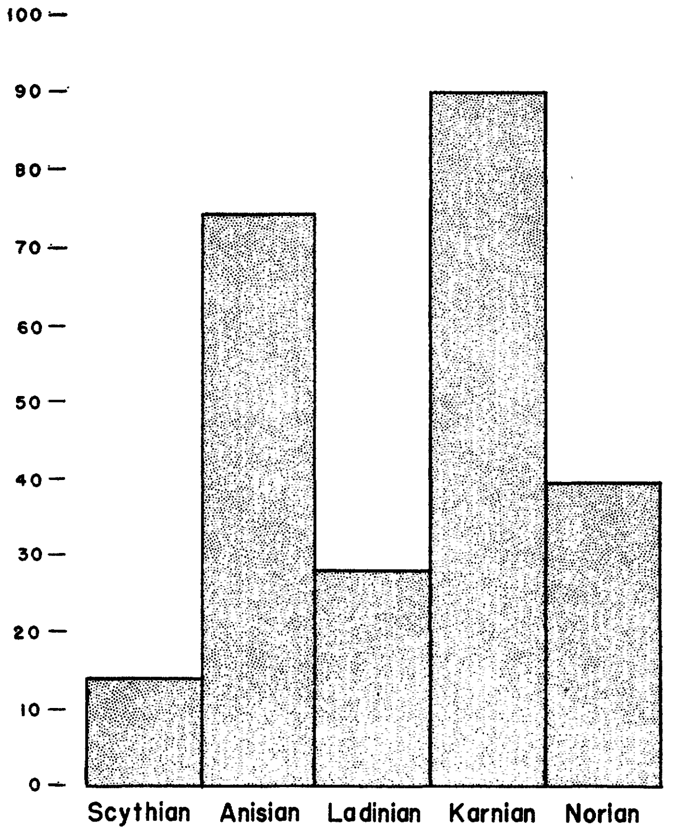

FIGURE 2.—Bar chart showing total number of species of Triassic nautiloids in each epoch.

nautilidae as proposed by Hyatt (1900), however, tentatively the author is following Mojsisovics and retaining them in the Tainoceratidae.

During the Ladinian only 3 genera, *Phloioceras*, *Thuringionautilus*, and *Clydonautilus* got their start; of these only *Clydonautilus* turned out to be a virile stock. There are 16 genera represented in the Ladinian. The acme was attained in the Karnian epoch with 20 genera and approximately 90 species of nautiloids. Only 4 genera (*Proclydonautilus*, *Cosmonautilus*, *Gryponautilus*, *Encoiloceras*) made their debut in the Karnian, whereas many of the well-established genera (including *Trachynautilus*, *Encoiloceras*, *Anoploceras*, *Holconautilus*, *Pleuronautilus*, *Mojsvaroceras*, and *Germanonautilus*) make their last appearance. Only 2 Karnian species, *Tainoceras klipsteini* and *Aulametacoceras rectangularis*, are placed in Permian genera. *Tainoceras* is a common Pennsylvanian and Permian nautiloid genus, and the Karnian species is assigned to it mainly on similarities of ornamentation. *Aulametacoceras* was originally described from beds of Leonard age in Arizona, and has only one Permian species. Whether placing Karnian species in Permian genera (in the absence of any intervening forms) is correct only time will tell.

There is only a slight decrease in total number of genera in the Norian (from 20 to 18). This is due mainly to the introduction of 6 new genera—*Juvavionautilus*, *Oxynautilus*, *Clymenonautilus*, *Indonautilus*, *Gonionautilus*, and *Callaionautilus*. Only *Juvavionautilus*, has more than one species or an extensive geographic distribution. *Menuthionautilus* in the Scythian, *Thuringionautilus* in the German Keuper, and *Encoiloceras* in the Karnian, are also monotypic genera. In the 18 genera represented in the Norian, about 80 percent of the species are in 5 genera—*Paranautilus*, *Clydonautilus*, *Proclydonautilus*, *Enoploceras*, and *Juvavionautilus*. Most of the remaining genera are represented by only one species each.

EVOLUTION

The whole evolutionary complex of late Paleozoic and Triassic nautiloids more or less follows a generalization concluded by Kieslinger (1925, p. 107) from his study of the Late Triassic nautiloids of Timor that the degree of involution and ornamentation are inversely proportional. There are eight families of late Paleozoic nautiloids (see Miller and Youngquist, 1949, p. v) but only the Grypoceratidae, Tainoceratidae, and Liroceratidae are thought to be involved in the direct ancestry of Triassic nautiloids and are discussed in this report. The Liroceratidae does not include Triassic genera. The families Paranautilidae, Clydonaitulidae, Gonio-

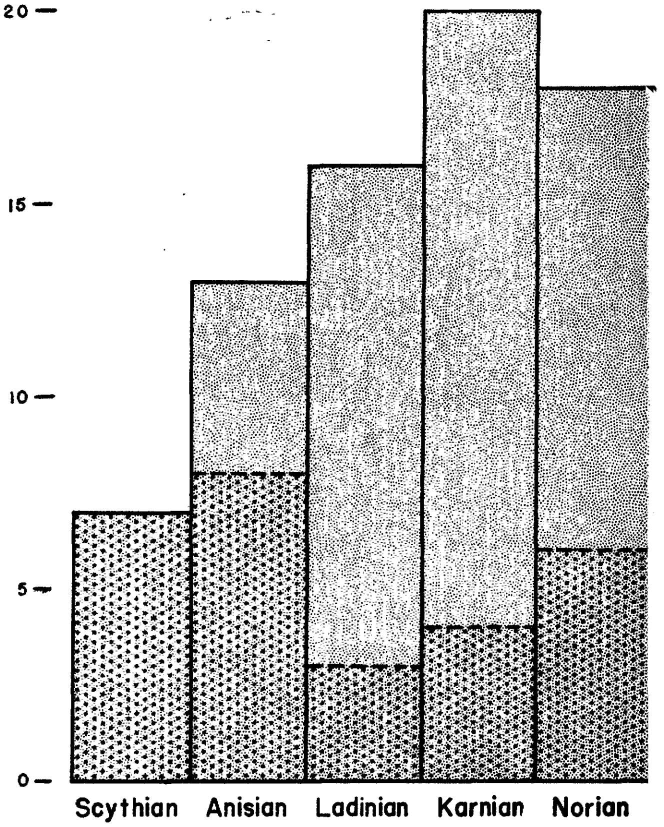

FIGURE 3.—Bar chart showing number of genera of nautiloid cephalopods present in each epoch (light stippling) and number of new genera appearing for the first time in each epoch of the Triassic period (dense stippling).

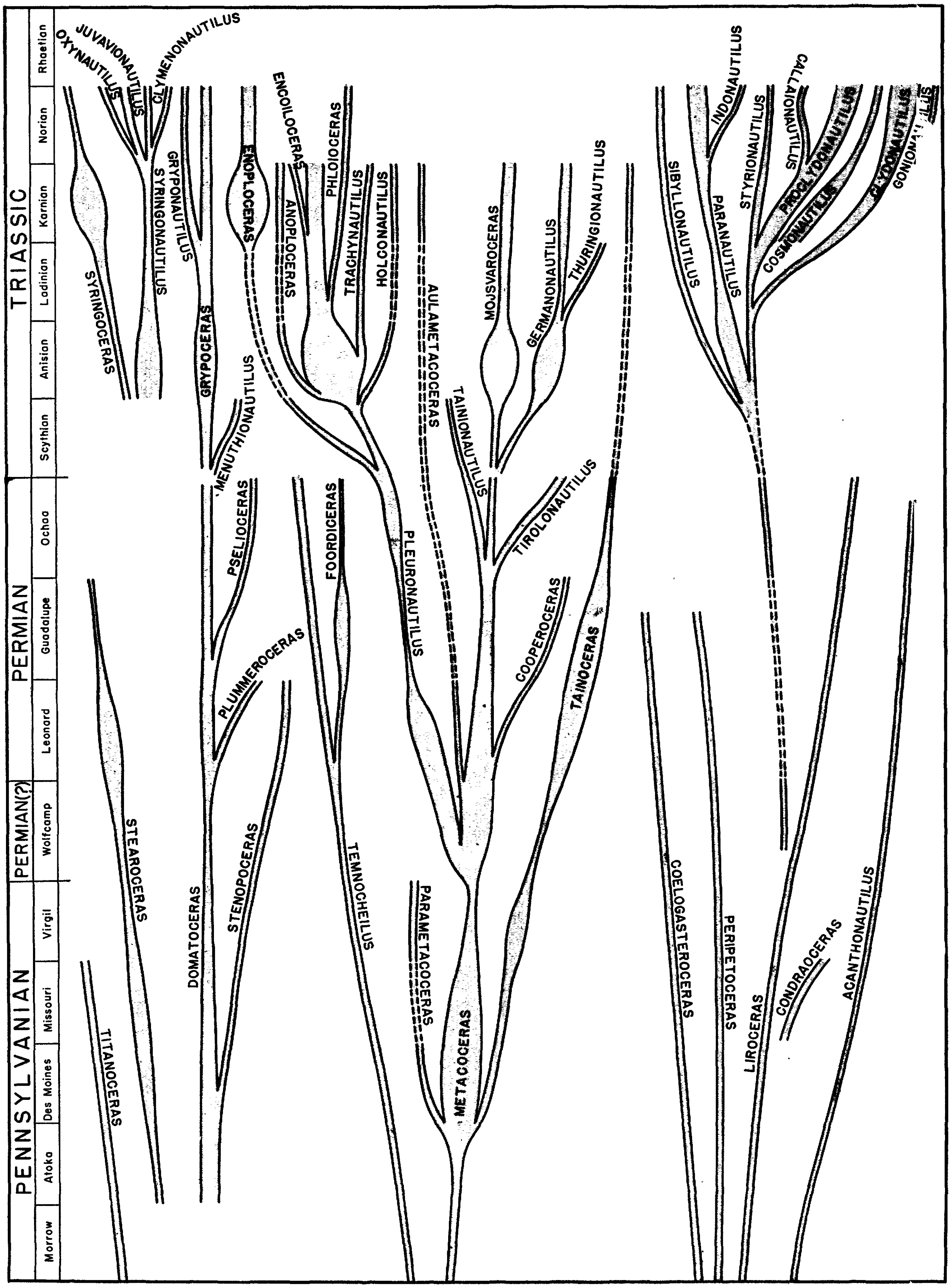

FIGURE 4.—Diagram showing inferred phylogeny and geologic distribution of late Paleozoic and Triassic coiled nautiloids.

nautilidae, and Syringonautilidae are confined to the Triassic (text fig. 4).

These seven families can be grouped into two phyletic lines that show a great deal of convergence throughout their history. The first group (the Tainoceratidae) includes most of the ornamented, generally evolute, nautiloids that have subquadratic whorl sections and very simplified sutures. The second, more complex, phyletic group includes forms that are smooth, generally involute, and tend towards modification and complication of the suture pattern. Three subdivisions of this group can be recognized. The first subgroup includes forms that have a smooth, involute conch and highly modified sutures (Clydonautilidae and Gonionautilidae). The second subgroup comprising the Paranautilidae and Liroceratidae, have a smooth, involute conch but very simple, practically straight, sutures. The third sub-group (Grypoceratidae and Syringonautilidae) is less homogeneous, and includes smooth, evolute to involute conchs, generally with flattened venters. The sutures include a broad lateral lobe with some modifications of the suture on the venter.

Although the grouping of late Paleozoic and Triassic families reveals the general evolutionary picture there are numerous anomalies. The acquisition of ornamentation occurred repeatedly in all or some species of genera Clydonautilidae and Grypoceratidae and in a sense shows a convergence towards some forms of the Tainoceratidae. *Cosmonautilus*, for example, has developed nodes on the ventral shoulders in some stages of its growth. Hyatt and Smith (1905, p. 207) used this as evidence of an ancestry in the genus *Metacoceras*, but the present author does not believe that this derivation is correct. In all other characters and especially its suture *Cosmonautilus* agrees with representatives of the Clydonautilidae. *Callaionautilus* is another ornamented genus of Clydonautilidae. *Clydonautilus cicatricosus* shows characters transitional to *Cosmonautilus* and the Tainoceratidae in having nodose ornamentation with a typical clydonautilid suture. A few other species of *Clydonautilus* show low folds on the flanks. *Domatoceras*, *Gryponautilus*, and *Plummeroceras* of the Grypoceratidae have nodes developed on either or both the ventral and umbilical shoulders in some or all of their species. However, the basic pattern of the conch and suture, are typical of the Grypoceratidae. The nodes and other ornamentation, especially developed on essentially smooth stocks are probably effects of late mutations superimposed on established conch patterns probably have no phyletic significance but merely represent local adaptations. However, the nature of adaptive advantage that ornamentated forms have over non-ornamented forms is not known for these invertebrates.

The conch pattern of each phyletic line retain, within broad limits, a certain homogeneity. but each shows some radiation that converges towards radiations of other groups. If each basic conch pattern reflects an adaptation to a certain environmental niche or way of life it appears that each phyletic line was well diversified and contributed toward the various environmental types.

Certain basic conch patterns were acquired independently by genera in one or more families during the late Paleozoic and Triassic. Highly compressed involute conchs in the late Paleozoic are confined to the genus *Stenopoceras*. Somewhat similar conch patterns, but of a more truly oxycone type, are seen in *Gryponautilus* and *Oxynautilus* of the Late Triassic. *Proclydonautilus ermollii* and *Styrionautilus discoidalis* of the family Clydonautilidae also have highly compressed involute conchs very similar to that of *Stenopoceras*. *Domatoceras* and *Plummeroceras* have compressed, evolute conchs with flattened venters. Some species of *Domatoceras* show transition to *Stenopoceras*. In the Triassic *Juvavionautilus* has a somewhat similar conch pattern. *Menuthionautilus* appears to combine features of domatoceratid and stenopoceratid conch patterns. *Sibyllonautilus* with its depressed but rapidly expanding conch is very reminiscent of *Acanthonautilus* of the late Paleozoic.

The greatest diversity in conch pattern intragenerically is found in the Clydonautilidae, the family which also has the most highly modified sutures. The Tainoceratidae, which include most of the ornamented late Paleozoic and Triassic nautiloids, maintain a remarkably uniform conch pattern, with only minor diversity. Some species in this family, especially in *Mojsvaroceras* and *Germanonautilus*, evolved toward loss of ornamentation, but did not greatly increase their involution.

Much of the similarity of the conch patterns of the genera and species of two families can be explained by convergence and adaptations to similar environments or modes of life. The repetition of similar conch patterns within a phyletic line may be partly explained on the same basis. *Domatoceras* and *Juvavionautilus* are very similar in conch patterns and each is thought to have given rise to highly compressed, involute genera, *Stenopoceras* and *Oxynautilus*. *Juvavionautilus* belongs in the family Syringonautilidae, which appears to have its origin in the Grypoceratidae. *Gryponautilus*, also of the Grypoceratidae, has a conch pattern reminiscent of a slightly inflated *Stenopoceras* and is somewhat similar to Oxynautilus. *Acanthonautilus* of the Liroceratidae has a counterpart in *Sibyllonautilus* of the Paranautilidae, the latter family being derived from the former.

In the example of the Grypoceratidae and Syringonautilidae the compressed, involute radiation comes near the beginning and near the end of the history of these families. This does not appear to be the case in the other example involving the Liroceratidae and Paranautilidae. The amount and kind of modifications that can be made on any one nautiloid conch pattern is limited. *Stenopoceras*, *Gryponautilus*, and *Oxynautilus* or *Domatoceras* and *Juvavionautilus* are similar in their basic conch pattern but differ in other features. The highly compressed involute shell was acquired by several distinct branches of the ammonoids throughout much of their history, and is also seen in the Cretaceous nautiloid *Heminautilus*. This form of the shell must have had some adaptive value and, when the genetic potential of the parent and the environment were in accord, it was possible to develop new stocks with this conch pattern completely independent of any previous or future radiation in this direction.

Most late Paleozoic and Triassic nautiloids have very simple suture patterns. Within the Tainoceratidae, sutures with shallow ventral and lateral lobes are the rule. The only exception is *Holconautilus*, which has a ventral saddle—a type of modification of the suture expressed in other completely independent lines. The Grypoceratidae, which have higher whorls than the Tainoceratidae generally, have a broad lateral lobe, but also show some modification on the ventral lobe. *Plummeroceras* has a very deep ventral lobe, almost equal to the width of the flattened venter. However, some species of *Domatoceras* are transitional to *Plummeroceras* in this character. *Grypoceras mesodiscus* of the Triassic has a deep ventral lobe similar to that of *Plummeroceras*. Most of the Syringonautilidae have highly simplified sutures. *Juvavionautilus* has a ventral saddle flanked by broad lateral lobes. *Clymenonautilus* has a conch pattern placing it in the Syringonautilidae, but shows strong convergence to the Clydonautilidae in the deep and peculiar lateral lobe of its suture. The Paranautilidae have simple, almost straight, sutures.

The only family that shows definite evolutionary changes in the suture is the Clydonautilidae, which also attained the highest diversity and modifications of the septa of any late Paleozoic and Triassic nautiloids. They are rivaled in complexity only by the early Cenozoic genera *Aturia*, *Aturoidea*, and *Hercoglossa*. The various genera of this family are largely defined on modifications of the suture on the venter, except for *Cosmonautilus* and *Callaionautilus*. For each genus there is a surprising uniformity in overall plan of the suture. The conch pattern, however, varies greatly.

Among late Paleozoic nautiloids the annular lobe has been found only in some species of *Stearoceras*. The annular lobe is characteristic of many Triassic genera; it is absent in the Clydonautilidae, and in all Paranautilidae except *Sibyllonautilus*. Welter (1914, p. 213) describes and illustrates a specimen of *Proclydonautilus gasteroptychus timorensis* that possesses an annular lobe. Mojsisovics used the annular lobe as a primary criterion in his taxonomic scheme for Triassic nautiloids. Most later authors do not consider this feature diagnostic by itself. In several post-Triassic nautiloid genera the annular lobe disappears early in the ontogeny (Spath, 1927b). The writer believes that the annular lobe generally cannot be used by itself to distinguish groups of taxonomic rank higher than subgenus and genus.

The siphuncle in most late Paleozoic and Triassic nautiloids remains nearly central. In the late Paleozoic only *Solenochilus* has its siphuncle in a marginal position. *Menuthionautilus* of the Scythian of Madagascar and Pakistan also has its siphuncle in a marginal position. *Syringoceras* has its siphuncle in a near marginal position, and on this criterion alone is separated from *Syringonautilus*. Data on the position of the siphuncle of most species are unpublished.

Most families of late Paleozoic and Triassic nautiloids follow a similar mode or pattern in their evolution: a central virile stock that slowly evolved from the Pennsylvanian through the Triassic, and periodically produced nearly equal virile stocks and isolated aberrant groups. The modifications of the aberrant groups are merely added to or superimposed on the conch pattern of the central stock. The Permian-Triassic boundary is not a very significant one in terms of nautiloid evolution. The two families, namely Tainoceratidae and Grypoceratidae, which best illustrate the above observations show only minor changes at the Permian-Triassic boundary.

In the Tainoceratidae, the main evolving stock is that of *Metacoceras*. This genus has a subquadrate cross section of the whorl, is somewhat evolute, and bears nodes on the shoulders. It is a very prolific stock in both numbers of species and individuals, and has a world-wide distribution in the Pennsylvanian and Permian. The late Paleozoic evolution of this group shows no definite trends; Permian and Pennsylvanian species are quite similar. *Metacoceras* evolved directly into or is replaced by *Mojsvaroceras* in the Triassic. *Mojsvaroceras* has the same general pattern of the conch as *Metacoceras*, and differs only in tighter coiling and the acquisition of an annular lobe. All of the remaining genera of the Tainoceratidae are either direct or indirect offshoots of the *Metacoceras*-*Mojsvaroceras* line. Each of these offshoots is characterized by a characteristic pattern of ornamentation, or modification of the conch shape, but at the same time shows clear affinities to *Metacoceras*. Many of these descendant forms have very narrow geographic distributions and stratigraphic ranges. It is very likely that they are the result of adaptations to changes in environmental conditions.

The most virile offshoot from *Metacoceras* is the complex of genera and subgenera evolving around *Pleuronautilus.* This group includes most of the ribbed, subquadratic late Paleozoic and Triassic nautiloids. *Pleuronautilus* seems to have arisen in early Permian time, and to have remained a rather singular and undiversified stock throughout the Permian. However, in the Triassic, and especially during the Anisian, the group began to radiate in many directions, and produced a complex association of highly ornamented nautiloids. Each subgroup of the pleuronautilid complex is characterized by a generally distinctive pattern of ornamentation or modification of the conch shape. Perhaps Hyatt (1900) was justified in placing this group in a separate family.

The Grypoceratidae have an evolutionary pattern very similar to that of the Tainoceratidae. *Domatoceras* and *Grypoceras* have the same relationships as *Metacoceras* and *Mojsvaroceras. Domatoceras* has an evolute compressed conch with a tabulate venter and is replaced in the Triassic by *Grypoceras* which is more involute, the venter more rounded, and the suture somewhat modified. The end members of this evolutionary line are quite different but there are numerous transitional forms. The offshoots of the *Domatoceras-Grypoceras* line are characterized by the extreme development of usually one of three main morphological changes that express the evolution in the parent stock. The trend towards involution is seen in *Stenopoceras*, *Menuthionautilus*, and *Gryponautilus.* Rounding of the ventral region of the conch is well developed in *Grypoceras*, but also expressed in *Pselioceras*, *Menuthionautilus*, and even in some *Stenopoceras.* Modification of the suture in the parent stock is mainly in development of a deeper ventral lobe adjoined by a large, broad, lateral lobe. In the parent stock this transition appears to be gradual. The subgenus *Plummeroceras* developed an extremely deep ventral lobe on a typical domatoceratid conch; the suture actually resembles that of some Late Triassic grypoceratids.

Stearoceras and *Titanoceras* of the Grypoceratidae are not fully understood but appear to be independent lines not involved in the *Domatoceras-Grypoceras* trend.

The Syringonautilidae are confined to the Triassic. They may have been derived from *Stearoceras-Domatoceras* transition complex in the Grypoceratidae. *Syringonautilus* and *Syringoceras* are very similar except for the position of the siphuncle. The writer considers them to be independent and parallel lines developing from the Grypoceratidae. *Syringonautilus* appears to have given rise to three aberrant offshoots in the Norian. These are *Juvavionautilus*, *Oxynautilus*, and *Clymenonautilus. Juvavionautilus* has a conch pattern very similar to that of *Domatoceras* except for a more rounded venter. *Oxynautilus* has a very compressed, involute conch similar to that of *Stenopoceras. Clymenonautilus* has a conch pattern like that of some grypoceratids but its suture develops a peculiar deep lateral lobe. Each of these Late Triassic offshoots of *Syringonautilus* takes on conch patterns resembling those seen in the Grypoceratidae, the ancestral group of the Syringonautilidae.

The evolutionary patterns in the Tainoceratidae Grypoceratidae, and Syringonautilidae are expressed primarily in the shape of the conch, degree of involution, and types of ornamentation, and only to a minor degree on modifications of the suture. The Liroceratidae, Paranautilidae, Clydonautilidae, and Gonionautilidae are characterized by involute conchs, generally devoid of ornamentation, and by a tendency towards extreme modification of the suture in the Clydonautilidae and Gonionautilidae. In all of these families there is a constancy in the suture pattern for any particular generic assemblage but at the same time the conch pattern may vary tremendously.

The Liroceratidae are a closely related group of several independent lines of Pennsylvanian and Permian nautiloids. The Paranautilidae are thought to be derived from *Liroceras* in the Permian. This family has a very simple, globular, smooth conch with an almost straight suture. *Paranautilus* is the main stock that gave rise to two aberrant developments and most important, it was ancestral to the Clydonautilidae. The Clydonautilidae show extreme modification of the suture. The complexity of the suture in such genera as *Proclydonautilus*, *Clydonautilus*, and *Cosmonautilus* is rivaled only by early Cenozoic forms like *Hercoglossa*, *Aturoidea*, and *Aturia.* The suture on the ventral region displays the most modification and is a feature of prime importance in distinguishing the various genera. The Gonionautilidae are represented by only one species, distinguished by its suture. This monotypic form represents the acme in sutural development of Triassic nautiloids.

One aberrant Permian form from Timor, *"Aganides" bitauniensis* Haniel (1915), has the conch form of an involute domatoceratid, but its suture (with its deep bluntly pointed ventral lobe and a very deep asymmetrical and pointed lateral lobe) resembles those of the Late Triassic Clydonautilidae. *"Aganides" bitauniensis* most surely belongs in a new genus, but the writer refrains from proposing one without actual specimens to study.

SYSTEMATIC PALEONTOLOGY

Family TAINOCERATIDAE Hyatt, 1883

Some of the most characteristic nautiloids in the late Paleozoic and Triassic sedimentary rocks are the ornamented forms bearing ribs, nodes, and spines. Most of these ornamented forms are placed in the family Tainoceratidae. When Hyatt first established this family he included in it a wide variety of forms. These are *Trocholites* Conrad and Hall, *Plectoceras* Hyatt, *Litoceras* Hyatt, *Diadiploceras* Hyatt, *Metacoceras* Hyatt, *Tainoceras* Hyatt, *Mojsvaroceras* Hyatt, *Grypoceras* Hyatt, *Clydonautilus* Mojsisovics, *Enclimatoceras* Hyatt, *Hercoglossa* Conrad, and *Aturia* Bronn. In his final work on the classification of the nautiloids, Hyatt (1900, p. 524) placed in this family *Tainoceras*, *Temnocheilus*, *Foordiceras*, *Metacoceras*, *Coelogasteroceras*, and *Diadiploceras*; and he listed *Endolobus* Meek and *Cryptoceras* d'Orb. as synonyms of *Temnocheilus* M'Coy.

Mojsisovics (1902, p. 204) placed the following genera in his family Temnocheilidae: *Temnocheilus*, *Metacoceras*, *Tainoceras*, *Foordiceras*, *Tainionautilus*, *Tirolonautilus*, *Mojsvaroceras*, *Germanonautilus*, *Thuringionautilus*, *Pleuronautilus*, *P.* (*Holconautilus*), *P.* (*Trachynautilus*), and *Phloioceras*. The two families Temnocheilidae Mojsisovics and Tainoceratidae Hyatt are almost identical in their scope and there are several genera that have been included in both families. As Temoncheilidae is synonomous with Tainoceratidae and the latter family has priority, Mojsisovics' family is suppressed as a synonym of Tainoceratidae. In this report the following genera and subgenera are included in this family: *Temnocheilus*, *Tainoceras*, *Parametacoceras*, *Foordiceras*, *Metacoceras*, *Tainionautilus*, *Cooperoceras*, *Tirolonautilus*, *Germanonautilus*, *Thuringionautilus*, *Mojsvaroceras*, *Aulametacoceras*, *Pleuronautilus*, *Enoploceras*, *Anoploceras*, *Encoiloceras*, *Holconautilus*, *Trachynautilus*, and *Phloioceras*.

As here defined this family includes nautiloids with thick subquadrate conchs in which the volutions are somewhat broader than high, slightly to moderately involute, umbilici usually wide and open, sutures sinuous, siphuncles subcentral and orthochoanitic. The family includes the typically "ornamented" nautiloids of the late Paleozoic and Triassic.

PHYLOGENY

Study of this evolutionary unit has led to several interesting observations. The genera included in this family comprise for the most part the "ornamented" nautiloids of the late Paleozoic and Triassic. Although 19 generic names used to differentiate the various phyletic elements there is a surprising uniformity among all of them. More important is the strong similarity and relationships between the Paleozoic and Triassic forms. Four and possibly 5 of the genera seem to range across this important boundary.

The ancestral form appears to be *Temnocheilus*, which ranges from the lower part of the Carboniferous into the Permian. *Temnocheilus* is characterized by a subtrigonal cross section of the conch with a row of nodes on the ventrolateral shoulders. In the Morrow (lowest Pennsylvanian) two members of this family, *Temnocheilus* and *Metacoceras*, lived side by side. *Metacoceras* appears to be a direct descendant of *Temnocheilus*. *Metacoceras* has a subquadrate conch with a row of nodes on the ventrolateral shoulders and perhaps a row of nodes on the umbilical shoulder. This genus is abundant throughout the Pennsylvanian and Permian. It has more species than any other genus of the Tainoceratidae and shows almost an infinite amount of variation. It is difficult to evaluate the validity of many of the species of this genus because no extensive studies have been made of any population—and the potential range of variation is not known, partly because of insufficient material. The shape of the conch and type of ornamentation of *Metacoceras* seem to have been the fundamental pattern upon which modifications were developed that form the basis for distinguishing many of the other genera of the Tainoceratidae. *Metacoceras* was a virile prolific stock of nautiloids that experienced no great evolutionary changes. The degree of variation seems to be just as large in the lower part of the Pennsylvanian as in the Permian. However, this basic stock periodically gave off mutants some of which had but a small stratigraphic and geographic extent, and others became the ancestors of independent phyletic lines.

Thus, in the early Pennsylvanian two basic phyletic lines were well defined, one of *Temnocheilus* and the other evolving from *Metacoceras*. *Temnocheilus* appears to belong to a comparatively sterile line with little variation and few species. *Temnocheilus* is thought to have given rise to only one genus, *Foordiceras*. This genus retained very closely the subtrigonal outline of the conch of *Temnocheilus*, but developed lateral ribs on the flanks. The broad definition of this genus by Miller and Youngquist (1949) is not held by the present writer, who believes that the earlier interpretation by Hyatt, Mojsisovics, and others are more nearly correct. *Nautilus goliathus* Waagen, the genotype of *Foordiceras*, has a subtrigonal outline and appears to show quite clearly affinities with *Temnocheilus*. Miller and Youngquist broadened the definition of this genus to include numerous forms with subquadratic cross sections.

Metacoceras is thought to be the ancestral stock from which the remaining genera of nautiloids of the Tainoceratidae were derived. *Parametacoceras*, Des Moines to Virgil in age, is one of the first groups to split off from *Metacoceras*. *Parametacoceras* has the subrectangular conch but with short transverse ribs on the mature portion of the conch. The complex of genera evolving from *Pleuronautilus* includes the prominently ribbed members of the Tainoceratidae. It is possible that *Parametacoceras* represents the ancestral elements of *Pleuronautilus* etc. However, the writer believes that altogether the evidence indicates descent from *Metacoceras*. Miller and Youngquist (1949, p. 96) recommended suppressing *Parametacoceras,* considering it a synonym of *Foordiceras*. The present author disagrees, and presents his views in his discussion of these genera (pp. 33–34).

One of the most unusual nautiloid genera of the family Tainoceratidae is *Tainoceras* which is characterized by a double row of nodes on the venter. There is one row of nodes on the ventral shoulder and perhaps another on the umbilical shoulder. *Tainoceras* ranges from the Des Moines to the Ochoan and it is suggested that a Triassic Karnian species should be included in this genus. The derivation of *Tainoceras* from *Metacoceras* has been generally agreed upon for many years. From the middle and late Permian several aberrant types of ornamented nautiloids that have narrow stratigraphic and geographic ranges, *Cooperoceras, Tainionautilus, Tirolonautilus, and Aulametacoceras,* are regarded as direct descendants of *Metacoceras*. *Cooperoceras* which ranges through the Leonard and Guadalupe, is characterized by the presence on the ventral shoulder of long, slender hollow paired spines that project ventrolaterally.

Tainionautilus includes nautiloids which on the mature portion of the conch have lateral ribs on the flanks that extend onto the venter and terminate at a ventral furrow. Recently Miller and Youngquist (1949, p. 96) proposed suppressing this genus as a synonym of *Foordiceras*. The view is not held tenable and a detailed discussion of this problem is given in the taxonomic treatment of these two genera (pp. 17, 26). The exact affinities of *Tainionautilus* are not well established. The older views (Mojsisovics 1902, p. 232) held *Tainionautilus* to be an aberrant development out of *Tainoceras,* with *T. tuberculatum* Trautschold a transitional form. Reed (1944, p. 356) considered *Tainionautilus* to be a subgenus of *Metacoceras* with *M. sulciferum* Miller and Thomas as a transitional form. The writer's interpretation somewhat resembles that of Reed.

Tirolonautilus also is derived directly from *Metacoceras* (Mojsisovics, 1902, p. 233) differing mainly in its slightly more involute outline and possession of a ventral furrow. *Tirolonautilus* has been reported only from the *Bellerophon* Limestone of the Alps. *Aulametacoceras* is another unique form; it has longitudinal ribs on the venter; the genotype *A. mckeei* is from beds of Leonard age in Arizona. The only other species placed in this genus is *A. rectangularis* (Hauer) from the Alpine Karnian. *Tainionautilus, Tirolonautilus, Aulametacoceras, Cooperoceras* retain the general shape of the conch and degree of involution of *Metacoceras*. The evolution and modifications which set the 4 genera apart from *Metacoceras* are changes that are confined mostly to the ventral regions of the conch. In *Cooperoceras* it is the development of spines, in *Tainionautilus* and *Tirolonautilus* the ventral furrow is distinctive and in the former genus there are also present lateral ribs which extend on to the venter. In *Aulametacoceras* the longitudinal ribs on the venter are the distinctive feature. These 4 genera have a total of only 11 species.

Metacoceras is thought to evolve directly into *Mojsvaroceras* at the end of the Permian and beginning of the Triassic. The two genera differ only in that the younger form is slightly more involute and has an annular lobe. The presence or absence of an annular lobe, however, is not known for most species of *Metacoceras*. On the phylogenetic diagram (text fig. 5), *Mojsvaroceras* is placed in a line directly continuous with that of *Metacoceras*. Mojsisovics (1902, p. 233) believed that the evolutionary trend within *Mojsvaroceras* was towards a loss of ornamentation; but the present writer does not agree. This genus ranges from the Scythian to the Karnian, with its acme in the Anisian. In the late Scythian a tribe of nautiloids, *Germanonautilus,* which tended towards greater involution and a loss of ornamentation, stemmed from *Mojsvaroceras* or possibly directly from *Metacoceras*. *Germanonautilus* ranges from the Scythian to the Karnian. Of the Triassic members of the Tainoceratidae *Mojsvaroceras, Thuringionautilus,* and *Germanonautilus* appear to be directly or indirectly derived from *Metacoceras*. *Aulametacoceras* and *Tainoceras,* both late Paleozoic genera, may each include one Triassic species.

The above discussion has attempted to summarize the lines of development stemming from the *Metacoceras*-*Mojsvaroceras* relationship. Another important phyletic line that also seems to have its ancestry in *Metacoceras* involves mostly Triassic nautiloids. This includes the genus *Pleuronautilus* and six closely related genera and subgenera. The writer believes that most of the ribbed nautiloids with subquadrate conchs of the late Paleozoic should be placed in the genus *Pleuronautilus*. These Paleozoic ribbed nautiloids developed out of *Metacoceras* in late Pennsylvanian or early Permian time. This branch remained fairly simple in its development in the Permian, but began a trend towards extreme modification and diversity in the early Triassic. There was actually a great expansion of this genetic line into

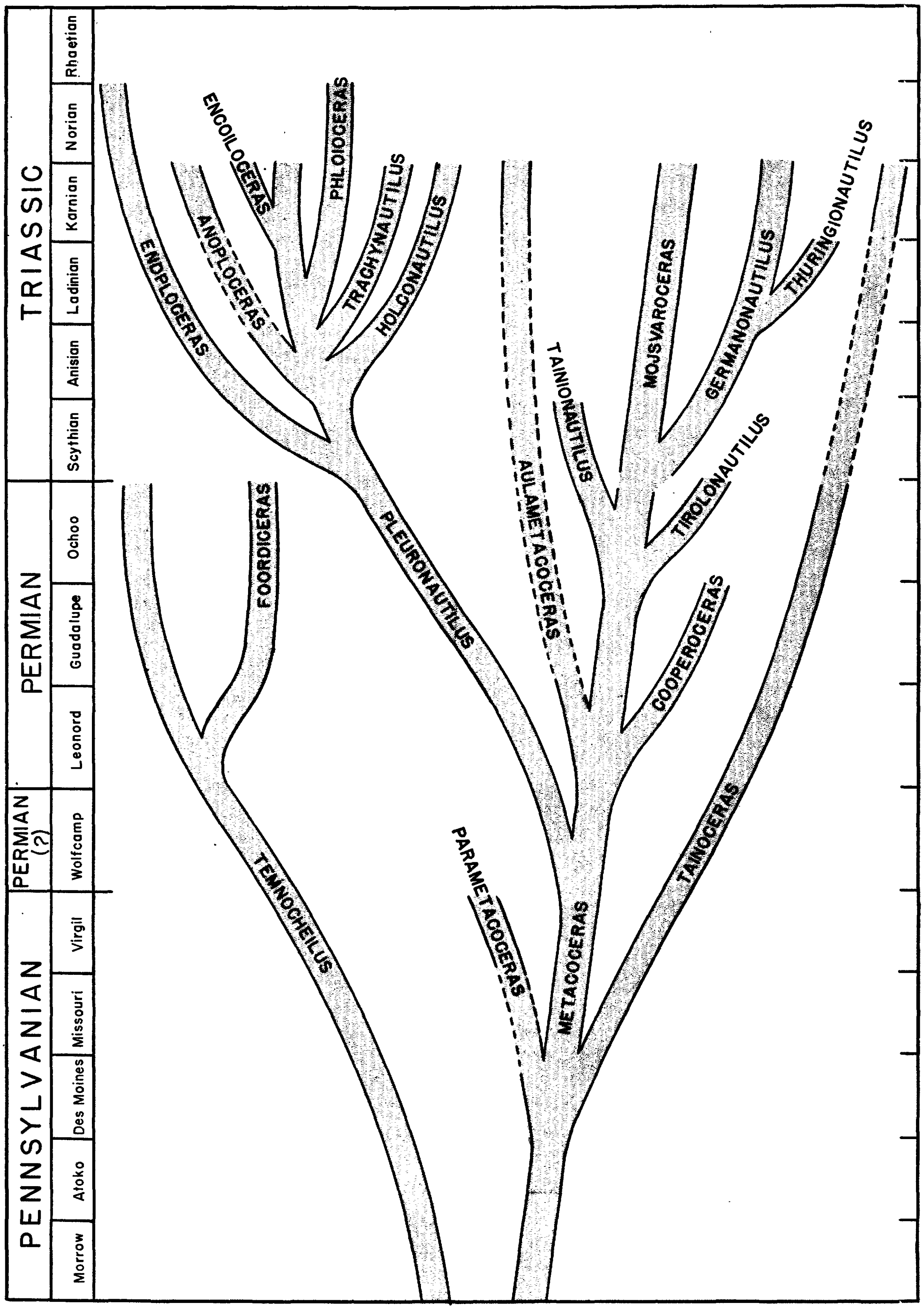

FIGURE 5.—Diagram showing inferred phylogeny and geologic distribution of the Tainoceratidae.

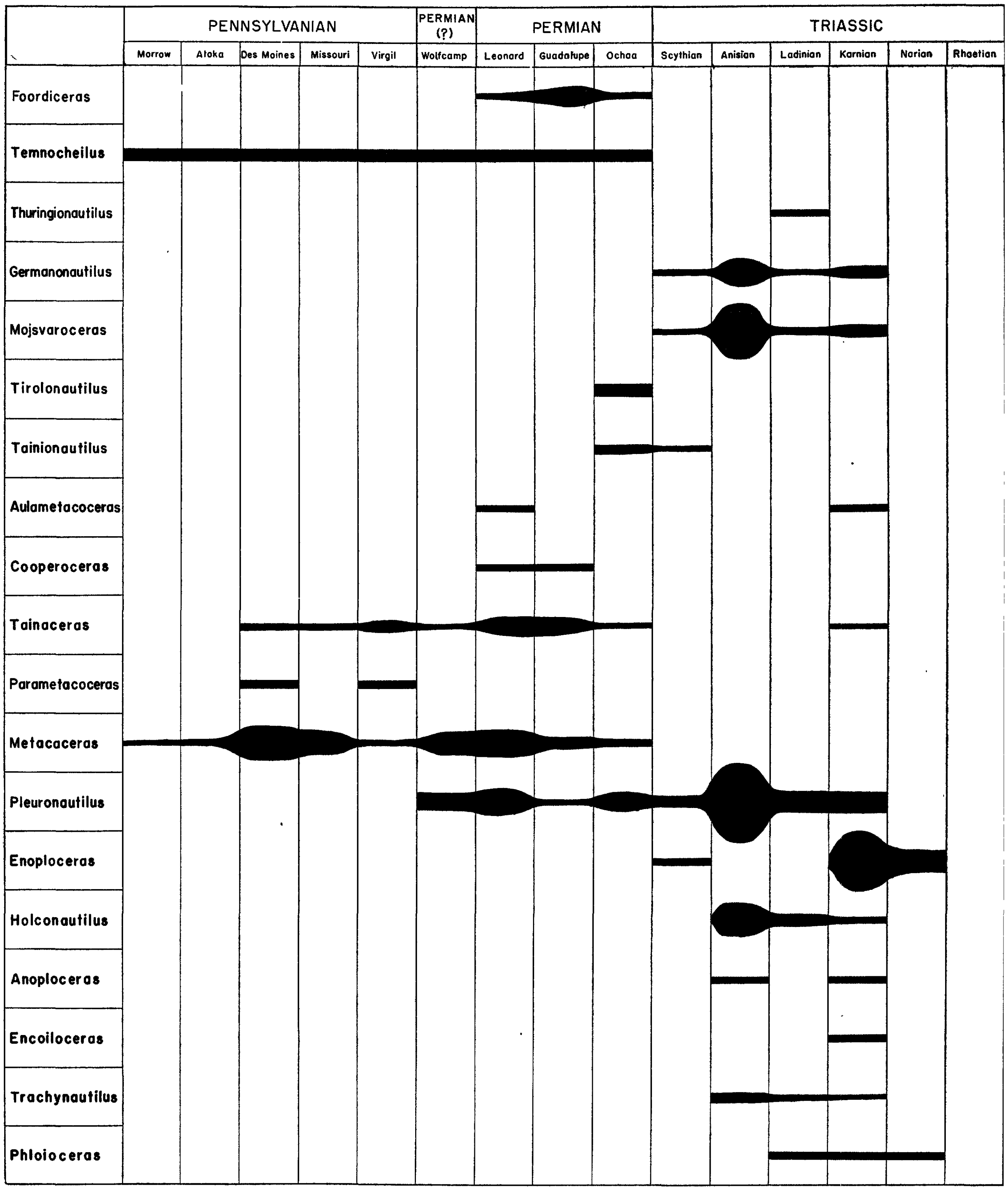

FIGURE 6.—Range chart showing known stratigraphic occurrence of the Tainoceratidae. The width of the line is proportional to the number of species.

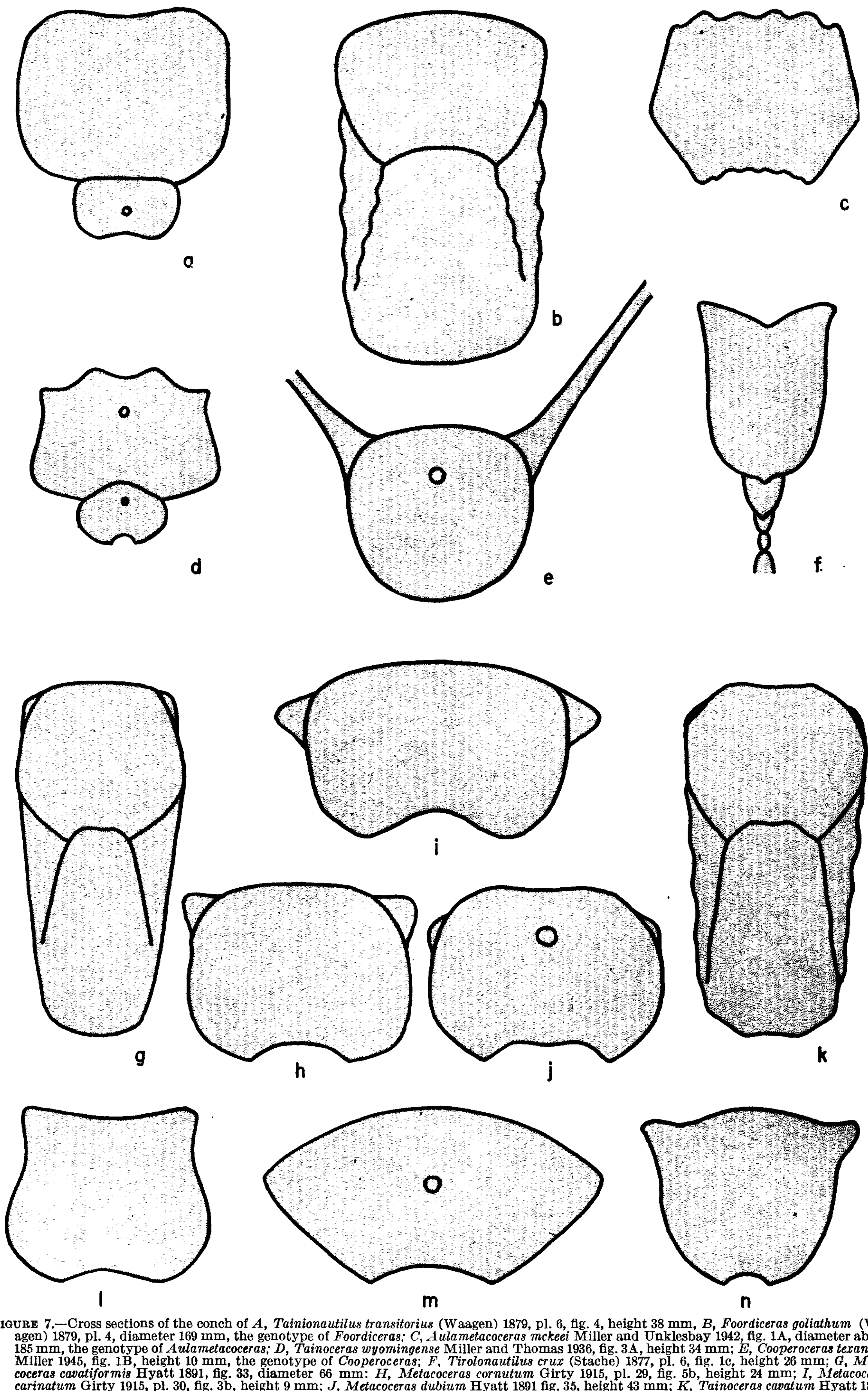

FIGURE 7.—Cross sections of the conch of *A*, *Tainionautilus transitorius* (Waagen) 1879, pl. 6, fig. 4, height 38 mm, *B*, *Foordiceras goliathum* (Waagen) 1879, pl. 4, diameter 169 mm, the genotype of *Foordiceras;* *C*, *Aulametacoceras mckeei* Miller and Unklesbay 1942, fig. 1A, diameter about 185 mm, the genotype of *Aulametacoceras;* *D*, *Tainoceras wyomingense* Miller and Thomas 1936, fig. 3A, height 34 mm; *E*, *Cooperoceras texanum* Miller 1945, fig. 1B, height 10 mm, the genotype of *Cooperoceras*; *F*, *Tirolonautilus crux* (Stache) 1877, pl. 6, fig. 1c, height 26 mm; *G*, *Metacoceras cavatiformis* Hyatt 1891, fig. 33, diameter 66 mm: *H*, *Metacoceras cornutum* Girty 1915, pl. 29, fig. 5b, height 24 mm; *I*, *Metacoceras carinatum* Girty 1915, pl. 30, fig. 3b, height 9 mm; *J*, *Metacoceras dubium* Hyatt 1891 fig. 35, height 43 mm; *K*, *Tainoceras cavatum* Hyatt 1891, fig. 42, diameter 106 mm; *L*, *Metacoceras nodosum* Miller, Dunbar and Condra 1933, pl. 15, fig. 7, height 20 mm; *M*. *Temnocheilus* sp. Miller and Owen 1934, fig. 2B, height 24 mm; *N*, *Metacoceras sinuosum* Girty 1915, pl. 30, fig. 1b, height 15 mm.

several more specialized lines. The most elaborate and complexly ornamented Triassic nautiloids belong in this phyletic line.

The directions of specialization in *Pleuronautilus* were twofold; the first towards changes in suture and the second towards changes in shape and ornamentation of the conch. Only one subgenus, *Holconautilus*, changed its suture pattern in developing a ventral saddle. The remaining subgenera are defined on changes in the form of the conch and patterns of ornamentation. *Enoploceras* has a quadratic conch with flattened venter, flanks, and umbilical walls. The ornamentation is not very unlike that of *Pleuronautilus*. *Anoploceras* has a depressed subquadratic conch with a broadly arched, smooth venter and steep umbilical walls. The flanks have sinuous ribs. In *Trachynautilus* the conch is characterized by longitudinal ribs and its small size. The last group, *Encoiloceras*, has a very evolute conch with strong fold-like ribs and modifications of the aperture. *Enoploceras* is the most heterogeneous, with 18 species. *Anoploceras* has only 2 species, *Trachynautilus* has 7, *Encoiloceras* has 1, and *Holconautilus* has 10.

Phloioceras developed longitudinal ridges on the flanks and venter. It is an independent development out of *Pleuronautilus*, but closely allied to *Trachynautilus*.

Genus TEMNOCHEILUS M'Coy, 1844

Genotype: *Nautilus* (*Temnocheilus*) *coronatus* M'Coy

This genus ranges from the early part of the Carboniferous to the middle part of the Permian period and is thought to be the ancestral form of the Tainoceratidae. Mojsisovics, Hyatt, Miller, and others have repeatedly pointed out its ancestral position in the phylogenetic history of this family. Miller, Dunbar, and Condra (1933) did much to clarify the complex taxonomic problems surrounding this genus, and gave the following clear, concise diagnosis of the genus:

> Conch nautiliconic, the whorls being greatly depressed, strongly flattened ventrally and laterally, narrowly rounded ventrolaterally and more broadly so dorsoventrally, and slightly impressed dorsally; lateral sides typically not parallel but converging toward the dorsum, the whorls therefore being subtrapezoidal in cross section. Umbilicus very broad, deep, and perforate. Prominent growth lines indicate the presence of a deep tongue-shaped hyponomic sinus. Ventrolateral shoulders of the conch marked by a single row of large, prominent nodes which are more or less confluent and are elongated in a direction parallel to the axis of the conch; these peculiar nodes are one of the most distinctive characters of the genus. Sutures simple and approximately transverse to long axis of the conch but slightly sinuous; they form broad, shallow, broadly rounded lobes as they cross the flattened lateral and ventral sides of the conch, rounded saddles as they cross the ventrolateral and dorsolateral zones, and deep, bluntly rounded lobes as they cross the dorsum. Septa likewise approximately transverse to long axis of conch and moderately convex apicad. Siphuncle small, subcentral in position, and orthochoanitic in structure; septal necks short but straight; connecting rings not expanded within camerae.

(See text fig. 8 and Pl. 1, figs. 1, 2.)

In this paper only two genera are considered direct descendants of *Temnocheilus: Foordiceras* and *Metacoceras*. The latter genus ranges through the Pennsylvanian and Permian, and is extremely varied and abundant. *Metacoceras* is thought to be the direct ancestor of several Paleozoic and Triassic genera. This is the virile branch of the family tree; it is also the branch which maintains a more or less subquadrangular cross section of the conch. The various descendants are differentiated mostly on the basis of differences in ornamentation.

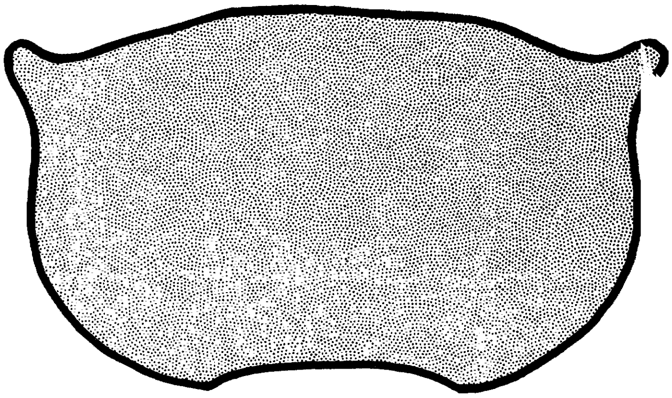

FIGURE 8.—Diagrammatic cross section of the holotype of *Temnocheilus latus* (Meek and Worthen) (Univ. Illinois X-438-A) from the Pennsylvanian, Carbon Cliffs, Rock Island County, Illinois, × 1.

Foordiceras is confined to the Permian. It has few species and appears to have a restricted geographic range (depending on the interpretation of the genus). *Foordiceras* maintains a subtrigonal type of conch which is similar to that of the ancestral *Temnocheilus*.

Temnocheilus ranges throughout the Pennsylvanian and Permian, and has been recorded from the United States and Eurasia. The species listed on page 18 have been assigned to it.

Genus FOORDICERAS Hyatt, 1893

Genotype: *Nautilus goliathus* Waagen

The genus *Foordiceras* has been generally neglected by American authors since Hyatt's time; however, Miller and Youngquist (1949) discussed the genus at length and included in it many species that had previously been assigned to *Metacoceras*, *Parametacoceras*, *Shansinautilus*, and *Tainionautilus*. They also suggested suppressing completely *Shansinautilus* Yabe and Mabuti, *Parametacoceras* Miller and Owen, and *Tainionautilus* Mojsisovics in favor of *Foordiceras* Hyatt. Much of their interpretation of this genus is

Distribution of species of the genus Temnocheilus

Species	Stratigraphic distribution	Geographic distribution
Temnocheilus ? acanthicus Tzwetaev 1888	Upper Carboniferous	Central Russia.
T. asiaticus Grabau 1924	Permian (Taiyuan series)	Shansi, China.
T. atuberculatus Tzwetaev 1888	Upper Carboniferous	Central Russia.
T. gemmellaroi Canavari 1935	Permian (Sosio beds)	Sicily.
T. grewingki Tschernyschew 1899	Permian (Bakhmout dolomite)	Kulogory, Russia.
T. harneri Miller and Owen 1934	Pennsylvanian (Cherokee formation)	Missouri.
T. inaequilateralis Miller and Youngquist 1949	Permian (Leonard formation)	Brewster County, Tex.
T. johnsoni Miller, Dunbar, and Condra 1933	Pennsylvanian	Colorado.
T. latus (Meek and Worthen) 1870	do	Illinois.
T. medioventralis Sturgeon 1946	Pennsylvanian (Allegheny formation)	Ohio.
T. multituberculatus (Waagen) 1879	Permian (Upper Productus limestone)	Salt Range, Pakistan.
T. multituberculatus simensis Kruglov 1928	Permian (Ashian)	Sims River, Russia.
T. multituberculatus tastubensis Kruglov 1928	do	Tastuba, Russia.
T. nikitini Loweneck 1932	Permian (*Schwagerina princeps* beds)	Tianschen, China.
T. ornatissimus Tzwetaev 1888	Upper Carboniferous	Central Russia.
T. posttuberculatus (Karpinsky) 1874	Permian (Artinskian)	Koswa River, Russia.
T. posttuberculatus kosswae Kruglov 1928	do	Do.
T. posttuberculatus waschkuricus Kruglov 1928	do	Tchussovaya River, Russia.
T. quinqueliratus Sturgeon 1946	Pennsylvanian (Allegheny formation)	Ohio.
T. subrectangularis Miller, Dunbar, and Condra 1933	Pennsylvanian (Upper part of Pottsville)	Floyd County, Ky.
T. tuberculatus Sowerby 1821	Carboniferous	Great Britain.
T. waageni Loczy 1898	Permo-Carboniferous	Yunnan, China.
T. winslowi (Meek and Worthen) 1870	Pennsylvanian	Illinois.

believed by the writer to be untenable. *Nautilus goliathus* Waagen of the Upper Productus limestone of the Salt Range, India, is the genotype of *Foordiceras* by original designation. Because it is pertinent to the analysis of ribbed nautiloids in the late Paleozoic and to the proper phylogenetic placement of *Foordiceras,* Waagen's discription of the genotype of *Foordiceras* is included here.

> The general form of the shell is that of a very thick disk. The umbilicus is very deep, but not very wide; the whorls are very thick and inflated with an extremely broad flattened external part. The transverse section of the whorl is broad trapezoidal, the broadest diameter being near the outer edge of the whorl. The lateral parts of the whorls unite with the external part in a rounded edge, which is ornamented with a row of thick elongated rib-like tubercles extending halfway down the height of the whorl. There are about fifteen of these tubercles on the specimen of a diameter of 168 mm. The lateral parts of the whorls slope down from the external edge regularly to the umbilical suture, only showing a slight curve, without forming any umbilical edge or a distinct umbilical wall.
>
> The septa of this species are slightly curved like those of the preceding one (*Nautilus flemingianus* de Koninck) but they are much less numerous. Besides this there is no relation between the air chambers and the tubercles, as in the case in *Nautilus flemingianus.* The specimen I have got for description is not sufficiently well preserved to count the number of septa on each whorl, but there may have been about thirty-two on the last circuit.
>
> The position of the siphon could not be ascertained.

From this description and examination of the figure of the holotype (Waagen 1879, Pl. 4; which Foord 1891, p. 156, states is "highly restored") it should be emphasized that the conch is trapezoidal in shape and that the flanks

> slope down from the external edge regularly to the umbilical suture, only showing a slight curve, without forming any umbilical edge or distinct umbilical wall (see fig. 7*B*).

The trapezoidal conch is very reminiscent of that seen only in typical representatives of *Temnocheilus.* The latter genus is also characterized by having ventrolateral nodes. Short ribs are common in several early Permian species of *Temnocheilus* described by Kruglov (1928) from Russia and Yin (1933) from China. *Temnocheilus* and *Foordiceras* are the only late Paleozoic or Triassic nautiloids with a similar trapezoidal conch. Mojsisovics (1902, p. 232) first observed that *Foordiceras* had a Temnocheilan cross section and he considered *Foordiceras* as a "directly descendant type from *Temnocheilus* in a somewhat more advanced evolutionary stage" [free translation]. In this interpretation the writer concurs. Many of the forms recently assigned to *Foordiceras* by Miller and Youngquist (1949) have a subquadratic to compressed conch and should be placed in the phyletic lines of *Metacoceras* and *Pleuronautilus.* The ornamentation is considered to be of secondary importance in this case and the shape of the conch a more vital basis of differentiation and indicator of genetic relationship. As demonstrated in several places in this study, the evolutionary history of Pennsylvanian, Permian, and Triassic nautiloids has several examples of convergent evolution and homeomorphic tendencies. The convergence may be in shape of the conch, in the ornamentation, or both. Thus it appears to be more correct to place *Foordiceras* as a direct derivative of *Temnocheilus* and confined to the Paleozoic, giving rise to no Triassic forms. Those nautiloids with more or less quadratic to compressed conchs should be kept in a completely different phyletic line.

Distribution of species of the genus Foordiceras

Species	Stratigraphic distribution	Geographic distribution
Foordiceras dyadicum (Haniel) 1915	Permian (Basleo beds)	Timor.
F. flemingianum (deKoninck) 1863	Permian (Middle Productus limestone)	Salt Range, Pakistan.
F. goliathum (Waagen) 1879	Permian (Upper Productus limestone)	Do.
F. grypoceroide Reed 1931	Permian (Productus limestone)	Do.
F. loczyi (Fliegel) 1901	Permian (middle)	Sumatra.
F. nodosocostatum (Gemmellaro) 1888	Permian (Sosio beds)	Sicily.
F. pleuronautiloide (Gemmellaro) 1888	do	Do.
F. sumatrense (Fliegel) 1901	Permian (middle)	Sumatra.
F.? ufimskensis Kruglov 1928	Permian (*Omphalotrochus* beds)	Russia.
F. wynnei (Waagen) 1879	Permian (Productus limestone)	Salt Range, Pakistan.

The writer believes that none of the species referred to *Foordiceras* by Miller and Youngquist (1949) belong to that genus and are more properly placed in *Metacoceras* and *Pleuronautilus*. The following species are thought to belong in the genus *Foordiceras*.

Genus **METACOCERAS** Hyatt, 1883

Genotype: *Nautilus* (*Discus*) *sangamonensis* Meek and Worthen

The most prolific Late Paleozoic nautiloid genus is *Metacoceras*, with about 50 species. The original generic designation by Hyatt (1883, p. 268) is as follows,

> *Metacoceras* includes Silurian and Carboniferous species with broad, ventral, lateral, and dorsal lobes but no annular lobes. Siphon near the ventrum or central. Whorls quadrate, sides with one row of nodes along the external border, umbilical shoulders smooth but gibbous, the type has this part of the whorls elevated into a ridge. The forms are evidently transitional from the genus *Plectoceras* to *Mojsvaroceras*.

A more recent and amended diagnosis of the genus is given by Miller, Dunbar and Condra (1933, p. 168–169). The many studies of the genus since Hyatt's original designation have tended to broaden the concept of it. Miller (1945) placed in this genus several ribbed forms from the middle Permian of West Texas that he later placed in *Foordiceras* (Miller and Youngquist, 1949). Girty (1915, p. 239–249) attempted to group the species of *Metacoceras* into four subdivisions. Fortunately, however, Girty applied no formal names to his groups (Miller, Dunbar, and Condra, 1933, p. 166) Study of the Literature, and a large collection of forms from the Late Paleozoic of Texas, show that the various "types" of ornamentation are gradational and that no practical or consistent subdivisions can be set up on this basis at the present time.

The basic pattern of ornamentation of *Metacoceras* is that of ventrolateral and umbilical nodes. The species can be separated into two groups, the first including those that have only ventrolateral nodes, and the second those that have both ventrolateral and umbilical nodes. Within these two groups there are countless variations and gradations. In the first group, there are species with weakly developed nodes (such as *M. sublaeve* and *M. inconspicuum*), and also species with strongly developed ventrolateral nodes (such as *M. sangamonense*, *M. mammiferum*, and *M. coloradoense*). Intermediate in development of the ventrolateral nodes are such species as *M. mutabile* and *M. cornutum*. Other species evolved elongated types of ventrolateral nodes such as are found in *M. hayi*, *M. walcotti*, and *M. cavatiformis*. Species of *Metacoceras* with both ventrolateral and umbilical nodes do not seem to be quite as common as those with only ventrolateral nodes. The binodal ornamentation is illustrated in such species as *M. angulatum*, *M. nodosum*, *M. biseriatum*, *M. medlicottianum* etc. The genotype of *Metacoceras*, *M. sangamonense* (Meek and Worthen) is characterized by large blunt, rounded ventrolateral nodes, with no nodes on the umbilical shoulder but with an acutely rounded umbilical shoulder (pl. 1).

Within recent years there has been a tendency to include in the genus *Metacoceras* Pennsylvanian and Permian nautiloids with the approximate gross form of the genotype, but with variously modified lateral ribs. The development of lateral ribs, which in some forms culminate in a ventro-lateral node and/or an umbilical node, appears to be a separate phyletic development that gave rise to the great complex of genera, subgenera, and species evolving around the genus *Pleuronautilus*. The evolutionary trend deriving *Mojsvaroceras* directly from *Metacoceras* does not appear to involve the development of primary ribs; however, some species of *Mojsvaroceras* do show connecting "pilae" or ribs between ventrolateral and umbilical nodes. Twenty-four species of Permian nautiloids, many previously referred to *Metacoceras*, are retained or placed in the genus *Pleuronautilus* and seem to represent the primitive early forms of *Pleuronautilus*, most of them showing marked affinities with *Metacoceras*. (See discussion of *Pleuronautilus* on pp. 33, 34.)

The genus *Metacoceras* ranges from the earliest Pennsylvanian to the latest Permian and is thought to be replaced in the Triassic by the subgenus *Mojsvaroceras*. *Metacoceras* shows two maxima in number of species, one in Des Moines-Missouri time and the other in Wolfcamp-Leonard time. The high degree of variation

Distribution of species of the subgenus Metacoceras (Metacoceras)

Species	Stratigraphic distribution	Geographic distribution
Metacoceras (*Metacoceras*) *angulatum* Sayre 1930	Pennsylvanian (Westerville limestone)	Missouri.
M. (*M.*) *armatum* (Sowerby) 1840	Carboniferous	Great Britain.
M. (*M.*) *baylorense* Miller and Youngquist 1949	Permian (Leuders formation)	Baylor County, Tex.
M. (*M.*) *biseriatum* Miller and Owen 1934	Pennsylvanian (Cherokee formation)	Henry County, Mo.
M. (*M.*) *bituberculatum* Miller and Youngquist 1949	Permian (Leonard formation)	Brewster County, Tex.
M. (*M.*) *carinatum* Girty 1911	Pennsylvanian (Wewoka formation)	Oklahoma.
M. (*M.*) *cavatiforme* Hyatt 1891	Permian (Fort Riley? limestone)	Geary County, Kans.
M. (*M.*) *cheneyi* Miller and Youngquist 1947	Permian (Admiral formation)	Coleman County, Tex.
M. (*M.*) *chittidilense* Reed 1944	Permian (Middle Productus limestone)	Salt Range, Pakistan.
M. (*M.*) *coloradoense* Miller, Dunbar, and Condra 1933.	Pennsylvanian	Colorado.
M. (*M.*) *cornutum* Girty 1911	Pennsylvanian (Wewoka formation)	Oklahoma.
M. (*M.*) *costatum* (Hind) 1911	Carboniferous	Great Britain.
M. (*M.*) *discoideum* Merla 1934	Permian (Bellerophon limestone)	Italy.
M. (*M.*) *dubium* Hyatt 1891	Permian (Fort Riley? limestone)	Geary County, Kans.
M. (*M.*) *falcatum* (Sowerby) 1840	Carboniferous	Great Britain.
M. (*M.*) *hayi* Hyatt 1891	Permian (Fort Riley? limestone)	Geary County, Kans.
M. (*M.*) *aff. M. hayi* (Fliegel) 1901	Permian (lower)	Sumatra.
M. (*M.*) *inaequiseptatum* Merla 1934	Permian (Bellerophon limestone)	Italy.
M. (*M.*) *inconspicum* Hyatt 1891	Permian (Fort Riley? limestone)	Geary County, Kans.
M. (*M.*) *jacksonense* Miller, Lane, and Unklesbay 1947.	Pennsylvanian (Winterset limestone)	Jackson County, Mo.
M. (*M.*) *knighti* Miller and Thomas 1936	Pennsylvanian (Casper formation)	Wyoming.
M. (*M.*) *lambi* Sturgeon 1946	Pennsylvanian (Allegheny formation)	Ohio.
M. (*M.*) *mammiferum* Miller 1945	Permian (Bone Spring limestone)	Hudspeth County, Tex.
M. (*M.*) *medlicottianum* (Waagen) 1879	Permian (Middle Productus limestone)	Salt Range, Pakistan.
M. (*M.*) *multituberculatum* Girty 1911	Pennsylvanian (Wewoka formation)	Oklahoma.
M. (*M.*) *mutabile* Miller and Owen 1934	Pennsylvanian (Cherokee formation)	Henry County, Mo.
M. (*M.*) *nodosum* Miller, Dunbar, and Condra 1933	Pennsylvanian (Kansas City group)	Missouri.
M. (*M.*) *ornatissimum* (Miller and Youngquist) 1941.	Permian (Admiral formation)	Coleman County, Tex.
M. (*M.*) *perelegans* Girty 1911	Pennsylvanian (Wewoka formation)	Oklahoma.
M. (*M.*) *pernodosum* (Tschernyschew) 1899	Permian (middle)	Russia.
M. (*M.*) *piszovi* Kruglov 1926	Permian	Ufa Plateau, Russia.
M. (*M.*) *piszovi artiense* Kruglov 1928	Permian (Artinskian)	Asha River, Russia.
M. (*M.*) *postcostatum* Bisat 1930	Carboniferous	Great Britain.
M. (*M.*) *pottsvillense* Morningstar 1922	Pennsylvanian (Pottsville formation)	Ohio.
M. (*M.*) *reedianum* Merla 1934	Permian (upper)	India.
M. (*M.*) *sangamonense* (Meek and Worthen) 1860	Pennsylvanian (McLeansboro formation)	Illinois.
M. (*M.*) *sinuosum* Girty 1911	Pennsylvanian (Wewoka formation)	Oklahoma.
M. (*M.*) *subglabrum* Kruglov 1928	Permian (Ashian)	Asha River, Russia.
M. (*M.*) *subquadrangularis* (Whitfield) 1882	Pennsylvanian	Ohio.
M. (*M.*) *tricarinatum* Sturgeon 1946	Pennsylvanian (Allegheny formation)	Do.
M. (*M.*) *tricarinatum parvinodosum* Sturgeon 1946	do	Do.
M. (*M.*) *trigonotuberculatum* Jakolew 1899	Permian (Bakhmout dolomite and Bellerophon limestone).	Donetz Basin, Russia; Alps, Italy.
M. (*M.*) *tschernyschewi* (Tzwetaev) 1888	Carboniferous (upper)	Central Russia.
M. (*M.*) *tuberosum* (McCoy) 1853	Carboniferous	Great Britain.
M. (*M.*) *unklesbayi* Miller and Youngquist 1949	Permian (Kaibab formation)	Arizona.
M. (*M.*) *vagans* Miller and Owen 1937	Pennsylvanian (Coffeyville formation)	Oklahoma.
M. (*M.*) *walcotti* Hyatt 1891	Pennsylvanian	Texas.

and few or poorly preserved specimens prevent a thorough understanding of most of the species. There are more than twice as many species of *Metacoceras* (50) as of any other Pennsylvanian and Permian nautiloid. The closest rival in numbers of species is *Domatoceras* with 22 species. *Metacoceras* and *Mojsvaroceras* are very similar in their gross form and show similar degrees of variation. *Mojsvaroceras* is slightly more involute and has an annular lobe. Hyatt (1883, p. 268) in his original designation of the genus *Metacoceras* states that no annular lobe is present. The number of species in which the dorsal suture pattern is known, however, is so few that the status of this feature in Pennsylvanian and Permian species of *Metacoceras* is not known. Recent studies on nautiloids (Diener, 1919, Kieslinger, 1924, and numerous publications by Miller) have cast grave doubt on the taxonomic significance of the annular lobe. Because the two genera are so closely related, differing mainly in the degree of involution and the presence or absence of an annular lobe, it is expedient to make *Mojsvaroceras* a subgenus of *Metacoceras*. This classification will also emphasize the close phyletic relationship between the two groups, that *Mojsvaroceras* appears to have been evolved directly from and to have replaced *Metacoceras*.

Miller, Dunbar, and Condra (1933, p. 167–168) assigned 33 species to the genus *Metacoceras*. Since then, taxonomic changes have raised to perhaps 50 the number of species the writer considers valid members of the genus.

Subgenus MOJSVAROCERAS Hyatt, 1883

Subgenotype: *Temnocheilus neumayri* Mojsisovics

According to Hyatt's original description (1883, p. 269) the genus

> Mojsvaroceras, nobis, of the Dyas and Trias includes the species described by Mojsisovics in the Mediterr. Trias Prov. as Temnocheili. These have two rows of lateral tubercles, the form quadrate and very stout, the siphons below the centre, and sutures with ventral lobes, but also according to Mojsisovics with minute annular lobes.

"Temnocheili" of Mojsisovics include *T. neumayri, T. augusti, T. morloti, T. cassianus,* and *T. schloenbachi.* The last three species are forms very different from the genotype and have subsequently been referred to other genera.

Mojsisovics (1902, p. 233) greatly amplified Hyatt's description of *Mojsvaroceras.* He characterized the genus as having straight ribs, by which it was differentiated from *Pleuronautilus,* and included Pennsylvanian and Permian species (*Nautilus nikitini* Tzwetaev (1888) and *Nautilus verae* Arthaber, and with question "*Temnocheilus*" *crassus* Hyatt). Mojsisovics visualized the ornamentation of *Mojsvaroceras* as consisting of either ventrolateral and umbilical nodes which may or may not be connected by lateral ribs, or lateral ribs only, or ventrolateral nodes only. He suggests an evolutionary trend towards a decrease in ornamentation. *Mojsvaroceras perarmatum* Mojsisovics of the Karnian with ventrolateral and umbilical nodes was considered a possible offshoot from the main evolutionary line.

There are 18 species of the subgenus *Mojsvaroceras:* 2 in the Scythian, 12 of Anisian age, 1 of Ladinian age, and 3 of Karnian age. This distribution appears to indicate an expansion in the Anisian and great reduction in the number of species in the Ladinian and Karnian. The two Scythian species are typical binodal forms showing strong affinities with *Metacoceras.* The Anisian species show a great amount of variation in the form of the conch and in ornamentation. One of the most striking characteristics of the Anisian species is the disappearance of the ornamentation leaving a smooth conch after the first or second whorl. This is well illustrated in *M. aureculatum* (Hauer), *M. ventricosum* (Hauer), and *M. kellneri* (Hauer). The Karnian species, namely *M. pironai* (Tommasi), and *M. perarmatum* Mojsisovics are all typical binodal forms; *M. turneri* Hyatt and Smith has only a row of elongated nodes along the midline of the flanks. The fact that the latest species of *Mojsvaroceras,* those of Karnian age, are typical binodal, quadrate forms appears to indicate that this ornamentational type is the main evolutionary pattern of this group. The principal modifications in these late species over the earlier species are the greater development of the ventral lobe, the presence of an annular lobe, and a slightly more involute conch. The Anisian species that led Mosisovics to believe in an evolutionary trend towards a decrease in ornamentation in *Mojsvaroceras* appear to be local aberrant forms that in effect show a great acceleration in their ontogenies and convergence towards *Germanonautilus.*

Only two species of *Mojsvaroceras* are known from the Triassic of North America, *M. turneri* Hyatt and Smith from the Hosselkus limestone, Shasta County, California and *M. frenchi* Kummel n. sp. from the Thaynes formation, southeastern Idaho. Most of the remaining species of *Mojsvaroceras* are known from the Alpine region of Europe, a few from Triassic rocks of the Himalayas, and one species from northern Siberia.

Distribution of species of the subgenus Metacoceras (Mojsvaroceras)

Species	Stratigraphic distribution	Geographic distribution
Metacoceras (*Mojsvaroceras*) *augusti* (Mojsisovics) 1882.	Triassic (Anisian)	Alps.
M. (*M.*) *auriculatum* (Hauer) 1892	Triassic (Anisian, Ladinian)	Alps, Yugoslavia.
M. (*M.*) *binodosum* (Hauer) 1887	Triassic (Anisian)	Do.
M. (*M.*) *bulogense* (Hauer) 1887	do	Yugoslavia.
M. (*M.*) *frenchi* Kummel n. sp	Triassic (Scythian)	Idaho.
M. (*M.*) *kagae* Diener 1907	Triassic (Anisian)	Himalayas, India.
M. (*M.*) *kellneri* (Hauer) 1887	do	Yugoslavia.
M. (*M.*) *morloti* (Mojsisovics) 1882	do	Alps, Yugoslavia.
M. (*M.*) *neumayri* (Mojsisovics) 1882	do	Alps.
M. (*M.*) *nivicola* Diener 1907	do	Himalayas, India.
M. (*M.*) *patens* (Hauer) 1896	do	Yugoslavia.
M. (*M.*) *perarmatum* (Mojsisovics) 1873	Triassic (Karnian)	Alps.
M. (*M.*) *pironai* (Tommasi) 1890	do	Do.
M. (*M.*) *polygonium* (Hauer) 1892	Triassic (Anisian)	Yugoslavia.
M. (*M.*) *subaratum* (Keyserling) 1860	Triassic (Scythian)	Siberia.
M. (*M.*) *turneri* Hyatt and Smith 1905	Triassic (Karnian)	California.
M. (*M.*) *ventricosum* (Hauer) 1896	Triassic (Anisian)	Yugoslavia.

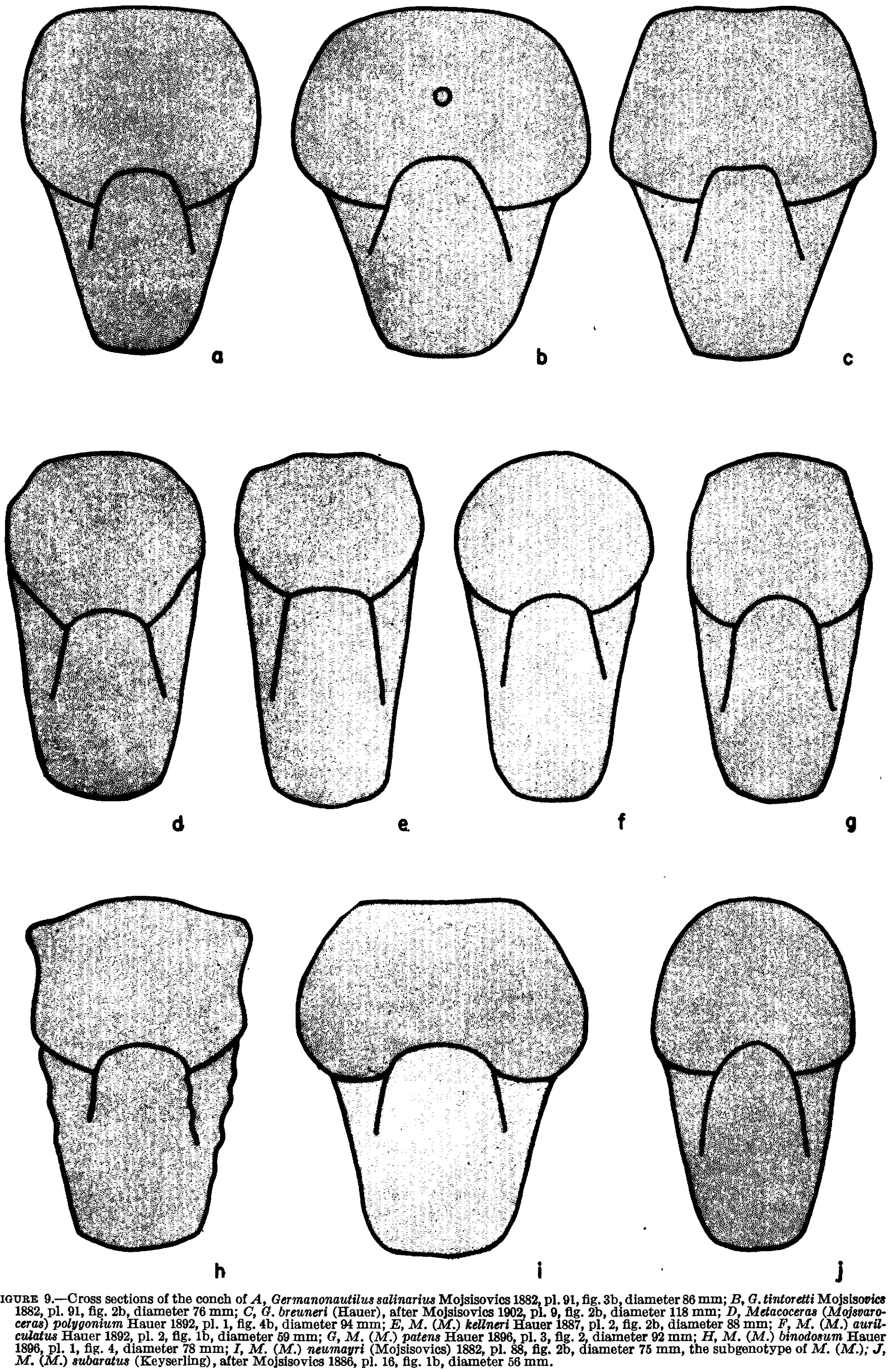

FIGURE 9.—Cross sections of the conch of *A*, *Germanonautilus salinarius* Mojsisovics 1882, pl. 91, fig. 3b, diameter 86 mm; *B*, *G. tintoretti* Mojsisovics 1882, pl. 91, fig. 2b, diameter 76 mm; *C*, *G. breuneri* (Hauer), after Mojsisovics 1902, pl. 9, fig. 2b, diameter 118 mm; *D*, *Metacoceras* (*Mojsvaroceras*) *polygonium* Hauer 1892, pl. 1, fig. 4b, diameter 94 mm; *E*, *M.* (*M.*) *kellneri* Hauer 1887, pl. 2, fig. 2b, diameter 88 mm; *F*, *M.* (*M.*) *auriculatus* Hauer 1892, pl. 2, fig. 1b, diameter 59 mm; *G*, *M.* (*M.*) *patens* Hauer 1896, pl. 3, fig. 2, diameter 92 mm; *H*, *M.* (*M.*) *binodosum* Hauer 1896, pl. 1, fig. 4, diameter 78 mm; *I*, *M.* (*M.*) *neumayri* (Mojsisovics) 1882, pl. 88, fig. 2b, diameter 75 mm, the subgenotype of *M.* (*M.*); *J*, *M.* (*M.*) *subaratus* (Keyserling), after Mojsisovics 1886, pl. 16, fig. 1b, diameter 56 mm.

Metacoceras (Mojsvaroceras) turneri Hyatt and Smith

Plate 2, figures 11–14; text figure 10

1905. *Mojsvaroceras turneri* Hyatt and Smith, U. S. Geol. Survey, Prof. Paper 40, p. 209, pl. 48, figs. 6–11.

1927. *Mojsvaroceras turneri* Hyatt and Smith, U. S. Geol. Survey, Prof. Paper 141, p. 106, pl. 48, figs. 6–11.

The holotype is a fragmentary specimen consisting of four camerae and about 65 mm of the living chamber. The whorls are subquadratic in cross section (text fig. 10). At the most adoral part of the conch the whorl is 60 mm wide and 40 mm high. The venter is broadly arched grading to distinct ventral shoulders. The flanks converge ventral and are only slightly arched. The umbilical shoulders are sharply rounded and the umbilical wall convex and steep. The impressed zone is moderately deep. The adoral part of the living chamber expands very rapidly.

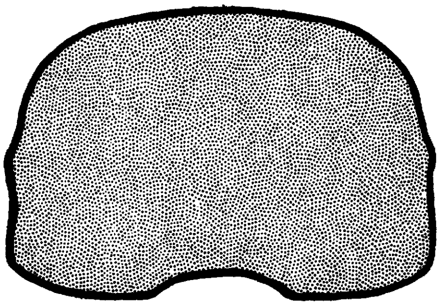

FIGURE 10.—Diagrammatic cross section of the holotype of *Metacoceras (Mojsvaroceras) turneri* Hyatt and Smith (U.S.N.M. 74026) from Hosselkus limestone, Shasta County, California, × 1.

Along the mid line of the flanks are large elongated low nodes spaced about 17 mm apart. There are no nodes on the ventral or umbilical shoulders. The sutures form shallow ventral and lateral lobes and have an annular lobe. A small paratype 30 mm in diameter has a flattened venter with well rounded ventral and umbilical shoulders. The flanks are also flattened. The nodose pattern of ornamentation is not present on this immature specimen.

Occurrence: Upper Triassic Hosselkus limestone, 3 miles east of Madison ranch, between Squaw Creek and Pit River, Shasta County, California.

Types: Holotype, U.S.N.M. 74026; paratype, U.S.N.M. 74026a.

Metacoceras (Mojsvaroceras) frenchi n. sp.

Plate 2, figures 1–10; plate 4, figures 8, 9, 10; text figure 11

This species is the most abundant form in the Lower Triassic nautiloid fauna from Idaho. Ten fairly complete specimens are available for study.

The conch is evolute, impressed zone being small. Cross-section of the adoral whorl is subquadratic in outline (text fig. 11) being broader than high. The venter is broad, flattened, and has a shallow depressed zone along the center in the maturer portions of the conch. The ventral shoulder is broadly rounded and the flanks flair distinctly outward. The umbilical shoulder is sharply rounded and passes on to a broadly arcuate umbilical wall which turns inward at the seam. The adapertural whorls are more rounded but still broader than high. The first one-half volution has no apparent umbilical shoulder, the flanks grade more or less gradually onto the dorsal area. The length of the living chamber is unknown. The umbilicus is broad, deep, and perforate. The umbilical perforation is 4 to 7 mm across in the specimens studied.

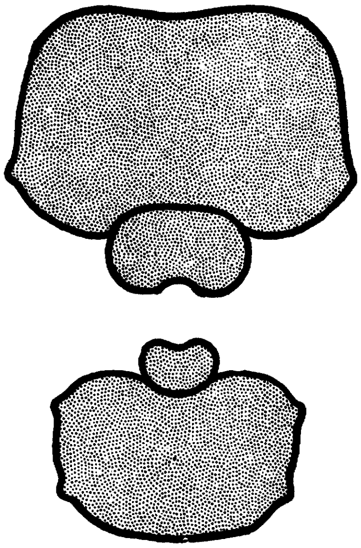

FIGURE 11.—Diagrammatic cross section of the holotype of *Metacoceras (Mojsvaroceras) frenchi*, n.sp. (U.S.N.M. 107069) from the *Columbites* beds, Thaynes formation, Montpelier Canyon, Idaho, × 1.

The test has strong prominent growth lines that pass aborally over the umbilical wall, curve adorally over the flanks and on the ventral shoulder the growth lines turn aborally to form a broad, deep ventral sinus. Delicate lirae oriented transverse to the growth lines have a wavy appearance. The lirae extend only between growth lines, but are more or less continuous. The most distinctive feature of the test is the presence of two sets of nodes, one set of nodes on the ventral shoulder or adjacent to it, and the other set of nodes on the umbilical shoulder. The nodes are high, slender and very distinct; there are no ribs or raised areas connecting the nodes. The nodes are also present on the internal mold but somewhat subdued. There is a slight variation in the prominence of the nodes on the internal mold. There is also some degree of variation in the nodes on the adapical half of the first volution. On this part of the conch there is essentially only one node, and it has the appearance of a short rib in some specimens. In other specimens there is a distinct node on the umbilical shoulder that slopes gradually towards the venter but there is no node on the ventral shoulder. One such specimen (pl. 4, figs. 8, 9, 10) shows strong similarities to *Parametacoceras* of the Pennsylvanian and Permian. The test of the adapertural first one-half volution is composed of delicate transverse and longitudinal ridges that give this portion of the conch a granular appearance. On one of the paratypes (pl. 2, fig. 8) there are, at a diameter of 15 mm, two depressed areas on the margins of the venter. These depressed areas are L-shaped and approximately 5 mm long. The borders of these depressed areas slope gradually on to the surface of the conch, producing no ridge or markings at the contact. The significance of these two symmetrical depressions is unknown.

The sutural elements are simple, consisting of a broad shallow ventral lobe, an adjacent shallow lateral lobe on the flanks, a short shallow lateral saddle on the umbilical shoulder following to the umbilical seam over the umbilical wall in almost a straight line. A short but distinct annular lobe is present. At a diameter of 15 mm the suture is essentially straight.

The siphuncle is subcentral and very small. In the immature part of the conch the siphuncle is central.

Dimensions (in millimeters) of holotype (U.S.N.M. 107069)

Diameter of conch	69. 5
Height of last whorl	30. 0
Width of last whorl	44. 8
Height of umbilical shoulder on the most adapical whorl	13. 5
Diameter of umbilicus	24. 5
Depth of umbilicus	15. 0
Impressed zone	3. 0

Remarks.—The type of *Mojsvaroceras* as picked by Hyatt and illustrated and described by Mojsisovics (1882, p. 267, pl. 88, figs. 1, 2) has a smooth conch for the first 1½ volutions; thereafter marginal nodes are developed on the ventral and umbilical shoulders. *Metacoceras* (*Mojsvaroceras*) *frenchi* has lateral nodes developed after the ½ volution and thus differs in this respect from the genotype. A study of other species included in this genus by Mojsisovics shows that he included forms that developed ornamentation at an early stage. *Metacoceras* (*Mojsvaroceras*) *frenchi* is a very distinctive form characterized by its rapidly expanding conch, the nodes on the ventral and umbilical shoulders, and the shape of its whorl section.

Mojsvaroceras has been recorded from the Alpine, the Himalayan, the northern Siberian, and the California Triassic regions. It ranges from the Scythian to the Karnian. The only other Scythian species of this subgenus known is *Metacoceras* (*Mojsvaroceras*) *subaratum* from the Olenek region of northern Siberia. *Mojsvaroceras* is very abundant in the Anisian in the Alpine and Himalayan regions. Smith (1927, p. 105) states that there are some forms in the middle Triassic of North America that may belong to this genus. One Ladinian species is known from the Alpine Triassic. In the Karnian only a few species are known from the Alpine region, one from the Himalayas and one from the Hosselkus limestone of California.

Occurrence.—Upper shale member (*Columbites* zone), Thaynes formation, Montpelier Canyon, Idaho, sec. 31, T. 12 S., R. 45 E. and Hot Springs, Idaho, sec. 18, T. 15 S., R. 45 E.

Types.—Holotype, U.S.N.M. 107069; paratypes 107070–107078.

Genus PARAMETACOCERAS Miller and Owen, 1934

Genotype: *Parametacoceras bellatulum* Miller and Owen

In their discussion of the genus *Foordiceras*, Miller and Youngquist (1949, p. 96) recommended suppressing *Parametacoceras* as a synonym of *Foordiceras*. This interpretation is held to be untenable for many of the reasons mentioned in the discussion of *Tainionautilus* and *Foordiceras* (pp. 17, 26). The subquadratic cross section of the whorl and the ornamentation show a close affinity to *Metacoceras* as originally pointed out by Miller and Owen (1934, p. 232–233); their original description is as follows:

> Conch tarphyceraconic and typically slightly evolute. Whorls subquadrate in cross section. Umbilicus large and perforate. Aperture marked ventrally by a broad deep rounded hyponomic sinus. On mature portion of the conch lateral sides of whorls bear short transverse ribs. Each suture forms very shallow broadly rounded ventral, lateral, and dorsal lobes and these are separated by similar but more narrowly rounded ventro-lateral and dorso-lateral saddles. Siphuncle small, subcentral or subventral in position, and orthochoanitic in structure.

Possibly *Parametacoceras* is actually the ancestral group of *Pleuronautilus*. It is only superficially similar to *Foordiceras* as defined by Miller and Youngquist (1949). As interpreted here, *Parametacoceras* includes only *P. bellatulum* Miller and Owen, the genotype, *P. schucherti* Miller, *P. crassus* (Hyatt), and possibly *P. nikitini* (Tzwetaev), all from the Pennsylvanian. "*Parametacoceras*" *praecursor* (Girty) from the Leonard formation of West Texas and "*Parametacoceras*" *venustum* Reed from the Upper Productus limestone of the Salt Range, India, the writer assigns to the genus *Pleuronautilus*.

Genus TAINOCERAS Hyatt, 1883

Genotype: *Nautilus quadrangulus* McChesney

The genus *Tainoceras* is well represented in rocks of middle Pennsylvanian to late Permian age throughout the world. It is here proposed to include a Triassic species. The best and most recent description of the genus is that by Miller and Youngquist (1949), quoted in part as follows:

> Conch nautiliconic but not deeply involute, and typically whorls are subrectangular in cross section as they are depressed dorsoventrally, flattened laterally and ventrally, and only slightly impressed dorsally [see text fig. 71]. The volutions are few in number. The umbilicus is large and open, the umbilical shoulders are abrupt, and the umbilical walls are steep. On each of the ventrolateral zones of the conch there is a single row of nodes that border a median sulcus or flattened zone. Growth lines indicate that the aperture bears a broad shallow lobe on the ventral, lateral, and dorsal sides of the conch—these are separated by very narrowly rounded or subangular saddles that center on the ventrolateral zones of the conch and the umbilical seams. As a result of the ventral nodes, the sutures are sinuous and commonly asymmetrical as they cross the ventral zone. At the umbilical shoulders which in some cases are nodose there is a marked change in the adoral curvature of the sutures. The siphuncle is orthochoanitic in structure and is more or less subcentral in position but typically located much closer to the venter than the dorsum. The septal necks are short but straight, the connecting rings are not expanded appreciably within the camerae, and the segments of the siphuncle are therefore essentially cylindrical in shape.

"*Trematodiscus*" *klipsteini* Mojsisovics from the Alpine Karnian resembles typical Paleozoic representatives of *Tainoceras* very closely. It bears prominent nodes on each ventrolateral shoulder and a double row of nodes on the venter. This species is more involute than any Paleozoic species of *Tainocreas*, the outer whorls inclosing more than half of the inner whorl. However, in all other morphologic features this Triassic form shows closer relationships to *Tainoceras* than to any other genus. Mojsisovics (1902, p. 236–237) placed this species in his new genus *Thuringionautilus* and noted its similarity to typical *Tainoceras*. He considered it to be nearer *Germanonautilus* because in the ontogeny the ventrolateral nodes appeared before the nodes on the venter. This is precisely what is found in at least some of the Paleozoic *Tainoceras*.

It is always difficult to ascertain the affinities of stratigraphically widely separated species. Pennsylvanian and Permian species are numerous and widespread; the only Triassic species even closely related is *Tainoceras klipsteini* whose morphological similarity is great. The same problem exists with bringing together in one genus *Aulametacoceras mckeei* and *Nautilus rectangularis* from the Alpine Karnian. One can easily ask, "Where are the intervening forms?" It is of course feasible to consider *T. klipsteini* as an aberrant development of *Germanonautilus* or keep it in the genus *Thuringionautilus* as suggested by Mojsisovics. However, it does not even reasonably resemble the genotype of *Thuringionautilus*, *T. jugatonodosus*. The writer believes that so striking a feature of ornamentation as the double row of ventral nodes, which is developed in only one stock of late Paleozoic nautiloids, is a monophyletic development and that provisionally it is best to place the Triassic species in this genus. It is well to note that no monographic works on Alpine Triassic nautiloids have appeared since those by Mojsisovics (1873–1902) and Diener (1919).

Distribution of species of the genus Tainoceras

Species	Stratigraphic distribution	Geographic distribution
Tainoceras cavatum Hyatt 1891	Permian (Leuders? formation)	Ballinger, Tex.
T. clydense Miller and Kemp 1947	Permian (Clyde formation)	Baylor County, Tex.
T. comptum Reed 1944	Permian (Upper? Productus limestone)	Salt Range, Pakistan.
T. debile Reed 1944	do	Do.
T. duttoni Hyatt 1893	Permian (middle)	New Mexico, Ariz.
T. klipsteini (Mojsisovics) 1882	Triassic (Karnian)	Alps.
T. mingshanense (Kayser) 1883	Permian (middle)	Kiangsi, China.
T. monolifer Miller, Dunbar, and Condra 1933	Pennsylvanian	Mid-Continent region, U. S. A.
T. murrayi Miller and Unklesbay 1942	Pennsylvanian (Lecompton limestone)	Oklahoma.
T. nebrascense Miller, Dunbar, and Condra 1933	Pennsylvanian-Permian (Wabaunsee group to lower Permian).	Nebraska.
T. nodocarinatum (McChesney) 1859	Pennsylvanian	Illinois.
T. noetlingi subglobosum Reed 1931	Permian (Productus limestone)	Salt Range, Pakistan.
T. occidentale (Swallow) 1858	Permian (lower)	Kansas.
T. orientale (Kayser) 1883	Permian (middle)	Kiangsi, China.
T. quadrangulum (McChesney) 1859	Pennsylvanian	Illinois.
T. rotundatum Miller, Dunbar, and Condra 1933	Pennsylvanian (Oread limestone)	Nebraska.
T. schellbachi Miller and Unklesbay 1942	Permian (Kaibab formation)	Arizona.
T. toulai (Gemmellaro) 1888	Permian (Sosio beds)	Sicily.
T. trautscholdi (Waagen) 1879	Upper Carboniferous	Russia.
T. trimuense Reed 1944	Permian (Lower Productus limestone)	Salt Range, Pakistan.
T. unklesbayi Miller and Youngquist 1949	Permian (Toroweap formation)	Arizona.
T. wyomingense Miller and Thomas 1936	Pennsylvanian (Casper formation)	Wyoming.
T. zmajevacense Simic 1933	Permian (upper)	Yugoslavia.

Genus COOPEROCERAS Miller, 1945

Genotype: *Cooperoceras texanum* Miller

This genus is another aberrant development out of *Metacoceras* that is present in the Permian. *Cooperoceras* is characterized by the presence of "long slender hollow paired ventrolateral spines that project ventrolaterally and are distinctly recurved" (see text fig. 7*E*). Only the genotype species is assigned with certainty to this genus. "*Metacoceras*" *spinosus* Kruglov of the Middle Permian Artinskian beds of Russia may belong to this genus. The genus as far as is known is confined to the Permian, and there are no Triassic nautiloids similar to it. A full discussion of the genus can be found in Miller (1945) and Miller and Youngquist (1949).

During the middle and late Permian there was extensive diversification of the *Tainoceratidae*. Four genera of nautiloids (*Tainionautilus*, *Tirolonautilus*, *Aulametacoceras*, and *Cooperoceras*) became established. Each of these genera has a restricted stratigraphic and geographic range. All these forms have a ventral furrow or furrows that is a new morphological feature not acquired previously by any stock of Pennsylvanian or Permian nautiloids except *Metacoceras sulciferum*. *Aulametacoceras* is represented in the Karnian by, possibly one species, and *Tainionautilus* in the Scythian by one species.

Genus TAINIONAUTILUS Mojsisovics, 1902

Genotype: *Nautilus transitorius* Waagen

When Mojsisovics first established this genus (1902, p. 232), he placed it in the family *Temnocheilidae*. He considered it to be transitional with the genus *Tainoceras* through *Nautilus trautscholdi* Waagen. Waagen (1879, pp. 54, 55) first pointed out the relationship between his species, *Nautilus transitorius* and *Nautilus trautscholdi* (=*Nautilus tuberculatus* Trautschold, non Sowerby). For the purpose of this study it probably would not have been necessary to make extensive comments on this genus except that recently Miller and Youngquist (1949) have discussed it and they recommended suppressing the genus and placing its forms in *Foordiceras*. The writer differs with this interpretation. For the sake of completeness it should be mentioned that Foord (1891, p. 136) included the group of *Nautilus trautscholdi* (*Tainionautilus*) in the genus *Pleuronautilus*.

The shape of the conch and ornamentation differ considerably from either of the above genera. Part of Waagen's description of *N. transitorius*, the genotype, is as follows:

> The general form of this species is very different according to the age of the shell.
>
> The whole shell appears thick disciform, with wide and rather shallow umbilicus. The transverse section of the whorls is somewhat squarish, the outer or ventral part of the shell being flat with a shallow depression in the middle. The lateral parts of the whorls are perpendicular, and form a distinct angle with the external part. The umbilicus is surrounded by a distinct umbilical wall, which forms a more or less distinct edge where it unites with the lateral parts of the whorls.
>
> In the young shell the first circuit has a diameter of about 17 mm, being pierced in the middle by a central aperture of about 5 or 6 mm in diameter. The commencement of the shell is quite smooth (the entire form of the "calotte" not being observable) and very depressed, the transverse section about twice as broad as high; but already towards the end of the first circuit the ornamentation of the shell begins to appear. This consists of a prominent crest along the umbilical edge and of low folds on the outer margin of the whorl, where the lateral and external parts of the shell unite. As the shell grows larger these folds increase considerably in height, and extend more and more towards the crest which surrounds the umbilicus. There may have been about fifteen of these folds on the third volution, how many there may have been on the second is not observable. On all these inner whorls the external part of the shell seems to have been entirely smooth, without marked depression on the middle.
>
> On the last whorl the sculpture changes considerably. Already towards the end of the third volution the crest on the umbilical margin thickens at certain intervals, and generally one of these nodular thickenings corresponds to two of those folds on the lateral parts of the whorl. On the last whorl now this crest is entirely resolved into single high knobs along the umbilical edge, and no proper crest remains. These knobs unite with alternate high thick ribs, which come from the external margin of the whorl, and are highest on that margin. Between these there are other ribs equally high on the outer margin of the whorl, but which disappear gradually towards the umbilical edge. The whole system of sculpture becomes less prominent towards the the mouth of the shell.
>
> The strong ribs which cover the lateral part of the last whorl extend on this whorl in a somewhat retrograde direction to the external or ventral part of the shell, up to near the middle of it, and terminate there as two very low longitudinal ridges which border a tolerable broad medial depression on both sides.
>
> It is very difficult to observe what form the sutures of the septa may have possessed, as the whole specimen is covered with its shell, but it seems that there were sinuosities both on the sides and on the external part of the whorl.
>
> I am not able to indicate anything as to the number of septa in one whorl, but the siphon is clearly observable on one of the septa. It is very narrow, and in its position nearer the internal than the external side of the whorl.

From the description and illustration of the genotype species by Waagen, it is readily seen that the shape of the whorl section is approximately square with abrupt imbilical walls (see text fig. 7 *A*). The genotype of *Foordiceras*, *F. goliathus* (Waagen) has no umbilical edge, or a distinct umbilical wall. The ornamentation of the two forms is different. In *Tainionautilus* the lateral folds or ribs extend onto the venter and terminate at the ventral furrow. The venter of at least the genotype of *Foordiceras* is smooth throughout growth. Also, *Foordiceras* shows no development of a crest and nodes on the umbilical shoulder such as are developed in *T. transitorius*. The trapezoidal conch of *Foordiceras* and differences in ornamentation appear to make it improbable that these two genera are related.

Only five species have been referred to this genus, *T. fugax* Mojsisovics, from the Bellerophon Limestone, the genotype *T. transitorius* (Waagen), *T. wynnei* (Waagen), *T. multicostatus* (Reed), and T. sp. Reed from the Productus Limestone of the Salt Range, Pakistan. *T. trachyceras* Frech from the Skythian beds of the Salt Range has also been placed in this genus (pl. 19, fig. 3). Thus the known range of the genus is upper Permian to Lower Triassic.

Reed (1944, p. 356) considered *Tainionautilus* to be a subgenus of *Metacoceras* and stated

> the nearest allied species to *M. wynnei* (Waagen) seems to be *M. sulciferum* Miller and Thomas (1936, p. 729, pl. 97, figs. 4–5) from the Casper formation of Wyoming, for they both possess the characteristic median groove on the venter.

Several species of *Metacoceras* show a binodal type of ornamentation in which the nodes are elongated onto the flanks and which have steep umbilical shoulders. To my knowledge, *M. sulciferum* is the only species of that genus possessing a median furrow. With only five isolated species of *Tainionautilus* so far recorded and none of these at the disposal of the writer, it is difficult to ascertain the affinities of this genus. The writer tentatively accepts Reed's (1944) interpretation as probably most correct (that *Tainionautilus* is an aberrant development derived from *Metacoceras*) but it it is here given generic rank. No North American species are referred to this genus.

Genus **TIROLONAUTILUS** Mojsisovics, 1902

Genotype: *Nautilus crux* Stache

Miller and Youngquist (1949, p. 80) questioned the validity of this genus and stated " * * * it seems rather doubtful if they [species of *Tirolonautilus*] differ sufficiently from typical *Tainoceras*, *Foordiceras*, and *Metacoceras* to be regarded as generically distinct." The four species assigned to this genus all come from the Bellerophon Kalk of the Alps. Neither the present author nor Miller and Youngquist have had an opportunity to study any specimens of these species, but it appears that the ornamentation is distinctive enough to distinguish this group from *Metacoceras* and *Tainoceras*. Middle and late Permian time was a period of great experimentation and diversification in the Tainoceratidae. This experimentation is well illustrated by such genera as *Cooperoceras*, *Tainionautilus*, and *Aulametacoceras*. Rather than place *Tirolonautilus* in synonymy of other genera, this genus is considered to be just another aberrant evolutionary development with a narrow stratigraphic and geographic range.

Mojsisovics (1902, p. 233) diagnosed the genus as follows:

> Die aus *Metacoceras* hervorgegangenen Formen, welche bis jetzt blos aus dem permischen Bellerophonkalk Südtirols bekannt sind, unterscheiden sich von *Metacoceras*, mit welcher Gattung sie sonst gut übereinstimmen, hauptsächlich durch die furchenförmige Längseinsenkung in der Mitte des Externtheiles. Die Involution ist nach den Abbildungen Stache's etwas stärker als wie bei dem geologisch älteren *Metacoceras* und nähert sich den Einrollungsverhältnissen von *Mojsvaroceras*. Die kräftig entwickelten Marginalknoten sind schräge gestreckt und setzen sich bei *Tirolonautilus crux* Stache von diesen schräge gestellten Randknoten rippenartige Verlängerungen auf den Externtheil fort, in dessen vertiefter Mittellinie sie von beiden Seiten unter einem spitzigen Winkel zusammenstossen. Eine Form, *Tirolonautilus Sebedinus* Stache besitzt auf der Mitte der Flanken schwielige, rippenartige Auftreibungen. Die dritte, in diese Gattung gehörige Art, welche den typischen Formen von *Metacoceras* am ähnlichsten sieht, ist *Tirolonautilus Hoernesi* Stache. Aber auch bei diesser Art sind wegen der stärkeren Einrollung die Marginalknoten des vorletzten Umganges im Nabelraume nicht mehr sichtbar.

Mojsisovics' description can be summarized as follows:

> This genus, derived from *Metacoceras*, is known only from the Bellerophon Kalk of the Alps. It differs from *Metacoceras* namely in the presence of a median furrow. Its involution is intermediate between that of *Metacoceras* and *Mojsvaroceras*. The strong nodes on the ventral shoulders of *Tirolonautilus crux* are elongated and oblique. They form a conspicuous angular ventral shoulder and there are ribs that project adapically from these marginal nodes, over the venter towards the deep median furrow. *Tirolonautilus sebedinus* Stache has radial fold-like ribs on the flanks. *Tirolonautilus hoernesi* Stache, which is most similar to *Metacoceras* is more involute and the ventrolateral nodes of the earlier whorls are not visible in the umbilicus.

Mojsisovics did not designate a type for his genus; *Tirolonautilus crux* (Stache) (text fig. 6*F*) is hereby selected as the type for this genus.

Tirolonautilus hoernesi is very similar to *Metacoceras sulciferum* Miller and Thomas of the *Stenopoceras* beds, Casper formation, Wyoming; both of these species have a characteristic median furrow. No other species of *Metacoceras* has a median furrow like *M. sulciferum*. The remaining two species of *Tirolonautilus* because of their distinctive ornamentation are not directly comparable to any other known Permian nautiloid.

Genus **AULAMETACOCERAS** Miller and Unklesbay, 1942

Genotype: *Aulametacoceras mckeei* Miller and Unklesbay

This genus is characterized by a conch with the general physiognomy of *Metacoceras* but with longitudinal ribs on the venter (see text fig. 7*C*). The genotype is from the Kaibab limestone, Arizona. Only one other species, *Nautilus rectangularis* Hauer from the Alpine Karnian, has been placed in this genus by its authors. This genus is well described by Miller and

Unklesbay (1942, p. 726) and by Miller and Youngquist (1949, p. 93), and need not be repeated here.

The Triassic species, *A. rectangulare*, has a similar development of ribs on the venter as in *A. mckeei* but has a subquadratic conch in contrast to a subhexagonal conch. The Triassic species also has no nodes on the umbilical shoulders. *A. rectangulare* has previously been placed in *Trematodiscus*, *Coelonautilus*, and *Thuringionautilus* but is not similar to any of these genera. Even though only two stratigraphically and geographically widely separated species of this genus are known, the writer believes that a tentative plan of following the procedure of Miller and Youngquist is the best one. With our present knowledge of Permian-Triassic nautiloids it is difficult to separate the two species on a logical basis except that of time and until more material is available it seems best to bring these closely similar species together into one genus.

Genus GERMANONAUTILUS Mojsisovics, 1902

Genotype: *Nautilus bidorsatus* Schlotheim

The original diagnosis of this genus by Mojsisovics (1902, p. 235) is quoted here in part:

> Als Typus dieser Gattung betrachte ich *Germanonautilus bidorsatus*. Die aus der Zone des *Ceratites trinodosus* von mir beschriebenen Formen *Nautilus privatus, N. Tintoretti, N. salinarius,* and *N.* ind. aff. *salinario,* welche in allem wesentlichen Merkmalen mit den glattschaligen Abänderungen des germanischen *Bidorsatus*-Typus übereinstimmen und offenbar derselben Gattung wie dieser zuerechnet werden müssen, unterscheiden sich von den in der gleichen Lagerstätte auftretenden Arten von *Mojsvaroceras* lediglich durch das vollständige Fehlen von Pilae und Knoten, und erscheint es zweckmässig, diesem glatten, offenbar aus *Mojsvaroceras* hervorgegangenen Typus unter einem selbständigen Gattungsnamen zusammenzufassen. Die rasch in die Höhe und Breite wachsenden Gehäuse besitzen in der Regel einen mehr winiger rechteckigen Querschnitt (text fig. 9). Dir Umgänge umfassen einander ziemlich stark, ohne aber den tiefen Nabel zu verschliessen. Die Breite der Umgänge überwiegt in der Regel bedeutend die Höhe. Der Externtheil ist breit, abgeflacht, manchmal auch leicht concav eingebogen. Der Nabelrand, in dessen nächster Nähe die grösste Breite der Umgänge erreicht wird, ist deutlich markirt, abgestumpft oder kantig. Die Schale ist in der Regel glatt, aber von kräftigen zuwachsstreifen bedeckt, welche auf den Flanken vom Nabelrande weg, schräge gegen rückwärts gewendet, dem kantigen Marginalrande zustreben und auf dem Externtheile einen starken, rückwärts gewendeten Sinus beschreiben (*G. Breunneri, G. Cassianus, G. Schloenbachi*). Bei einigen Formen treten Marginalknoten auf, was im Hinblick auf die genetischen Relationen als eine atavistische, an *Mojsvaroceras* oder *Temnocheilus* erinnernde Erscheinung aufgefasst werden Kann. Da diese Arten in allen übrigen Merkmalen vollständig mit den glattschaligen Repräsentanten übereinstimmen, erscheint es wohl über flüssig, sie unter einer besonderen generischen Bezeichnung abzutrennen.
>
> Die Loben von *Germanonautilus* schliessen sich den Loben mit steiler Nabelwand versehenen Arten. von *Mojsvaroceras* an. Die Kammerwände stehen sehr gedrängt, bilden auf der Externseite einen seichten, flachen Lobus oder übersetzen den Externtheil geradlinig; auf den Flanken ist ein gleichfalls ziemlich weiter, etwas tieferer Lobus vorhanden, Kleine, abgerundete Sättel stehen auf dem Aussen- und dem Nabelrande.
>
> Ein Internlobus (Annularlobus) ist vorhanden * * * Der dicke Sipho steht, ähnlich wie bei *Mojsvaroceras,* in oder unter der halben Mündungshöhe.

Mojsisovics' diagnosis can be summarized as follows:

> The type of this genus is *Germanonautilus bidorsatus. Germanonautilus* is undoubtedly derived from *Mojsvaroceras* and differs from that genus in the complete lack of ribs or nodes The whorl section is subquadrate, generally wider than high. The venter is broad, flattened, and often slightly concave. The umbilical shoulder is sharply rounded. The shell is smooth except for growth lines which trend adapically over the whorl sides and form a sinus on the venter. The suture forms a shallow ventral and a broad, deeper lateral lobe. An annular lobe is present. The siphuncle is approximately central in position as in *Mojsvaroceras.*

Mojsisovics included in this genus two species (*G. cassianus* and *G. schloenbachi*), which have distinct nodes on the ventral shoulders, but he expressed the possibility that these two species did not belong to *Germanonautilus* and should perhaps be placed in a new genus. The shape of the conch agrees quite closely with that of the genotype of *Germanonautilus*. However, without having seen specimens of these species

Distribution of species of the genus Germanonautilus

Species	Stratigraphic distribution	Geographic distribution
Germanonautilius advena (Fritsch) 1902	Triassic (Muschelkalk)	Germany.
G. bidorsatus (Schlotheim) 1832	do	Do.
G. breunneri (Hauer) 1847	Triassic (Karnian)	Alps.
G. brooksi Smith 1927	do	Alaska.
G. cassianus (Mojsisovics) 1882	do	Alps.
G. dolomiticus (Quenstedt) 1849	Triassic (Muschelkalk)	Germany.
G. furlongi Smith 1914	Triassic (Anisian)	Nevada.
G. johnstoni Kummel n. sp	do	Do.
G. montpelierensis Kummel n. sp.	Triassic (Scythian)	Idaho.
G. nodosus (Münster) 1831	Triassic (Muschelkalk)	Germany.
G. salinarius (Mojsisovics) 1882	Triassic (Anisian)	Alps, Yugoslavia.
G. schloenbachi (Mojsisovics) 1873	Triassic (Karnian)	Alps.
G. spumosus (Fritsch) 1902	Triassic (Muschelkalk)	Germany.
G. suevicus (Philippi) 1898	do	Do.

the writer refrains from changing the taxonomic status of these forms. *Germanonautilus* appears to be a derivative of *Mojsvaroceras* or *Metacoceras* sensu stricto differing mainly in the greater involution and general loss of ornamentation.

Germanonautilus brooksi Smith

Plate 3, figures 1–10.

1927. *Germanonautilus brooksi* Smith, U. S. Geol. Survey Prof. Paper 141, p. 105, pl. 52, figs. 7–10.

Smith's description of this species is as follows:

> Shell moderately evolute, with open umbilicus, whorls broader than high, deeply embracing. Cross section low, crescentic, with broadly arched venter, more sharply curving flanks, and steep umbilical walls. There is only a faint suggestion of the ventral shoulders usually characteristic of the group and no remnant of the nodes. Surface shows fine striae of growth and spiral lines. The striae of growth bend backward on the venter, forming a deep broad sinus. The septa show a broad, shallow ventral lobe, and a short funnel shaped ventral [dorsal] or annular lobe. Siphuncle central.

The specimens figured and described by Smith came from U.S.G.S. locality 9384, south bank of Yukon River opposite mouth of Nation River, Alaska. In addition to this holotype and paratype there are available one specimen from the same locality which can thus be considered a topotype, U.S.N.M. 107087, and a specimen from U.S.G.S. locality 9385, Yukon River ⅛ mile northeast of the mouth of Nation River, Alaska. Both the holotype and topotype seem to be immature specimens, thus accounting for the broadly rounded ventro-lateral and umbilical shoulders. The fourth specimen, U.S.N.M. 107086, and the paratype are presumably late adolescent or early mature individuals. The ventral and umbilical shoulders are distinct, the flanks converge towards the venter, and the venter is broadly rounded. The umbilical walls are gently rounded but steep and the umbilicus is deep. The sutures have a very shallow ventral lobe and a broad shallow lateral lobe with a slight saddle on the umbilical shoulder. The first one-half volution of specimen U.S.N.M. 107086 has delicate reticulate ornamentation. The siphuncle is central and large, measuring 3 mm in diameter.

Occurrence.—Holotype, paratype, and topotype from U.S.G.S. locality 9384, south bank of Yukon River opposite mouth of Nations River, Alaska, in Upper Triassic beds of Karnic age. Plesiotype U.S.N.M. 107086 from U.S.G.S. locality 9385, Nation River, hillside ⅛ mile northeast of mouth of Yukon Valley, Alaska.

Types.—Holotype, U.S.N.M. 74206; paratype, U.S. N.M. 74206a; topotype, U.S.N.M. 107087; plesiotype, U.S.N.M. 107086.

Germanonautilus furlongi Smith

Plate 3, figures 12, 13; text figure 12

1914. *Germanonautilus furlongi* Smith, U. S. Geol. Survey Prof. Paper 83, p. 142, pl. 95, figs. 1, 2.

Smith's description of this species is as follows:

> Form robust, whorls low, broad and trapezoidal in cross section, little embracing, and little indented by the inner whorls. Sides converging toward venter. Umbilicus about one-fourth of the diameter of the shell. Umbilical shoulders subangular, inner walls very steep. Ventral shoulders rounded, venter broad and flat, without concavity. Siphuncle a little below the middle of the chamber.
>
> Septa close together, with gentle backward curve or the lobe on the flanks. Surface smooth, outer shell unknown.

Dimensions of the type specimen of Germanonautilus furlongi

	(mm)
Diameter	87
Height of last whorl	43
Width of last whorl	60
Width of umbilicus	23
Involution	8

> *Germanonautilus furlongi* is very closely related to G. *salinarius* Mojsisovics of the same horizon in the Alpine province but has the sides of the whorl somewhat more convergent and the umbilicus narrower. It is still closer to *Germanonautilus* sp. ind. Mojsisovics and may be identical with that unnamed species.

Two fragmentary specimens are referred with question to this species. One is from the same locality as the holotype. This specimen, U.S.N.M. 32631, has only part of the phragmocone and living chamber of only one side of the conch preserved. It is 118 mm in

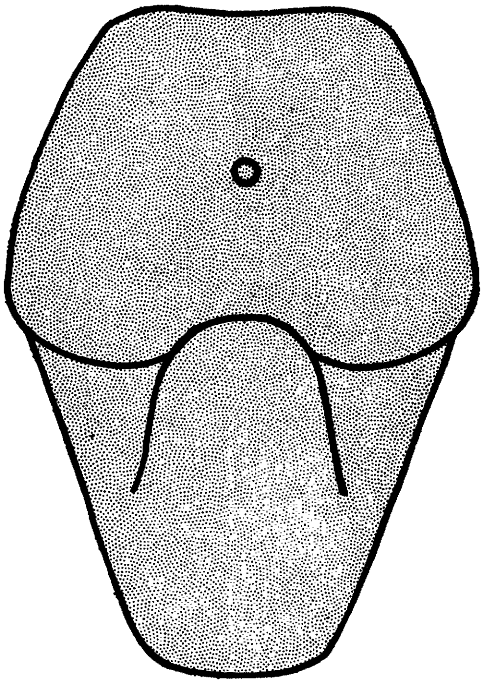

FIGURE 12.—Diagrammatic cross section of the holotype of *Germanonautilus furlongi* Smith (U.S.N.M. 74444) from *Daonella dubia* zone of Star Peak formation, Fossil Hill, West Humboldt Range, Nevada, × 1.

diameter, but does not have the subangular umbilical shoulders of the holotype. This, however, may be an ontogenetic feature as the holotype is much smaller than this specimen. The other fragmentary specimen, consists of only two camerae plus a small part of the living chamber. The specimen is more quadratic in outline of the conch than the holotype but appears to belong to this species.

Occurrence.—The holotype U.S.N.M. 74444 and specimen U.S.N.M. 32631 came from the *Daonella dubia* zone, *Ceratites trinodosus* subzone of the Star Peak formation, South Fork of American Canyon, Fossil Hill, West Humboldt Range, Nevada. Another specimen came from the same formation and horizon, on the north side of South Canyon, New Pass Range, Nevada.

Types.—Holotype U.S.N.M. 74444; specimen U.S.N.M. 32631.

Germanonautilus johnstoni n. sp.

Plate 3, figures 14, 15; text figure 13

One small specimen of 1¼ volutions, 42 mm across, is available. The specimen is especially noteworthy because it represents a nodose form of *Germanonautilus* related to *G. cassianus* and *G. schloenbachi.* The conch is rapidly expanding and at its maximum diameter the whorl has a subquadratic cross-section about 20 mm in height and 27 mm in width; the flanks converge toward the venter. The venter is essentially flat and the ventral shoulders well rounded. The flanks are convex and the umbilical shoulders subangular (text fig. 13). The umbilical wall is only slightly convex and practically vertical. The umbilicus is deep and measures 11 mm at the maximum diameter of the conch. Up to the end of the first volution the flanks and both shoulders are more rounded.

On the ventral shoulders are low distinct ribs that curve adapically parallel to the trend of the growth lines, which form a deep hyponomic sinus. The ribs are discernable only over the rounded ventral shoulder and do not extend far on the venter or the flanks. The most adoral rib visible is 10 mm in length.

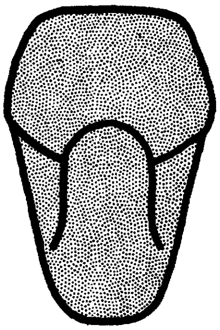

FIGURE 13.—Diagrammatic cross section of the holotype of *Germanonautilus johnstoni*, n. sp. (U.S.N.M. 107088) from the Star Peak formation, South Canyon, New Pass, Desatoya Range, Nev., × 1.

The suture forms a distinct lobe on the venter and a broad concave lateral lobe. The siphuncle was not observed.

Remarks.—Only three species of *Germanonautilus* with ribs or elongated nodes on the ventral shoulders have been described. These are *G. cassianus*, *G. schloenbachi*, and *G. johnstoni.* The first two species from the Alpine Karnian have very rapidly expanding conchs with angular to subangular ventral shoulders. In *G. cassianus* the nodes are elongated parallel to the angular ventral shoulder. In *G. schloenbachi* the nodes are not parallel but elongated at a small angle from the subangular ventral shoulder. In neither species do the elongated nodes parallel the growth lines as in *G. johnstoni.*

Occurrence.—Star Peak formation, South Canyon, New Pass, Desatoya Range Nevada. Collected by F. N. Johnston.

Holotype.—U.S.N.M. 107088.

Germanonautilus montpelierensis n. sp.

Plate 3, figure 11; text figure 14

A rather poorly preserved phragmocone from the *Columbites* zone at Hot Springs, Idaho is referred to *Germanonautilus.* The right side of the specimen and most of the venter has been crushed. The conch is evolute, rapidly expanded orad, and has a rather deep perforate umbilicus. The phragmocone is the only portion of the conch preserved and consists of about 1½ volutions. The outline of the adoral camera is quadrate, measuring 42.6 mm wide and 33 mm high (text fig. 14). The venter is broadly arched and the ventral shoulders are obliquely rounded. The flanks are flattened and slope obliquely outward passing on to a strongly rounded umbilical shoulder. The um-

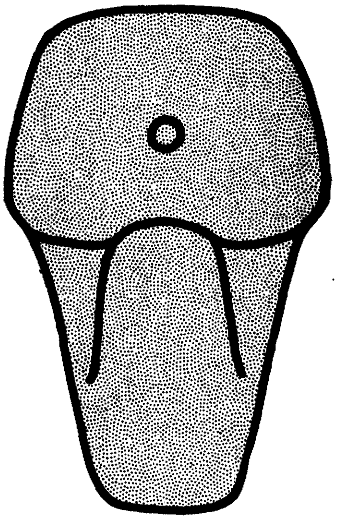

FIGURE 14.—Diagrammatic cross section of the holotype of *Germanonautilus montpelierensis*, n. sp. (U.S.N.M. 107089) from the *Columbites* beds, Thaynes formation, Hot Springs, Idaho, × 1.

bilical wall is oblique and arched; the extreme lower edge of the umbilical wall is turned in sharply into the umbilical seam. The inner whorls are much more rounded in cross section but still broader than high and the umbilical wall is more nearly vertical. The first adapertural one-half volution is ovoid in cross section and has no apparent umbilical shoulder. The umbilicus is rather narrow, deep, and perforate. It measures 25 mm in width and is 15 mm deep. The umbilical perforation is 6 mm in diameter.

Only a few isolated parts of the conch have the test preserved. The growth lines are very delicate, closely spaced, and slightly sinuous on the flanks. The test is distinctive, however, in having delicate transverse striations or ridges. This feature is best observed on the umbilical wall, where slightly weather portions of the test emphasize the lines. The test also has delicate undulating longitudinal lines. This feature is not very conspicuous however, as the test is not well preserved. There is a small node on the flanks of the adapical half of the adapertural first one-half volution. As there are no other nodes on this specimen, probably because it is poorly preserved, the significance of this node is not known. The suture is preserved only on the flanks where it forms a broad concave lateral lobe. The siphuncle is central in position and is about 3 mm in diameter.

Remarks.—*Germanonautilus montpelierensis* does not seem to be closely similar to any other species of the genus. It is more evolute than most species of *Germanonautilus*. This species shows some affinities in form of its conch to species of *Syringonautilus*. *G. montpelierensis* is the first record of a Scythian representative of this genus; all the other species occur in Ansian and Karnian formations.

Occurrence.—Upper shale member, *Columbites* zone, Thaynes formation, Hot Springs, Idaho, sec. 18, T. 15 S., R. 45 E. Collected by the author.

Holotype.—U.S.N.M. 107089

Germanonautilus spp. (of Nevada)

Two incomplete specimens from the Upper Triassic of Nevada can be assigned to *Germanonautilus* but are not well enough preserved to identify specifically. The first specimen U.S.N.M. 107090 (U.S.G.S. loc. 11782) has only 2 cm of living chamber and 5 cm of phragmocone (measured along the venter) preserved. The venter is broadly rounded, flanks slightly convex and sloping sharply ventrad. Sutures are practically straight with only a slight ventral and lateral lobe. The growth lines are very coarse and show a broad rather deep sinus on the venter. The label accompanying this specimen reads as follows:

> Upper Triassic, massive limestone Shoshone Range; by roadside ½ mile south of spring in mouth of Union Canyon, west front of Shoshone Range, Tonopah Quadrangle, Nevada.

This is presumably from the Luning formation (see Muller and Ferguson, 1939).

The second specimen U.S.N.M. 107091 (U.S.G.S. loc. 14344) consists of one half whorl with only one side and part of the venter preserved. No septa are visible, most of the specimen probably represents living chamber. The venter is broadly arched, grading to a sharp, subangular ventral shoulder. The flanks are convex and the umbilical shoulders are well rounded. This specimen came from the Cedar Range, 3½ miles south of Bench Mark 6679, Tonopah Quadrangle, Nevada, in the Luning formation.

Germanonautilus spp. (of Alaska)

Two specimens are available for study from Alaska that clearly belong in *Germanonautilus* but are too incomplete to warrant specific assignment. The first, U.S.N.M. 107092 (U.S.G.S. loc. 12393), is from the Gold Bay District, Alaska Peninsula, Alaska and was collected by W. R. Smith in 1924. The specimen is an essentially complete living chamber with part of the crushed phragmocone. The conch is very robust, measuring 57 mm in width and 54 mm in height on the most adoral part of the living chamber. The venter is broadly rounded, flanks slightly convex grading on to a rounded and sloping umbilical wall. There is a broad shallow constriction on the flanks and venter about 2 cm back of the most adoral part of the specimen. The phragmocone is badly crushed but appears to be very much smaller in its general dimensions than the living chamber, indicating a rapidly expanding conch. Only part of a broad lateral lobe of the suture is visible. Position of the siphuncle is not known.

The second Alaskan specimen, U.S.N.M. 107093 U.S.G.S. loc. 8895), is also the living chamber of a very robust individual. The specimen is 42 mm high and 58 mm wide, measuring the conch along the midpoint of the specimen and 110 mm in length along the venter. The venter and flanks are only broadly arched, ventral and umbilical shoulders well defined and rounded. The umbilical wall is convex and steep. This specimen is from a 10-ft bed of dark noncrystalline limestone that is separated from Carboniferous limestones by a 50-ft covered interval along the south bank of the Yukon River about 1 mile above the Nation River, Alaska (see Martin, 1926, p. 96). Stanton (in Martin, 1926) has identified the following genera from this limestone bed: *Rhynchonella, Terebratula, Spiriferina, Halobia, Aviculopecten, Natica,* and *Nautilus*. Thirty feet above this limestone bed characteristic Upper Triassic fossils were obtained. Stanton's conclusions that the lower limestone (U.S.G.S. loc. 8895) was probably Triassic is correct. However, the nautiloid described here does not aid in a more specific age determination.

Genus **THURINGIONAUTILUS** Mojsisovics, 1902

Genotype: *Trematodiscus jugatonodosus* Zimmermann

Mojsisovics' original description is quoted here in full (1902, p. 236–237):

> Von *Germanonautilus* sich abzweigende Gattung, welche sich durch die Erwerbung einer Externsculptur von *Germanonautilus* unterscheidet. Als Typus ist der durch eine auffallend lange Wohnkammer Umgang bemerkenswerte *Thuringionautilus jugatonodosus* Zimmermann anzusehen.
>
> Diese Art, welche aus dem Grenzdolomit des thüringischen Keupers stammt, erwirbt auf dem letzten Umgange eine an den permischen *Tainionautilus* erinnernde Externsculptur. Die Mitte des Externtheiles ist ausgehöhlt und wird beiderseits durch Längsleisten begrenzt, welche durch schräge gegen vorne laufende Querjoche mit den auf der Marginalkante stehenden, in der Richtung der Spirale verlängerten Marginalknoten verbunden sind. Auf dem vorletzten Umgange fehlen die Querjoche sowie die Randknoten und sind nach Zimmermann's Beschreibung blos die Längsleisten vorhanden. Es geht hieraus klar hevor, dass ein directer genetischer Zusammenhang mit *Tainionautilus* nicht besteht. Da in dem sonstigen Verhalten die grösste Uebereinstimmung mit *Germanonautilus* besteht, so ist es evident, dass *Thuringionautilus* blos als ein von *Germanonautilus* derivirter, selbständiger Typus zu betrachten ist.
>
> Die zweite, in diese Gattung einzubeziehende Art ist der von mir früher zu *Trematodiscus* gestellte *Thuringionautilus rectangularis* (Hau.), welcher ebenso wie *Th. jugatonodosus* sehr evolut ist und bei ganz übereinstimmendem Entwicklungsgange sich durch eine grössere Anzahl von Externrippen unterscheidet.
>
> Eine etwas weitergehende Verschiedenheit zeigt die dritte bekannte Art, *Thuringionautilus Klipsteini* Mojs., welche sich durch stärkere Involution auszeichnet und durch die Sculptur ihrer Externseite mehr an *Tainoceras* erinnert. Die Abstammung von *Germanonautilus* ist aber auch bei dieser Art leicht aus der ontogenetischen Entwicklung nachzuweisen. Es erscheinen nämlich auf dem ersten Umgang die Marginalknoten früher als die durch rückwärts gewendete Querjoche mit diesen verbundenen Externknoten und sieht in diesem Stadium das Gehäuse vollkommen dem *Germanonautilus Cassianus* ähnlich.
>
> *Thuringionautilus* besitzt wie *Germanonautilus* gedrängt stehende Kammerwande mit breiten Extern-und Laterallobus. Umbilicalsattel und Internlobus vorhanden. Sipho subcentral.

Mojsisovics' description can be summarized as follows:

> The type of this genus is *Thuringionautilus jugatonodosus* (Zimmermann). *Thuringionautilus* is derived from *Germanonautilus* and differs from that genus in the presence of sculpture on the ventral region. The modifications on the venter are reminiscent of that found in the Permian *Tainionautilus.* The venter has a conspicuous ventral furrow with sharp borders. The sharply rounded ventral shoulder has oblique, elongated nodes that project adapically over the venter toward the border of the ventral furrow. The ventral nodes disappear adorally. A direct relationship with *Tainionautilus* is not indicated but rather a close relationship to *Germanonautilus.* A second species, *T. rectangularis* (Hauer), was previously placed in *Trematodiscus.* It is evolute like *T. jugatonodosus* and is distinguished by its numerous ventral ribs. *T. klipsteini* Mojsisovics is more involute and similar in its ornamentation to *Tainoceras.* Its derivation from *Germanonautilus* is evident from its ontogenetic development. The ventrolateral nodes appear earlier on the first volution than the ventral nodes and in this stage the conch is similar to *Germanonautilus cassianus. Thuringionautilus,* as *Germanonautilus,* has a depressed whorl section. The suture has a wide ventral and lateral lobe. An umbilical saddle and a dorsal lobe are present. The siphuncle is subcentral.

Of the three species assigned to this genus by Mojsisovics *T. rectangularis,* has subsequently been placed in *Aulametacoceras* (Miller and Unklesbay 1942, p. 726). The similarity between the genotype species, *A. mckeei,* from beds of Leonard age, Arizona to the Karnian *A. rectangulare* is remarkable. "*Thuringionautilus*" *klipsteini* is tentatively placed in *Tainoceras* and is discussed under that genus. The existence of longitudinal ribs on the ventral reigon is found in four genera of the *Tainoceratidae,* namely *Phloioceras, Trachynautilus, Thuringionautilus,* and *Aulametacoceras.* The first two genera are clearly related to *Pleuronautilus* and need no further mention here. The last two belong to the *Metacoceras-Mojsvacoceras* evolutionary complex. In *Thuringionautilus* the presence of a deep ventral furrow offers additional problems. There are only two species of *Aulametacoceras* and one of *Thuringionautilus* so far reported. The only species of *Thuringionautilus* comes from the Keuper of Germany. The writer tentatively accepts the present taxonomic status of these forms. The derivation of *Thuringionautilus* from *Germanonautilus,* as proposed by Mojsisovics is also believed to be correct. Possibly this genus descended directly from *Mojsvaroceras.* The similarity of *Thuringionautilus jugatonodosus* to the Permian *Tainionautilus* is thought to be superficial. With so few specimens and species of this genus it appears unwise to speculate too widely as to its affinities. This genus has not been reported from any North American strata of Triassic age.

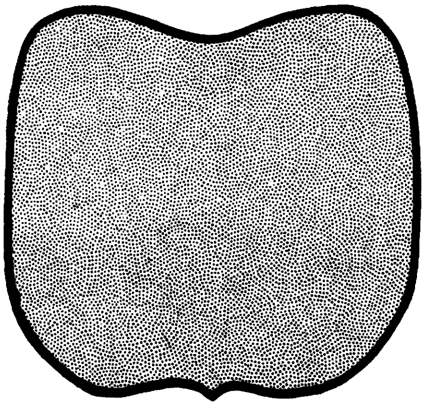

FIGURE 15.—Diagrammatic cross section of the holotype of *Thuringionautilus jugatonodosus* (Zimmermann) from the Keuper of Germany, × 1. After Zimmermann.

Genus PLEURONAUTILUS Mojsisovics, 1882

Genotype: *Pleuronautilus trinodosus* Mojsisovics

This genus, with its 5 subgenera and approximately 95 species, includes most of the highly ornamented Triassic nautiloids. The group includes Permian and Triassic nautiloids which have ribs with or without associated nodes. Mojsisovics' original description is given here (1882, p. 273):

> Der Externtheil der rechteckigen, einander nur sehr wenig umhüllenden, weitnabeligen Formen ist, wie bei *Temnocheilus*, glatt, sculpturfrei, die Seiten sind dagegen in der Regel mit kräftigen, geraden oder leicht geschwungenen Rippen bedeckt, welche bei den meisten Formen mit einer oder mehreren Knotenspiralen versehen sind. Die mit blos einer, marginal stehenden Knotenreihe ausgestatteten Formen erinnern an *Temnocheilus*, von welchem sie jedoch liecht durch die kräftigen Rippen unterscheiden werden können.
>
> Die erste Hälfte der ersten Windung ist bei einer Anzahl von Formen blos mit einfachen Querstreifen versehen, bei anderen (*Pleuronautilus marmolatae*, *Pleuronautilus subgemmatus*) kommen auf den Seitentheilen gekornte Längsrippen vor, wie bei *Trematodiscus*. Die Perforation des Nabels erreicht bei manchen Formen, wie bei *Pleuronautilus superbus*, einen sehr bedeutenden Umfang.
>
> Kammerwände bei einigen älteren Formen, wie *Pleuronautilus semicostatus* und *Pleuronautilus distinctus*, gerade über den Externtheil verlaufend und seitlich einen flachen, breiten Laterallobus bildend, oder aber, wie bei der Mehrzahl der triadischen Formen, auch auf dem Externtheil zu einem flachen Externlobus eigebogen. Bei allem, in dieser Beziehung näher untersuchten Formen konnte ein kleiner Internlobus constatirt werden. (Text fig. 16.)

Mojsisovics' description can be summarized as follows:

Conch evolute, widely umbilicate, venter smooth, whorl sides with strong, straight or slightly sinuous ribs which in most forms have one or more spiral row of nodes. The first half volution in many species has merely simple cross striae, but other species have nodose strigations as in *Trematodiscus*. The umbilical perforation in several species, such as *Pleuronautilus superbus*, is very large. The suture is straight over the venter or with a shallow ventral lobe; the lateral lobe is broad and shallow. A small annular lobe is present.

Mojsisovics continued his description of *Pleuronautilus*, explaining his reasons for establishing the genus, and its probable affinities. This part is pertinent to the following discussion and will be quoted here in full (translation from Foord p. 135–136, 1891).

> I was at first disposed to make *Pleuronautilus* a distinct division of *Temnocheilus;* but the near relationship between *Pleuronautilus* and *Trematodiscus* on the one hand, and the distinctness of these two genera from the coexisting *Temnocheilus*-stock on the other hand, determined me to introduce *Pleuronautilus* as a distinct genus.
>
> The near relationship between *Trematodiscus* and *Pleuronautilus* can easily be made out. First, the variation in certain species of Carboniferous *Trematodiscus* must be pointed out; this consists in the development in advanced age of a full, rounded shell, free from sculpture. The union of the typical *Trematodiscus* sculpture with the lateral ribs of *Pleuronautilus* is observable in *Gyroceras tessellatum*, de Koninck, *G. binodosum*, Sandberger, *G. costatum*, Goldfuss, *Cyrtoceras rugosum*, Fleming, as well as in *Nautilus nodoso-carinatus*, F. Roemer, of the Coal Measures. Secondly, the characters presented by *Pleuronautilus marmolatae* (in which the *Trematodiscus* sculpture passes directly into the *Pleuronautilus* sculpture), added to the appearance in other *Pleuronautili* of several nodose-ridged species (*Pleuronautilus trinodosus, P. Mosis, P. Cornaliae, P. Fischeri* etc.) which are apparently equivalent to the nodose-keeled species of *Treamtodiscus*, speak in such a convincing manner in favour of the genetic connection between the two genera that we do not hesitate to place forms with smooth surface and crenulated ridges, such as *P.* (*Phloioceras*) *gemmatus*, in the genus *Pleuronautilus*.
>
> As is indicated in *Gyroceras aigoceras*, de Koninck (which possesses the sculpture of *Pleuronautilus*), it seems quite possible that some *Pleuronautili* have been developed from forms with open whorls without passing through a *Trematodiscus* stage * * *
>
> The oldest *Pleuronautili* known to me are found in the Productus Limestone of the Salt Range, and in the Permian-Kalkstein of the Araxes Pass in Armenia.

Foord (1891, p. 134-138) emended this genus to include a variety of Late Paleozoic forms. However, species referred by Foord to *Pleuronautilus* have since been placed in at least six other genera. Foord's broad interpretation of the genus is untenable and cannot be followed.

Arthaber (1896) slightly emended the description of *Pleuronautilus* by Mojsisovics and established three form groups into which he placed all the species of *Pleuronautilus* known at that time. Arthaber's groups are those of *Pleuronautilus ampezzanus*, *Pleuronautilus mosis*, and *Pleuronautilus subgemmatus*.

Hyatt (1900, p. 525) proposed the family Pleuronautilidae, and included in it *Pselioceras* Hyatt, *Pleuronautilus* Mojsisovics, *Enoploceras* Hyatt, *Encoiloceras* Hyatt, and *Anoploceras* Hyatt. The last three genera were newly described by Hyatt in the 1900 edition of the Zittel-Eastman Textbook of Paleontology. The genotype of *Enoploceras* is *Nautilus wulfeni* Mojsisovics, that of *Encoiloceras* is *Pleuronautilus superbus* Mojsisovics, and that of *Anoploceras* is *Pleuronautilus ampezzanus* (Loretz). Since Hyatt's publication these three genera have generally been considered subgenera of *Pleuronautilus* by most authors and this procedure is followed here. Mojsisovics (1902, p. 237–239) established two more subgenera of *Pleuronautilus; P.* (*Holconautilus*) for the forms with ventral saddles and *P.* (*Trachynautilus*) for the group of *Pleuronautilus subgemmatus*.

Ribbing as a dominant ornamentational type is present in relatively few Paleozoic Tainoceratidae: *Foordiceras*, *Tainionautilus*, *Tirolonautilus* and *Pleuronautilus*. *Foordiceras*, which has a Temnocheilan outline, has lateral ribs that extend half way up the flank from the venter as seen in the genotype *Nautilus goliathus* Waagen.

Tainionautilus was established by Mojsisovic in 1902, type *Nautilus transitorius* Waagen 1879, to include nautiloids with quadratic whorl sections and sinuous lateral ribs that extend up the venter to a ventral furrow. Mojsisovics considered the genus an offshoot of the genus *Tainoceras*. The writer considers *Tainionautilus* a specialized offshoot of *Metacoceras* with a limited geologic and geographic range. This genus was suppressed by Miller and Youngquist (1949) as a synonym of *Foordiceras*, but this view cannot be held. The quadratic conch, the type of ornamentation, and the ventral furrow are quite distinct from the genotype of *Foordiceras*, so much so that direct comparison is difficult.

The genus *Huanghoceras* was established by Yin (1933, p. 19) for ribbed nautiloids with whorl section more trapezoidal than that of *Pleuronautilus*. Yin's descriptions and illustrations are inadequate, and it is difficult to evaluate the true character of his genus. The species he assigned to his new genus are so closely allied to *Pleuronautilus* that *Huanghoceras* is here placed in synonymy of *Pleuronautilus*. Possibly the species of *Huanghoceras* more properly belong in *Foordiceras*. The species assigned to *Huanghoceras* by Young (1942, p. 123) are so poorly preserved and his descriptions so brief that the correct affinities of these forms remain in doubt.

The other ribbed representatives of the Paleozoic Tainoceratidae have been shifted from one genus to another by nearly every paleontologist working with these forms. One can almost make the generalization that specialists on Paleozoic nautiloids have tended to put these forms in *Metacoceras* or *Foordiceras* and specialists on Triassic nautiloids have tended to place them in *Pleuronautilus*. Within the Tainoceratidae, the development and elaboration of ribbing as the basic ornamentational pattern is most fully attained in one generic group, that evolving around *Pleuronautilus*. There are about 24 Permian species and 34 Triassic species of *Pleuronautilus*, 4 in the Scythian, 20 in the Anisian, 6 in the Ladinian, and 4 in the Karnian. The widest range in form and in ornamentational variation is attained in the Anisian where the most species have so far been recognized. Many of the Triassic species have simple straight ribs. Similar forms with more or less quadratic whorl sections and straight ribs are recognized in Permian rocks throughout the world. Many of these species appear to be transitional between *Metacoceras* and the Triassic *Pleuronautilus* and should be placed in the latter genus. It is interesting to note how the generic assignments of many of these species by various authors vacillates between the above two genera. The phylogenetic study of the Tainoceratidae as an entity seems to support placing the ribbed Permian species in *Pleuronautilus* and deriving that genus directly out of *Metacoceras*. Schmidt (1929, p. 60) considered *Metacoceras* as a subgenus of *Pleuronautilus*.

The Permian species placed in *Pleuronautilus* have a world wide distribution. Only two Triassic species of *Pleuronautilus* from North America are known, these are *P. idahoensis* Kummel, n. sp. from Scythian rocks of southeast Idaho and *P. alaskensis* Kummel, n. sp. from Karnian beds in Alaska. Most of the other Triassic species of *Pleuronautilus* are found in the region of the Tethyian geosyncline.

Pleuronautilus (p.) alaskensis n. sp.

Plate 4, figures 5, 6

This species is based on a single well-preserved internal mold of an immature individual. The specimen, comprising one and one half whorls, is septate throughout and no portion of the living chamber is preserved. It measures 51 mm in diameter. The most adoral camera is subquadratic, and is 24 mm wide and 19 mm high. The umbilical and ventral shoulders are sharply rounded, the flanks flattened, and the nearly flat umbilical wall slopes at a high angle to the umbilical seam. The impressed zone is about 1 mm deep. At the end of the first one-half volution the conch height and width are about equal, with a distinctly arched venter. The umbilicus measures 20 mm across and is also perforate.

The lateral flanks are ornamented with two rows of nodes. On the ventral shoulders is a row of small rounded nodes spaced approximately 5 mm apart, measured from crest to crest. Adapically the nodes are closer together and appear to form a distinct continuous ridge. Along the midline of the flank is another set of nodes similar to those on the ventral shoulders. A low distinct ridge connects the two rows of nodes. On the first one-half volution these nodes coalesce and form a ridge following the midline of the flanks. There may have been a row of nodes along the umbilical shoulder, but this is difficult to determine from the internal mold. No part of the shell is preserved, but the appearance of the two sets of nodes suggests they probably were joined to form a nodose rib.

The suture forms a shallow ventral lobe and a broadly rounded lateral lobe. There is a rounded saddle on the ventral shoulder, with the apex ventral to the nodes on the ventral shoulders. Over the umbilical wall the suture slopes adorally in a straight line. There is a well-defined angular dorsal lobe with a small annular lobe.

The siphuncle is 3 mm in diameter in the most adoral

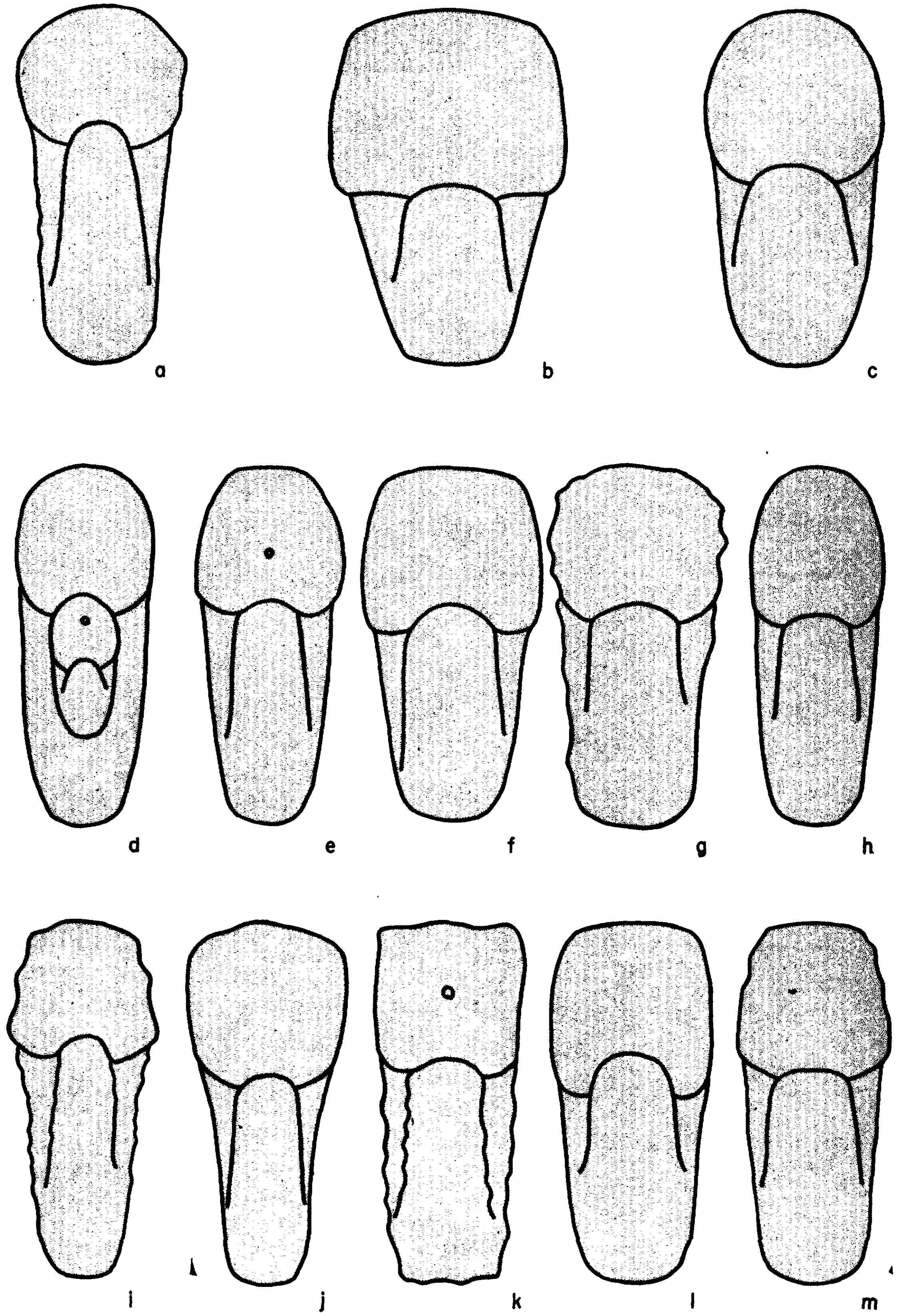

FIGURE 16.—Cross sections of the conch of *A*, *Pleuronautilus* (*Encoiloceras*) *superbus* Mojsisovics 1873, pl. 4, fig. 1b, diameter 98 mm, the subgenotype of *Encoiloceras; B*, *Phloioceras gemmatum*, Mojsisovics 1873, pl. 3, fig. 1b, diameter 140 mm, the genotype of *Phloioceras*, *C*, *Pleuronautiluis* (*Trachynautilus*) *subgemmatum* Mojsisovics 1882, pl. 85, fig. 22, diameter 24 mm, the subgenotype of *Trachynautilus; D*, *Pleuronautilus esinensis* Mojsisovics 1882, pl. 86, fig. 5b, diameter 60 mm; E, *P. mosis* Mojsisovics 1882, pl. 85, fig. 3b, diameter 95 mm; *F*, *P. crassescens* Arthaber 1896, pl. 3, fig. 1b, diameter 34 mm; *G*, *P. strangulatus* (Hauer) 1892, pl. 2, fig. 4b, diameter 45 mm; *H*. *P. cornaliae* (Stoppani), after Mojsisovics 1882, pl. 84, fig. 2b, diameter 68 mm; *I*, *P. triserialis* (Hauer) 1896, pl. 5, fig. 4, diameter 61 mm; *J*, *P. furcatus* Arthaber 1896, pl. 2, fig. 3b, diameter 75 mm; *K*, *P. verae* Arthaber 1898, pl. 13, fig. 4b, diameter 51 mm; *L*, *P. ambigus* Arthaber 1896, pl. 3, fig. 3b, diameter 39 mm; *M*, *P. trinodosus* Mojsisovics 1882, pl. 85, fig. 1b, diameter 90 mm, the genotype of *Pleuronautilus*.

Distribution of species of the subgenus Pleuronautilus (Pleuronautilus)

Species	Stratigraphic distribution	Geographic distribution
Pleuronautilus (*Pleuronautilus*) *ambiguus* Arthaber 1896.	Triassic (Anisian)	Alps.
P. (*P.*) *ambiquus* var. *spirata* Reis 1905	do	Do.
P. (*P.*) *alaskensis* Kummel n. sp	Triassic (Karnian)	Alaska.
P. (*P.*) *carbonarius* Kruglov 1928	Permian (Ashian and Krasnoufimskian)	Sterlitamak, Russia.
P. (*P.*) *cooperi* (Miller) 1945	Permian (Leonard series)	Texas.
P. (*P.*) *cornaliae* (Stoppani) 1859	Triassic (Ladinian)	Alps.
P. (*P.*) *crassescens* Arthaber 1896	Triassic (Anisian)	Do.
P. (*P.*) *crassescens* var. *jugulata* Arthaber 1896	do	Do.
P. (*P.*) *crassescens* var. *semijugulata* Alma 1926	do	Do.
P. (*P.*) *dieneri* Krafft and Diener 1909	Triassic (Scythian)	Himalayas, India.
P. (*P.*) *dolomiticus* Koken 1913	Triassic (Karnian)	Alps.
P. (*P.*) *dorini* Caneva 1906	Permian (Bellerophon limestone)	Italy.
P. (*P.*) *dorso-armatus* (Abich) 1878	Permian (Djulfa beds)	Armenia.
P. (*P.*) *esinensis* Mojsisovics 1882	Triassic (Ladinian)	Alps.
P. (*P.*) *externelobatus* Gemmellaro 1904	Triassic (upper)	Sicily.
P. (*P.*) *furcatus* Arthaber 1896	Triassic (Anisian)	Alps.
P. (*P.*) *gregarium* (Miller) 1945	Permian (Leonard series)	Texas.
P. (*P.*) *idahoensis* Kummel n. sp	Triassic (Scythian)	Idaho.
P. (*P.*) *incertus* (Abich) 1878	Permian (Djulfa beds)	Armenia.
P. ? (*P.*) *kasarmenskensis* Kruglov 1928	Permian (Ashian)	Sims River, Russia.
P. (*P.*) *kokeni* Frech 1905	Triassic (Scythian)	Salt Range, Pakistan.
P. ? (*P.*) *latissimus* (Waagen) 1879	Permian (Upper Productus limestone)	Do.
P. (*P.*) *linchengense* (Yin) 1933	Permian (Taiyuan series)	China.
P. (*P.*) *longinodosus* Turina 1912	Triassic (Anisian)	Yugoslavia.
P. (*P.*) *magnicostatum* (Miller) 1945	Permian (Leonard series)	Texas.
P. (*P.*) *mariani* Airaghi 1902	Triassic (Ladinian)	Alps.
P. (*P.*) *marmolatae* Mojsisovics 1882	do	Do.
P. (*P.*) *megaporum* (Miller) 1945	Permian (Leonard series)	Texas.
P. (*P.*) *mosis* Mojsisovics 1882	Triassic (Anisian, Ladinian)	Alps, Yugoslavia.
P. (*P.*) *mutatum* (Miller) 1945	Permian (Leonard series)	Texas.
P. (*P.*) *narcissae* Toula 1896	Triassic (Anisian)	Turkey.
P. (*P.*) *nodosostriatus* Yin 1933	Triassic (Taiyuan series)	China.
P. (*P.*) *oenanus* Mojsisovics 1882	Triassic (Karnian)	Alps.
P. (*P.*) *ornatissimus* Yin 1933	Permian (Taiyuan series)	China.
P. (*P.*) *ornatus* (Hauer) 1887	Triassic (Anisian)	Yugoslavia.
P. (*P.*) *paronai* Airaghi 1902	Triassic (Ladinian)	Alps.
P. (*P.*) *pernodosus* Yin 1933	Permian (Taiyuan series)	China.
P. (*P.*) *praecursor* (Girty) 1908	Permian (Leonard series)	Texas.
P. (*P.*) *ptychoides* Arthaber 1896	Triassic (Anisian)	Alps.
P. (*P.*) *quadrangulus* (Hauer) 1892	do	Yugoslavia.
P. (*P.*) *schafhäutli* Reis 1900	do	Alps.
P. (*P.*) *seminodosus* Arthaber 1896	do	Do.
P. (*P.*) *shumardianum* (Girty) 1908	Permian (Capitan limestone)	Texas.
P. (*P.*) *simplicostatum* (Yin) 1933	Permian (Taiyuan series)	China.
P. (*P.*) *strangulatus* (Hauer) 1892	Triassic (Anisian)	Yugoslavia.
P. (*P.*) *subquadrangulus* Tien 1933	Triassic (Scythian)	China.
P. (*P.*) *taramelli* Tommasi 1894	Triassic (Anisian)	Alps.
P. (*P.*) *tommasi* (Parona) 1889	Triassic (Karnian)	Do.
P. (*P.*) *trinodosus* Mojsisovics 1882	Triassic (Anisian)	Do.
P. (*P.*) *iriserialis* (Hauer) 1896	do	Yugoslavia.
P. (*P.*) *tschihatscheffi* Toula 1896	do	Turkey.
P. (*P.*) *tubercularis* (Abich) 1878	Permian (Djulfa beds)	Armenia.
P. (*P.*) *venustum* (Reed) 1944	Permian (Upper Productus limestone)	Salt Range, Pakistan.
P. (*P.*) *verae* (Abich) 1878	Permian (Djulfa beds)	Armenia.
P. (*P.*) *wangi* (Yin) 1933	Permian (Taiyuan series)	China.

part of the phragmocone and is dorsal of the center of the whorl.

Remarks.—There is no previous record of *Pleuronautilus* from the Upper Triassic of North America. This present species is from the Chitistone limestone of Alaska. From the whole Karnian there are only four species of nautiloids previously assigned to *Pleuronautilus.*

Pleuronautilus alaskensis is similar in ornamentation to the genotype species, *P. trinodosus* Mojsisovics. In the latter species three rows of nodes are on the flanks, and the whorl section of the conch is higher than wide. Comparisons with any other species of *Pleuronautilus* are futile because our specimen lacks the shell material, which would show the ornamentation more clearly. Nevertheless, it appears that our species is a valid member of the genus, and it is important because it represents the first representative of the genus recorded from the Upper Triassic of North America.

Occurrence.—U.S.G.S. loc. 13749, Chitistone limestone (Upper Triassic, Karnian) from the flats at the base of cliff along edge of Kennicott glacier, 5 miles north of Kennicott, Chitna Valley, Copper River Region, Alaska.

Holotype.—U.S.N.M. 107082.

Pleuronautilus idahoensis n. sp.

Plate 4, figures 2, 3, 4; text figure 17

The holotype of this species is a well-preserved internal mold 105 mm in diameter. The first 1½ volutions have the shell preserved. The conch is involute, consists of 2½ whorls, and is a mature specimen. The living chamber is 105 mm in length measured on the venter, and expands rapidly orad. The living chamber is apparently incomplete, as there are no indications of an apertural margin. The cross-section of the living chamber (text figure 17) is subquadrate with a flattened venter, a well-rounded ventral shoulder, weakly concave flanks, and steeply rounded umbilical shoulders. The living chamber is 10.6 percent wider than high, measuring 57 mm in width and 51 mm in height. The impressed zone is 5 mm deep, being 9.83 percent of the height of the living chamber. The phragmocone is 79 mm in diameter and has 15 camerae in the last one-half volution. The last camera of the phragmocone (the adoral one) is 37 mm high and 39 mm wide. At an estimated diameter of 58 mm the height is 26 mm and the width 31 mm. At an estimated diameter of 44 mm the height is 21 mm and the width 25 mm.

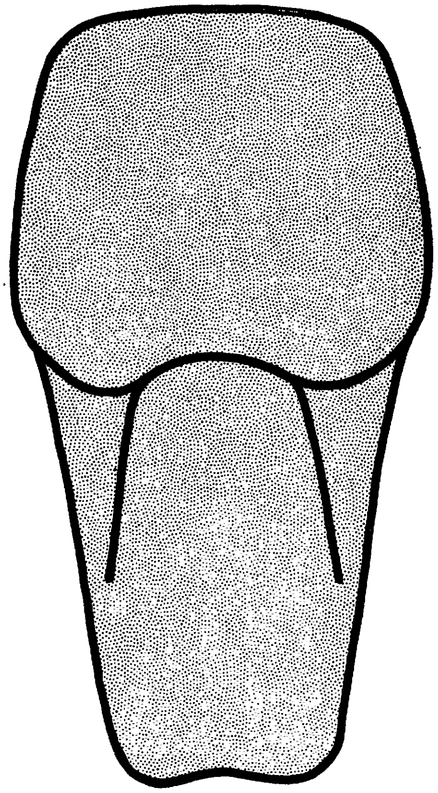

FIGURE 17.—Diagrammatic cross section of the holotype of *Pleuronautilus idahoensis*, n. sp. (U. S. N. M. 107079) from the Columbites beds, Thaynes formation, Hot Springs, Idaho, × 1.

The adapertural three-quarters volution of the phragmocone is smooth and consists of numerous relatively thin subquadrate camerae. The venter of the phragmocone at its most adoral portion is broadly rounded, almost flattened, and the flanks are smooth and nearly flat. The ventral shoulder and the umbilical shoulder are will rounded and the umbilical wall is broadly rounded and vertical. Adapically the whorl section of the phragmocone becomes more rounded. The venter becomes broadly curved, the flanks are only slightly curved and the ventral shoulder is obtusely rounded, the umbilical shoulder being more broadly rounded. The second volution has a broadly curved flank with a well-rounded and deep umbilical shoulder. The first one-half volution is apparently ovoid in shape; the flanks of this portion of the conch are broadly curved, and no distinct umbilical shoulder is present.

The umbilicus is fairly narrow and deep, measuring 30 mm in width, which is 28.5 percent of the height of the conch; the depth of the umbilicus measures 20 mm. The height of the umbilical shoulder is 14 mm at the adoral portion of the living chamber, 11 mm at the most adapertural portion of the phragmocone, 7 mm at the end of the second volution and 4 mm at the end of the first volution. A small umbilical perforation is present and measures 4 mm in diameter (estimated). The perforation could not be completely excavated and the extreme adapical end of the conch is not present, but the above measurement is undoubtedly fairly accurate.

The surface of the test is for the most part smooth. The second volution, which has the shell preserved, has narrow well-defined ribs that extend from the umbilical shoulder to the ventral shoulder. The ribs are radial and straight and about 4 mm apart, measured from crest to crest. Adaperturally the phragmocone is smooth, with no indications of ribs or nodes. The adapical part of the living chamber has four slight nodes on the ventral shoulder. These nodes, though not conspicuous on an internal mold, must have been rather high on the shell. A small area of the shell is preserved on the living chamber. It is 1.75 mm thick and has distinct growth lines. The extreme adapical part of the phragmocone, consisting of the first ½ volution, has conspicuous transverse lirae. The lirae can be studied only on the flanks of the whorls. This feature is similar to that described by Miller (1936, p. 96, fig. 10) for an immature specimen of *Metacoceras* sp.

The sutural elements are relatively simple. The suture at 75 mm consists of a broad shallow ventral lobe, an acutely rounded saddle whose apex is on the ventral shoulder, and a broad concave lateral lobe occuping the entire flank. It passes over the umbilical shoulder to the umbilical seam forming a short simple lateral saddle. At 59 mm the suture has a more primitive aspect. The ventral lobe is smaller and is flanked by two broadly rounded ventral saddles whose apices are on the venter and not on the ventral shoulder as they are adaperturally. The lateral lobe is distinctly concave and the deepest part of the lobe is in the dorsal half of the flank. The lateral saddle curves up over the umbilical shoulder.

The siphuncle is subcentral in position, being 20 mm from the venter and 12 mm up from the dorsum, and it is 3 mm in diameter.

Remarks.—The rapidly expanding conch, shape of the whorl section, and the ornamentation distinguish this unique form. It superficially resembles several Hallstatt forms described by Mojsisovics but since the test for the most part is lacking and only one mature specimen is available, relationships are difficult to point out and are inadvisable. Smith (1932) referred a specimen to *Nautilus* (*Pleuronautilus*) sp. from the *Columbites* zone of the Thaynes formation, Idaho. He did not describe or illustrate the specimen, however.

Only one mature specimen of this species is available for study; however, two smaller immature specimens in the collection are assigned to this species. The first (U.S.G.S. loc. 7588) is from the same locality and probably the same horizon as the holotype. The specimen was collected by T. W. Stanton in 1910 from a "dark shaly limestone 300 or 400 ft. above the basal limestone of the Thaynes formation on the west slope of the second ridge east of Hot Springs, Idaho." The adoral part of the specimen is broken however, enough of the features are preserved to indicate clearly its affinities with the holotype.

The second immature specimen (pl. 4, figs. 3, 4) from the *Columbites* zone, Montpelier Canyon, is 33 mm in diameter and also doubtfully referred to this species. The specimen has straight lateral ribs and the outline of the adoral camera is subquadratic, measuring 24.5 mm wide and 15 mm high; the venter is slightly arched. It has a well-defined ventral lobe that passes over the umbilical wall in a straight line.

Diener recorded *Pleuronautilus dieneri* from the *Hedenstroemia* beds, southeast of Muth, Spiti in the Himalayas, and Frech referred a doubtful specimen to this genus, *Pleuronautilus*? *kokeni*, from the Scythian of the Salt Range. During the Triassic period *Pleuronautilus* was present in the Germanic, Alpine Mediterranean, the Himalayan regions, Timor, Alaska, and Idaho. In the Anisian, *Pleuronautilus* became very abundant and diversified and developed highly ornate conchs. The largest number of species and of specimens known was in the Alpine Triassic. The Germanic province has yielded only one species. The eastern regions of the Tetheys have yielded a few species in the Himalayas and in Timor. *Pleuronautilus* has not been recorded from the Middle Triassic of North America. In the Ladinian and Karnian stages *Pleuronautilus* declined in number of species considerably, foreshadowing the great decline of the nautiloids which took place at the end of the Triassic period.

Occurrence—Upper shale member, (*Columbites* zone) Thaynes formation, Hot Springs, Idaho, sec. 18, T. 15 S., R. 45 E.

Types.—Holotype, U.S.N.M. 107079; paratype, 107080, unfigured plesiotype, U.S.N.M. 107081.

Pleuronautilus sp. (of Idaho)

The only representative of this species is a poorly preserved internal mold from the *Tirolites* limestone Thaynes formation, Paris Canyon, Idaho. The conch is 101 mm in diameter and consists of about 2 volutions, 1½ volution being phragmocone and ½ volution living chamber. The incomplete living chamber is 120 mm long, as measured on the venter, expands rapidly orad, and shows no indications of an apertural margin. The outline of the living chamber is subquadratic, having a flattened venter with a median furrow, rounded ventral shoulders, broadly convex flanks and a steep well-rounded umbilical shoulder. The cross section of the living chamber measures 46.5 mm high and 54 mm wide, the ratio of height to width is 14.8 percent. The impressed zone is 5 mm deep.

The phragmocone is 77 mm in diameter and consists of numerous thin subspherical to subquadrate camerae. The most adapertural camera is 33 mm high and 40 mm wide, height-width ratio is 17.5 percent. At a diameter of 40 mm (estimated) the height and width are 21 mm and 28 mm respectively, the ratio is 25 percent. The cross section of the phragmocone at a diameter of 40 mm is subspherical, the venter is broadly arched, the flanks weakly convex and the umbilical shoulder is well rounded and steep. Adorally the venter of the phragmocone is badly weathered and the true shape of the venter is not preserved.

The umbilicus is narrow and deep, measuring 30 mm in width and 23 mm in depth. The width of the umbilicus is 29.7 percent the diameter of the conch. The umbilical shoulder measures 16 mm at the adoral end of the living chamber and 14 mm at the adoral end of the phragmocone. Presumably, an umbilical perforation is present. It could not be completely excavated, however, but from the nature of the inner volutions a measurement of 9.5 mm for the width of the umbilical perforation is thought to be fairly accurate.

The surface of the test is, for the most part, weathered and not much detail is present. There are, however, strong radial ribs on the first one and ¼ volutions which are confined to the flanks of the conch. These ribs are broad and high, and are about 12 mm apart, measured from crest to crest.

The suture is not preserved on the venter but forms a broad shallow lobe on the flanks and a straight course on the umbilical wall.

The siphuncle is not preserved.

Remarks.—This specimen may be conspecific with *Pleuronautilus idahoensis;* although there are significant differences. *Pleuronautilus* sp. has fewer whorls, a more rapidly expanding conch, and the ribs are of a very different nature.

Occurrence.—Middle limestone member of Thaynes formation, Paris Canyon, Idaho. (Kummel, 1950). Collected by the author.

Specimen.—U.S.N.M. 107083.

Pleuronautilus sp. (of Montana)

One complete but weathered specimen from the Thaynes formation in Little Water Canyon, southwestern Montana is available for study. The specimen measures 127 mm in diameter. The most adoral part of the living chamber is 45 mm high and 40 mm wide. The cross section of the whorl is subquadratic with well defined ventrolateral and umbilical shoulders. The venter has a median furrow. The umbilicus measures 40 mm in diameter.

The most adoral part of the living chamber appears to flare outward and is not in contact with the preceding whorl dorsally. The specimen cannot be identified specifically but can definitely be assigned to the genus *Pleuronautilus*. The specimen is of special interest as the first Triassic nautiloid reported from Montana. It is not unlike the few other pleuronautilids from southeastern Idaho.

Occurrence.—From beds above the *Meekoceras* zone, Thaynes formation, Little Water Canyon, 6 miles west of Dell, southwestern Montana. Collected by the the author.

Specimen.—U.S.N.M. 107084

Subgenus ENOPLOCERAS Hyatt, 1900

Subgenotype: *Nautilus wulfeni* Mojsisovics

Of the five subgenera of *Pleuronautilus*, the subgenus *Enoploceras* is the most adundant and widespread form. It is characterized by a whorl section that at maturity is subquadratic with flattened venter, flanks, and umbilical walls (text fig. 18). The ventral and umbilical shoulders are generally sharply rounded. No other group of pleuronautilids is so striking in form of conch. Hyatt did not describe the genus, but the description of the subgenotype by Mojsisovics (1873, p. 10) is given here in part:

> Die ziemlich rasch anwachsenden Windungen dieser mit *Nautilus perarmatus, Nautilus planilateratus* und *Nautilus Fischeri* eine Formenreihe bildenden Art sind viel breiter als hoch und während des ersten halben Umganges gerundet, späterhin aber platten sich die Seiten stark ab, der Convextheil erscheint mässig gewölbt und zur Naht senkt sich eine hohe Nabelwand von einer scharfen Nabelkante schräge herab. Zwischen Seiten und Convextheil befindet sich eine stumpfe Seitenkante. Die Involution erstreckt sich nur auf den Convextheil des vorhergehenden Umganges. Der tiefe Nabel ist in der Mitte von einem kleinen Loche durchbrochen. Mit Beginn der zweiten Hälfte, des ersten Umganges stellen sich auf den Seiten Radialfalten ein, welche an der Nabelkante mit einem Knoten ansetzen und an der Seitenkante mit einem solchem abschliessen. An einem Exemplare bemerkt man ausserdem, aber nur vom Beginn der zweiten Hälfte des ersten Umganges bis zum Beginn des zweiten Viertels des zweiten Umganges ganz feine, auf der Mitte der Radialfalten stehende Knötchen; die andern Exemplare zeigen sie nicht. Die Radialfalten, welche bei manchen Stücken schon auf den inneren Umgängen sehr schwach sind und deren man auf eimen ganzen Umgange nicht mehr als 14–15 zählt, verflachen sich auf den aüsseren Windungen, insbesondere auf der Wohnkammer fast bis zur Unkenntlichkeit; dagegen bleiben die Knoten auf dem Nabel- und Seitenrand constant und nehmen immerfort an Stärke zu.
>
> Die schalenoberfläche überziehen zahlreiche gedrängte, feine Querstreifen, über welche sehr schöne undulirte Längsstreifen hinwegziehen. Auf der Mitte des Convextheiles bleibt ein ziemlich breiter Streifen frei von den Langsstreifen.—Sobald die Schalenoberfläche durch Verwitterung etwas gelitten hat, treten nur mehr die Querstreifen scharf hervor.
>
> Auf der Wohnkammer plattet sich der Convextheil stärker ab und es bildet sich in der Mitte desselben eine flache Rinne.
>
> Die Kammerscheidewände zeichnen sich durch besondere Stärke der in mehrfachen Lagen sich abblätternden Perlmuttersubstanz aus. Auf dem Convextheile befindet sich ein flacher Lobus, dem ein tieferer Laterallobus folgt. Auf dem Concavetheile steht ein kleiner Spindellobus.
>
> Der grosse Sipho steht im ersten Drittel der Kammerwandhöhe, nahe über dem Spindellobus. Normallinie auf der Perlmutterschicht deutlich, auf dem Steinkern nur schwach sichbar.

Mojsisovics' description of *Nautilus wulfeni* can be summarized as follows:

> The whorls are wider than high and in the first half volution are rounded. The whorls then become flattened on the sides and the venter moderately arched. The ventral shoulders are blunt. The involution is such that only the venter of the preceding whorls are covered. The umbilicus is deep and with a small perforation. Radial ribs with nodes on the umbilical shoulder commence at the end of the first half volution. There are 14 to 15 radial ribs per volution and they diminish in prominence adorally. On the living chamber they are almost unrecognizable; the nodes, however, remain. The shell has delicate, crowded cross striae with undulating longitudinal lines. The longitudinal lines are not present on the central part of the venter. On the living chamber the venter is flattened and slightly concave. The suture has a shallow ventral and lateral lobe. An annular lobe is present. The siphuncle is subcentral in position.

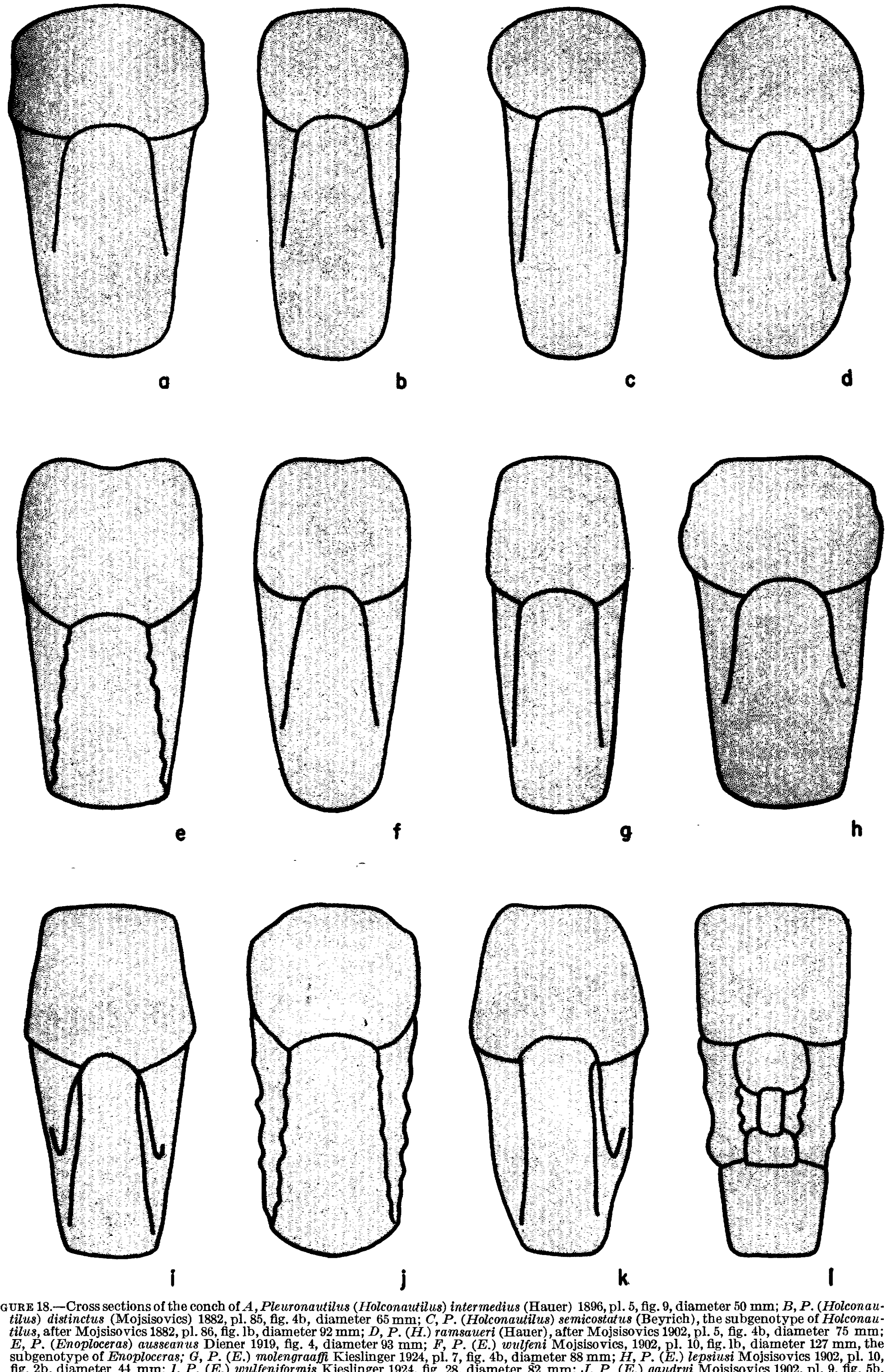

FIGURE 18.—Cross sections of the conch of *A*, *Pleuronautilus* (*Holconautilus*) *intermedius* (Hauer) 1896, pl. 5, fig. 9, diameter 50 mm; *B*, *P.* (*Holconautilus*) *distinctus* (Mojsisovics) 1882, pl. 85, fig. 4b, diameter 65 mm; *C*, *P.* (*Holconautilus*) *semicostatus* (Beyrich), the subgenotype of *Holconautilus*, after Mojsisovics 1882, pl. 86, fig. 1b, diameter 92 mm; *D*, *P.* (*H.*) *ramsaueri* (Hauer), after Mojsisovics 1902, pl. 5, fig. 4b, diameter 75 mm; *E*, *P.* (*Enoploceras*) *ausseanus* Diener 1919, fig. 4, diameter 93 mm; *F*, *P.* (*E.*) *wulfeni* Mojsisovics, 1902, pl. 10, fig. 1b, diameter 127 mm, the subgenotype of *Enoploceras*; *G*, *P.* (*E.*) *molengraaffi* Kieslinger 1924, pl. 7, fig. 4b, diameter 88 mm; *H*, *P.* (*E.*) *lepsiusi* Mojsisovics 1902, pl. 10, fig. 2b, diameter 44 mm; *I*, *P.* (*E.*) *wulfeniformis* Kieslinger 1924, fig. 28, diameter 82 mm; *J*, *P.* (*E.*) *gaudryi* Mojsisovics 1902, pl. 9, fig. 5b, diameter 109 mm; *K*, *P.* (*E.*) *pseudowulfeni* Kieslinger 1924, fig. 29c, diameter 122 mm; *L*, *P.* (*E.*) n. sp. ex. aff. *wulfeni* Kieslinger 1924, fig. 30, diameter 112 mm.

Sixteen species of *Enoploceras* have been described to date. There are also numerous specimens that have been described as being related to or similar to previously designated species. Most of the species of *Enoploceras* occur in rocks of Karnian age, only three are known from the Norian. The only North American species is *Pleuronautilus* (*Enoploceras*) *newelli* n. sp., from the Thaynes formation (Scythian) of southeastern Idaho. With the exception of the single North American species all the species of *Enoploceras* occur in localities within the Tethyian geosyncline, namely the Alpine region, the Himalayas, and the Island of Timor.

Distribution of species of the subgenus Pleuronautilus (Enoploceras)

Species	Stratigraphic distribution	Geographic distribution
Pleuronautilus (*Enoploceras*) *ausseeanus* Diener 1919	Triassic (Karnian, Norian)	Alps.
P. (*E.*) *fischeri* (Mojsisovics) 1873	Triassic (Karnian)	Do.
P. (*E.*) *gaudryi* Mojsisovics 1902	do	Do.
P. (*E.*) *kossmati* Diener 1901	do	Do.
P. (*E.*) *lepsiusi* Mojsisovics 1902	Triassic (Norian)	Alps, Timor.
P. (*E.*) *lepsiusiformis* Diener 1919	Triassic (Karnian, Norian)	Alps.
P. (*E.*) *malayicus* Welter 1914	Triassic (upper)	Timor.
P. (*E.*) *molengraaffi* Kieslinger 1924	do	Do.
P. (*E.*) *newelli* Kummel n. sp	Triassic (Scythian)	Idaho.
P. (*E.*) *planilateratus* (Hauer) 1860	Triassic (Karnian)	Alps.
P. (*E.*) *pseudoplanilateratus* Kieslinger 1924	do	Timor.
P. (*E.*) *pseudowulfeni* Kieslinger 1924	Triassic (upper)	Do.
P. (*E.*) *semseyi* Frech 1903	Triassic (Karnian)	Alps.
P. (*E.*) *tibeticus* Mojsisovics 1896	do	India, Timor.
P. (*E.*) *wulfeni* (Mojsisovics) 1873	do	Alps.
P. (*E.*) *wulfeniformis* Kieslinger 1924	do	Timor.

Pleuronautilus (Enoploceras) newelli n. sp.

Plate 4, figure 1; text figure 19

Only one specimen, well-preserved and fairly complete, is available for study. About a third of the conch is missing and the test is not present over the venter. The conch is evolute, robust, has a deep perforate umbilicus, and is rapidly expanded orad; it measures 84 mm in diameter. The cross section of the living chamber is quadratic, is much broader than high, and measures 61 mm wide and 40 mm high (text fig. 19). The venter is flattened and contains a shallow central furrow. The ventral shoulder is abruptly rounded and has large prominent nodes. The flanks are very gently arched, converge slightly ventrally, and have an acutely rounded umbilical shoulder. The umbilical wall is vertical and sinuous. The umbilicus is very deep and the umbilical perforation is about 8 mm in diameter. The incomplete living chamber measures 55 mm along the venter. The phragmocone is much more rounded in cross section and is also much broader than high. The cross section of the phragmocone at a diameter of about 55 mm measures 46 mm wide and 27 mm high. The venter is distinctly arched passing on to the flattened flanks at a definite line of contact. The umbilical shoulder is sharply rounded and the umbilical wall is steep but slightly oblique. The extreme lower portion of the umbilical shoulder curves inward toward the seam. The depth of the impressed zone at this diameter of the conch is about 10 mm.

The surface of the test is well preserved and ornate. There are two sets of nodes present, one on the umbilical shoulder and one on the ventral shoulder. Insofar as can be determined from the specimen the nodes begin near the adoral end of the first volution. The nodes here are rather slender, high, and very distinct. The umbilical wall of the next whorl extends down to the ventrolateral set of nodes. There are no ridges or ribs connecting the nodes. On the ventral shoulder of the living chamber the nodes are much larger, blunter, and

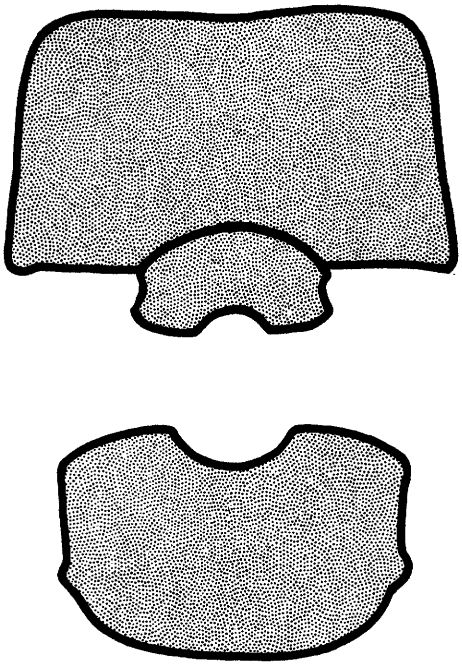

FIGURE 19.—Diagrammatic cross section of the holotype of *P.* (*Enoploceras*) *newell* n. sp. (U. S. N. M. 107085), from the *Columbites* beds, Thaynes formation, Montpelier Canyon, Idaho × 1.

essentially more subdued than they are on the phragmocone. On the umbilical shoulder of the living chamber the nodes are large, narrow, and very much subdued. The nodes are also very conspicuous on the internal mold. The test on the adapetural first two-thirds volution consists of delicate transverse and longitudinal striae, or ridges, which give the conch at this place a granular appearance.

The growth lines on the phragmocone are moderately distinct. They curve adapically over the umbilical wall, straighten out over the flanks and form a deep broad sinus on the venter. On the living chamber the growth lines are much more distinct. Over the umbilical wall they are arcuate in shape, being concave orally. On the flanks the growth lines form a broad orally concave arc, the curvature of the arc decreasing towards the venter; at a distance of 30 to 40 mm from the aperture this arc, formed by the growth lines, is about 8 mm deep, adjacent to the aperture the arc is very shallow. As the test is not preserved on the venter, the shape of the growth lines there is unknown. The test has numerous delicate undulating longitudinal ridges or striations. This type of shell ornamentation gives the test a more or less corrugated appearance and is characteristic of many representatives of this group of nautiloids. The aperture is preserved in only a small area around the umbilical shoulder. The apertural margins are short and abruptly curved, folding slightly under the margins of the conch. The thickness of the test varies considerably at different portions of the conch. Adjacent to the umbilical shoulder on the living chamber the test is 0.8 mm thick, adjacent to the ventral shoulder 2 mm thick, and on the venter of the phragmocone less than 1 mm thick.

The septa and the siphuncle are not preserved.

Remarks.—*Pleuronautilus* (*Enoploceras*) *wulfeni* is the only Scythian representative of this subgenus; all other species of *P.* (*Enoploceras*) are confined to the Karnian and the Norian. The Idaho species is much more depressed than *P.* (*E.*) *wulfeni* and has no radial folds that connect the nodes.

Occurence.—The only known representative of this species came from the upper shale member, *Columbites* zone, Thaynes formation, Montpelier Canyon, Idaho, sec. 31, T. 12 S., R. 45 E. Collected by the author.

Holotype.—U.S.N.M. 107085

Subgenus HOLCONAUTILUS Mojsisovics, 1902

Subgenotype: *Nautilus semicostatus* Beyrich

This subgenus was proposed by Mojsisovics (1902, p. 238) to include those pleuronautilids which have a ventral saddle instead of the more typical ventral lobe. In practically every other respect the forms included in *Holconautilus* are similar to *Pleuronautilus* (see text figs. 16, 18, pl. 17, figs. 3, 4).

Only nine species of this subgenus have been described, six are from the Anisian, one from the Ladinian, and two from the Karnian. Many described specimens have been placed in this subgenus with *cf.* or *aff.* to one of described species. All of the species of *Holconautilus* come from the Germanic region, the Mediterranean region, or from the Island of Timor.

Distribution of species of the subgenus Pleuronautilus (Holconautilus)

Species	Stratigraphic distribution	Geographic distribution
Pleuronautilus (*Holconautilus*) *distinctus* (Mojsisovics) 1882.	Triassic (Anisian)	Alps.
P. (*H.*) *intermedius* (Hauer) 1896	do	Alps, Yugoslvaia.
P. (*H.*) *pichleri* (Hauer) 1865	do	Alps.
P. (*H.*) *ramsaueri* (Hauer) 1855	Triassic (Karnian)	Do.
P. (*H.*) *scabiosus* (Arthaber) 1896	Triassic (Anisian)	Do.
P. (*H.*) *semicostatus* (Beyrich) 1865	do	Do.
P. (*H.*) *singularis* (Welter) 1914	Triassic (upper)	Timor.
P. (*H.*) *stautei* (Fritsch) 1902	Triassic (Muschelkalk)	Germany.
P. (*H.*) *striatus* (Hauer) 1892	Triassic (Anisian)	Alps.

Subgenus ENCOILOCERAS Hyatt, 1900

Subgenotype: *Encoiloceras superbus* Mojsisovics

Hyatt (1900, p. 525) originally proposed *Encoiloceras* as a distinct genus in his family Pleuronautilidae. However, most subsequent authors have treated *Encoiloceras* as a subgenus of *Pleuronautilus*. It is a monotypic genus and since Hyatt did not give any diagnosis of his new genus the description of the holotype by Mojsisovics (1873, p. 18) is quoted here in part (see pl. 17, figs. 9, 10):

> Diese schöne Art aus der Verwandtschaft des *Nautilus Ramsaueri* Hauer zeichnet sich vor allen mir bekannten Nautilen durch die Grösse des von der inneren Windung offen Gelassenen Raumes aus, welche nicht weniger als 25–26 mm in Durchmesser misst.
>
> Der Anfang der ersten Windung ist völlig frei, bald aber wird dieselbe vom nächstfolgenden. Umgange berührt und kurz darauf stellt sich das normale Involutionsverhältniss her, indem

⅓ der vorhergehenden Windung vom folgenden Umgange bedeckt wird.

Während des ersten Umganges wachsen die Windungen langsam an und sind breiter als hoch. Der Uebergang der Seiten zur Nabelwand und zum Convextheil ist gerundet, ohne irgend welche Andeutung einer Kantenbildung. Auf der Mitte des Concavtheiles ist die Schale seicht rinnenförming vertieft. Die Schalenoberfläche ist mit feinen Querstreifen bedeckt, ähnlich wie bie *Nautilus brevis* und *Nautilus evolutus*. Kreuzende Längsstreifen wurden nur auf dem Concavtheil, hier aber in ausgezeichneter Schärfe bemerkt.

Auch auf dem zweiten Umgange sind die Windungen breiter als hoch; die Form des Querschnittes und die Sculptur ändern sich aber ausserordentlich. Es bildet sich am Anfange des zweiten Umganges, zugleich mit dem Erscheinen radialer Falten auf den Seiten, eine stumpfe Nabelkante, welche späterhin, wo aus den Falten förmliche Rippen werden, weniger markirt hervortritt. Der Convextheil bleibt noch geraume Zeit schön gewölbt; auf der Wohnkammer jedoch plattet er sich bedeutend ab und der Querschnitt erscheint in Folge dessen eher viereckig als gerundet.

Die Zahl der Falten betragt 27. Dieselben sind leicht geschwungen mit nach aussen gekehrter Concavität. Gegen den Rand zum Convextheil verdicken sie sich allmälig und enden mit undeutlichen Knoten.

Gegen die Mundung der beiläufig ⅓ Umgang einnehmenden Wohnkammer zu stellt sich auf der Mitte des Convextheiles eine leichte, ziemlich breite rinnenartige Vertiefung ein und am Rande des Convextheiles gegen die Seiten erfolgt eine Contraction der Windung, gegen die Naht zu hingegen eine Erweiterung derselben, indem die letzten Rippen geradezu das verkehrte Verhältniss gegen alle vorhergehenden zeigen, nämlich innerhalb des Seitenrandes erst ansetzen, gegen den Nabel zu sich allmälig verbreitern und auf der Nabelwand mit einer knotenförmigen Verdickung endigen.

Die dicht auf einander folgenden Kammerwände beschreiben auf dem ersten Umgang auf dem Convextheil einen flach gewölbten Sattel, auf dem zweiten Umgang dagegen einen flachgewölbten Lobus; auf den Seiten folgt ein weiterer Laterallobus; auf dem Concavtheile schliessen zwei flache Sättel einen namentlich auf der ersten Windung verhältnissmässig grossen Spindellobus ein.

Der Sipho steht tief, ganz nahe über dem Spindellobus.

Ueber die Mitte des Convextheiles verläuft eine auf über die ganze Wohnkammer sich erstreckende Normallinie.

Mojsisovics' description can be summarized as follows:

This beautiful species, related to *Nautilus ramsaueri* has the largest umbilical performation of any Triassic nautiloid known to me. The initial part of the first volution is completely free but soon becomes partially inclosed by the succeeding whorls. The normal involution is about one-third the whorl height. In the first volution the whorls are wider than high and the whorl sides rounded. The dorsal area has longitudinal striae. The shell surface bears fine cross striae. The whorls on the second volution are also wider than high and radial folds begin to develop. The whorl shape on the living chamber is subquadratic. There are about 27 slightly sinuous ribs per volution that thicken towards the ventral shoulder where they form a slight node. On the last third volution prior to the aperture the venter has a median furrow. The whorl sides are more convergent and the ribs thicken towards the umbilical shoulder. The suture has a shallow ventral, lateral, and dorsal lobe with an annuler lobe. On the first volution there is a ventral saddle instead of a ventral lobe. The siphuncle is close to the dorsum.

The holotype is from the Karnian of the Alps (pl. 17, figs. 9, 10). Kutassy (1928) records *P.* (*Encoiloceras*) sp. ex. aff. *superbus* from Karnian rocks of Hungary.

Subgenus ANOPLOCERAS Hyatt, 1900

Subgenotype: *Anoploceras ampezzanus* (Loretz)

This is another of the new genera placed in his family Pleuronautilidae by Hyatt in the 1900 edition of the Ziteel-Eastman Textbook of Paleontology. The two species that have been placed in *Anoploceras* are very closely related to *Pleuronautilus* and it seems best to treat this group as a subgenus. *Anoploceras* is characterized by an evolute conch with a subquadratic and depressed whorl section. The flanks have thick, foldlike, slightly sinuous ribs and the venter is smooth pl. 17, figs. 62.

Hyatt did not describe his new genus so the description of the subgenotype by Loretz (1875, p. 809) is quoted here in part:

Die Seitenfläche der Windung verläugt flach und ist mit dicht aufeinander folgenden gleichbreiten Furchen und Rippen versehen, deren auf die halbe Windung je circa 18 bis 19 kommen; sie reichen von der Nabekante bis an den Beginn der Wölburg, welche die Seitenfläche mit der Aussenfläche verbindet. Die Rippen sind in ihrer grössten Länge radial gerichtet, in der Nähe der Nabelkante jedoch sind sie etwas abgelenkt und nehmen eine Richtung vorwärts an.

Mit der Naht ist die Seitenfläche durch eine ziemlich steil abfallende, anscheinend glatte Nahtfläche verbunden; zwischen beiden Flächen ist eine markirte Nabelkante. Die Aussenfläche der Windung ist sehr breit, gegen die mitte zu nur sehr liecht eingesenkt, ohne Rippen und Furchen, und mit den Seitenflächen, zu denen sie rechtwinklig steht, durch eine continuirliche Wölbung verbunden, so dass sich keine Aussenkante bildet.—Die Schale ist in der Mitte der Aussenfläche der Windung nur dünn, wird nach den Seitenflächen zu stärker und ist auf letzteren von beträchtlicher Dicke.

Die Lobenlinie bildet auf der Mitte der Seitenflache, sowie auf der Mitte der Aussenfläche eine sanft nach rückwärts geschwungene Bucht. Etwa die Hälfte des vorliegenden Stückes ist Wohnkammer; nur die beiden letzten Lobenlinien konnten beobachtet werden, sie stehen auf der Mitte der Aussenfläche circa 11 mm. von einander ab.—Der Sipho liegt der concaven Seite der Windungsröhre nahe.

This description is summarized as follows:

The whorl sides are flattened and have thick radial ribs and furrows; there are approximately 18 to 19 ribs on a half volution. In the region of the umbilical shoulder the ribs project adorally. The unbilical shoulder is sharply rounded and the umbilical wall steep and smooth. The venter is very broad and slightly concave. The ventral shoulders are rounded. The suture forms a shallow ventral and lateral lobe. The siphuncle is below the center of the whorl.

The type species comes from Karnian rocks of the Alpine region. The only other species assigned to this subgenus, *P.* (*A.*) *rollieri* (Arthaber) 1896, is from Anisian rocks of the Alps.

Subgenus TRACHYNAUTILUS Mojsisovics, 1902

Subgenotype: *Pleuronautilus subgemmatus* Mojsisovics

When Mojsisovics (1902, p. 239) proposed his subgenus *Trachynautilus* he made the following comments:

> Als eine weitere Untergattung von *Pleuronautilus* möchte ich *Trachynautilus* oder die Gruppe des *Pleuronautilus subgemmatus* auffassen, welche den Uebergang zur Gattung *Phloioceras* vermittelt. Die Abstammung dieser durch laterale Längsrippen ausgezeichneten kleinen Gruppe von *Pleuronautilus* lehrt deutlich der von G. v. Arthaber aus dem Reiflinger Kalke beschriebene *Pleuronautilus scabiosus* und insbesondere der von v. Arthaber als Varietät dieser Art bezeichnete *Pl. jugulatus*, welcher in den mittleren Lebensstadien deutlich die Verbindung der typischen *Pleuronautilus*–Sculptur mit der Trachynautilus—Sculptur zeigt, auf der Wohnkammer aber ausschliesslich die longitudinale *Trachynautilus*-Sculptur besitzt. Bei dem julischen *Trachynautilus Telleri* ist das Uebergreifen der lateralen Längsrippen auf die Externseite zu beobachten, wodurch sich die allmähliche Annäherung an den Typus von *Phloioceras* deutlich zu erkennen gibt.

The type specimen is refigured on plate 17.

Mojsisovics' comments can be summarized as follows:

> As another subgenus of *Pleuronautilus* I propose *Trachynautilus* for the group of *Pleuronautilus subgemmatus*, which is transitional to *Phloioceras*. The derivation of this group with longitudinal ribs on the flanks from *Pleuronautilus* is especially demonstrated in *Pleuronautilus scabiosus* and P. *jugulatus* described by Arthaber from the Reiflinger Kalk which in there ontogeny show the combination of *Pleuronautilus* and *Trachynautilus* ornamentation. *Trachynautilus telleri* has the longitudinal ribs spreading onto the venter and in this respect is transitional to *Phloioceras*.

Distribution of species of the subgenus Pleuronautilus (Trachynautilus)

Species	Stratigraphic distribution	Geographic distribution
Pleuronautilus (*Trachynautilus*) *clathratus* Hauer 1896.	Triassic (Anisian)	Yugoslavia.
P. (*T.*) *laevis* Schnetzer 1934	Triassic (Muschelkalk)	Germany.
P. (*T.*) *minuens* Kittl 1908	Triassic (Ladinian)	Roumania.
P. (*T.*) *nodulosus* Arthaber 1896	Triassic (Anisian)	Alps.
P. (*T.*) *subgemmatus* Mojsiovics 1882	do	Do.
P. (*T.*) *telleri* Mojsisovics 1902	Triassic (Karnian)	Do.
P. (*T.*) *trilineatus* Frech 1903	Triassic (Ladinian)	Do.

Genus PHLOIOCERAS Hyatt, 1883

Genotype: *Nautilus gemmatus* Mojsisovics

When Hyatt (1883, p. 286) first established this genus he diagnosed it as follows:

> The shells are ridged longitudinally, and the ridges in the type roughened by transverse striae. Mojsisovics considers them as allies of *Nautilus cariniferus*, and he may be right, but we have placed them in this series on account of the resemblance of [*N.*] *gemmatus* to *Kophinoceras*. The sutures have simple, lateral, ventral and dorsal lobes, with small annular lobes. Siphon is central or below the centre.

(see pl. 17, figs. 5, 6).

In the very next generic description of that paper, Hyatt discussed the genus *Pleuronautilus* and remarked

> The young of one species, *Pleuronautilus* (now *Trachynautilus*) *subgemmatum*, as figured by Mojsisovics (1883, p. 85) is similar to the adult *Phloioceras gemmatum*, and appears to settle the question of affinity.

At this time he included both of these genera in his family Rutoceratidae. However, in the 1900 edition of the Zittel-Eastman Text-book of Paleontology he placed *Phloioceras* in the family Rhineceratidae. Mojsisovics (1902, p. 239) expressed the opinion that *Phloioceras* is somewhat similar to *Trachynatilus* and is actually an offshoot of *Pleuronautilus* and thus belongs in the family Temnocheilidae (Tainoceratidae of the present paper). Mojsisovics also pointed out that as yet no intermediate forms are known that link *Phloioceras* and *Trachynautilus*. The latter genus has the peculiar longitudinal ridges confined to the flanks and do not occupy the venter, and also all the species of *Trachynautilus* are rather small. *Phloioceras* has the longitudinal ridges developed both on the flanks and the venter, and the robust shell attains a much larger size than in any known representative of *Trachynautilus*. The writer is inclined to agree with Mojsisovics and in depicting the phylogenetic development of the Tainoceratidae *Phloioceras* is placed close to *Trachynautilus* but regarded as having been derived directly from *Pleuronautilus*.

Phloioceras sp.

Plate 4, figure 7; text figure 20

Only one fragmentary specimen in the present collection can be assigned to the genus *Phloioceras*. The writer refrains from naming the form because the specimen is not sufficiently complete. The specimen consists of about 25 mm of the living chamber with the shell preserved and the ventral region of an inner whorl. The preserved part of the living chamber measures 22 mm in height and 33 mm in width. The venter is broadly arched, the flanks slightly divergent, and the umbilical shoulder is subangular (see text fig. 20). The umbilical wall slopes at an angle of approximately 35 degrees.

Distribution of species of the genus Phloioceras

Species	Stratigraphic distribution	Geographic distribution
Phloioceras deliciosum Diener 1908	Triassic (Ladinian)	Himalayas, India.
P. gemmatum (Mojsisovics) 1882	Triassic (Karnian)	Alps.
P. welteri Kieslinger 1924	Triassic (Norian)	Timor.
P. sp	Triassic (Karnian)	Alaska.

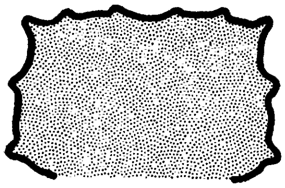

FIGURE 20.—Diagrammatic cross section of *Phloioceras* sp. (U. S. N. M. 107094) from the Upper Triassic on Admiralty Islands, Alaska, × 1.

The surface of the conch is highly ornamented. Along the venter are four longitudinal and parallel rows of low elongate nodes. The nodes along the median portion of the venter are spaced slightly farther apart than those of the adjacent row of nodes on either side. There is a row of rather high rounded nodes on the ventral shoulder and one on the umbilical shoulder. Along the middle of the flank between the shoulders is another row of nodes, which are likewise large and rounded. There are thus ten distinct longitudinal rows of nodes on the flanks and venter. The ventral region of an inner whorl shows four distinct longitudinal ridges. The ridges are in pairs on each side of the venter, and the space between the two central ridges is nearly twice that between the outer two ridges. This is very similar to the type of ornamentation seen in *Trachynautilus*.

Remarks.—*Phloioceras* sp. of Alaska is very similar to *Phloioceras welteri* Kieslinger from the Norian of Timor. *P. welteri* has six rows of nodes on the ventral region, a row of nodes on the ventral and umbilical shoulders, but no median row of nodes on the flanks as seen in *P.* sp. Both species differ from the genotype, which has a much more highly developed ornamentation, with longitudinal ridges that seem to be formed by the coalescing of elongated nodes, and much more numerous rows of nodes. The basic form of the conch, however, is similar in all three forms.

Occurrence.—Point at north entrance to Herring Bay, Admiralty Islands, Alaska. Bed 9 in section (Martin 1926, p. 90) from a "fossiliferous limestone."

Type.—U.S.N.M. 107094.

Family GRYPOCERATIDAE Hyatt, 1900

The genera now included in Grypoceratidae are *Grypoceras, Gryponautilus, Domatoceras, Stenopoceras, Menuthionautilus, Plummeroceras, Stearoceras, Titanoceras,* and *Pselioceras.* Mojsisovics (1902) established the family Gryponautilidae for *Grypoceras* and *Gryponautilus.* He separated these genera from the Clydonautilidae mainly on the presence of an annular lobe. Diener (1919) objected to the taxonomic scheme of Mojsisovics (1902), especially to the importance that Mojsisovics attached to the annular lobe. Diener (1919) combined the Gryponautilidae and Clydonautilidae of Mojsisovics (1902) into the family Grypoceratidae Hyatt (1900). In this latter family Hyatt (1900) originally had only included *Grypoceras* and *Syringoceras.*

It now seems quite clear that the relationship of *Grypoceras* to *Domatoceras* links that genus closely to its Paleozoic ancestors and that they should be included in the same family. As will be discussed below *Domatoceras* Hyatt 1891, is placed as a subgenus of *Grypoceras* Hyatt 1883, which has priority. Miller and Youngquist (1949, p. 41) erected the family Domatoceratidae for five very similar late Paleozoic nautiloid genera that probably directly or indirectly evolved from *Koninckioceras* "or some very similar form." These genera are *Domatoceras, Stearoceras, Stenopoceras, Titanoceras,* and *Pselioceras.* These genera are now all included in the Grypoceratidae. A new subgenus, *Plummeroceras,* is proposed for late Paleozoic grypoceratids with deep ventral lobes. *Menuthionautilus* is a monotypic development known only in the Scythian beds of Madagascar and Pakistan. In its ontogeny and morphological features it appears to be an aberrant offshoot of *Domatoceras.*

As an evolutionary unit this family appears to be closely integrated. The extensive variations experimented with in this family keep an over-all unity in both the shape of the conch and sutural development. The Paleozoic genera are mostly widely umbilicate forms except for *Stenopoceras* and those species of *Domatoceras* transitional to *Stenopoceras.* The principal Triassic representative, *Grypoceras,* is slightly more involute than *Domatoceras* but *Menuthionautilus* and *Gryponautilus* are highly involute forms similar to *Stenopoceras.* The group as a whole has compressed conchs that tend to be flattened laterally and may or may not be flattened ventrally. The sutures form ventral, lateral, and dorsal lobes. An annular lobe is present in *Stearoceras, Grypoceras,* and *Gryponautilus* but not present or not recognized as yet in the remaining genera. Nodes on the ventral shoulders are developed at full maturity in some of the Paleozoic repre-

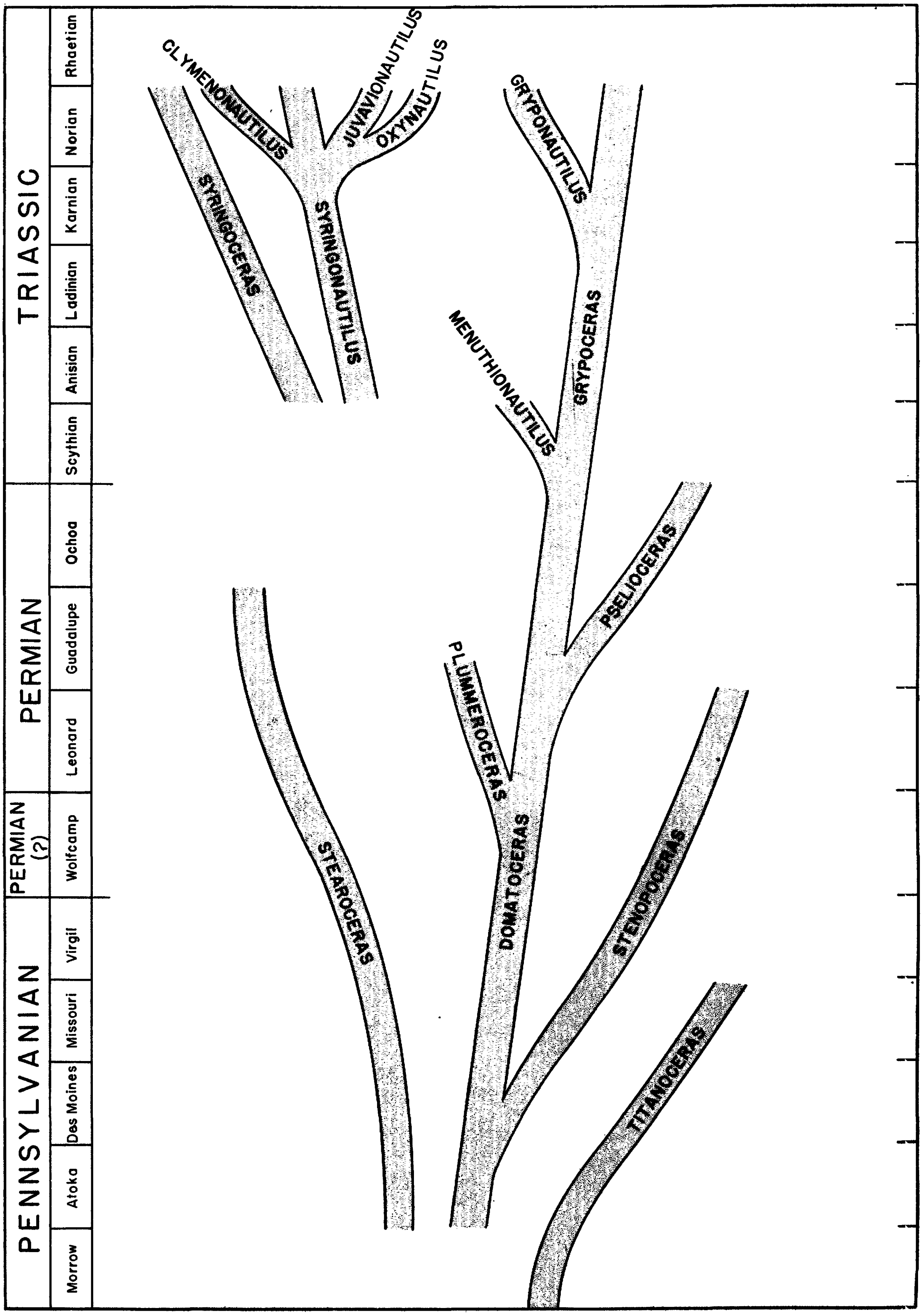

FIGURE 21.—Diagram showing inferred phylogeny and geologic distribution of the Grypoceratidae and the Syringonautilidae.

sentatives of this group. Similar types of nodes are found in youthful *Gryponautilus* but they are not considered to indicate any affinity with the Tainoceratidae. The sum total of all the characteristics of these forms refutes any genetic relationship to that family. The siphuncle is orthochoanitic in structure and is extremely variable in position; it ranges from subcentral in most genera to an extreme ventral position in *Menuthionautilus*.

Geographically this family is very wide spread. The Paleozoic forms are rather wide-spread in North America, Europe, Asia, and Australasia. The Triassic forms have a closely limited distribution in North America but are quite common in the region of the Triassic Tethyian geosyncline.

PHYLOGENY

The evolution of the Gypoceratidae is similar to that of the Tainoceratidae in the existance of a dominant, slowly evolving stock from which several varied forms developed (text figs. 21, 22). *Domatoceras* is a very abundant nautiloid in late Paleozoic rocks and practically world wide in distribution. It does show a great range of variation in the Pennsylvanian and Permian, but these variations appear to be random and of no stratigraphic significance. *Grypoceras* is considered to be a direct offshoot of *Domatoceras* and replaces it in the Triassic. The main changes are toward a rounding of the venter, and greater involution. Scythian species of *Grypoceras*, as *G. brahmanicum*, *G. hexagonalis*, and *G. milleri* n. sp. (p. 53) have rectangular whorl sections with rounded ventral and umbilical shoulders and somewhat flattened flanks. These species are actually difficult to distinguish from several species of Pennsylvanian and Permian *Domatoceras*. Middle and Late Triassic species of *Grypoceras* show more rounding of the venter and greater involution.

The suture in *Domatoceras* has in general rather moderate ventral and lateral lobes, those in *Grypoceras* are somewhat deeper and there is an annular lobe. This relationship is very similar to that between *Metacoceras* and *Mojsvaroceras*. *Plummeroceras* (p. 54) is an aberrant offshoot of *Domatoceras* that maintained a typical evolute domatoceratid conch but acquired a very deep ventral lobe similar to that of some Triassic species of *Grypoceras*.

Both *Domatoceras* and *Grypoceras* gave rise to more specialized offshoots that have more limited geologic and geographic distributions. A trend towards greater involution is found in *Stenopoceras*, Pennsylvanian to Permian in age; *Menuthionautilus*, Scythian in age; and in *Gryponautilus*, Late Triassic in age. *Stenopoceras* has a highly involute and compressed conch. The venter is generally narrow and may be rounded, subacute, or even concave. *Stenopoceras* is connected with *Doma-*

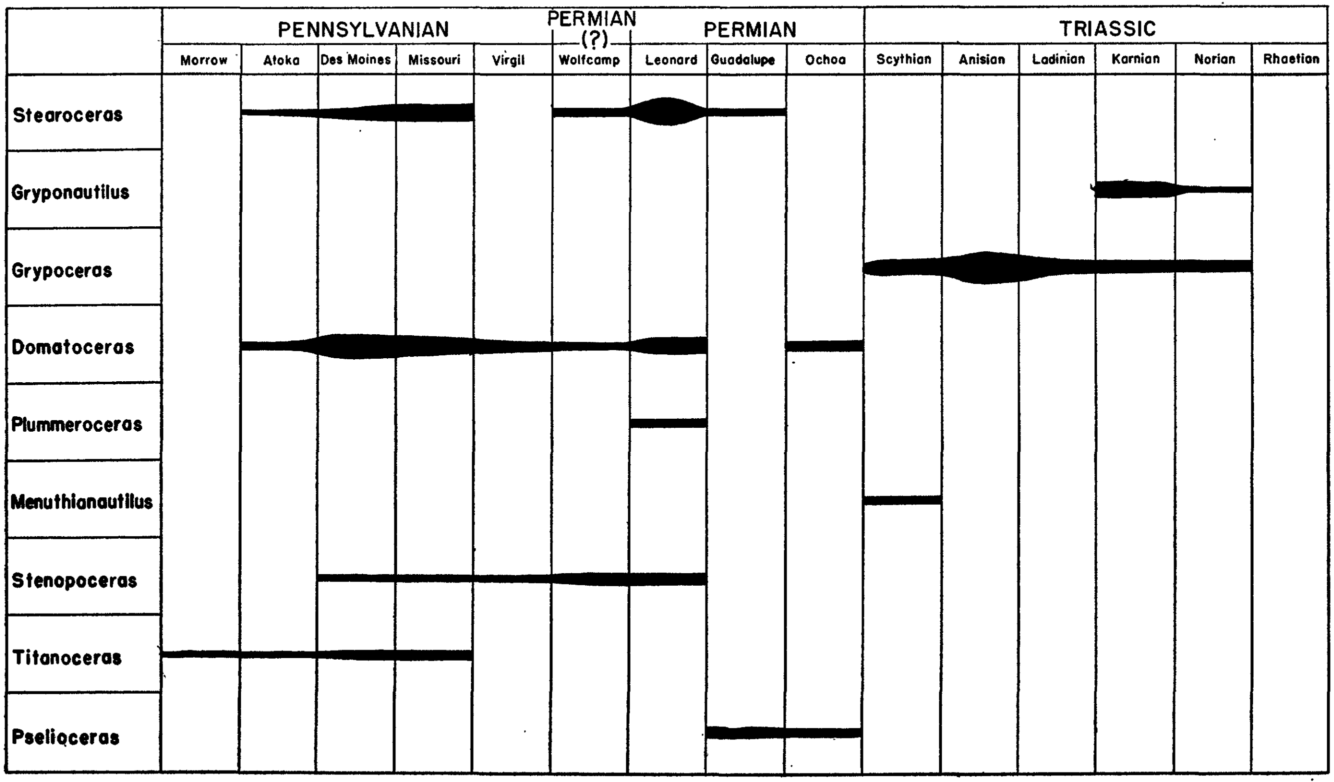

FIGURE 22.—Range chart showing known stratigraphic occurrence of the Grypoceratidae. The width of the line is proportional to the number of species in each epoch.

toceras through such involute species as *D. kleihegei* and *D. moorei*. *Stenopoceras* did not give rise to any other groups of nautiloids and represents merely an involute offshoot of the more slowly evolving domatoceratid stock.

Menuthionautilus is another involute offshoot of *Domatoceras*. It has a rapidly expanding, smooth, and involute conch. On the early whorls the venter is flattened and becomes broadly convex on the mature portion of the conch. The conch form, suture, and ontogeny appear to indicate a close relationship with a domatoceratid ancestry. Along with the greater involution of the conch there was a shifting of the siphuncle to an extreme ventral position. The parent stock, *Domatoceras*, shows a great deal of variation in the position of the siphuncle. Some of the more involute species, as *D. kleihegei*, have the siphuncle only 12.5 percent of the whorl height from the venter. Shifting of the siphuncle to an extreme ventral position is a relatively rare ocurrence in late Paleozoic and Triassic nautiloids. This phenomenon is present only in *Solenochilus* of the late Paleozoic and in *Menuthionautilus* of the Early Triassic.

Gryponautilus is incompletely known. The genotype, *G. galeatus*, has an inflated involute conch with a very narrow keel-like venter. The inner whorls have a broad flatly convex venter, and there are nodes along the ventral shoulders. The suture and general form and ontogenetic development of the conch clearly point to its ancestry in *Grypoceras* in the Late Triassic. Ornamentation is not characteristic in the Grypoceratidae—most species have smooth conchs. There are some species of *Domatoceras*, as *D. williamsi*, that have nodes on the ventral shoulder. The presence of nodes in members of the Grypoceratidae do not appear to have any phylogenetic significance—they merely show some convergence towards the Tainoceratidae.

The relationships of *Pselioceras*, *Stearoceras*, and *Titanoceras* are uncertain. *Pselioceras* is a widely umbilicate form known only from the Salt Range of Pakistan. *Titanoceras* occurs in the Pennsylvanian but not in the Permian. It gave rise to no other genera, and its ancestry and relationships with other genera of the Grypoceratidae are not well understood. *Stearoceras* appears to be an independent development out of *Koninckioceras* paralleling *Domatoceras* (Miller and Youngquist, 1949, p. 42). According to the broad interpretation of this genus as proposed by Miller and Youngquist *Stearoceras* now includes a wide assortment of forms. There are forms intermediate between *Stearoceras* and *Domatoceras*. The Syringonautilidae are thought to arise from these.

Genus **GRYPOCERAS** Hyatt, 1883

Genotype: *Nautilus mesodicum* Hauer

Hyatt first diagnosed this genus as follows:

> *Grypoceras*, nobis, includes species of the Trias which are described by Mojsisovics, "Das Gebirge um Hallst.," with compressed and more involute whorls than the above (*Mojsvaroceras*), abdomen, however, truncated at some stage of growth, though acute in some species in the later adolescent and adult stages. Siphon below the centre, sutures like the above (*Mojsvaroceras*), but with deeper lateral lobes and narrow V-shaped ventral lobes. The forms have annular lobes according to Mojsisovics.

The forms with acute venters included by Hyatt in this genus were later placed by Mojsisovics in a subgenus, *Gryponautilus*, which is raised to full generic rank in the present report.

Mojsisovics (1902, p. 228), in discussing this genus made several pertinent comments as to its probable affinities, pointing out the close relationship of *Grypoceras* with *Domatoceras*. As his comments are important and generally inaccessible they are quoted in part here (free translation)

> The closest similarity is with *Domatoceras* Hyatt, a characteristic nautiloid of the Pennsylvanian and Permian that Hyatt had placed in the family Koninckioceratidae. This conclusion does not rest solely on the suture but also in the form of the conch in the older species of *Grypoceras*, from which they differ in being less involute and lacking an annular lobe. Prof. Diener showed me a specimen of *Domatoceras hunicum* from the Permian limestone of Chitichun, Himalayas, India in which one would have doubt as to whether both these species should not be placed in the same genus

Most compressed Triassic nautiloids with flattened ventral and lateral areas have been placed in the genus *Grypoceras*. This Triassic genus shows remarkable similarity with typical representatives of *Domatoceras* (text figs. 23, 24). *Grypoceras*, however, is generally more involute than *Domatoceras* and has an annular lobe. These differences are precisely the same as those between *Metacoceras* and *Mojsvaroceras*.

The degree of involution of the conch in species of *Domatoceras* is varied. Calculation taken from the literature on 12 species show the diameter of the um-

FIGURE 23.—Cross sections of the conch of *A*, *Pselioceras ophioneus* (Waagen) 1879, pl. 5, fig. 2b, Height 48 mm; *B*, *Stenopoceras cooperi* Miller and Unklesbay 1942, fig. 1E, Height 56 mm; *C*, *Menuthionautilus kieslingeri* Collignon 1933, fig. 4, Height 54 mm; the genotype of *Menuthionautilus;* *D*, *S. smithi* Miller and Unklesbay 1947, fig. 1, Height 52 mm; *E*, *P. convolutum* (Waagen) 1879, pl. 6, fig. 2b, Height 31 mm; *F*, *S. whitei* Miller and Youngquist 1949, fig. 22A, Height 37 mm; *G*, *S. abundum* Miller and Thomas 1936, pl. 99, fig. 1, Diameter 120 mm; *H*, *S. abundum* Miller and Thomas, 1949, fig. 21A, Diameter 61 mm; *I*, *S. dumblei* (Hyatt) 1891, fig. 50, Diameter 138 mm; the genotype of *S.*; *J*, *S.* sp. Miller 1945, fig. 2B, Height 51 mm; *K*, *Grypoceras* (*Domatoceras*) *umbilicatum* Hyatt 1891, fig. 47, Height 73 mm; *L*, *G.* (*D.*) *williamsi* Miller and Owen 1934, pl. 17, fig. 4, Height 27 mm; *M*, *G.* (*D.*) *convergens* (Abich), after Arthaber 1900, pl. 18, fig. 2b, Height 30 mm; *N*, *G.* (*D.*) *bradyi* Miller and Unklesbay 1942, fig. 1H, Height 55 mm; *O*, *G.* (*D.*) *walteri* Miller and Unklesbay 1942, fig. 1F, Height 55 mm: *P*, *G.* (*D.*) *sculptile* (Girty) 1915, pl. 31, fig. 2a, Diameter 73 mm: *Q*, *G.* (*D.*) *umbilicatum* Hyatt, 1891, fig. 46, D. 100 mm±; the genotype of *G.* (*D.*)*;* *R*, *G.* (*D.*) *moorei* Miller, Dunbar, and Condra 1933, pl. 21, fig. 2, Diameter 106 mm+; *S*, *G.* (*D.*) *mosquensis* Tzwetaev 1888, pl. 6, fig. 37, Diameter 110 mm: *T*, *G.* (*D.*) *hunicus* Diener 1903, pl. 1, fig. 1b, Diameter 74 mm.

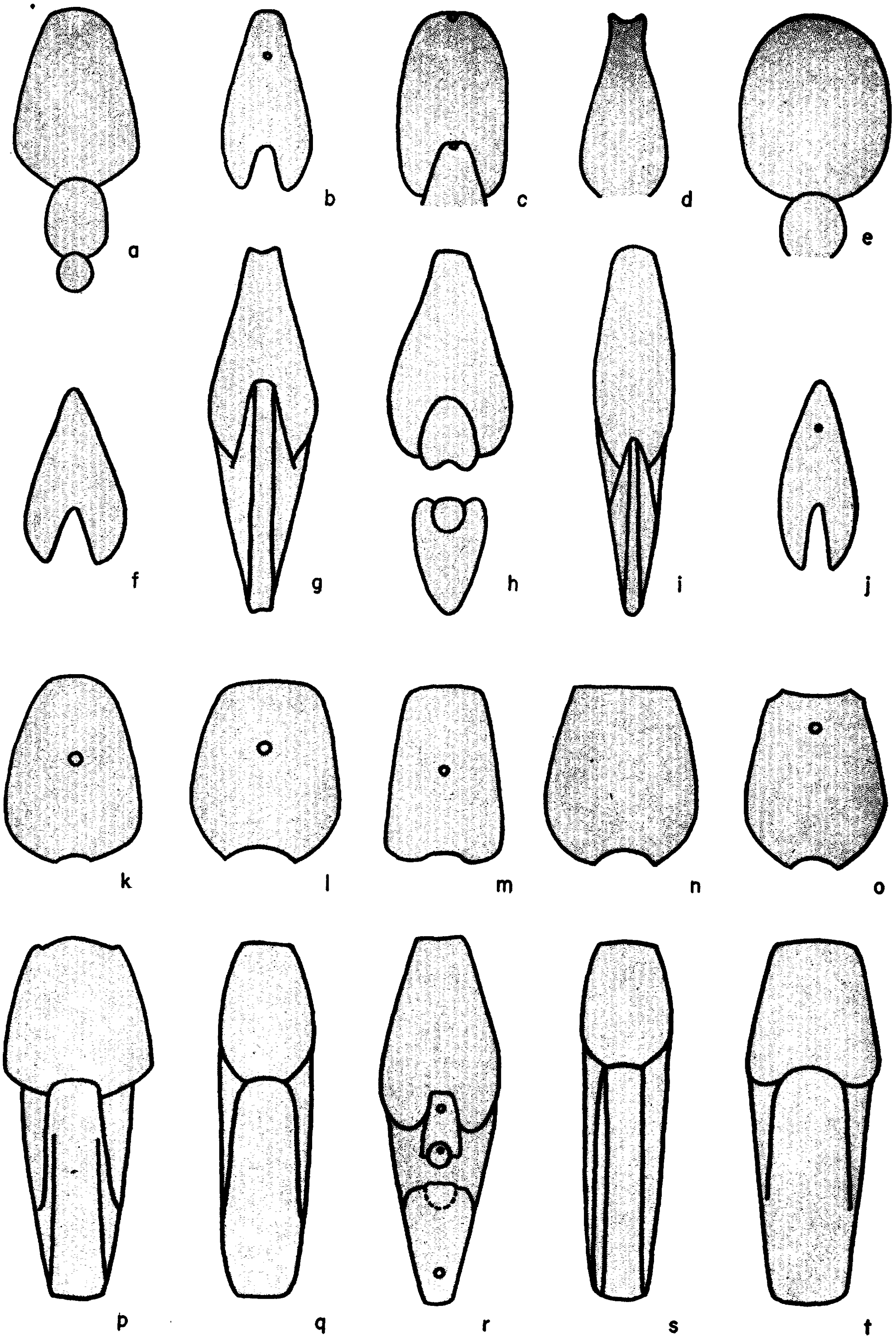

FIGURE 23

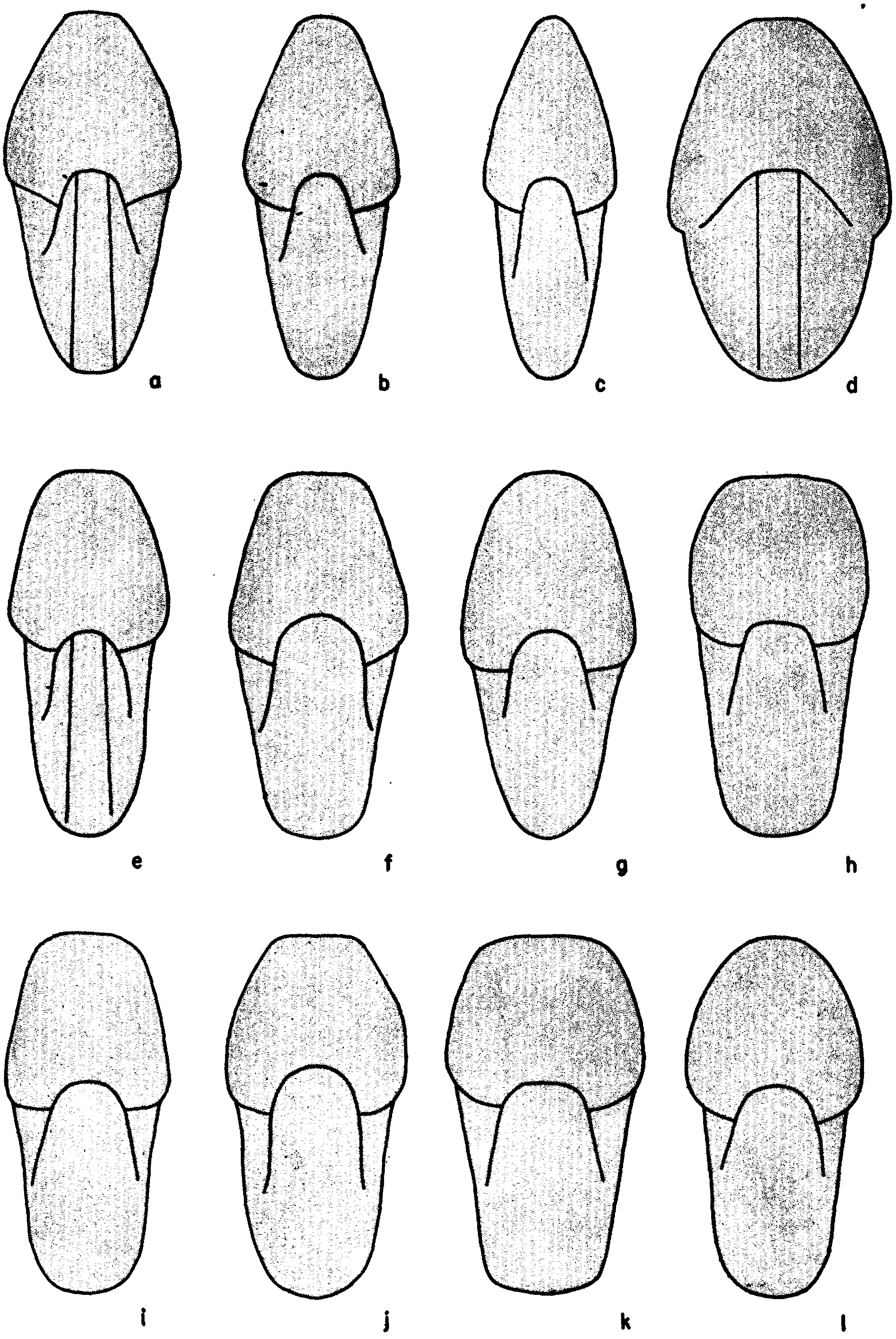

FIGURE 24.

bilicus to range from 16 to 50 percent the diameter of the conch.

Range of diameter of umbilicus in 12 species of Domatoceras, *expressed as percent of diameter of the conch*

Species	*Percent of diameter of conch*
D. williamsi	50
D. bradyi	50
D. northropi	50
D. walteri	50
D. obsoletum	43
D. umbilicatum	35
D. shepherdi	35
D. sculptile	30
D. hunicum	30
D. arthaberi	30
D. kleighegei	17
D. moorei	16

The last two species are generally thought to be transitional forms to *Stenopoceras*, which is a highly involute and compressed offshoot of *Domatoceras*.

Within the genus *Grypoceras* the percentage of the diameter of the umbilicus to diameter of the conch ranges from 8.5 to 30.

Range of diameter of umbilicus in 9 species of Grypoceras, *expressed as percent of diameter of the conch*

Species	*Percent of diameter of conch*
G. obtusum	30
G. laubei	27
G. gumbeli	24
G. whitneyi	24
G. privatum	22
G. palladi	18
G. haloricum	17
G. mesodicum	14
G. involutum	8. 5

Whereas the range in width of the umbilicus to the diameter of the conch in *Grypoceras* is 8.5 to 30 percent, that of *Domatoceras*, if one leaves out of consideration the two species which are transitional to *Stenopoceras*, is from 30 to 50 percent. In neither genus is there any obvious correlation between the percentage and geologic age, perhaps because available data are insufficient.

The position of the siphuncle in *Domatoceras* is generally subcentral, but varies in the different species. Unfortunately, for many species data on the siphuncle are unavailable. Measurements and descriptive data on the position of the siphuncle for 10 species were analyzed.

Variation in position of the siphuncle in 7 species of Domatoceras, *expressed as percent of the distance from the venter to the siphuncle, to the height of the whorl*

Species	*Percent of whorl height*
D. kleighegei	12. 5
D. walteri	14. 2
D. toddanum	20
D. northropi	24. 5
D. moorei	25
D. williamsi	38. 5
D. sculptile	50

Domatoceras umbilicatum, *D. parallelus*, and *D. mosquensis* have the siphuncle "above the center of the whorl." The same measurements for *Grypoceras* range from 30 to 50 percent.

Quantitative or diagrammatic data on the suture pattern are rather meager. In general, *Grypoceras* has deeper lobes than are found in *Domatoceras*, and it also has an annular lobe which is unknown as yet in *Domatoceras*.

Many species of *Grypoceras* lose the angularity of the ventral shoulders. It is significant that Mojsisovics (1902), in describing *Grypoceras*, pointed out that on comparing *Domatoceras hunicum* with *G. brahmanicum* the marked similarity made him wonder if the species should not be placed in the same genus. The writer believes that the presence or absence of an annular lobe is not of great taxonomic importance. The difference between *Grypoceras* and *Domatoceras* being mainly degree of involution and the presence or absence of an annular lobe, the Triassic genus is considered to have descended directly from *Domatoceras* and the latter genus is retained as a subgenus of *Grypoceras* which has priority. This is in accord with the treatment given *Metacoceras* and *Mojsvaroceras* where a rather similar relationship exists.

Grypoceras (*Plummeroceras*) *plummeri* Kummel, n. subgen., n. sp., from the Permian of Texas, is very similar to the type species of *Grypoceras*. It has an unusually large ventral lobe, similar to that of *G.* (*G.*) *mesodicum* (see pl. 5, figs. 2, 3, 4; text fig. 27). The lateral lobe of this specimen is not so concave as Mojsisovics' specimen and also the Texas form is more evolute.

Grypoceras is widely distributed geographically, and is fairly common in the Alpine and Himalayan Triassic regions. It is also reported in Triassic rocks from North America, the Ussuri region, Timor, and New Zealand.

FIGURE 24.—Cross sections of the conch of *A*, *G. mesodicum* (Hauer), after Mojsisovics 1873, pl. 8, fig. 1b, Diameter 150 mm; *B*, *G. haloricum* (Mojsisovics) 1873, pl. 7, fig. 4b, Diameter 112 mm; *C*, *G. obtusum* (Mojsisovics) 1873, pl. 7, fig. 1b, Diameter 90 mm: *D*, *G. involutum* Kieslinger 1924, pl. 1, fig. 7b, Diameter 82 mm: *E*, *G. gumbeli* (Mojsisovics) 1873, pl. 7 fig. 2b, Diameter 39 mm: *F*, *G. whitneyi* (Gabb) 1863, pl. 3, fig. 3, Diameter 60 mm; *G*, *G. cancellatum* Hauer 1896, pl. 5, fig. 6, Diameter 54 mm; *H*, *G. quadrangulum* (Beyrich) after Mojsisovics 1882, pl. 83, fig. 3b, Diameter 54 mm; *I*, *G. brahmanicum* (Griesbach) after Diener 1897, pl. 1, fig. 1b, Diameter 63 mm: *J*, *G. hexagonalis* Diener 1897, pl. 1, fig. 2, Diameter 39 mm; *K*, *G. privatum* (Mojsisovics) 1882, pl. 40, fig. 3b, Diameter 80 mm; *L*, *G. laubei* (Mojsisovics) 1873, pl. 6, fig. 10a, Diameter 30 mm.

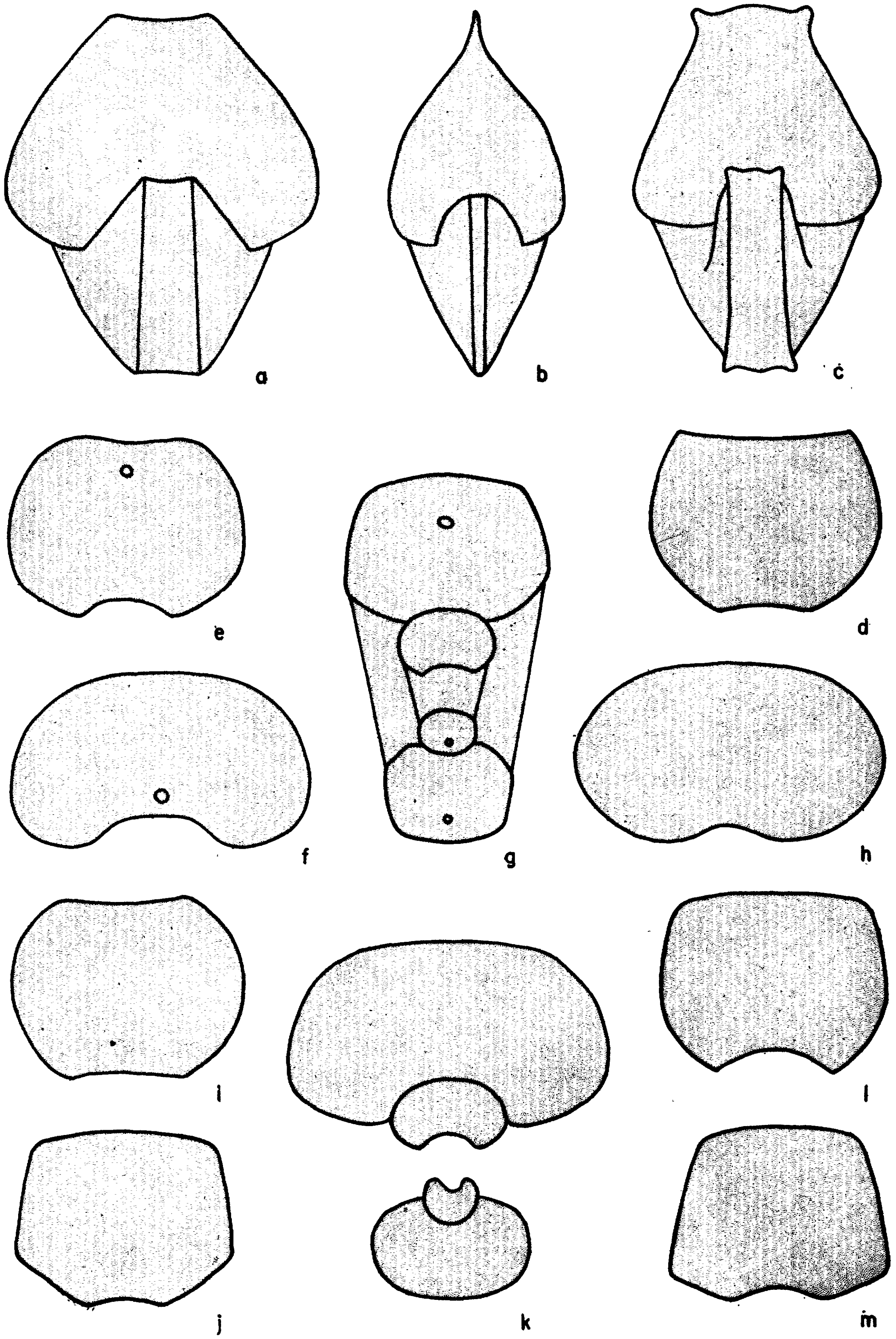

FIGURE 25.—Cross sections of the conch of *A*, *Gryponautilus suessi* Mojsisovics 1873, pl. 13, fig. 2b, Diameter 70 mm; *B*, *G. galeatus* Mojsisovics 1873, pl. 12, fig. 1, Diameter 390 mm; the genotype of *Gryponautilus; C*, *G. cooperi* Smith, based on the holotype at a diameter of about 67 mm; *D*, *Titanoceras ponderosum* (Meek), the genotype of *Titanoceras*, after Miller and Unklesbay 1942, fig. 1J, Height 61 mm: *E*, *Stearoceras sublaeve* (Miller, Dunbar, and Condra), after Miller and Youngquist 1949, fig. 19, Height 20 mm: *F*, *S. phosphoriense* (Branson), after Miller and Youngquist 1949, fig. 11, Height 33 mm; *G*, *S. militarium* (Hyatt), after Miller and Youngquist 1949, fig. 10A, Diameter 49 mm: *H*, *Stearoceras conchiferous* (Hyatt) 1891, fig. 24, Height 11 mm: *I*, *S. rotundatum* (Miller and Unklesbay), 1942, fig. 1B, Height 40 mm: *J*, *S. aberrans* (Miller and Unklesbay) 1942, fig. 1C, Height 49 mm: *K*, *S. gibbosus* (Hyatt) 1891, fig. 56, Height 82 mm the genotype of *S. L. S. sanandresense* (Miller, Dunbar, and Condra), after Miller and Unklesbay 1942, fig. 1D, Height 34 mm; *M*, *S. simplex* (Hyatt,) after Miller and Youngquist 1949, fig. 18, Height 68 mm.

Distribution of species of the subgenus Grypoceras (Grypoceras)

Species	Stratigraphic distribution	Geographic distribution
Grypoceras (*Grypoceras*) *brahmanicum* (Griesbach) 1880.	Triassic (Scythian)	Himalayas, India.
G. (*G.*) *cancellatum* (Hauer) 1896	Triassic (Anisian)	Yugoslavia.
G. (*G.*) *griesbachi* (Diener) 1895	do	Himalayas, India.
G. (*G.*) *guembeli* (Mojsisovics) 1873	Triassic (Anisian, Karnian)	Alps.
G. (*G.*) *haloricum* (Mojsisovics) 1873	Triassic (Norian)	Do.
G. (*G.*) *hexagonalis* (Diener) 1897	Triassic (Scythian)	Himalayas, India.
G. (*G.*) *involutum* Kieslinger 1924	Triassic (Karnian)	Timor.
G. (*G.*) *laubei* (Mojsisovics) 1873	do	Alps.
G. (*G.*) *lilangense* Krafft and Diener 1909	Triassic (Scythian)	Himalayas, India.
G. (*G.*) *mesodicum* (Hauer) 1846	Triassic (Norian)	Alps.
G. (*G.*) *milleri* Kummel n. sp	Triassic (Scythian)	Idaho.
G. (*G.*) *obtusum* (Mojsisovics) 1873	Triassic (Norian)	Alps.
G. (*G.*) *palladi* (Mojsisovics(1869	Triassic (Anisian)	Alps, Yugoslavia.
G. (*G.*) *privatum* (Mojsisovics) 1883	do	Alps.
G. (*G.*) *quadrangulum* (Beyrich) 1866	do	Do.
G. (*G.*) *vihianum* Diener 1913	do	Himalayas, India.
G. (*G.*) *whitneyi* (Gabb) 1864	do	California, Nevada.

Grypoceras (Grypoceras) milleri n. sp.

Plate 6, figures 5, 6; text figure 26

One poorly preserved specimen from the Lower Triassic Dinwoody formation of southeastern Idaho is available for study. The specimen includes only the living chamber and part of the crushed and recrystallized phragmocone. The living chamber measures 100 mm along the venter. The whorl section is subrectangular, with a broad slightly convex venter; the flanks are flattened and converge gradually towards the venter (text fig. 26). The ventral shoulders are abruptly rounded. The umbilical shoulders are not well preserved but seem to be well rounded and steep. The living chamber expands rapidly, the most adapical part measuring 31 mm and 21 mm in height and witdh and the most adapertural part 48 mm and 27 mm respectively.

The suture can be made out in a general way on the most adapical part of the living chamber. There is a deep ventral lobe and a broad lateral lobe. The siphuncle is subventral in position, lying only 5 mm from the venter. No surface markings of any kind are preserved.

Remarks.—The most interesting and distinctive feature of this species is the shape of the whorl section. In this feature it is very similar to such species of *Grypoceras* (*Domatoceras*) as *G.* (*D.*) *hunicum*, *G.* (*D.*) *parallelum*, and *G.* (*D.*) *williamsi*. With the exception of a doubtful species of *Grypoceras* recorded from the Ussuri region of eastern Siberia (Diener, 1895) all the previously recorded Scythian species are from the Himalayan region. All three of the Himalyayan species (*G.* (*G.*) *brahmanicum*, *G.* (*G.*) *hexagonalis*, and *G.* (*G.*) *lilangense*) have compressed subrectangular whorl sections with distinct ventral and umbilical shoulders. *Grypoceras* (*G.*) *lilangense* also shows an extraordinary expansion of the living chamber. *Grypoceras* (*G.*) *milleri* is more similar to these Scythian species than to any other species of *Grypoceras*. Muller and Ferguson (1939, p. 1584) report *G.* (*G.*) cf. *G.* (*G.*) *brahmanicum* from the Candelaria formation of Nevada. The geologically younger species of *Grypoceras* generally show more highly arched venters and less distinct ventral shoulders. *Grypoceras* (*G.*) *milleri* can be considered a transitional form between (*G.*) (*Domatoceras*) and *G.* (*Grypoceras*).

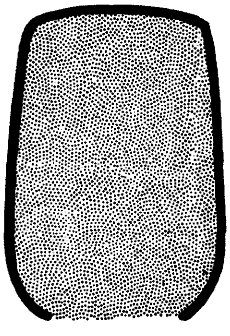

FIGURE 26.—Diagrammatic cross section of holotype of *Grypoceras milleri*, n. sp. (U.S.N.M. 107095) from the Dinwoody formation, Slight Canyon, southeastern Idaho.

Occurrence.—Slight Canyon, Paris-Bloomington region, southeastern Idaho; from limestone near middle of Dinwoody formation, along road, 600 ft from abandoned mine shaft. Collected by the author.

Holotype.—U.S.N.M. 107095.

Grypoceras (Grypoceras) whitneyi (Gabb)

Plate 5, figure 1; plate 6, figures 1–4

1863. *Nautilus whitneyi* Gabb, Geol. Surv Calif. Paleontology vol. 1, p. 19, pl. 3, figs. 5–7.

1914. *Grypoceras whitneyi* (Gabb.) Smith, U. S. Geol. Survey Prof. Paper 83, p. 141, pl. 16, fig. 2, 3, pl. 99, figs. 5–7.

Gabb described this species as follows:

> Shell moderate in size; last volution expanding somewhat rapidly towards the aperture, enveloping about two-thirds of the preceding whorl. Sides flat, converging towards the dorsum,

and gradually rounding into it. Dorsum slightly arched. Umbilicus large, being nearly one-third the diameter of the whole disk; the umbilical margin slopes outwards and unites the surface of the shell by a rounded angle. Septa deeply arched on the sides; separated from each other by about one-third the width of the volution. Surface marked by fine lines, which arise in the umbilicus; curve slightly backwards and then forwards on the side, and, as they pass over the angle between the side and back, again curve backwards, making a deep sinus on the dorsum.

The holotype was not available for study. A pleisotype (pl. 6, figs. 1–4) was assigned to this species by Smith (1914, p. 141). This specimen measures 88 mm in diameter, 46 mm for width of the last whorl, 45 mm for height of last whorl and it has an umbilicus 21 mm in diameter. The conch is smooth, compressed, and evolute. The venter is well rounded, grading onto the flanks with no distinct ventral shoulders. The flanks are flattened grading onto sharply rounded umbilical shoulders and steep umbilical walls. The surface of the conch is smooth except for fine growth lines that form a rounded sinus on the venter. The siphuncle is centrally located. The sutures form rounded ventral and lateral lobes.

Smith (1914, p. 141) correctly noted that this species is very similar to *Grypoceras palladi* Mojsisovics "differing only in the shallower lateral lobe of the septa."

Occurrence—Holotype from the Buena Vista District, Humboldt Mining region. Plesiotype from Middle Triassic, zone of *Ceratites trinodosus*, Wheeler mine, Buena Vista Canyon, near Unionville, West Humbolt Range, Nevada.

Types—Plesiotype, U.S.N.M. 74459.

Subgenus DOMATOCERAS Hyatt, 1891

Subgenotype: *Domatoceras umbilicatum* Hyatt

Hyatt (1900, p. 523, 525) placed *Domatoceras* in the family Koninckioceratidae. Miller and Yongquist (1949) followed Hyatt in the derivation of *Domatoceras* from *Koninckioceras* but felt these forms were far enough removed to be established in a distinct family. It has already been pointed out in the discussion of *Grypoceras* that *Grypoceras* and *Domatoceras* are intimately related and that *Domatoceras* is placed as a subgenus of *Grypoceras* which has priority. For this reason also the family Domatoceratidae Miller and Youngquist cannot be used and it falls in the synonymy of Grypoceratidae. The morphological characters of the subgenus *Domatoceras* were discussed in the chapter on *Grypoceras*.

The subgenus *Domatoceras* occupies a position in the family Grypoceratidae similar to that of *Metacoceras* in the Tainoceratidae. It seems to be the persistent evolving stock from which forms like *Stenopoceras*, *Grypoceras*, and *Menuthionautilus* are thought to have been derived. Miller and Youngquist consider *Stearoceras* to be an independent development out of *Koninckioceras* paralleling *Domatoceras* and that *Stearoceras* and *Domatoceras* are more or less gradational and connected by intermediate forms.

Subgenus PLUMMEROCERAS Kummel, n. subgenus

Subgenotype: *Grypoceras (Plummeroceras) plummeri* Kummel, n. sp.

The single specimen upon which this new subgenus is based is a compressed evolute conch with a flattened venter. The conch agrees in essentially all features with representatives of *G.* (*Domatoceras*), such as *G.* (*D.*) *williamsi* Miller and Owen except in having a very deep ventral lobe. The species that have been assigned to *G.* (*Domatoceras*) have very shallow ventral lobes or sutures which pass straight over the venter. The remaining Paleozoic genera of the Grypoceratidae likewise have very shallow ventral lobes. *Menuthionautilus* is an involute compressed nautiloid with a deep ventral lobe, but not nearly so well developed as in *G.* (*Plummeroceras*). Within the subgenus *G.* (*Grypoceras*) well-developed ventral lobes are present. The genotype *G.* (*G.*) *mesodicum* has a ventral lobe very similar to that in *G.* (*Plummeroceras*), but again it does not appear to be so deep.

G. (*Grypoceras*) is belived to be a direct evolutionary development out of *G.* (*Domatoceras*), actually replacing the latter subgenus in the Triassic. The Paleozoic species of *G.* (*Domatoceras*) do not show much evolution in any particular direction or feature. However, in *G.* (*Grypoceras*) there are definite trends towards a more involute conch, rounding of the ventral shoulders and the venter, and increased differentiation of the suture. Early Triassic species of *G.* (*Grypoceras*) seem more similar to Permian species of *G.* (*Domatoceras*) than to late Triassic species of *G.* (*Grypoceras*). *G.* (*Plummeroceras*) has an advanced and specialized type of suture developed on a conch that is fairly primitive for this evolutionary line and is interpreted as a specialized development of the subgenus *G.* (*Domatoceras*) not belonging in the group that eventually produced the forms included in *G.* (*Grypoceras*).

The only specimen of this subgenus available is from the Belle Plains formation (Leonard), Callahan County, Texas.

Grypoceras (Plummeroceras) plummeri, n. sp.

Plate 5, figure 4; text figure 27

The conch is compressed and evolute, with flattened venter, angular ventral shoulders. The flanks of the phragmocone are flattened to slightly arched, becoming more arched on the living chamber. The umbilical shoulders are sharply rounded and the umbilical walls steep. The greatest diameter of the conch is 168

Distribution of species of the subgenus Grypoceras (Domatoceras)

Species	Stratigraphic distribution	Geographic distribution
Grypoceras (*Domatoceras*) *arthaberi* (Haniel) 1915	Permian (Bitauni and Amarrassi beds)	Timor.
G. (*D.*) *bradyi* (Miller and Unklesbay) 1942	Permian (Kaibab limestone)	Arizona.
G. (*D.*) *complanatum* (Sowerby) 1821	Carboniferous	Isle of Man.
G. (*D.*) *fredericksi* (Kruglov) 1928	Permian (Artinskian and Kungurian)	Ural Mountains, Russia.
G. (*D.*) *hunicum* (Diener) 1903	Permian (Chitichum formation)	Himalayas, India.
G. (*D.*) *inostranzewi* (Tzwetaev) 1888	Upper Carboniferous	Central Russia.
G. (*D.*) *kleihegei* (Miller, Lane, and Unklesbay) 1947	Pennsylvanian (Winterset limestone)	Jackson County, Mo.
G. (*D.*) *krotovi* (Kruglov) 1928	Permian (Artinskian and Kungurian)	Ural Mountains, Russia.
G. (*D.*) *minimum* (Kruglov) 1928	Upper Carboniferous (Uralian)	Do.
G. (*D.*) *moorei* (Miller, Dunbar, and Condra) 1933	Pennsylvanian (Kansas City group)	Kansas.
G. (*D.*) *mosquensis* (Tzwetaev) 1888	Upper Carboniferous	Central Russia.
G.? (*D.*) *nikitowkensis* (Jakowlew) 1899	Permian (middle)	Donetz Basin, Russia.
G. (*D.*) *northropi* (Miller and Unklesbay) 1942	Permian (Chupadero formation)	New Mexico.
G. (*D.*) *obsoletum* (Strugeon) 1946	Pennsylvanian (Allegheny formation)	Ohio.
G. (*D.*) *parallelus* (Abich) 1900	Permian (Djulfa beds)	Armenia.
G. (*D.*) *planovolve* (Shumard) 1858	Pennsylvanian	Nebraska.
G. (*D.*) *sculptile* (Girty) 1911	Pennsylvanian (Wewoka formation)	Oklahoma.
G. (*D.*) *shepherdi* (Sturgeon) 1946	Pennsylvanian (Allegheny formation)	Ohio.
G. (*D.*) *subquadrangulare* (Grabau) 1924	Permian (Paotechow limestone)	Shansi, China.
G. (*D.*) *umbilicatum* (Hyatt) 1891	Pennsylvanian (lower)	Kansas.
G. (*D.*) *walteri* (Miller and Unklesbay) 1942	Permian (San Andres limestone)	New Mexico.
G. (*D.*) *williamsi* (Miller and Owen) 1934	Pennsylvanian (Cherokee formation)	Missouri.

mm, width and height of the most adoral part of the living chamber are 47 mm and 59 mm respectively. The living chamber measures 160 mm along the venter. At the junction of the living chamber and the phragmocone the venter is 25 mm wide.

The umbilicus is broad, measuring 67 mm, and the umbilical perforation is 6 mm. in diameter. The whorls are very little embracing. The specimen is an internal mold with a perfectly smooth surface. There appear to be, however, low, small, and indistinct elongated nodes on the ventral shoulders of the most adoral half volution of the phragmocone. There are also two low, large, blunt nodes on the umbilical shoulders of the living chamber.

The suture is the most distinctive feature of this species (text fig. 27). The ventral lobe is deep and acutely rounded. The most adoral suture has a ventral lobe 23 mm wide and 23 mm deep. In the more adapical sutures the depth of the ventral lobe is always slightly less than the width of the lobe. There is an acute saddle on the ventral shoulder which passes to a broad deep lateral lobe spanning the whole flank. On the umbilical wall, the suture trends slightly adorally and is faintly concave. The septa are closely spaced, with 27 camerae in the last volution. The siphuncle was not observed.

Remarks.—This species is very similar to such species of *G.* (*Domatoceras*) as *G.* (*D.*) *williamsi* Miller and Owen and *G.* (*D.*) *umbilicatum* Hyatt. The only essential difference is in the deep ventral lobe. In this it is similar to *G.* (*Grypoceras*) *mesodicum* (Hauer) of the Upper Triassic, although it differs in being more evolute and compressed. *G.* (*D.*) *williamsi* is of special interest because it has nodes developed on portions of the ventral and umbilical shoulders very similar to that seen in (*G.*) (*Plummeroceras*) *plummeri*.

Occurrence. Belle Plains formation, 2½ miles west of Baird, Callahan County, Texas; Bureau of Economic Geology loc. 30–T–9; the type specimen was collected by F. B. Plummer, for whom it is named.

Holotype.—Bureau of Economic Geology, University of Texas, no. 7173.

Genus GRYPONAUTILUS Mojsisovics, 1902

Genotype: *Nautilus galeatus* Mojsisovics

Mojsisovics (1902, p. 229) erected this group as a subgenus of *Grypoceras* and most authors have accepted this arrangement. The writer believes that this group of nautiloids should be given full generic rank. *Gryponautilus* has been recorded from only the Karnian and Norian and seems to be a specialized offshoot of *Grypoceras*; four species, and four specimens referred with question or with affinities to one of the four species, have so far been recorded. Of these eight forms one occurs in the Norian, and seven in the Karnian.

Gryponautilus is a highly involute nautiloid with a very narrow venter on the mature portions of the conch. The inner whorls have broad concave to convex truncated venters and inflated flanks (text fig. 25). According to Mojsisovics, in the genotype species, the venter becomes very narrow and almost forms a sharp keel at a whorl height of 130–150 mm. In such species as *G. suessi* and *G. cooperi*, both much smaller than *G. galeatus* and not having the acute ventered last whorl, there is a row of nodes along the sharp ventrolateral margins. Likewise *G. suessi* and *G. cooperi* have very simple sutures with very shallow

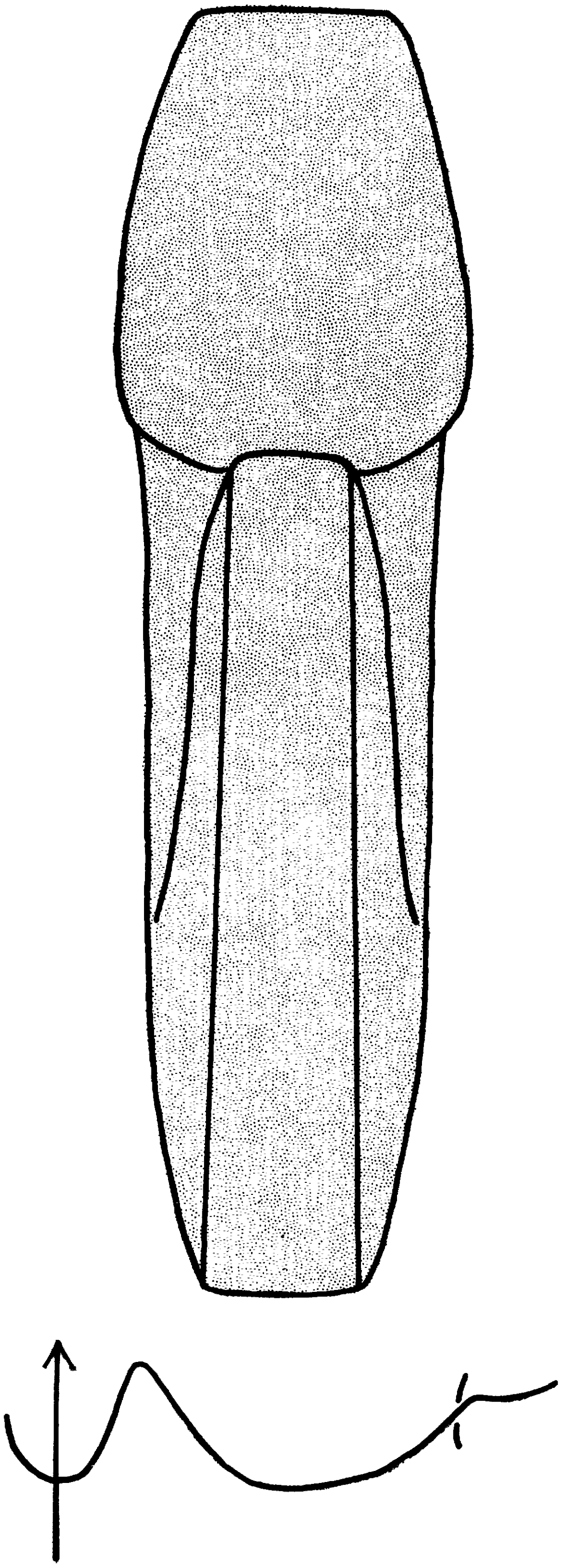

FIGURE 27.—Diagrammatic cross section and representation of suture of the holotype of *Grypoceras* (*Plummeroceras*) *plummeri* n. sp. (Bureau of Economic Geology Coll., 7173) from the Belle Plains formation, Callahan County, Texas, ×0.8.

ventral and lateral lobes. In *G. galeatus* there is a shallow ventral lobe, a deep lateral lobe, and a lateral saddle that separates the lateral lobe from the umbilical lobe (Mojsisovics 1902, p. 229). *Gryponautilus* also has an annular lobe.

None of the species assigned to *Gryponautilus* have the highly contracted venter in the adoral whorls of the genotype. They all, however, have inner whorls that closely resemble those of *G. galeatum* and are probably correctly assigned to this genus. Mojsisovics believed *Gryponautilus* to be an aberrant involute offshoot of Grypoceras, and the present writer has found no evidence to the contrary.

Gryponautilus cooperi (Smith)

Plate 7, figures 1–5

1927. *Grypoceras* (*Gryponautilus*) *cooperi* Smith, U. S. Geol. Survey, Prof. Paper 141, p. 107, pl. 88, figs. 1–5.

The holotype and one paratype are available for study. The conch is involute, robust, and has a slightly arched truncated venter. The living chamber of the holotype is 75 mm long and of the paratype 48 mm. The greatest width of the conch is just ventral to the umbilical shoulder and the broadly rounded flanks converge strongly towards the venter. The ventral shoulders are acute and have conspicuous elongated nodes that coalesce to form an almost continuous carinate ridge along the shoulder. The nodes on the ventral shoulder are nearly paired on the phragmocone, but on the living chamber they are alternate in position.

The suture has a very shallow ventral and lateral lobe. The siphuncle was not observed. No part of the shell is preserved on either available specimen.

	Dimensions (in millimeters)	
	Holotype	Paratype
Diameter	67	25. 5
Height of last whorl	38	15.
Width of last whorl	41	22. 5
Diameter of umbilicus	8	5.
Width of venter	18	10.

Gryponautilus cooperi appears to be closely related to *G. suessi* Mojsisovics and *G. suessiforme* Diener, but is sufficiently different to be easily distinguished. These three forms differ from the genotype, *Gryponautilus galeatus* Mojsisovics, in lacking the nearly acute venter in the mature portion of the conch.

Occurrence.—From the Upper Triassic limestone, upper or *Juvavites* subzone of the zone of *Tropites subbullatus*, Bear Cove, north end and east side of

Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.

Types.—Holotype, U.S.N.M. 74127; paratype 74127a.

Genus MENUTHIONAUTILUS Collignon, 1933

Genotype. *Nautilus (Menuthionautilus) kieslingeri* Collignon

Unique among Triassic nautiloids is this monotypic genus from Scythian rocks in northern Madagascar. Few late Paleozoic or Triassic nautiloid genera have the siphuncle in an extremely ventral position. *Solenochilus* is the only late Paleozoic form with the siphuncle in this position. *Menuthionautilus* is the only Triassic genus with the siphuncle against the venter. *Syringoceras* has a siphuncle that is somewhat ventrally placed but it is not in so extreme a position as in *Solenochilus* or *Menuthionautilus*.

The conch is involute, rapidly expanding, and smooth. Whorls are compressed with a broadly convex venter on the mature portion of the conch. The inner whorls, according to Collignon's cross section (text fig. 28 of present report) have a flattened venter. The flanks are broadly convex. The umbilicus measures approximately 12 percent of the diameter of the conch. The umbilical shoulders are sharply rounded, unbilical walls steep. The suture forms a ventral lobe and a broad lateral lobe that occupies nearly the whole flank. The siphuncle is in an extreme ventral position and about 1 mm in diameter.

The shape of the conch and the suture clearly place this form in the Grypoceratidae. It shows closest affinities with the subgenus *Grypoceras (Domatoceras)*. The compressed involute conch with a flattened convex venter on the inner whorls and a more broadly convex venter on the mature portion of the conch also seem to indicate affinities with *G. (Domatoceras)*. The sutures are similar, both forms having rounded ventral and lateral lobes. Such involute species of *G. (Domatoceras) as G. (D.) kleihegei* and *G. (D.) moorei* are very similar in their main features to *Menuthionautilus kieslingeri*. Likewise in both of these species the siphuncle lies in a somewhat ventral position, *G. (D.) kleihegei* having its siphuncle only 12.5 percent of the height of the whorl from the venter. *G. (Domatoceras)* was also the ancestral form of *Stenopoceras*, a highly compressed genus with a very narrow venter. *Menuthionautilus* shows some affinities to *Grypoceras*, also considered a derivative of *G. (Domatoceras)*. However, *Grypoceras* appears to be a more advanced form and differs in the proportions of its sutural elements and in general form of the conch. It seems best to consider *Menuthionautilus* an aberrant offshoot of *G. (Domatoceras)*.

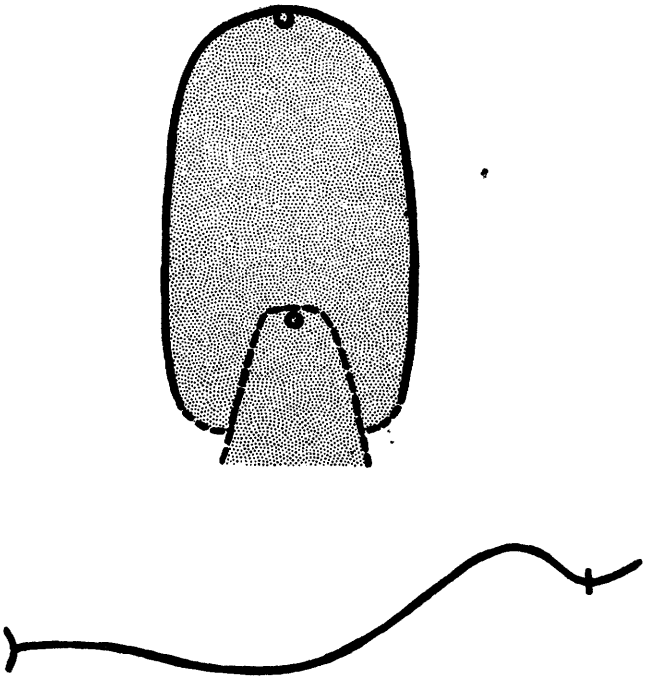

FIGURE 28.—Diagrammatic cross section of the holotype of *Menuthionautilus kieslingeri* Collignon from the Lower Triassic of Madagascar, × 1. After Collignon 1933, fig. 4.

Genus STENOPOCERAS Hyatt, 1893

Genotype: *Phacoceras dumblei* Hyatt

Late Paleozoic nautiloids with strongly compressed and involute smooth conchs are generally placed in the genus *Stenopoceras*. The suture forms a deep ventral saddle, a broad rounded lateral lobe, a smaller rounded dorsolateral saddle in the region of the umbilical shoulder, a similar lobe that centers on or near the umbilical seam, and a similar internal lateral saddle which extends to a moderately deeply depressed V-shaped truncated dorsal lobe. The siphuncle is small and lies ventral of the center of the conch.

Stenopoceras is clearly related to *G. (Domatoceras)* (Miller and Youngquist, 1949, p. 70). It is connected with the latter genus through such species as *G. (D.) kleihegei and G. (D.) moorei*. Hyatt (1891, p. 349) made the following comments in his discussion of the genotype species of *Stenopoceras, Phacoceras dumblei:* The aspect of the adults and the sutures in this genus are like Triassic species such as *Grypoceras (Nautilus) galeatus*, Mojsisovics, [now *Gryponautilus*] and at first they appear to have occurred before their proper geologic period. When, however, their young are studied, it is plain that their shells at early stages have the ordinary characteristics of normal members of the Carboniferous faunas, and that the peculiarities of later stages were evolved from purely Carboniferous forms. There mimicry of Triassic shells in later stages must therefore be regarded simply as good examples of parallel progressive complications arising independently in different genetic series during different periods of time.

Distribution of species of the genus Stenopoceras

Species	Stratigraphic distribution	Geographic distribution
Stenopoceras abundans Miller and Thomas 1936	Pennsylvanian (Casper formation)	Wyoming.
S. cooperi Miller and Unklesbay 1942	Pennsylvanian (Neva limestone)	Kansas.
S. dumblei (Hyatt) 1891	Permian (Fort Riley? limestone)	Geary County, Kans.
S. inexpectans Miller 1945	Permian (Leonard formation)	Brewster County, Tex.
S. rouillieri (deKoninck) 1878	Upper Carboniferous	Central Russia.
S. smithi Miller and Unklesbay 1947	Pennsylvanian (Conemaugh series)	Pennsylvania.
S. tularosense Miller 1932	Pennsylvanian (Abo? sandstone)	New Mexico.
S. whitei Miller and Youngquist 1949	Permian (Clyde formation)	Baylor County, Tex.

This genus represents a specialized compressed offshoot of *G.* (*Domatoceras*) and does not seem to have given rise to any other forms. *Stenopoceras* ranges from the lower part of the Upper Carboniferous up into the middle part of the Permian in North America and central European Russia.

Genus STEAROCERAS Hyatt, 1893

Genotype: *Endolobus gibbosus* Hyatt

Miller and Youngquist (1949) in their monograph on American Permian Nautiloids discussed this genus extensively. They recognized that a wide assortment of both quadratic and compressed forms had been included in *Domatoceras*. Very little attention has been given the genus *Stearoceras* since Hyatt described it. As now defined by Miller and Youngquist it includes forms with subtrapezoidal conchs that are depressed dorsoventrally, and flattened laterally and ventrally (text fig. 25). The umbilicus is moderate in size, deep and probably perforate. The umbilical shoulders are fairly distinct, and the umbilical walls are steep. The sutures form slight ventral, lateral, and dorsal lobes and there is a small annular lobe.

The above authors broadened the interpretation of this genus by including several species with a wide umbilicus and rather abrupt umbilical shoulders. Their conclusions on this genus are tentatively followed by the present writer. Actually, *Stearoceras*, includes many nautiloids with subtrapezoidal conchs that were once included in *Domatoceras*. Several species previously placed in *Titanoceras* and *Metacoceras* were also placed in *Stearoceras* by Miller and Youngquist. Their interpretation is very different from earlier authors and it is not considered at all certain that all the species now referred to this genus are properly placed.

Stearoceras seems to be an independent development out of *Koninckioceras* paralleling *G.* (*Domatoceras*). As pointed out by Miller and Youngquist (1949, p. 42) there are intermediate forms between *Stearoceras* and *G.* (*Domatoceras*). It is known to range from the lower part of the Pennsylvanian to the middle Permian.

Genus PSELIOCERAS Hyatt, 1883

Genotype: *Nautilus ophioneus* Waagen

Of the nine genera included in the Grypoceratidae *Pselicoceras* is the most widely umbilicate form. Hyatt erected this genus for the "Ophionei" of Waagen (1879, p. 58) designating *Nautilus ophioneus* Waagen as the genotype. The group includes compressed nautiloids with whorls little embracing and having an umbilical perforation. The conch is smooth, ventral and lateral areas are slightly convex, and umbilical shoulders broadly rounded (text fig. 23). The suture is straight over the venter and forms a shallow lateral lobe. The siphuncle is about central. Only the three species described by Waagen from the *Productus* limestone of

Distribution of species of the genus Stearoceras

Species	Stratigraphic distribution	Geographic distribution
Stearoceras aberrans (Miller and Unklesbay) 1942	Permian (Chupadera formation)	New Mexico.
S. conchiferum (Hyatt) 1891	Late Paleozoic	Texas.
S. gibbosus (Hyatt) 1893	Pennsylvanian (lower)	Do.
S. hesperium Miller and Youngquist 1949	Permian (Leonard formation)	Do.
S. highlandensis (Meek and Worthen) 1873	Pennsylvanian (McLeansboro formation)	Illinois.
S. ingens (Miller, Dunbar, and Condra) 1933	Pennsylvanian (middle)	Nebraska.
S. lasallensis (Meek and Worthen) 1873	Pennsylvanian (McLeansboro formation)	Illinois.
S. militarium (Hyatt) 1893	Permian (Clyde formation)	Baylor County, Tex.
S.? permianum (Swallow) 1858	Permian	Kansas.
S. phosphoriense (Branson) 1930	Permian (Phosphoria formation)	Wyoming.
S. rotundatum (Miller and Unklesbay) 1942	Permian (San Andres limestone)	New Mexico.
S. sanandreasense (Miller, Dunbar, and Condra) 1933.	Permian (San Andres limestone and Kaibab formation).	New Mexico, Ariz.
S. simplex (Hyatt) 1893	Permian (Clyde formation)	Baylor County, Tex.
S. sublaeve (Miller, Dunbar, and Condra) 1933	Pennsylvanian (Neva limestone)	Texas.
S. toddanum (Gurley) 1883	Pennsylvanian	Missouri.

the Salt Range have been assigned to this genus: *P. ophioneus* from the lowest part of the Middle Productus limestone, *P. connectens* from the upper part of the Middle Productus limestone, and *P. convolutus* from the Upper Productus limestone.

Miller and Youngquist (1949, p. 41) placed *Pselioceras* in the Domatoceratidae, and they also pointed out the general similarity of that genus with *Domatoceras* but suggested that it may have had a different ancestry. Miller and Unklesbay (1942, p. 721–722) had placed these three species in the genus *Domatoceras*. Waagen (1879, p. 63) pointed out the similarity of *P. convolutus* with *Nautilus spitiensis* Stoliczka. Waagen recognized an evolutionary trend in his "Ophionei" toward greater involution and believed that *Nautilus spitiensis* now *Syringonautilus* was merely a continuation of this developmental series.

Genus TITANOCERAS Hyatt, 1884

Genotype: *Nautilus ponderosus* White

Miller and Youngquist (1949, p. 69–70) characterized this genus as follows:

> The whorls are subquadratic in cross section, being distinctly wider than high, slightly impressed dorsally, rounded dorsolaterally, flattened but nevertheless convex laterally, subangular ventrolaterally, and concave ventrally. The umbilicus is large, open, and perforate. At full maturity each of the ventrolateral shoulders of the conch bears a row of relatively small elongate nodes. The mature sutures form broad rounded ventral, lateral and almost certainly dorsal lobes. No information is available in regard to the siphuncle.

These authors placed no late Paleozoic nautiloids in this genus in their monograph on Permian Nautiloids. It is not clear how many Carboniferous species should be placed here in addition to the genotype. *Titanoceras* is possibly an offshoot of *G.* (*Domatoceras*) and does not seem to have been a direct ancestor of any Triassic species.

Family SYRINGONAUTILIDAE Mojsisovics, 1902

The interpretation of this family followed here is very similar to that of Mojsisovics when he first established it. Only five genera, more or less closely related, are included: *Syringonautilus*, *Syringoceras*, *Juvavionautilus*, *Oxynautilus* and *Clymenonautilus*. *Syringonautilus* and *Syringoceras*, which differ only in the position of the siphuncle, are the dominant forms Distinguishing the two genera on that basis alone is open to question. Study of large collections of both genera would probably decide the validity of the distinction, but such collections were not available. For the present, *Syringoceras* and *Syringonautilus* are considered independent offshoots from the complex between *G.* (*Domatoceras*) and *Stearoceras* of the Grypoceratidae.

Juvavionautilus, *Oxynautilus*, and *Clymenonautilus* are aberrant developments of the Late Triassic. The last two genera are monotypic and the first has only six species. *Juvavionautilus* has a conch pattern similar to some late Paleozoic domatoceratids, and *Oxynautilus* has a highly involute compressed conch similar to that found in *Stenopoceras*. *Clymenonautilus* has a conch pattern like that of *Syringonautilus* but a suture that passes straight over the venter and forms a narrow, deep lateral lobe. In this last feature it shows convergence to the Clydonautilidae. Cross sections of the conch of species of each of these genera are illustrated in text figure 32.

Syringoceras and *Syringonautilus* range from the Anisian to the Norian (text fig. 29). Only one species of *Syringoceras* is known from North America. The two genera are confined mainly to Triassic areas within the Tethyian geosyncline. *Juvavionautilus* is Norian in age and found in the Alpine and Timor Triassic areas. *Clymenonautilus* is found only in the Norian of the Alps. *Oxynautilus* is found in the Norian of the Alps and of California (Smith, 1927).

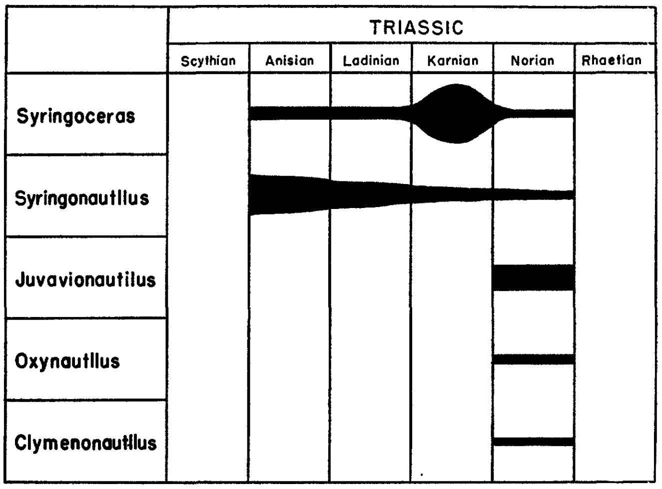

FIGURE 29.—Range chart showing known stratigraphic occurrence of the Syringonautilidae. The width of the line is proportional to the number of species.

PHYLOGENY

The origin of the Syringonautilidae is much less obvious than the other families of Triassic nautiloids (text fig. 21). Their origin in the Grypoceratidae is based on the similarity of the basic conch patterns found in some groups of these two families. The most important evolutionary lines in Pennsylvanian and Permian Grypoceratidae are *Stearoceras* and *G.* (*Domatoceras*), which show a wide divergence in conch form and have transitional forms between them. It is in these transitional forms that one can find nautiloids with the essential morphological features from which it was possible to derive two independent lines, that is, one leading to *Syringonautilus* and the other to *Syringoceras.* It is difficult to imagine any other late Paleozoic ancestors for these two Triassic genera.

The evolution of *Syringonautilus* and that of *Syringoceras* have interesting and contrasting patterns. *Syringonautilus* has the largest number of species at the beginning of its recorded history and declines rapidly in numbers of species. *Syringoceras* begins slowly and reaches its acme in numbers of species late in its history. The reason for such a pattern is not known.

In the Late Triassic three aberrant forms developed out of *Syringonautilus: Juvavionautilus, Oxynautilus,* and *Clymenonautilus. Juvavionautilus* and *Oxynautilus* have conch patterns similar to those found in the Paleozoic ancestral family Grypoceratidae. *Clymenonautilus* is convergent with the Clydonautilidae in its suture but retains the conch pattern of typical *Syringonautilus.* All three Late Triassic genera are unsuccessful experiments coming near the end of the family history.

Genus SYRINGONAUTILUS Mojsisovics, 1902

Genotype: *Nautilus lilianus* Mojsisovics

Syringonautilus is distinguished from *Syringoceras* by the subcentral position of its siphuncle (pl. 18, figs. 3, 4). *Syringoceras* has a nearly marginal siphuncle, but the literature reveals neither the amount of variation in position of the siphuncle within either genus, nor whether there is gradation between the two genera.

A diagram showing the number of species per epoch (text fig. 29) reveals an interesting distribution that may or may not be significant. Of *Syringonautilus* there are no species in the Scythian, 9 in the Anisian, 5 in the Ladinian, 3 in the Karnian, and 1 indeterminate species in the Norian. For *Syringoceras* there are no Scythian species, 2 in the Anisian, 2 in the Ladinian, 13 in the Karnian, and 1 species in the Norian. The pattern of diversification between these two genera is exactly opposite. *Syringonautilus* has a great period of expansion near the beginning of its range and gradually declines. *Syringoceras* develops slowly and has its period of expansion in the Karnian, which is followed by a great decline in the Norian where only one species is recorded. The significance of the above distribution patterns is difficult to interpret in absence of careful first hand study of all the species involved. Admittedly also the paleontologic record is incomplete and the relationship of distribution may be merely a coincidence. Possibly the forms with the siphuncle in a nearly marginal position now included in *Syringoceras* are merely intrageneric variants that have been set apart on this one character. If this is true, the proportion of variants towards a nearly marginal siphuncle progressively increases.

No species of *Syringonautilus* have as yet been recorded from the North American Triassic. However, the genus is widespread in Eurasia, having been reported from the Alps, Hungary, Germany, Greece, Himalayas, Timor, Japan and Spitzbergen.

Distribution of species of the genus Syringonautilus

Species	Stratigraphic distribution	Geographic distribution
Syringonautilus bosnesis (Hauer) 1892	Triassic (Anisian)	Alps, Yugoslavia.
S. bullatus (Mojsisovics) 1873	Triassic (Karnian)	Alps, Hungary.
S. carolinus (Mojsisovics) 1882	Triassic (Anisian)	Alps, Greece, Timor.
S. japonicus Yabe and Shimizu 1927	Triassic (Anisian, Ladinian)	Japan.
S. lilianus (Mojsisovics) 1882	Triassic (Anisian)	Alps, Yugoslavia.
S. linearis (Münster) 1841	Triassic (Karnian)	Alps.
S. longobardicus (Mojsisovics) 1882	Triassic (Ladinian, Karnian)	Do.
S. nordenskjöldi (Lindstroem) 1865	Triassic (Anisian)	Spitzbergen.
S. obtusicarinatus (Reis) 1900	do	Alps.
S. primoriensis (Martelli) 1904	do	Yugoslavia, Greece.
S. spitiensis (Stoliczka) 1865	do	Himalayas, India.
S. subbullatus Schnetzer 1934	Triassic (Muschelkalk)	Germany.
S. subcarolinus (Mojsisovics) 1882	Triassic (Anisian, Ladinian)	Alps, Yugoslavia.
S. zinnae (Airaghi) 1902	Triassic (Ladinian)	Alps, Roumania, Greece?
S. nov. f. ind. Mojsisovics 1896	Triassic (Norian)	Alps.

Genus SYRINGOCERAS Hyatt, 1894

Genotype: *Syringoceras granulosostriatus* (Klipstein)

When Hyatt (1894, p. 546), first described this genus he made the following comments:

> This genus has been framed for Triassic species like the type, *Syringoceras granulosostriatus,* which have a tubular, nepionic volution with the siphuncle subventran. The early nepionic shell is also ornamented with very closely set transverse ridges, but it has no longitudinal ridges until a comparatively late stage. This nepionic ornamentation is like that of the genus *Hercoceras* at the same age. The impressed zone is present only after contact and is not deep. The genus includes the group of *Nautilus barrandei* of Mojsisovics, the equivalent of *Nautilus linearis,* Laube, and *S.* (*Naut.*) *evolutum,* sp. Mojsisovics.

In the above description Hyatt quite clearly designates *Syringoceras granulosostriatus* as the type (pl. 18, figs. 5–8). However, Mojsisovics (1902, p. 214) listed *Syringoceras barrandei* (Hauer) as genotype (pl. 18, fig. 13). Every subsequent author who has referred to this genus has followed Mojsisovics' interpretation.

Syringoceras includes forms with rapidly expanded conchs and usually a small umbilical perforation. The early whorls are tubular, but grade into whorls that have well-defined and steep to broadly rounded umbilical shoulders and rounded but distinct ventral shoulders (text fig. 30). The cross section of a mature conch is subquadratic to slightly compressed. The width of the umbilicus averages 25 to 30 percent the diameter of the conch. The only ornamentation consists of a delicate network of lirae. The sutures show only a faint ventral saddle, a shallow lateral lobe, and an annular lobe. The siphuncle is very near the venter.

The ancestry of *Syringoceras* is problematic, and its affinities to any Permian forms are less obvious than for many other Triassic genera. This genus differs from *Syringonautilus* only in position of the siphuncle, the latter genus having the siphuncle more nearly central. Waagen (1879, p. 63–64) considered *Pselioceras convolutum* (Waagen) to be closely related to *Syringonautilus spitiensis* (Stolizska) of the Himalayan Anisian. He also mentions the shifting of the siphuncle to a more nearly marginal position in some Triassic species, citing *Syringoceras brevis*, *S. evolutus*, and *S. eugyrus*, which he considered as probable descendants of *Syringonautilus spitiensis*. *Pselioceras* is poorly known, and only by the three species from the Salt Range described by Waagen (1879). Waagen concluded from a study of these three species that there was an evolutionary trend towards tighter coiling, and rounding of the whorl section. The Triassic genera *Syringonautilus* and *Syringoceras* he considered to be in a direct line of this trend. Waagen's interpretations may be correct but the meager data do not constitute proof.

The writer believes that a more convincing argument can be made for deriving *Syringoceras* and *Syringonautilus* from forms probably transitional between *Stearoceras* and *G.* (*Domatoceras*). The former genus has a depressed subquadratic conch with flattened venter and flanks, a moderate and deep umbilicus, and a simple suture with an annular lobe. *G.* (*Domatoceras*) includes compressed nautiloids with a more diversified suture. Between these two genera are many transitional forms. Whether all the species assigned to *Stearoceras* by Miller and Youngquist (1949) belong in that genus is not known but typical species, and those transitional to *G.* (*Domatoceras*), have a conch very similar to typical *Syringonautilus* and *Syringoceras* except for being more evolute. The oldest species of *Syringoceras* and *Syringonautilus* are from the Anisian. *Syringonautilus* and *Syringoceras* are considered independent developments from the *Stearoceras-Domatoceras* transition complex, but only large collections can prove that they are different genera. Vagaries of the position of the siphuncle in *Stearoceras* and *G.* (*Domatoceras*) is great. *Menuthionautilus*, a descendant of *G.* (*Domatoceras*) from the Early Triassic of Madagascar has the siphuncle in a marginal position. *Syringoceras* is considered to be another experimental form, the siphuncle shifting to a position near the margin but it was a great deal more successful than *Menuthionautilus*.

Distribution of species of the genus Syringoceras

Species	Stratigraphic distribution	Geographic distribution
Syringoceras acis (Münster) 1841	Triassic (Karnian)	Alps.
S. altius Mojsisovics 1902	do	Alps, Greece.
S. barrandei (Hauer) 1847	do	Alps, Roumania, Greece.
S. breve (Hauer) 1860	do	Alps.
S. brevius (Mojsisovics) 1873	do	Do.
S. credneri Mojsisovics 1902	do	Do.
S. doubreeanum Mojsisovics 1902	do	Do.
S. eugyrum (Mojsisovics) 1873	do	Do.
S. evolutum (Mojsisovics) 1873	Triassic (Ladinian, Karnian)	Alps, Greece.
S. externecavatum Welter 1915	Triassic (Anisian)	Timor.
S. granulosostriatum (Klipstein) 1843	Triassic (Ladinian, Karnian)	Alps, Greece.
S. malayicum Welter 1914	Triassic (upper)	Timor.
S. renzi Frech 1907	Triassic (Anisian)	Greece.
S. spurri Smith 1927	Triassic (Norian)	California.
S. tenuireticulatum (Assmann) 1925	Triassic (Muschelkalk)	Germany.
S. zitteli Mojsisovics 1902	Triassic (Karnian)	Alps, Greece?
S. zitteli timorense Welter 1914	Triassic (upper)	Timor.

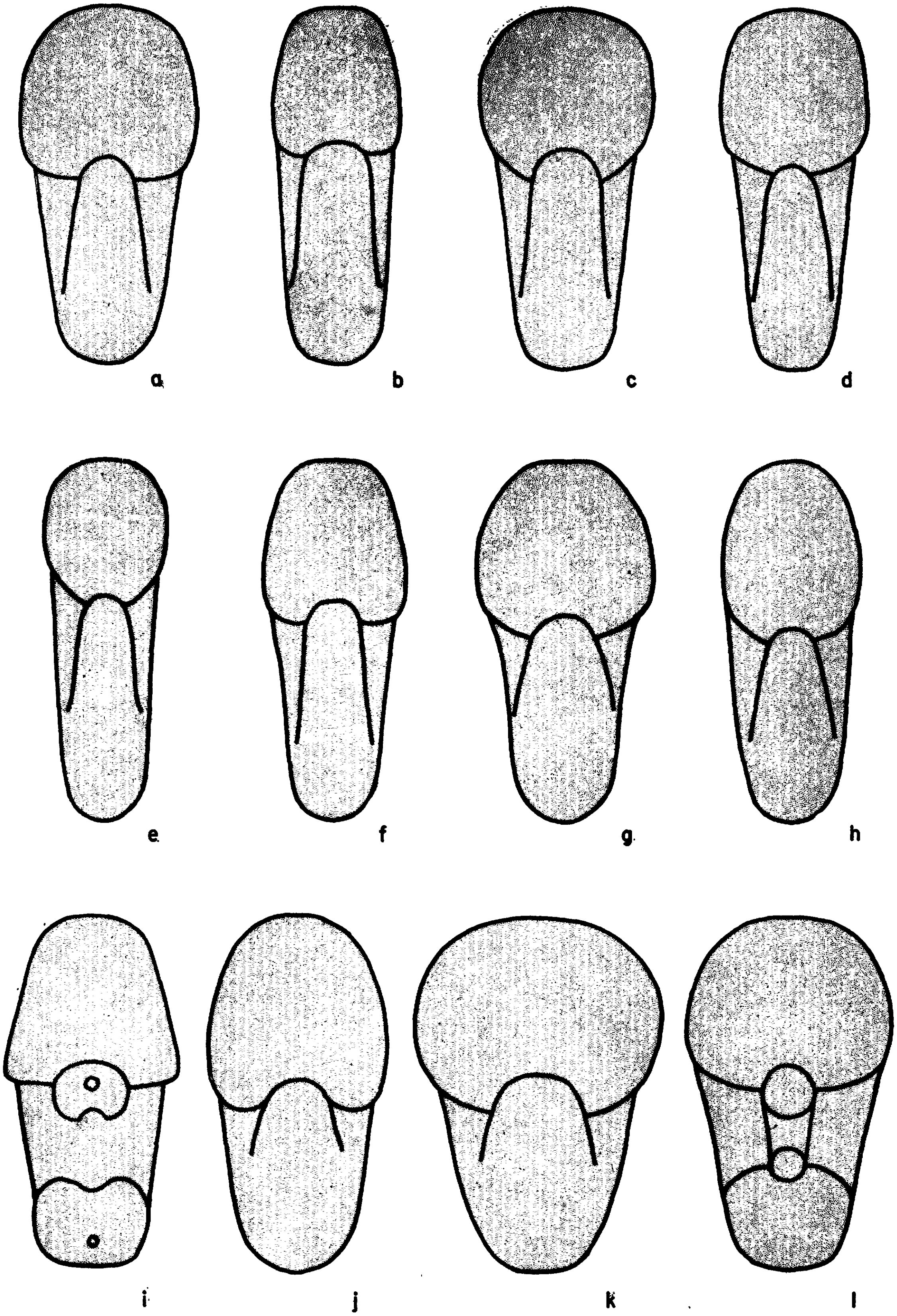

FIGURE 30.—Cross sections of the conch of *A*, *Syringoceras credneri* Mojsisovics 1902, pl. 6, fig. 1b, Diameter 110 mm; *B*, *Syringoceras zitteli* Mojsisovics 1902, pl. 6, fig. 3b, Diameter 67 mm; *C*, *Syringoceras breve* (Hauer), after Mojsisovics 1902, pl. 9, fig. 1b, diameter 42 mm; *D*, *Syringoceras barrandei* (Hauer), after Mojsisovics 1902, pl. 5, fig. 2b, Diameter 85 mm; *E*, *Syringoceras eugyrum* (Mojsisovics) 1873, pl. 6, fig. 3b, Diameter 48 mm; *F*, *Syringoceras evolutum* Mojsisovics 1902, pl. 7, fig. 1b, Diameter 136 mm; *G*, *Syringoceras daubreeanum* Mojsisovics 1902, pl. 5, fig. 1b, Diameter 37 mm; *H*, *Syringoceras altius* Mojsisovics 1902, pl. 6, fig. 2b, Diameter 60 mm; *I*, *Syringonautilus lilianus* (Mojsisovics) 1882, pl. 82, fig. 4b, Diameter 40 mm, the genotype of *Syringonautilus*; *J*, *Syringonautilus bosnensis* (Hauer) 1892, pl. 1, fig. 3b, Diameter 40 mm; *K*, *Syringonautilus bullatus* (Mojsisovics) 1873, pl. 5, fig. 1b, Diameter 126 mm; *L*, *Syringonautilus nordenskjöldi* (Mojsisovics) 1886, pl. 16, fig. 3b, Diameter 90 mm.

Syringoceras spurri Smith

Plate 7, figures 6, 7; text figure 31

1927. *Syringoceras spurri* Smith, U. S. Geol. Survey Prof. Paper 141, p. 106, pl. 104, figs. 8, 9.

The original description by Smith is quoted here:

> Form moderately robust, somewhat compressed laterally, with open though not very wide umbilicus and rounded venter. Surface shows fine, sharp backward-curving growth lines. Septa have only gentle curves; no real lobes nor saddles on the outside. Annular lobe not observed.
>
> *S. spurri* resembles *S. altius* Mojsisovics but differs in being more compressed and less widely umbilicate.

Occurrence.—Upper Triassic *Pseudomonotis subcircularis* zone of the Star Peak formation, in Muttleberry Canyon, in the West Humboldt Range, about 8 miles southeast of Lovelock, Nevada.

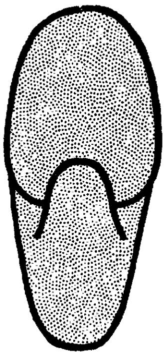

FIGURE 31.—Diagrammatic cross section of the holotype of *Syringoceras spurri* Smith (U.S.N.M. 74219) from Star Peak formation, Muttleberry Canyon, West Humbolt Range, Nevada, × 1.

Genus JUVAVIONAUTILUS Mojsisovics, 1902

Genotype: *Nautilus heterophyllus* Hauer 1849

The surficial features of the forms included in this Upper Triassic genus closely resemble those of *G.* (*Domatoceras*). *Juvavionautilus* includes widely umbilicate perforate shells with flattened to broadly rounded ventral and lateral areas. The younger whorls are usually more rounded. The conch expands slowly and the impressed zone is usually a third the height of the whorl. The greatest width of the whorl is above the umbilical shoulder (pl. 18, figs. 1, 2; text fig. 32). The sutures form a ventral saddle, a broad lateral lobe, a small saddle on the umbilical wall, and there is an annular lobe. The siphuncle is subcentral in position.

Mojsisovics discussed this genus rather thoroughly (p. 222–223, 1902) and believed that *Juvavionautilus* was derived out of *Syringonautilus*. He pointed particularly to *S. longobardicus* as a transitional form. In this species a definite umbilical shoulder is developed in the phragmocone, whereas in most other species the umbilical shoulder is well developed only on the living chamber. Mojsisovics also offered the possibility of a genetic relationship between *Pselioceras* and *Juvavionautilus* but any similarity between these two genera appears to be quite superficial. Both genera have a ventral saddle or a straight suture over the venter. *Syringonautilus* has a faint ventral saddle also. This genus (*Syringonautilus*) probably has its ancestry in the *Stearoceras-Domatoceras* complex whose members possess a ventral lobe. Two species from Timor described by Kieslinger (p. 98–100, 1924) as *J. brouweri* and *J. geyeriformis*, posses shallow ventral lobes in contrast to ventral saddles found in all other species of *Juvavionautilus*. In all other characters these two species agree with typical representatives of this genus and are therefore retained in it. It is difficult to consider *Pselioceras* an ancestral form of *Juvavionautilus*. As pointed out by Mojsisovics, *Pselioceras* is little known and seems to be confined to the Permian. No forms that could possibly be transitional to the Upper Triassic *Juvavionautilus* are known. The writer feels that for the time being it is best to follow Mojsisovics' interpretation of deriving *Juvavionautilus* out of *Syringonautilus*.

Genus OXYNAUTILUS Mojsisovics, 1902

Genotype: *Nautilus acutus* Hauer

This aberrant form derived from *Juvavionautilus* was considered by Mojsisovics to be a subgenus of *Juvavionautilus*. Diener (p. 777, 1919) considered this form to be sufficiently distinct to be raised to full generic rank, and his procedure is followed here. The genus includes nautiloids that have compressed conchs with a very narrow to acute venter and with or without a keel. Whorls expand rapidly, are extremely high with the widest portion just above the umbilical shoulders (pl. 19. figs, 1, 2; text, fig. 32). Each whorl embraces more than a third of the preceding whorl. The umbilicus is well defined, moderate in size and perforate, and the umbilical shoulders are abruptly

Distribution of species of the genus Juvavionautilus

Species	Stratigraphic distribution	Geographic distribution
Juvavionautilus brouweri Kieslinger 1924	Traissic (upper)	Timor.
J. geyeri Diener 1919	Triassic (Karnian, Norian)	Alps.
J. geyeriformis Kieslinger 1924	Triassic (upper)	Timor.
J. heterophyllus (Hauer) 1849	Triassic (Norian)	Alps.
J. subtrapezoidalis Mojsisovics 1902	do	Do.
J. trapezoidalis (Hauer) 1860	do	Alps, Timor.

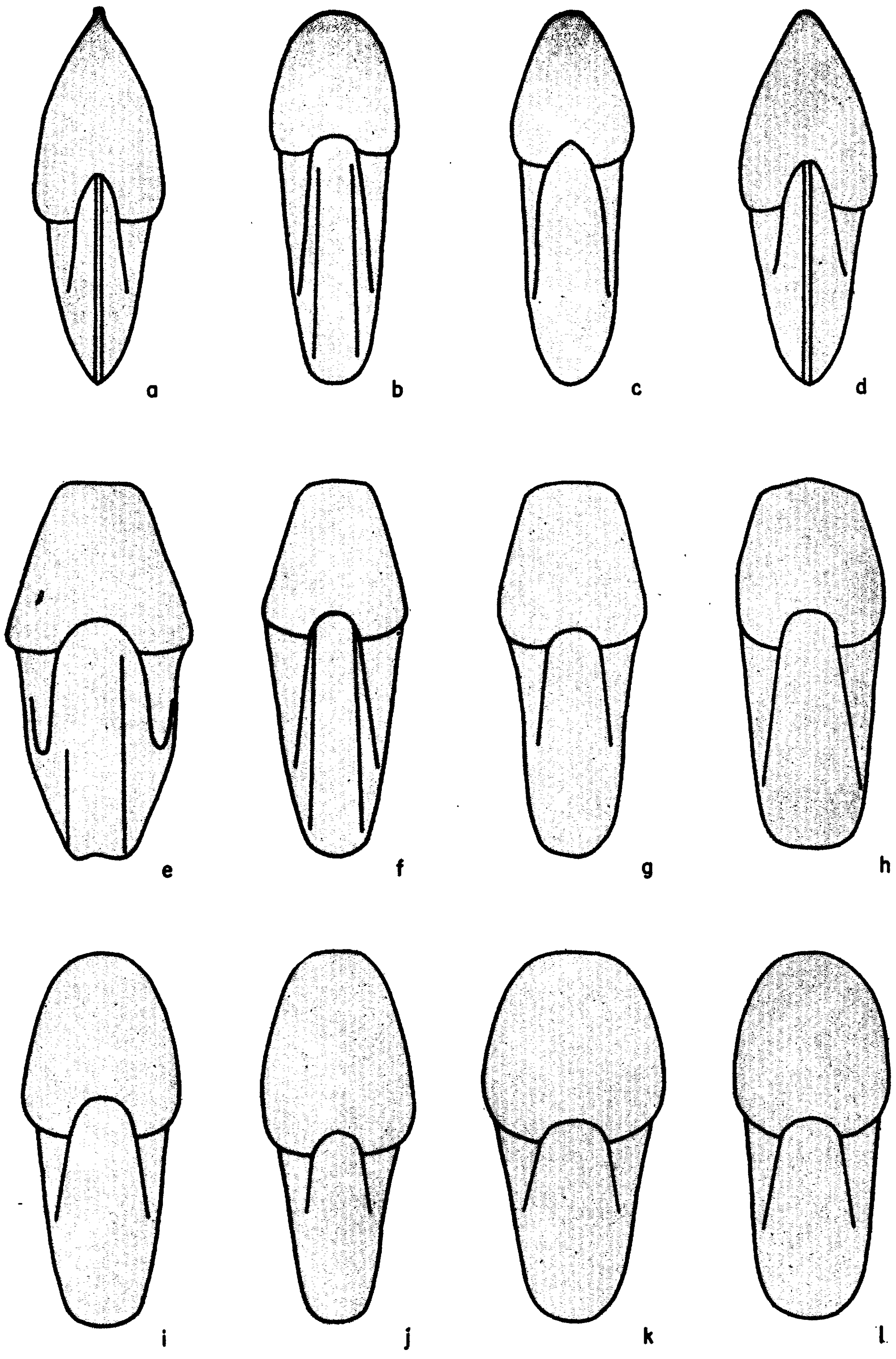

FIGURE 32.—Cross sections of the conch of *A*, *Oxynautilus acutus* (Hauer), after Mojsisovics 1902, pl. 3, fig. 1b, Diameter 138 mm; *B*, *Juvavionautilus trapezoidalis* (Hauer), after Mojsisovics 1902, pl. 4, fig. 1b, Diameter 116.5 mm; *C*, *J. heterophyllus* (Hauer), after Mojsisovics 1902, pl. 4, fig. 2b, Diameter 128 mm; *D*, *Oxynautilus acutus* (Hauer), after Mojsisovics 1902, pl. 2, fig. 1b, Diameter 163 mm; *E*, *Juvavionautilus brouweri* Kieslinger 1924, fig. 24, Diameter 124 mm; *F*, *J. subtrapezoidalis* Mojsisovics 1902, pl. 3, fig. 2b, Diameter 89 mm; *G*, *J. geyeriformis* Kieslinger 1924, fig. 25a, Diameter 52 mm; *H*, *J. geyeri* Diener 1919, fig. 19, Diameter 49 mm; *I*, *Clymenonautilus ehrlichi* (Mojsisovics) 1873, pl. 6, fig. 9b, Diameter 55 mm; *J*, *Syringonautilus zinae* (Airaghi) 1902, pl. 4, fig. 4b, Diameter 35 mm; *K*, *S. longobardicus* (Mojsisovics) 1882, pl. 83, fig. 6b, Diameter 62 mm; *L*, *S. subcarolinus* (Mojsisovics) 1882, pl. 83, fig. 2b, Diameter 65 mm.

rounded, and the umbilical flanks are slightly convex and vertical. The suture forms a narrow to pointed ventral saddle, a broad lateral lobe, and a small lobe on the umbilical wall, with a saddle on the umbilical shoulder. An annular lobe is present. The siphuncle lies three-quarters the height of the whorl from the venter.

Oxynautilus is a monotypic genus known from the Norian of the Alps. Smith (p. 106–107, 1927) records the occurrence of *Oxynautilus acutus* from the

> Upper Triassic Hosselkus limestone, above the coral zone at the base of the beds of Norian age at the east side of the north end of Brock Mountain, between Pit River and Squaw Creek, Shasta County, California.

Smith also states that

> This specimen was completely shattered in the attempt to get it out of the splintery rock matrix and could not be illustrated.

Genus CLYMENONAUTILUS Hyatt, 1900

Genotype: *Nautilus ehrlichi* Mojsisovics

As no definition of this monotypic genus was given by Hyatt, the original description of the genotype by Mojsisovics (1873, p. 15) is quoted here in part.

> Rasch anwachsende Windungen von grösserer Höhe als Dicke involviren beiläufig ein Drittel der vorhergehenden Windung und bilden einen tiefen in der Mitte durchbrochenen Nabel. Der Uebergang von den Seiten in den Convextheil und zur Nabelwand ist gerundet. Die Seiten erscheinen ziemlich platt. Auf den inneren Windungen seiht man auf der Oberfläche der Schale feine Querstreifen, gekreuzt von ebenso feinen Längsstreifen. Die aüssere Windung scheint völlig glatt zu werden; doch kann dies vorläufig nicht mit voller Sicherheit constatirt werden. Die Kammer-Scheidewände verlaufen über den Convextheil nahezu gerade; innerhalb der Involutionsspirale bilden sie einen ziemlich tiefen zungenförmigen Laterallobus, kehren jedoch noch vor Erreichung des Nabelrandes in die frühere gerade Richtung zurück und wenden sich auf der Nabelwand etwas nach vorn. Die Stellund des Sipho konnte nicht ermittelt werden; derselbe scheint sich dicht am Convextheil zu befinden. Dimensionen—Durchmesser, 55 mm; Höhe des letzten Umganges, 28 mm; Dicke des letzten Umganges, 24 mm; Nabelweite, 16 mm.

(see pl. 7, figs. 8, 9).

Mojsisovics' description can be summarized as follows:

> The conch is rapidly expanding; the whorls higher than wide and inclosing a third of the preceding whorls and forming a deep and perforate umbilicus. The ventral and umbilical shoulders are rounded. The whorl sides are flattened. On the inner whorls the shell has fine cross striae and longitudinal lines. The outer whorls appear to be smooth. The suture passes straight over the venter and forms a deep, tongue shaped lobe on the whorl sides. The position of the siphuncle is not known.

When Hyatt proposed the genus *Clymenonautilus* he placed it in the family Clydonautilidae. Mojsisovics (1902, p. 221) differed with Hyatt on the taxonomic position of *Clymenonautilus* and made the following comments:

> Diese Gattung wurde von Hyatt in die Familie der Clydonautilidae gestellt, wozu wohl nur der tiefe, zungenförmige Laterallobus die Veranlassung darbot. Ich kann diese Auffassung nicht theilen und erblicke in *Clymenonautilus* einen durch die tiefe Ausbiegung eines schmalen Laterallobus abgeänderten Nachkommen des *Syringonautilus*-Stammes. Die ganze Gestaltung des Gehäuses und die Beschaffenheit der Schale weisen deutlich darauf hin.
>
> Die Involution der Umgänge ist die gleiche wie bei *Syringonautilus*.
>
> Ausser dem Laterallobus besitzt *Clymenonautilus* noch die Andeutung eines schwachen Lateralsattels, welche durch die flache Einsenkung eines Umbilicallobus hervorgerufen wird.

Mojsisovics' comments can be summarized as follows:

> This genus was placed by Hyatt in the Clydonautilidae in which the only relationship is in the deep, tongue shaped lateral lobe. In this conclusion I can not agree and see in the character of the conch and the lateral lobe relationship to *Syringonautilus*. The involution is the same as in *Syringonautilus*. In addition to the lateral lobe *Clymenonautilus* has an indication of a weak lateral saddle which is caused by a shallow umbilical lobe.

There has always been considerable disagreement among students of nautiloids as to the value of certain morphologic features in taxonomy. Recent work on Tertiary nautiloids by Spath (1927), and Miller and Youngquist (1949) have stressed the priority of differences in the suture pattern and ornamentation over the shape of the conch in the determination of the taxonomic position of a genus or species of nautiloid cephalopod. In the present case, however, a species agrees perfectly with the one group (Syringonautilidae) in the shape of its conch and degree of involution text (fig. 32), and with another group (Clydonautilidae) it agrees only in the over-all plan of the suture, that of having a deep lateral lobe. The lateral lobe in *Clymenonautilus* is rather narrow and confined to the mid point of the flanks. The straight course over the venter, in so far as the suture is concerned, indicates affinity between *Clymenonautilus* and *Styrionautilus*. However, the over-all similarity in the plan of the conch between *Clymenonautilus* and *Syringonautilus*, and the Syringonautilidae in general, is impressive. *Clymenonautilus* may represent a late evolutionary experiment on a relatively simple conch pattern that is convergent towards the Clydonautilidae. *Clymenonautilus* is a monotypic form from Norian rocks of the Alps, and until more material is found the question of its affinities will remain in doubt. For the present the classification of Mojsisovics are followed.

Family PARANAUTILIDAE Kummel, 1950

This new family is proposed to include two genera that Mojsisovics (1902) had placed in the family Clydonautilidae, along with genera that possessed no annular lobe (with the exception of *Gonionautilus*), involute conchs, and tended towards increased sinuosity of the suture. Two of the most primitive forms (*Paranautilus* and *Indonautilus*) are different from the remaining members of *Clydonautilidae* (namely *Styrionautilus, Clydonautilus, Proclydonautilus, Cosmonautilus,* and *Callaionautilus*) in that their conchs are generally not so involute and the sutures remain essentially straight with only minor inflections. Spath (1927b, p. 24) was the first to suggest a new family, commenting

> * * * *Paranautilus* and *Indonautilus*, Mojsisovics, though equally devoid of an annular lobe, must perhaps be referred to a separate family distinct also from Grypoceratidae.

Sibyllonautilus, which has an involute depressed conch and is characterized by the extraordinary expansion of the whorl section (especially in the living chamber) is also included in this new family. *Sibyllonautilus,* however, differs in one important characteristic from *Paranautilus* and *Indonautilus*—it has an annular lobe. Mojsisovics believed the annular lobe was of great systematic importance but other students, such as Diener, Kieslinger, Spath, and Miller, have minimized the absolute importance of this one character. Spath (1924b, p. 24) says:

> There seems to be no doubt that this annular lobe cannot be used, by itself, for the classification of Jurassic and Cretaceous nautili, for it disappears early in *Bisiphytes* and may persist in forms that otherwise cannot be separated from *Eutrephoceras.*

The similarity in conch pattern and suture between *Paranautilus* and *Sibyllonautilus* is striking. Even more impressive is the similarity to *Liroceras* of the family Liroceratidae, from which the Paranautilidae are thought to have developed. Mojsisovics (1902, p. 235) considered *Sibyllonautilus pertumidus* to be most closely related to *Germanonautilus*. The only similarity between these two genera is the presence in both of annular lobes, the patterns of the conchs are very different. Arthaber (1896) favored a relationship of *Sibyllonautilus pertumidus* to *Acanthonautilus cornutus* (Golovkinsky) (family Liroceratidae) of the Permian of Russia.

The family Paranautilidae is thus proposed to include Triassic nautiloids having involute globular to compressed conchs and simple sutures, but which may or may not have an annular lobe. Only three genera are included in this family: *Paranautilus, Indonautilus,* and *Sibyllonautilus.*

Geographically, the only genus in this family that is widespread is *Paranautilus.* It has been reported from beds ranging in age from Permian through the Triassic from North America, China, Timor, Himalayas, Sicily, Alpine region, and Germany. *Indonautilus* is a monotypic genus known only from Norian beds of the Himalayas. *Sibyllonautilus* ranges from the Anisian to the Norian, and has been reported from Nevada, British Columbia, Spitzbergen, and the Alpine region.

PHYLOGENY

In most features *Paranautilus* is closely related to *Liroceras* and allied genera of the Liroceratidae (text figure 33, 34). Even though no Scythian species of *Paranautilus* are known, it is suggested that two Permian species should be placed in this genus. The Liroceratidae Miller and Youngquist (1949) as now interpreted contains the following genera: *Liroceras* Teichert, *Coelogasteroceras* Hyatt, *Peripetoceras* Hyatt, *Condraoceras* Miller and Unklesbay, and *Acanthonautilus* Foord. All these forms have smooth, involute, nautiliconic conchs which are considerably impressed dorsally. These features also characterize the Paranautilidae. *Liroceras* seems to be the main evolving stock of the Liroceratidae with the other genera representing specializations of a Liroceratid conch. *Coelogasteroceras* and *Peripetoceras* have conchs that are slightly flattened ventrally and laterally. *Coelogasteroceras* likewise has a ventral groove. *Condraoceras* has a more compressed conch than *Liroceras. Acanthonautilus* has a very rapidly expanded conch with spine-like projections on the unbilical shoulder.

The relationship of *Liroceras* to *Paranautilus* is very similar to that between *Metacoceras* and *Mojsvaroceras, Domatoceras* and *Grypoceras.* In the latter case the Triassic forms were reduced to subgeneric rank to express the closeness of their relationships with the late Paleozoic stocks. *Liroceras* and *Paranautilus* may well have a similar relationship, however, the available data are insufficient to establish it.

The Paranautilidae are a small family of unspectacular Triassic nautiloids. Of the three genera included in this family *Paranautilus* is by far the most important and abundant. It gave rise to *Sibyllonautilus* and *Indonautilus.* Even more important, however, it appears to be the stock from which the Clydonautilidae arose. In its own evolutionary history *Paranautilus* shows a general trend towards more compression of the conch. *Sibyllonautilus* is an aberrant offshoot developing an extraordinarily expanded conch. This same type of specialization is found in *Acanthonautilus* of the late Paleozoic. *Sibyllonautilus* also has an annular lobe. *Indonautilus* is a monotypic form from Norian formations of the Himalayas. The form of the conch is similar to that of some grypoceratids with distinct ventral shoulders and rounded umbilical shoulders. A monotypic form like *Indonautilus* is difficult to place but in the sum total of its characters it appears to lie closest to *Paranautilus.*

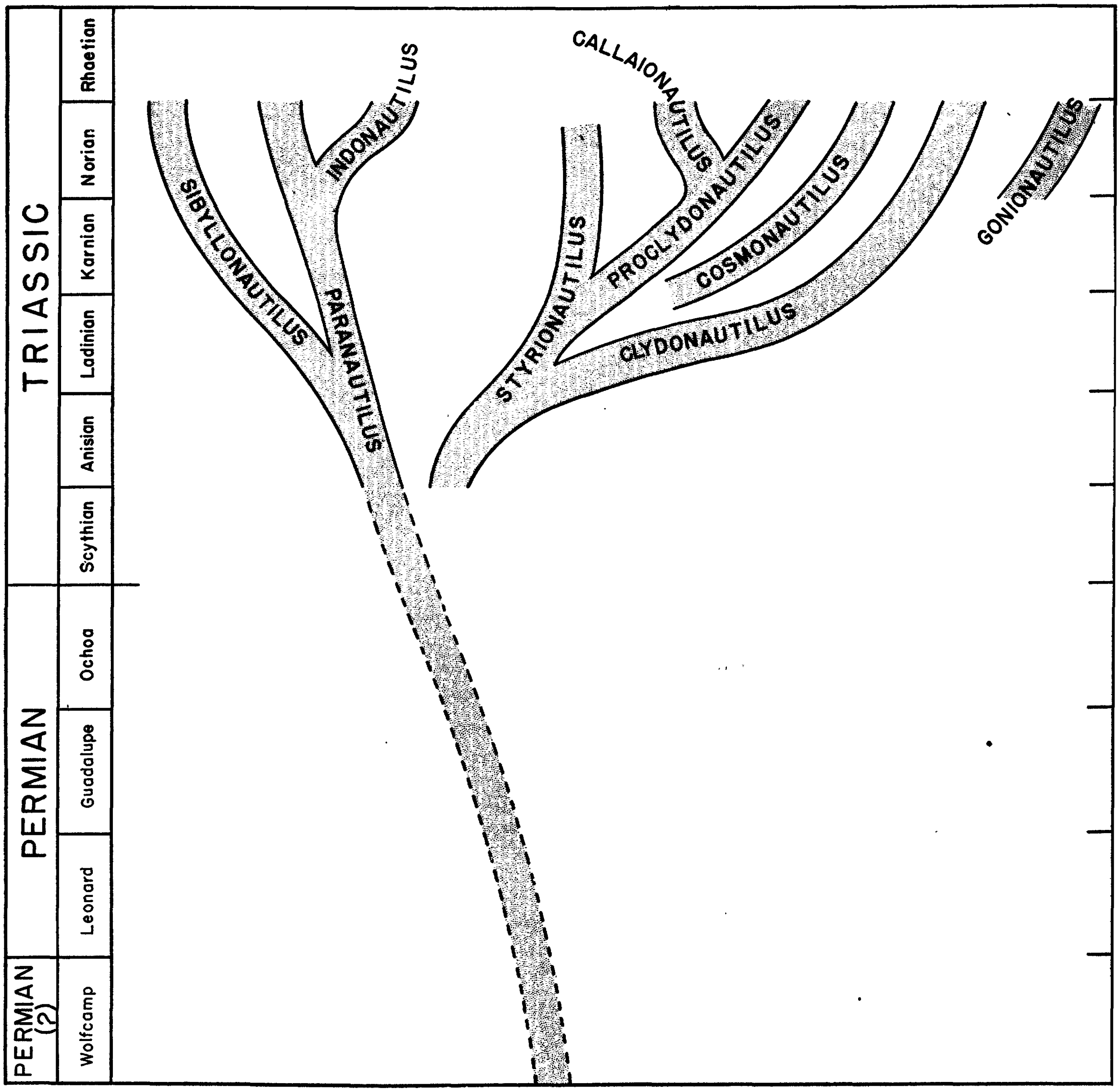

FIGURE 33.—Diagram showing inferred phylogeny and geologic distribution of the Paranautilidae, Clydonautilidae, and Gonionautilidae.

Genus PARANAUTILUS Mojsisovics, 1902

Genotype: *Paranautilus simonyi* (Hauer)

When Mojsisovics first described this genus (1902, p. 205, he diagnosed it as follows:

> Extern abgerundete, hochmündige, enge genabelte, glattschalige Gehäuse mit einfachen, nur leicht gebogenen und gedrängt stehenden Kammerwänden ohne Internlobus. Sipho bei der typischen Art unterhalb der halben Mündungshöhe der Internseite genähert, bei anderen Formen auch höher. Mundrand bei altersreifen, ausgewachsenen Individuen auf den Flanken eingebogen. Laterallobus blos einen flachen Sinus bildend. Umbilicalsattel kaum angeduetet. Externsattel bei den typischen Formen schwach angeduetet, einen breiten flachen Bogen beschreibend.

Mojsisovics' description can be summarized as follows:

> Conch smooth, narrowly umbilicate, whorls higher than wide, venter rounded with only slightly sinuous septa and no annular lobe. Siphuncle generally below the center of the whorl section. Growth lines concave on the whorl sides. Lateral lobe shallow, umbilical saddle hardly noticable, ventral saddle broad and low.

Paranautilus has the simplest plan of conch of all the Triassic nautiloid (text fig. 35). Mojsisovics con-

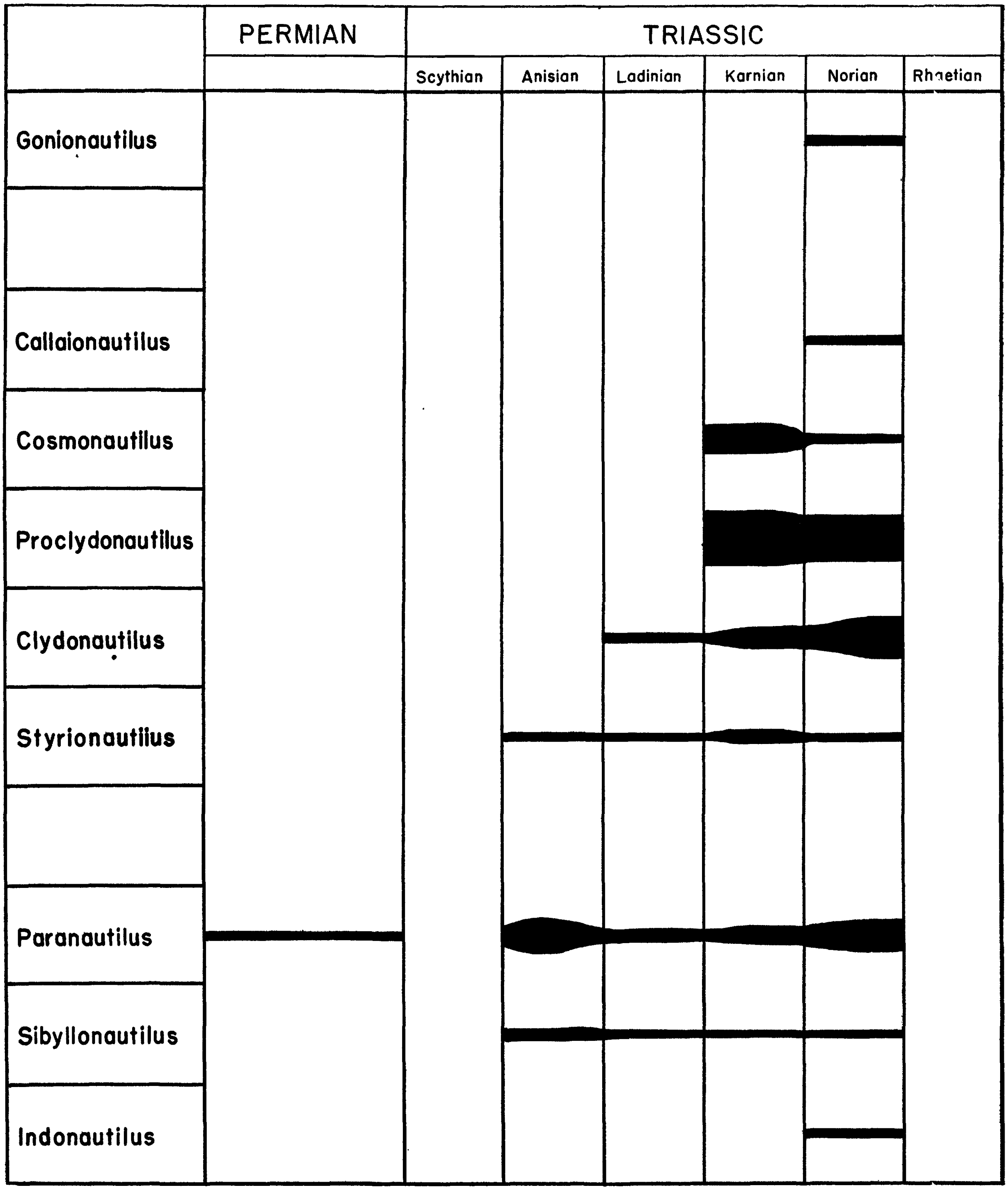

FIGURE 34.—Range chart showing known stratigraphic occurrence of Paranautilidae, Clydonautilidae, and Gonionautilidae. The width of the line is proportional to the number of species.

sidered *Nautilus peregrinus* Waagen, an unusual species from the Middle Productus limestone of the Salt Range, as possibly the oldest species of this genus. Miller and Unklesbay (1942, p. 721) had tentatively placed this species in *Stenopoceras*. Reed (1944, p. 362–363) considered it highly probable that *Nautilus peregrinus* should be placed in *Paranautilus*, but points out its close resemblance to *Solenochilus mokouensis* Yin (1933, p. 28, pl. 5, figs. la-b) of the Penchi Series North China and *Solenochilus buriensis* Reed (1944, p. 362, pl. 62, figs. 1, la-b) of the Upper Productus Limestone, Salt Range, India. The surficial features of the conch of *Nautilus peregrinus* and *Solenchilus buriensis* are very similar, but in the latter species the siphuncle is in a ventromarginal position, whereas in *Nautilus peregrinus* the siphuncle is more nearly central. *Solenochilus mokouensis* Yin is not a *Solenochilus*—one of the most diagnostic features of the genus is the ventromarginal position of the siphuncle. "*Solenochilus*" *mokouensis* has the siphuncle in a subcentral position "nearer the outer than the inner margin" and the species appears to be closely related to *Nautilus peregrinus.*

Unfortunately Waagen's *Nautilus peregrinus* is based on one poorly preserved and crushed specimen, making it difficult to ascertain all the morphological features. The conch is involute, compressed, and has a small and deep umbilicus. The venter is broadly rounded and the umbilical shoulders are rounded. The specimen has a shell diameter of 91 mm, diameter of the umbilicus 6 mm, height of the last whorl 58 mm, and width of the last whorl 35? mm. The suture is nearly straight, showing a broad shallow lateral lobe and a shallow dorsal saddle. The siphuncle appears to be "within the outer third of the radial diameter of the section".

The assignment of *Nautilus peregrinus* to *Stenopoceras* by Miller and Unklesbay does not seem to be justified. *Stenopoceras* is a highly compressed form with a narrow venter (text fig. 23). There are no other genera of late Paleozoic nautiloids to which *Nautilus peregrinus* can be assigned. There are, however, affinities to *Paranautilus*. In general the height and width of the whorl section of *Paranautilus* are about equal. However, there are several species that show a compressed conch as in Waagen's species. The present writer agrees with Mojsisovics' conclusion as to the relationships of *Nautilus peregrinus* and assigns the species to *Paranautilus*. "*Solenochilus*" *mokouensis* Yin from the Penchi series of North China is also tentatively assigned to this genus. Yin's description of this species is very incomplete and his illustrations do not aid greatly in diagnosing the characteristics of this species. *Paranautilus mokouensis* is not as compressed as *Paranautilus peregrinus* but is a much larger shell—in fact, if the generic assignment is correct, it is the largest species of *Paranautilus* known, measuring more than 20 cm in diameter.

The various species of *Paranautilus* show a large variation in the shape of the conch (text fig. 35).

Variation in the shape of the whorls of 12 species of Paranautilus, *expressed as percent of the height to the width of the whorl*

Species	*Percent of height to width*
P. multicameratus	72
P. tommasi	76
P. anisi	84
P. brembanus	84
P. simonyi	92
P. indifferens	92
P. cassis	106
P. bambanagensis	113
P. sundaicus	120
P. modestus	148
P. meridianus	157
P. peregrinus	165

Within the Triassic there appears to be a correlation of the percentage of height to width of whorl with geologic age. In general those species with compressed conchs and high percentages are confined to the Ladinian and Anisian. The high percentage for *Paranautilus peregrinus* may be due to error in measurement of Waagen's crushed specimen. Variations in the shape of the conch itself can best be studied by referring to figure 35.

Paranautilus seems to show affinities with only one genus of Permian nautiloids, *Liroceras* of the family Liroceratidae. *Liroceras* has a globular rounded conch, deep, narrow umbilicus, and straight or very simple suture. The conch is in general much more depressed than in *Paranautilus*. However, the Triassic species of *Paranautilus* appear to show a trend towards a more compressed conch and if *Liroceras* is actually the ancestral form it fits into this evolutionary trend. There are few other distinct and important differences between *Liroceras* and *Paranautilus*. Umbilical plugs are common in species of both genera. The sutures are, likewise, simple and have various minor inflections. *Liroceras greenei* has a shallow lateral lobe, *L. obsoletum* has a broad shallow dorsal lobe, *L. liratum* has a slight ventral lobe, and *L. globulare* may have an obscure ventral saddle. In *Paranautilus* the suture generally shows a weak ventral saddle and a broad shallow lateral lobe. However, shallow ventral lobes are present in *Paranautilus meridianus*, *P. brembanus*, *P.* cf. *sundaicus*, and possibly in *P. bambanagensis*. Neither of these two genera possess an annular lobe. The position of the siphuncle is varied in both genera.

Paranautilus shows general affinities with the other genera in the Liroceratidae but these genera have

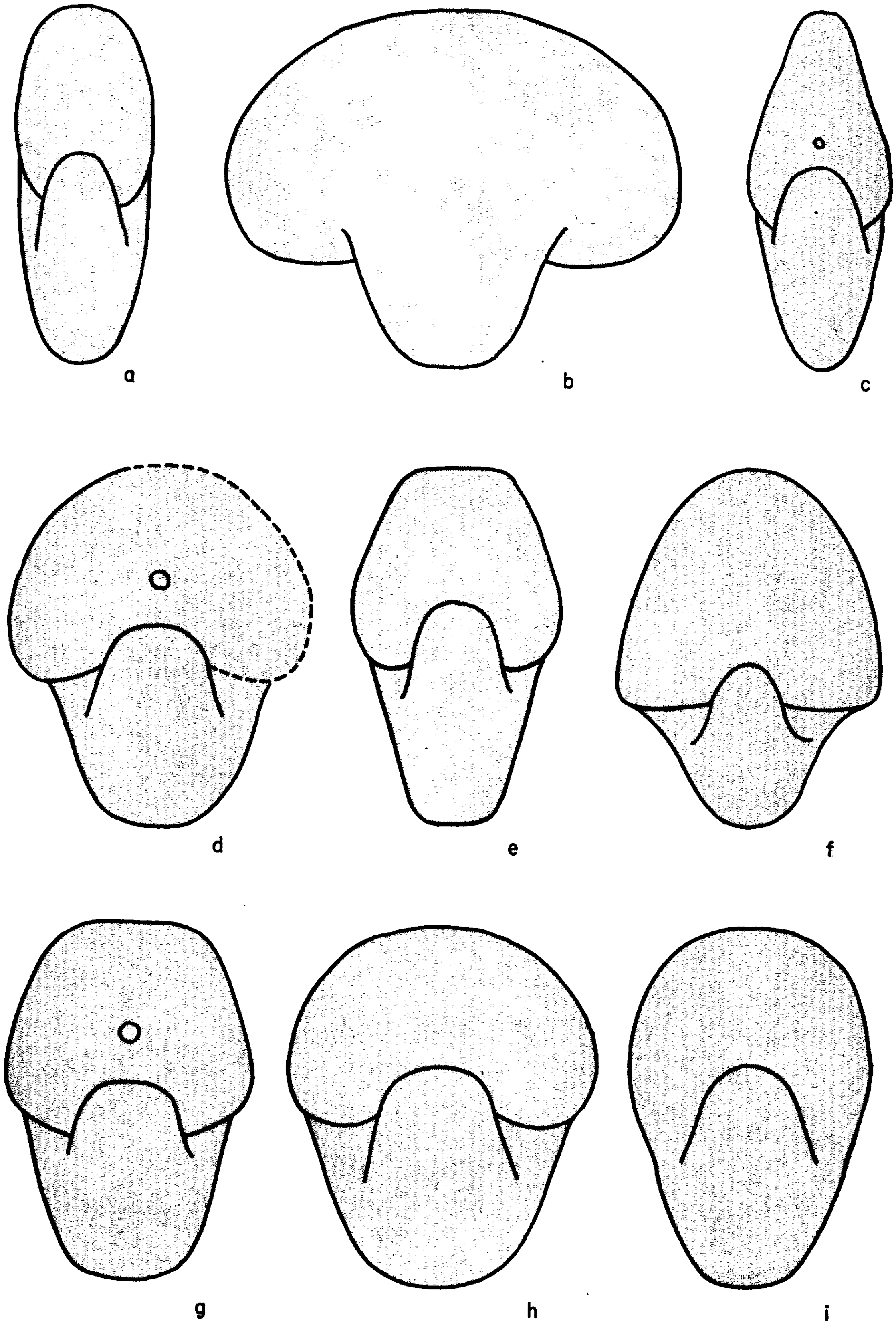

Figure 35.—Cross sections of the conch of *A, Paranautilus modestus* (Mojsisovics) 1873, pl. 15, fig. 2b, Diameter 70 mm; *B, Sibyllonautilus pertumidus* (Arthaber) 1896, pl. 3, fig. 6, Diameter 90 mm; posterior ventral view; *C, P. meridianus* Welter 1914, pl. 31, fig. 5, Diameter 85 mm; *D, P. tommasi* Airaghi 1902, pl. 1, fig. 6b, Diameter 55 mm; *E, Indonautilus kraffti* Mojsisovics 1896, pl. 21, fig. 2b, Diameter 48 mm, the genotype of *Indonautilus*; *F, P. anisi* (Arthaber) 1896, pl. 27, fig. 4b, Diameter 57 mm; *G, P. brembanus* (Mojsisovics) 1882, pl. 90, fig. 4b, Diameter 53 mm; *H, Liroceras liratum* (Girty), after Miller, Dunbar, and Condra 1933, pl. 6, fig. 3, Diameter 29 mm; *I, P. simonyi* (Hauer), the genotype of *Paranautilus*, after Mojsisovics 1902, pl. 1, fig. 2b, Diameter 76 mm.

Distribution of species of the genus Paranautilus

Species	Stratigraphic distribution	Geographic distribution
Paranautilus anisi (Arthaber) 1896	Triassic (Anisian)	Alps.
P. arcestiformis Diener 1908	Triassic (Norian)	Himalayas, India.
P. bambanagensis (Mojsisovics) 1896	do.	Do.
P. brembanus (Mojsisovics) 1882	Triassic (Karnian)	Alps.
P. bullocki Diener 1907	Triassic (Anisian)	Himalayas, India.
P. cassis Kieslinger 1924	Triassic (upper)	Timor.
P. indifferens (Hauer) 1892	Triassic (Anisian)	Yugoslavia.
P. kashmiricus Diener 1913	do.	Himalayas, India.
P. meridianus Welter 1914	Triassic (upper)	Timor.
P. modestus (Mojsisovics) 1873	Triassic (Norian)	Alps.
P.? mokouensis (Yin) 1933	Permian (Penchi series)	China.
P. multicameratus (Gabb) 1864	Triassic (Anisian)	Nevada.
P.? peregrinus (Waagen) 1879	Permian (Middle Productus limestone)	Salt Range, Pakistan.
P. pseudobrembanus Assmann 1925	Triassic (Muschelkalk)	Germany.
P. siculus (Gemmellaro) 1868	Triassic (Norian)	Sicily.
P. simonyi (Hauer) 1849	do.	Alps.
P. smithi Kummel n. sp	Triassic (Anisian)	Nevada.
P. subbambanagensis (Krumbeck) 1913	Triassic (Norian)	Indonesia, Iran.
P. sundaicus Welter 1914	Triassic (upper)	Timor.
P. tommasi (Airaghi) 1902	Triassic (Ladinian)	Alps.

individual specializations that probably preclude considering them ancestral to *Paranautilus.*

Paranautilus is widely distributed in Eurasia and narrowly in North America. There are two Permian species tentatively assigned to this genus. The range of *Paranautilus* in the Triassic is Anisian to Norian. Only two species are known from the North America, the remaining species are from Triassic areas within the Tethyian geosyncline.

Paranautilus multicameratus (Gabb)

Plate 14, figures 7, 8

1864. *Nautilus multicameratus* Gabb, Geol. Surv. California, Paleontology, vol. 1, p. 20, pl. 3, figs. 4, 5.

1914. *Paranautilus multicameratus* (Gabb). Smith, U. S. Geol. Survey Prof. Paper 83, p. 143, pl. 16, figs. 4, 5 (not pl. 95, figs. 3, 4).

The description of the holotype by Gabb is as follows:

> Shell broad, subglobose; whorls deeply embracing; sides compressed and rapidly converging; dorsum broadly grooved; umbilicus apparently quite small, partially obliterated in the specimen. Septa numerous, crowded, arching forward on the sides, and curving slightly backwards on the back. Siphuncle unusually large. Surface marked by revolving, somewhat irregular elevated lines.

The holotype was not available for study, but, Gabb's original description and figures of this species are sufficient to show the main characters. It is not even closely similar to the specimen placed in this species by Smith (1914, pl. 95, figs. 3, 4). *Paranautilus multicameratus* is unique in having a broad ventral groove and some ornamentation. Smith's specimen has a very rapidly expanded smooth conch and is made the holotype of a new species, *Paranautilus smithi* n. sp.

Occurrence.—"A single specimen was found by Mr. R. Hamfray at Dun Glen, near the Auld Lang Syne Mine, Sierra District, Humboldt County, Nevada Territory." (Gabb, p. 20, 1864.)

Holotype.—Location unknown.

Paranautilus smithi n. sp.

Plate 4, figs. 11, 12; pl. 8, figures 12, 13; text figure 36

1914. *Paranautilus multicameratus* (Gabb). Smith, U. S. Geol. Survey Prof. Paper 83, p. 143, pl. 95, figs. 3, 4.

The specimen assigned by Smith (1914) to Gabb's species does not seem to be conspecific. This specimen (and holotype) measures 102 mm in diameter, 66.5 mm in height of the most adoral part of the last whorl, and 77 mm in width. The conch is globose, involute, and rapidly expanding. The venter is flattened and grades imperceptably onto broad rounded ventral shoulders. The flanks are also broadly rounded, convergent towards the venter (text fig. 36). The living chamber measures 115 mm along the venter. The suture is almost straight over the venter and has a very shallow lateral lobe. No surface markings are present. The siphuncle is not visible.

Three conspecific specimens are available for study. One large one is complete, but somewhat distorted. An immature specimen (pl. 4, figs. 12, 13) that consists of the phragomcone only agrees in all essential features with the holotype.

This species is very similar to *Paranautilus mokouensis* Yin from the Penchi series of North China. The involute globose conch with the slight flattening of the venter of the last whorl shows strong affinities between these two species. *Paranautilus smithi* differs from *P. multicameratus* in lacking the ventral furrow and the surface ornamentation.

Occurrence.—Holotype and figured plesiotype from Middle Triassic *Daonella dubia* zone, *Ceratites trino-*

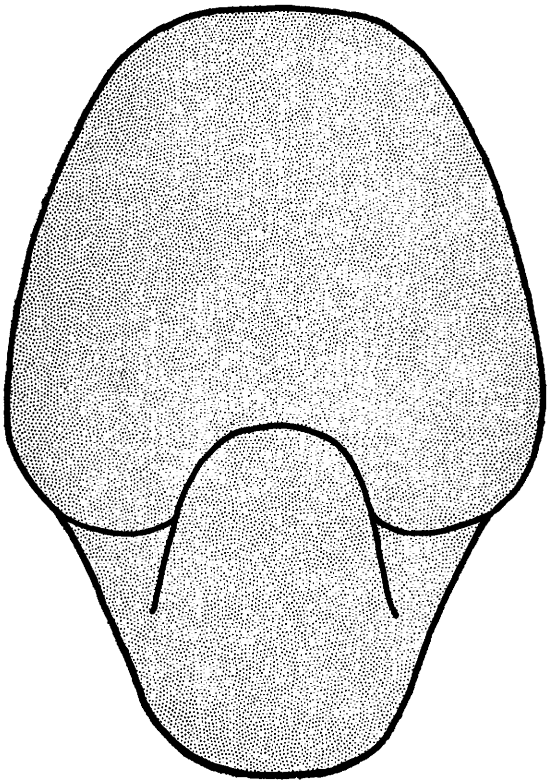

FIGURE 36.—Diagrammatic cross section of holotype of *Paranautilus smithi* n. sp. (U.S.N.M. 7445) from *Daonella dubia* zone of Star Peak formation, Fossil Hill, West Humboldt Range, Nevada, × 1.

dosus subzone, of the Buena Vista district; and of Fossil Hill, South Fork of American Canyon, 4 miles south of Fitting Post Office (formerly Foltz), West Humboldt Range, Nevada. Unfigured plesiotypes from *Daonella dubia* zone north side of South Canyon, New Pass, Desatoya Range, Lander County, Nevada.

Types.—Holotype, U.S.N.M. 74445; figured plesiotype, U.S.N.M. 32644; unfigured plesiotypes, U.S.N.M. 107096 and 107097.

Paranautilus sp.

Plate 8, figures 8, 9

One small immature specimen, consisting of only one half of the conch, is available from the Upper Triassic Luning (?) formation, Shoshone Mountains, Nevada. It is 33 mm in diameter, 23 mm in maximum width of whorl, and 17 mm in height. The specimen is subglobular, and appears to represent one half of the first and second volutions. The penultimate half whorl height and width are 10 and 16 mm respectively. The whorl at this point is broadly elliptical with a slight amount of flattening on the flanks. The whorl at the most adoral part of the conch shows a little more flattening of the flanks, grading to a broadly rounded ventrolateral region and to a smooth flatly rounded venter.

The umbilicus is small and deep, measuring 7 mm in diameter, 5 mm in depth. The umbilical shoulders are sharply rounded and the umbilical wall descends almost vertically to the umbilical seam. The only surface markings on the test are delicate but distinct growth lines that extend essentially straight across the umbilical wall and flanks of the conch, and form a broad deep sinus on the venter.

There are 16 septa in about half volution of the conch. A very small part (about 5 mm) of the living chamber is also present. The suture forms a very shallow ventral and lateral lobe, and it passes across the umbilical wall to the seam in a straight line. The siphuncle is not visible.

Remarks.—The only available specimen seems to represent an immature individual. The septa are relatively widely spaced and the distance between septa increases adorally. It is considered inadvisable to name a new species or to postulate its affinities on this specimen only.

Occurrence.—U.S.G.S. 11773, the label accompanying this specimen reads as follows: "North side of Union Canyon about 1½ miles above its mouth. From Triassic limestone above contact with Volcanic Rocks. Shoshone Range, Tonopah Quadrangle, Nevada." This is presumably from the Luning formation (Karnian). Collected by Ferguson, Cathcart, Heigs, and T. W. Stanton, July 6, 1923.

Figured plesiotype.—U.S.N.M. 107098.

Genus INDONAUTILUS Mojsisovics, 1902

Genotype: *Nautilus krafft* Mojsisovics

The description of the genotype by Mojsisovics (1899, p. 122) is as follows:

> This cast chambered throughout shows a great resemblance to *Nautilus mesodicus*, Hau., and has a considerably more concentrated growth. The perforation of the umbilicus, which in *Nautilus mesodicus* amounts to about 12 mm., is in the present cast only 2 mm. There are about one and a half whorls at the diameter of 48 mm. Sharp edges are not yet present at the beginning of the last whorl, but they are formed in the course of the latter. The flattening and the individualisation of the external part occurs simultaneously with the appearance of marginal angles.
>
> *Siphuncle.*—The position of the siphuncle is very deep, near the internal part.
>
> *Sutures.*—An internal lobe is not present.
>
> The development of the flat external lobe occuping the breadth of the external part goes hand in hand with the appearance of the marginal angles. There is a broad flat lateral lobe at the sides as in *Nautilus mesodicus*. The crowded condition of the septa, which considerably increases towards the anterior fractured edge, is still remarkable. From this increasing shortness of the distance of the septa it must be concluded that the specimen was broken off near the beginning of the body chamber.

(pl. 18, figs. 11, 12; text fig. 35).

When Mojsisovics (1902, p. 205) proposed the genus *Indonautilus* he made the following comments:

> Ich habe in meiner Arbeit über die obertriadischen Cepha-

> lopoden des Himalaya (1896, p. 672) unter der Bezeichnung *Nautilus* ind. ex. aff. *mesodici* einen Typus beschrieben, welcher bisher in der europäischen Trias noch nicht beobachtet wurde. Gleichwohl erscheint es aber angezeigt, diesen Typus hier zu erwähnen und für denselben sowohl eine eigene subgenerische Bezeichnung vorzuschlagen, als auch einen Artnamen nachzutragen. Ich wähle als sochen J. Krafft*i*.
>
> *Indonautilus* unterscheidet sich von *Grypoceras*, mit welchem sonst die grösste Uebereinstimmung besteht, durch das Fehlen eines Internlobus und dies dürfte wohl darauf hindeuten, dass *Indonautilus* in genetischer Beiziehung zunachst an *Paranautilus* anzureihen sein dürfte. Die kantige Abplattung der Externseite und die hiermit gleichzeitige Herausbildung eines Externlobus kennzeichnen die gleiche Variationsrichtung, welche auch von *Styrionautilus* zu *Clydonautilus* führt. Die grosse äussere Aehnlichkeit mit *Grypoceras* wäre daher als eine Convergenzerscheinung aufzufassen.

Mojsisovics' comments can be summarized as follows:

> *Nautilus* ind. ex. aff. *mesodici* which I have described from the Upper Triassic of the Himalayas is now considered as a distinct new form which I designate as *Indonautilus kraffti.*
>
> *Indonautilus* differs from *Grypoceras*, with which it is closely similar, in the absence of an annular lobe, and in which it is similar to *Paranautilus*. The angular, flattened venter and the character of the ventral lobe are similar to variations found in the *Styrionautilus-Clydonautilus* line. The great similarity with *Grypoceras* must be due to convergence.

Two species have been referred to the genus: *Indonautilus kraffti* and *I. subbambanagensis*. The latter species does not appear to be properly classified and is referred to the genus *Paranautilus*. It is very closely related to *Paranautilus bambanagensis*. *Indonautilus* superficially resembles *Grypoceras* in general shape of the conch, but is much more involute, has a slightly different suture, and no annular lobe. It appears to be most closely related to and derived from *Paranautilus*. Monotypic genera such as *Indonautilus*, in which data are insufficient, are difficult to classify and at best can be only tentatively assigned to a family. In this report *Indonautilus* is considered a late evolutionary development out of *Paranautilus*. The genotype species comes from Norian beds of the Himalayan region. Jaworski (1915, p. 131-132) described a specimen from Norian rocks on the Island of Misol that he believes is related to *Indonautilus kraffti.*

Genus Sibyllonautilus Diener, 1915

Genotype: *Nautilus sibyllae* Mojsisovics

In Part 8 of the Fossilium Catalogus, "Cephalopoda Triadica," Diener 1915 erected two new genera, *Sybyllonautilus* and *Tumidonautilus* (Genotype, *Nautilus pertumidus* Arthaber). Both genera include tightly coiled nautiloids that show a great expansion in the width of the whorl in mature specimens. *Tumidonautilus* differs from *Sybyllonautilus* essentially only in the greater expansion of the conch. The illustrations of *Sibyllonautilus sibyllae* and *S. liardensis* show that not much of the living chamber is preserved in these specimens, which may explain the differences in the whorl expansion between these two genera. *Nautilus sibyllae* and *N. pertumidus* appear so closely related and similar that they should be brought together into one genus. Because *Sibyllonautilus* was listed first in Part 8 of the Fossilium Catalogus, *Tumidonautilus* is suppressed and its one species place in *Sibyllonautilus.*

Diener gave no description of *Sibyllonautilus,* but the description of the type species is quoted here in full (Mojsisovics, 1886, p. 100):

> Die sehr rasch in die Breite wachsende Art besteht in dem abgebildeten Exemplare blos aus anderthalb Umgängen. Der gewölbte, nicht abgeplattete Externtheil trennt sich kaum von den leicht gewölbten Seitentheilen. Der Nabelrand ist auf dem äusseren, noch durchaus gekammerten Umgange deutlich markirt. Die hohe Nabelwand fällt von demselben in schräger Fläche zum tiefen, trichteförmigen Nabel ab. Die Involution umfasst die halbe Windungshöhe der umhüllten Windungen. Die grösste Dicke der Windungen fällt in die halbe Windungshöhe etwas ausserhalb des Nabelrandes.
>
> Die Schale ist von kräftigen, eigenthümlich verlaufenden Zuwachstreifen bedeckt. Auf den tiefen Sinus des Externtheiles folgt ein gegen vorne convexer Bogen am Rande zwischen Seiten- und Externtheil. Hierauf biegen sich die Streifen abermals zu einem kleinen Sinus zurück, während dieselben auf dem Nabelrande neuerdings einen gegen vorne convexen Bogen bilden und auf der Nabelwand ziemlich gerade zur Naht sich abwärts senken. Dieser, insbesondere durch den auf den Nabelrand fallenden zweiten Bogen bemerkenswerthe Verlauf der Zuwachsstreifen findet sich unter den europäischen Triasnautilen wieder bei *Nautilus Suessi* aus den Hallstätter Kalken, sowie man durch denselben auch an den Mundrand des permischen *Nautilus cornutus* Golovinski erinnert wird.
>
> Loben. Gedrängt stehende Kammerwände, welche mit kaum merklichem Sinus über den Externtheil ziehen und auf den Seiten einen gleichfalls nur sehr schwachen, seichten Laterallobus bilden. Internlobus vorhanden.
>
> Sipho. Konnte nicht beobachtet werden.
>
> Dimensionen: Durchmesser—73 mm., Höhe derr letzten Windung—43 mm, Dicke—59 mm., Nabelweite—9 mm, Perforation—2 mm.

Mojsisovics' description of *Nautilus sibyllae* can be summarized as follows:

> The conch is rapidly expanding, venter broadly arched and hardly separated from the rounded whorl sides. The umbilical shoulder is very distinct and the high umbilical wall slopes gradually to a deep funnel shaped umbilicus. The conch is involute, the whorls embracing about one-half of the preceding whorls. The shell has strong growth lines that form a deep sinus on the venter and a shallow sinus on the whorl sides. The suture is almost straight across the venter and with a shallow lateral lobe. An annular lobe is present. The position of the siphuncle is not known.

Mojsisovics (1902, p. 235) believed that *Sibyllonautilus sibyllae* occupied a more or less isolated position, but he pointed similarity to *Nautilus cornutus.*

Sibyllonautilus pertumidus is one of the most unusual of all the Triassic nautiloids. No other Triassic nautiloid shows such rapid expansion of the living chamber; Arthaber's specimen (1896, p. 42) measured 75 mm in diameter, 40 mm for the height of the last whorl and 102 mm for the width of the last whorl (test fig. 35). The venter is flatly rounded on the early whorls, becoming arched on the living chamber. No distinct ventral shoulders are developed. The umbilical walls are steep, becoming arched where the whorls begin to expand rapidly. The whorls first begin their extraordinary expansion on the living chamber of a mature individual. The part of the living chamber preserved in Arthaber's specimen is one-third of a volution in length. The suture shows very shallow ventral and lateral lobes. An annular lobe is also present. The siphuncle is subcentral in position.

Arthaber recognized the unusual features of his species and thought it occupied a more or less isolated position among known Triassic nautiloid faunas but he did point out similarities to *Nautilus tintoretti* Mojsisovics and *N. sibyllae* Mojsisovics. However, Arthaber favored a possible relationship to *N. cornutus* Golovkinsky, which develops very long extended horn-like projections or rolls from the area of the umbilical shoulders. It was made the genotype of the genus *Permonautilus* Kruglov (1933), but Miller and Youngquist (1949, p. 120) suppressed *Permonautilus* as a synonym of *Acanthonautilus* Foord. The genotype of *Acanthonautilus* is *A. bispinosis* Foord of the Lower Carboniferous of Ireland. *A. cornutus* is from the Upper(?) Permian of Russia. *Sibyllonautilus* differs from these two Paleozoic species in lacking the spine-like projections mentioned above.

Mojsisovics (1902, p. 235, footnote) suggested that the phragmocone of *Nautilus pertumidus* was very similar to *Mojsvaroceras* or *Germanonautilus* and that *N. pertumidus* could be considered an aberrant offshoot of *Germanonautilus* with subgeneric rank. It seems incorrect to place *Sibyllonautilus* in the Tainoceratidae as suggested by Mojsisovics. *Sibyllonautilus* does not have any type of ornamentation characteristic of the genera in that family. Likewise, with few exceptions, the genera of the Tainoceratidae are much more evolute than *Sibyllonautilus*. The general shape of the conch and simplified suture ally *Sibyllonautilus* with *Paranautilus*. The earliest representatives of *Sibyllonautilus* appear in the Anisian. *Paranautilus* is believed to be decended from *Liroceras* and *Sibyllonautilus*, to represent an aberrant offshoot of *Paranautilus*, or possibly be a direct development from *Liroceras*. A genetic relationship between *Acanthonautilus* and *Sibyllonautilus* seems unlikely. In the former genus the development of the extended horn-like projection from the area of the umbilical shoulder is considered an independent line of specialization.

Distribution of species of the genus Sibyllonautilus

Species	Stratigraphic distribution	Geographic distribution
Sibyllonautilus fergusoni Kummel n. sp	Triassic (Norian)	Nevada.
S. liardensis (Whiteaves) 1889	Triassic (Ladinian, Karnian)	British Columbia.
S. pertumidus (Arthaber) 1896	Triassic (Anisian)	Alps.
S. sibyllae (Mojsisovics) 1886	do	Spitzbergen.

Sibyllonautilus fergusoni n. sp.

Plare 8, figures 10, 11; text figure 37

The Gabbs formation of Nevada has yielded two specimens that belong in the genus *Sibyllonautilus*. One of these specimens is fairly well preserved and is septate throughout; the other is only a fragment of one-third volution and only the ventral part of the conch.

The holotype specimen is involute, subglobular, has a maximum diameter of 49 mm, a maximum width of 65 mm, and height of the conch of about 30 mm. The conch is expanded orad very rapidly; height and width of the penultimate whorl are about 15 mm and 25 mm, respectively. The whorls are broadly rounded ventrally, showing no trace of a ventral shoulder, the flanks curve gradually to the venter (text fig. 37).

The umbilicus is very small and may be completely closed by successive whorls; the umbilical shoulders are sharply defined. The umbilical walls are flattened and slope at a steep angle. No trace of surface markings is discernible.

The septa are only moderately close together and slope steeply adorally. The sutures are essentially straight, showing only a faint indication of ventral and lateral lobes. The siphuncle is subcentral, and closer to the dorsum than the venter.

Remarks.—The rate of expansion of the whorls in *S. fergusoni* is much greater than that of *S. liardensis* or *S. sibyllae* but approaches that of *S. pertumidus*. However, in the latter species the great expansion of the whorls begins on the living chamber, in *S. fergusoni* the expansion is already very marked on the phragmocone. The umbilicus is much larger and the umbilical wall less steep in *S. sibyllae*. *S. liardensis* has a cross section more elliptical than that of *S. fergusoni*. The species is named for H. G. Fergusson, who collected the specimens.

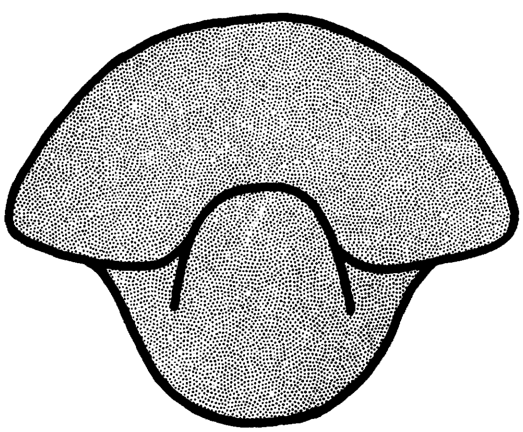

FIGURE 37.—Diagrammatic cross section of holotype of *Sibyllonautilus fergusoni* n. sp. (U.S.N.M. 107099) from Gabbs formation Gabbs Valley Range, Nevada, × 1.

Occurrence.—U.S.G.S. 13420, Gabbs formation, 2½ miles north of the mouth of New York Canyon, Gabbs Valley Range, Nevada.

Types.—U.S.N.M. 107099 (holotype), 108000 (paratype).

Sibyllonautilus liardensis (Whiteaves)

Plate 14, figures 9, 10

1889. *Nautilus liardensis* (Whiteaves), Contr. Canadian Paleontology, vol. 1, pt. 2, p. 137, pl. 18. figs. 1, 1a.

1927. *Paranautilus liardensis* (Whiteaves). Smith, U. S. Geol. Prof. Paper 141, p. 102, pl. 107, figs. 1, 2.

The description of the species by Whiteaves is as follows:

> Shell broad, subglobose, but deeply though rather narrowly umbilicated: maximum breadth of the aperture about equal to the entire length, as measured from the centre of the outer lip to a corresonding point on the periphery of the opposite side. Volutions very closely embracing, the inner ones almost completely covered, the outer one increasing rapidly in size, but expanding much more rapidly in a lateral than in a dorso-ventral direction: periphery somewhat flattened, but probably abnormally so: sides and umbilical margin both rounded, the latter not at all angular: aperture a little more than twice as broad as high, transversely subreniform, or transversely and broadly elliptical but shallowly emarginate in the centre of the base by the encroachment of the preceeding volution.
>
> Septa somewhat closely approximated, their average distance apart on the periphery, where their margins are nearly straight, being about six millimetres. Position of the siphuncle unknown.
>
> Surface apparently almost smooth, and marked only by transverse striae of growth.
>
> Dimensions of the only specimen collected: maximum length, fifty-seven millimetres; maximum breadth at the aperture, where the shell is broadest, fifty-eight mm; height of aperture in the centre, twenty-seven mm.
>
> Liard River, about twenty-five miles below Devil's Portage, R. G. McConnell, 1887: a slightly distorted cast of the interior of the shell, with small portions of the test preserved, but with the greater portion of the chamber of habitation broken off. The number of septa whose margins are visible in this specimen is twenty-one, and the portion of the body chamber that remains is about three-quarters of an inch in length.
>
> This shell appears to bear such a close resemblance to the *Nautilus sibyllae* of Mojsisovics, from the Trias of Spitzbergen in almost every respect, that it may possibly prove to be only a local variety of that species. Still in the figures of *N. sibyllae* the umbilical margin is represented as rather distinctly angular, whereas that of *N. liardensis* is very regularly rounded.

Family CLYDONAUTILIDAE Hyatt, 1900

Hyatt (1900, p. 521–522) included in this family, a wide range of forms from the Mesozoic and Cenozoic eras—*Clymenonautilus, Clydonautilus, Hercoglossa, Pseudonautilus,* and *Aturia.* Mojsisovics (1902) greatly restricted this family to Triassic genera, and added several new ones. Mojsisovics placed in it *Paranautilus Indonautilus, Styrionautilus, Clydonautilus, Proclydonautilus,* and *Gonionautilus.* Kummel (1950) placed *Paranautilus* and *Indonautilus* in the Paranautilidae, and *Gonionautilus,* in the Gonionautilidae. The Clydonautilidae are now thought to include *Clydonautilus, Proclydonautilus, Styrionautilus, Cosmonautilus,* and *Callaionautilus.* Spath (1927b, p. 24) suggested that *Callaionautilus* does not belong in the Clydonautilidae and, although he gave no reason for his proposal, it may well be valid. *Callaionautilus* is a monotypic genus known only from Norian beds of Timor and is very difficult to classify, as are most more or less isolated monotypic forms. The writer is leaving *Callaionautilus* in the Clydonautilidae on the basis of its early ontogenetic development, which is so similar to that of *Proclydonautilus* and *Cosmonautilus.* Kieslinger (1924, p. 133) in fact, suppressed his new genus *Callaionautilus* along with *Cosmonautilus* in a supplement believing them to lie within the sphere of variation of *Proclydonautilus.*

The Clydonautilidae as here interpreted form a very closely integrated group. The family includes Triassic nautiloids with involute subglobular to compressed conchs and highly differentiated sutures (text figs. 39–41). One of the most distinctive features of the genera in this family is the suture pattern, which forms the best evidence for interpreting phylogenetic relationships within the family. Variation in the shape of the conch is rather great in all of the genera but the basic plan of the suture remains constant. In all the genera there is a large, deep lateral lobe and the main difference between the various groups lies in the character of the suture in the ventral region of the conch. In *Styrionautilus* the suture is straight over the venter, in *Clydonautilus* the ventral lobe is divided by a small saddle, in *Proclydonautilus* there is only a large ventral lobe. *Cosmonautilus* and *Callaionautilus* are differentiated on features of ornamentation developed at some stage in their ontogeny and have a suture similar to that of *Proclydonautilus.*

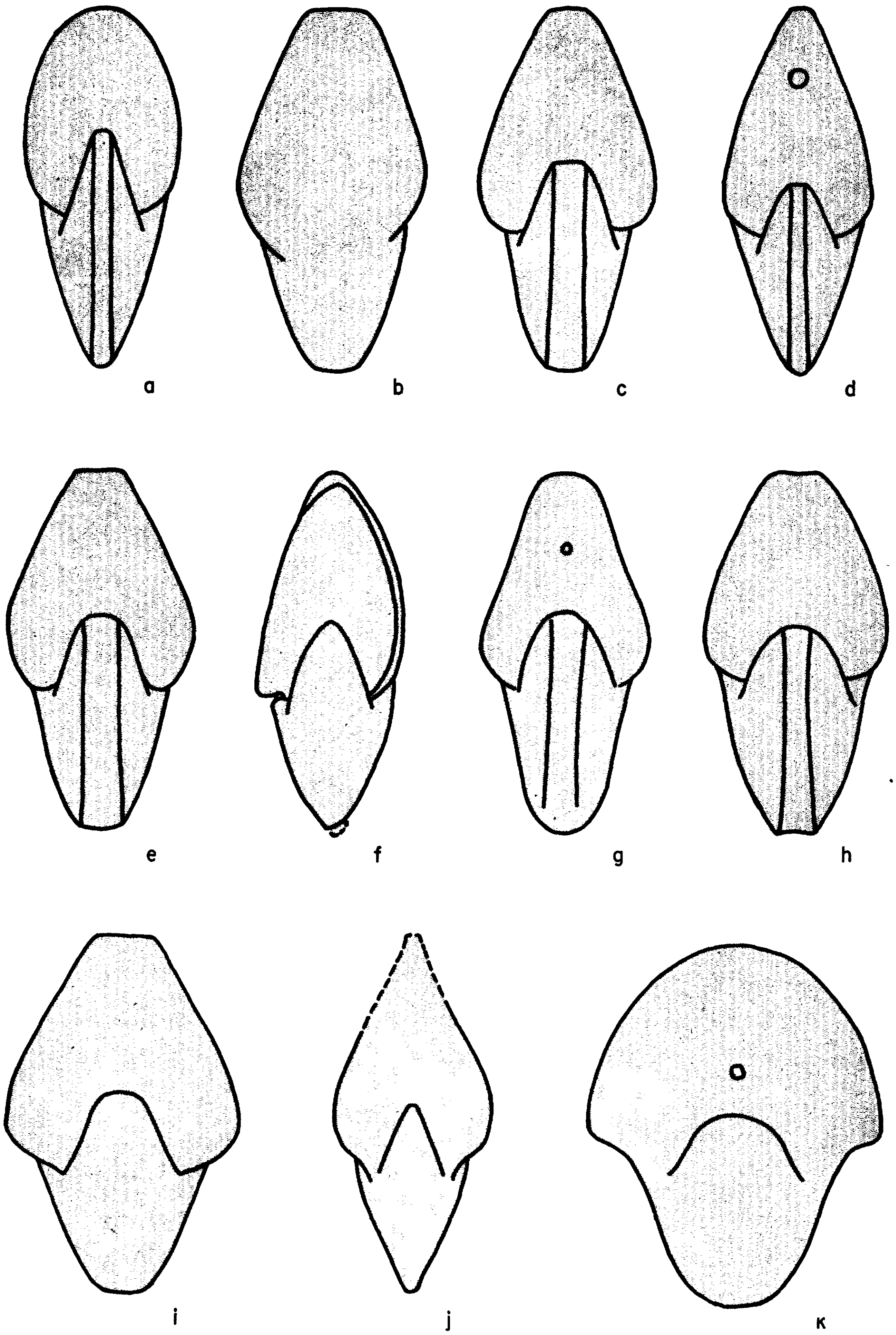

FIGURE 38.—Cross sections of the conch of *A*, *Clydonautilus salisburgensis* (Hauer), after Mojsisovics, 1902, pl. 12, fig. 1b, Diameter 184 mm; *B*, *C. compressus* Welter 1914, p. 217, fig. 92, Diameter 65 mm; *C*, *C. salisburgensis* (Hauer), after Kieslinger, 1924, pl. 3, fig. 1b, Diameter 89 mm; *D*, *Gonionautilus securis* (Dittmar), the genotype of *Gonionautilus*, after Mojsisovics, 1902, pl. 1, fig. 1b, Diameter 110 mm; *E*, *C. biangularis* Mojsisovics 1896, pl. 22, fig, 2b, Diameter 83 mm; *F*, *C. salisburgensis timorensis* Welter 1914, p. 222, fig. 99, Diameter 194 mm; *G*, *C. glaber* Kieslinger 1924, pl. 2, fig. 2b, Diameter 55 mm; *H*, *C. quenstedti* (Hauer), after Mojsisovics, 1873, pl. 9, fig. 1b, Diameter 290 mm; *I*, *Styrionautilus sauperi* (Hauer), after Mojsisovics, 1873, pl. 15, fig. 1b, Diameter 122 mm; *J*, *S. discoidalis* (Welter) 1914, pl. 31, fig. 9 Diameter 50 mm; *K*, *S. styriacus* Mojsisovics 1873, pl. 14, fig. 7b, Diameter 74 mm, the genotype of *Styrionautilus*.

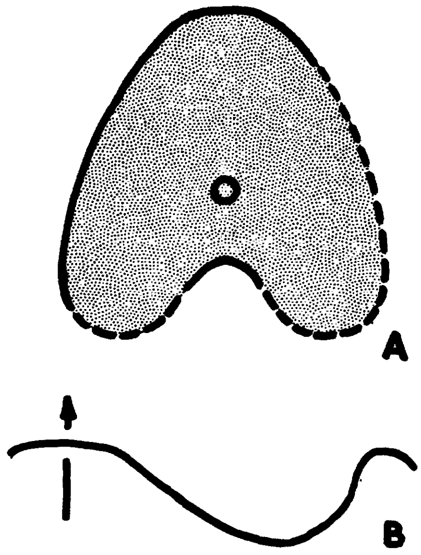

FIGURE 39.—Diagrammatic cross section and representation of suture of *Styrionautilus* sp. (U.S.N.M. 108001) from Middle Triassic, South Canyon, New Pass, Desatoya Range, Nev., both × 1.

Geographically the genera in this family are world wide in their distribution. *Cosmonautilus* and *Callaionautilus* are more closely limited in their distribution than *Styrionautilus*, *Clydonautilus* and *Proclydonautilus*. *Stryionautilus* ranges from the Anisian to the Norian, *Clydonautilus* from Ladinian to Norian, *Proclydonautilus* and *Cosmonautilus* from Karnian to Norian, and *Callaionautilus* is known only from the Norian.

PHYLOGENY

The dominant evolutionary trends within the family Clydonautilidae are the increasing sinuosity and the modifications of the suture pattern. The conch for the most part remained smooth, involute, and subglobular in shape. Minor elements of ornamentation are present such as the nodes on the early whorls of *Cosmonautilus* and *Callaionautilus*, but these features have no phylogenetic significance and are merely abberrant mutations superimposed on a basic conch pattern. The family reveals no distinct evolutionary trend in the shape of the conch. The affinities of the various genera and their interrelationships can best be studied on the basis of the evolution in the suture pattern (text fig. 41). The complexity of the suture of the Triassic Clydonautilidae is rivaled only by that shown in such Tertiary nautiloids as *Aturia*, *Aturoidea*, and possibly *Hercoglossa* (see Miller, fig. 7, 1947).

Among late Paleozoic nautiloids only "*Aganides*" *bitauniensis* Haniel (1915) from the Permian of Timor has a suture rivaling the complexity of that in the Clydonautilidae. The conch form places this species in the Grypoceratidae. The suture, however, is very uncommon for late Paleozoic nautiloids and is similar only to the Late Triassic Clydonautilidae. This species should be placed in a separate new genus.

The family seems to stem from a paranautilid stock in the Ladinian. *Paranautilus* has a very simple globular conch with a nearly straight suture. On this basic conch and sutural pattern the genera of the Clydonautilidae were derived either directly or indirectly. Mojsisovics (1902, p. 206) indicated the great similarity in shape of the conch of *Stryionautilus* to *Paranautilus anisi*. *Styrionautilus* is characterized by a suture passing straight over the venter, and a deep lateral lobe. Forms such as *Paranautilus meridianus* with a deep but very broad lateral lobe and *Paranautilus sundaicus* with a shallower lateral lobe and a ventral saddle seem to be somewhat transitional, at least in their suture pattern, to *Stryrionautilus*. Five species of *Styrionautilus* are recognized, one from the Ladinian and the remaining species from the Karnian. *Styrionautilus* shows more similarity to its descendants in the shape of the conch than it does to the ancestral *Paranautilus*.

Proclydonautilus, an involute subglobose nautiloid, has a small ventral lobe dividing the ventral saddle. Forms such as *Styrionautilus sauperi* have such a ventral lobe developed on the last few septa and are believed to indicate clearly the genetic relationships of *Styrionautilus* and *Proclydonautilus*. Closely related to *Proclydonautilus* are two groups of nautiloids that develop features of ornamentation during at least part of their ontogeny on a Proclydonautilid conch and at the same time maintain a suture pattern very similar to that of the parent stock. The first, *Cosmonautilus*, develops nodes on the ventral shoulders, usually only on the inner whorls, and at maturity has a completely smooth conch very difficult to differentiate from typical *Proclydonautilus*. The second genus, *Callaionautilus*, has an ontogeny similar to that of *Cosmonautilus* in the formation of nodes on the ventral shoulders, but this phase grades into one in which the conch is ovoid in shape, smooth, and with a ventral nodose keel. Both of these genera are thought to be aberrant evolutionary offshoots, and the ornamentation consists of coenogenetic characters with no phylogenetic significance. *Proclydonautilus* and *Cosmonautilus* range through the Karnian and Norian, *Callaionautilus* is known only from the Norian.

From *Paranautilus* evolved the genus *Clydonautilus*, which has a suture pattern similar to that of *Proclydonautilus* except that a small saddle divides the ventral lobe. These two genera lived side by side throughout the Karnian and Norian and seem to represent two closely related but independent lines developing out of *Paranautilus*.

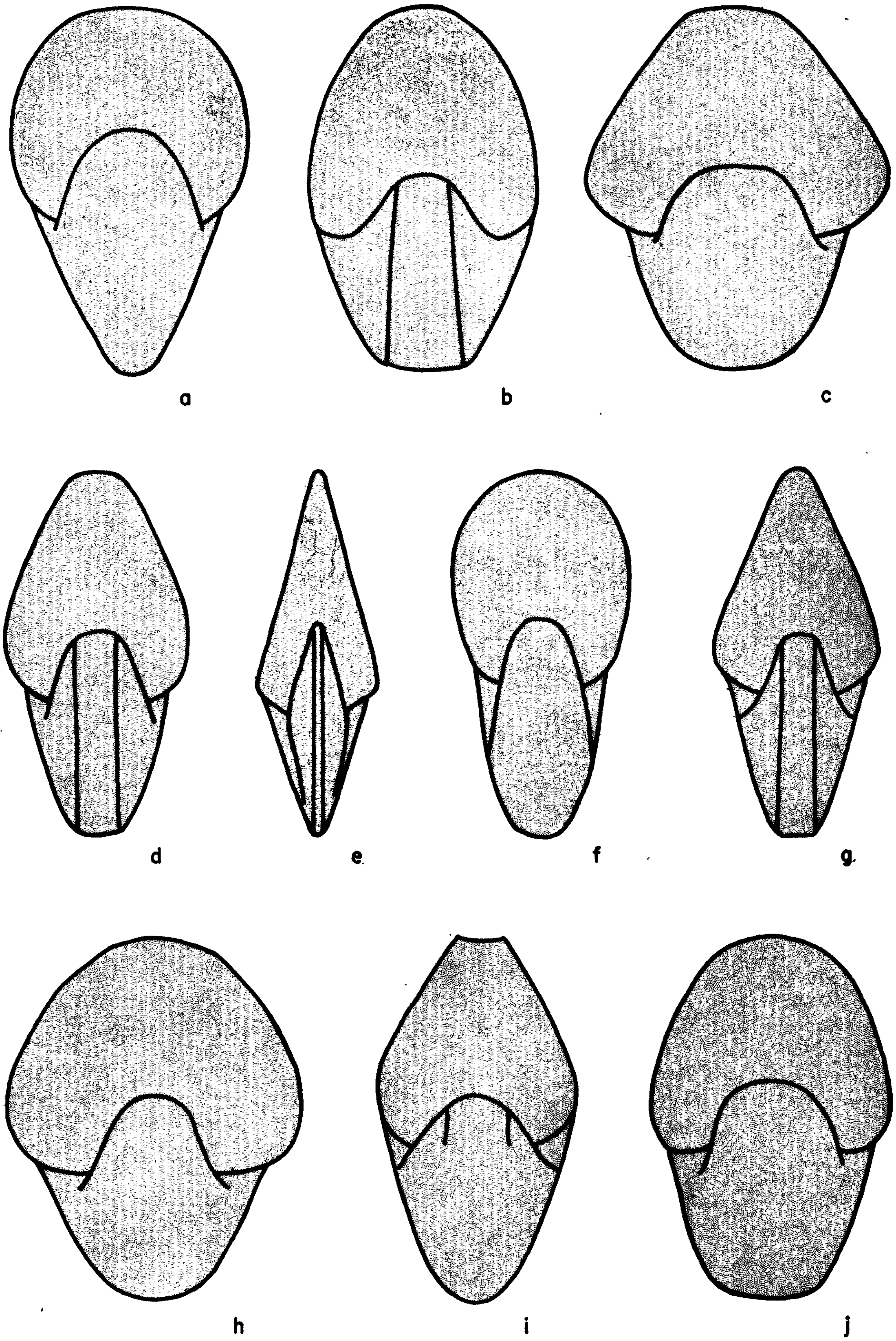

FIGURE 40.—Cross sections of the conch of *A*, *Proclydonautilus gasteroptycus* (Dittmar), after Mojsisovics 1873, pl. 10, fig. 1b, Diameter 100 mm; *B*, *P. ernesti* Diener 1919, p. 773, fig. 14, Diameter 73 mm; *C*, *P. singularis* Welter, after Kieslinger, 1924, p. 78, fig. 11, Diameter 106 mm; *D*, *P. griesbachi* Mojsisovics, 1896, pl. 22, fig. 1b, Diameter 87 mm, the genotype of *Proclydonautilus; E*, *P. ermollii* Diener 1919, p. 775, fig. 16, Diameter 117 mm; *F*, *P. triadicus* Mojsisovics, after Diener 1919, p. 766, fig. 6a, Diameter 138 mm; *G*, *P. buddhaicus* Diener 1919, p. 769, fig. 9, Diameter 113 mm; *H*, *P. spirolobus* (Dittmar), after Mojsisovics 1902, pl. 10, fig. 3b, Diameter 73 mm; *I*, *P. tuvalicus* Diener 1919, p. 772, fig. 12, Diameter 150 mm; *J*, *P. inflatus* Welter 1914, p. 212, fig. 83, Diameter 94 mm.

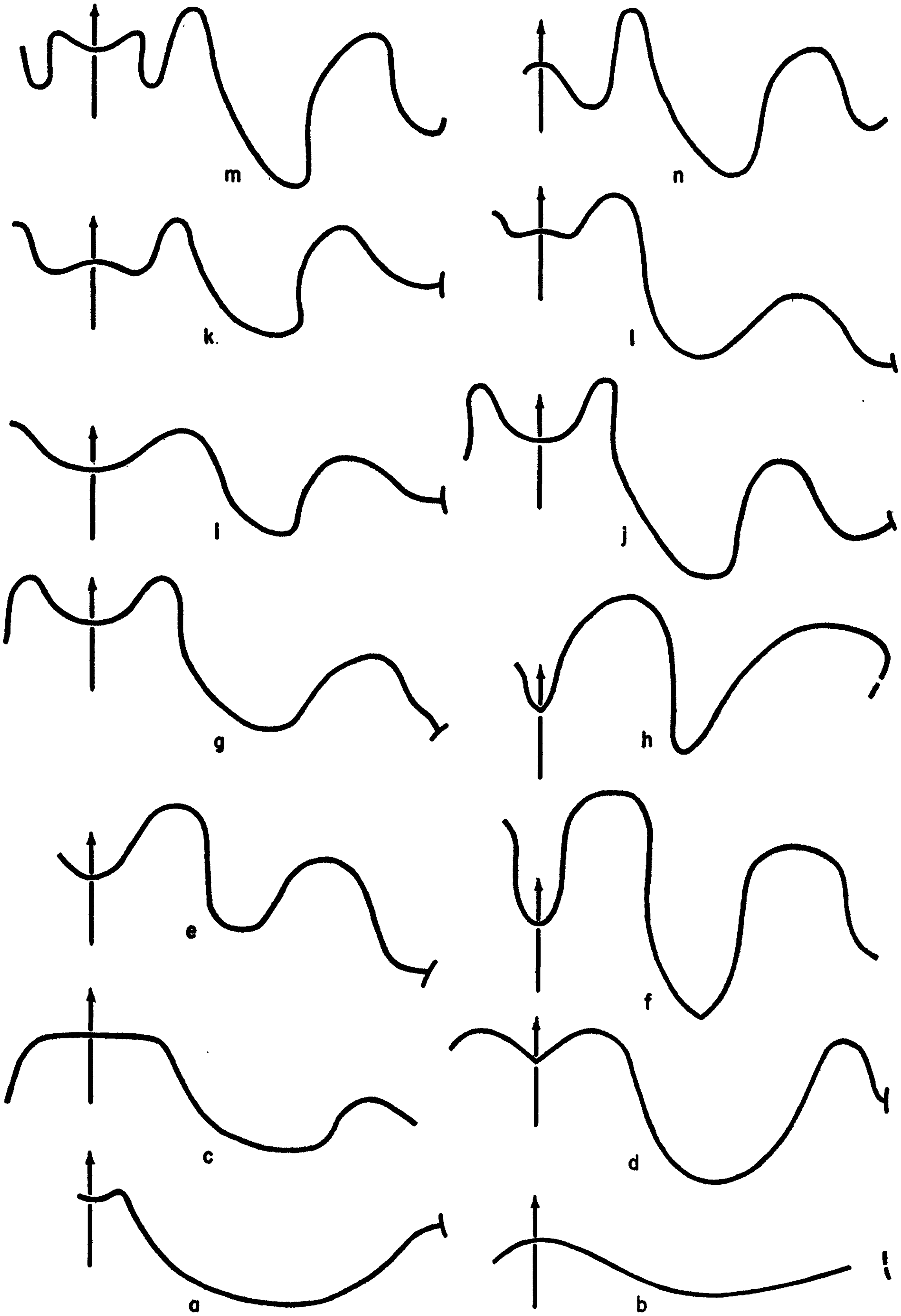

FIGURE 41.—Diagrammatic representation of sutures of *A*, *Paranautilus meridianus* Welter, 1914, pl. 31, fig. 6, ×1; *B*, *Paranautilus sundaicus* Welter, 1914, pl. 31, fig. 3, ×1; *C*, *Styrionautilus discoidalis* (Welter) 1914, pl. 31, fig. 8, ×2.34; *D*, *Styrionautilus sauperi* (Hauer), after Mojsisovics, 1902, p. 209, fig. 6, ×0.8, a very late stage suture; *E*, *Proclydonautilus ernesti* Diener, 1919, p. 774, fig. 15, ×1.6; *F*, *Proclydonautilus goniatites* (Hauer), after Kieslinger, 1924, p. 77, fig. 10, ×0.81; *G*, *Proclydonautilus griesbachi* (Mojsisovics), 1896, pl. 22, fig. 1c, ×1.1, the genotype of *Proclydonautilus; H*, *Proclydonautilus natosoni* McLearn, 1946, pl. 2, fig. 2, ×1.4; *I*, *Callaionautilus turgidus* Kieslinger, 1924, p. 94, fig. 21, ×1.46; *J*, *Cosmonautilus dilleri* Hyatt and Smith, after Smith, 1927, pl. 54, fig. 2, ×0.6; *K*, *Clydonautilus biangularis* Mojsisovics, 1896, pl. 22, fig. 2c, ×1.1; *L*, *Clydonautilus salisburgensis* (Hauer), after Kieslinger, 1924, p. 68, fig. 6, ×1; *M*, *Clydonautilus noricus* Mojsisovics, 1873, pl. 11, fig. 2, ×0 23; *N*. *Clydonautilus quenstedti* (Hauer), after Mojsisovics, 1873, pl. 9, fig. 3, ×0.28.

Genus STYRIONAUTILUS Mojsisovics, 1902

Genotype: *Nautilus styriacus* Mojsisovics

Mojsisovics (1902, p. 206) diagnosed his genus as follows:

> Involute globose Gehause mit abgerundeter Eternseite. Geradlinig den Externtheil ubersetzender Externsattel, tiefer spitz gerundeter Laterallobus, grosser Lateralsattel, welcher sich aus dem kleinen Umbilicalsattel von *Paranautilus* entwickelt hat, und tiefer Nachtlobus. Kein Internlobus. Sipho subcentral. (pl. 18, figs. 9, 10).

Mojsisovics' diagnosis can be summarized as follows:

> Conch globose, involute, with rounded venter. Ventral saddle straight, lateral lobe deep, acutely rounded, lateral saddle larger and developed from the small umbilical saddle of *Paranautilus*. No annular lobe. Siphuncle subcentral.

The general shape of the conch of *Styrionautilus* is very similar to that of *Proclydonautilus* and *Clydonautilus*. It differs mainly in that the sutures form a straight line over the venter (text fig. 41). Mojsisovics pointed out the great similarity to *Paranautilus anisi* and believed *Styrionautilus* to be derived from *Paranautilus* and to be the forerunner of *Proclydonautilus*. The evolutionary development was confined mainly to changes in the suture and especially in the ventral saddle. *Styrionautilus sauperi* has a small lobe developed in the last few septa and is thought to be a form transitional to typical *Proclydonautilus*. No known forms show a transition between the shallow lobes of *Paranautilus* to the deep lobes of *Styrionautilus*.

There are great differences in shape of the conch among the species of *Styrionautilus*. The genotype has an involute subglobular conch with an arched venter and rounded flanks (see text fig. 38). *S. sauperi* has a more compressed conch with a flattened venter and *S. discoidalis* is a very compressed form with a very narrow venter. All the species, however, agree in their suture pattern, that of a straight ventral saddle with deep lateral lobes. This relationship reflects the general evolutionary pattern of the family Clydonautilidae—the suture lines of the various genera are fairly constant in form, but the variation in shape of the whorl section between the species may be great. *Proclydonautilus* illustrates this relationship even more strikingly than *Styrionautilus*.

Distribution of species of the genus Styrionautilus

Species	Stratigraphic distribution	Geographic distribution
Styrionautilus discoidalis (Welter) 1914	Triassic (upper)	Timor.
S. occidentalis (Tornquist) 1898	Triassic (Ladinian)	Alps.
S. sauperi (Hauer) 1846	Triassic (Karnian)	Alps, Hungary.
S. styriacus (Mojsisovics)	do	Alps.
S. sp	Triassic (Anisian)	Nevada.

Styrionautilus sp.

Plate 15, figure 16; text figure 39

One fragmentary specimen consisting of two camerae can confidently be placed in this genus. The specimen is from the Middle Triassic, Desatoya Range, Nevada. The camerae measure 43 mm in height and approximately 44 mm in width near the umbilical shoulders. The venter is 10 mm wide and flattened, the flanks are also flattened to broadly arched, and converge towards the venter. The ventral shoulders are distinct and rounded (text fig. 39). The siphuncle lies closer to the dorsum than to the venter. The specimen is characterized by its suture, which traces a straight line across the venter, forms a deep, broad lateral lobe, and passes to a small saddle near the umbilical shoulder. The nature of the suture pattern and shape of the conch clearly place this specimen in *Styrionautilus*, and the shape of the whorl section suggests affinities to *Styrionautilus sauperi*.

Occurrence.—The specimen was collected by F. N. Johnston and the label with the specimen reads "Middle Triassic, South Canyon, New Pass, Desatoya Range, Nevada." This is presumably from bed 2b of Johnston's generalized stratigraphic section (1941, p. 448) *Daonella* zone of late Anisian age.

Figured specimen.—U. S. N. M. 108001

Genus PROCLYDONAUTILUS Mojsisovics, 1902

Genotype: *Nautilus griesbachi* Mojsisovics

When Mojsisovics first described this genus, he considered the group a subgenus of *Clydonautilus* which, however, has a small median saddle dividing the ventral lobe. The taxonomic status of *Proclydonautilus* has been changed several times. Smith (1904, p. 401) raised *Proclydonautilus* to full generic rank, and Hyatt and Smith (1905, p. 205) Welter (1914, p. 208), Kieslinger (1924, p. 66) and Smith (1927, p. 102) concurred. Diener (1919, p. 766) maintained the classification first proposed by Mojsisovics.

Proclydonautilus may be briefly described as follows: The conch is nautiliconic and subglobular to compressed (text fig. 40), the whorls are generally rounded although the flanks may be somewhat flattened and converge towards the venter. The venter is broadly rounded to flattened, with well defined ventral shoulders. The umbilicus is small, umbilical shoulders well rounded.

Conch is smooth. The suture consists of a broad, shallow to deep ventral lobe dividing a large ventral saddle. The flanks are occupied by a large lateral lobe with a smaller lateral saddle and a second lateral lobe. Generally no annular lobe is present. However. Welter (1914, p. 213) described and illustrated specimens of *Proclydonautilus*(?) *gasteroptychus timorensis* that have an annular lobe but the external suture is of a typical proclydonautilid type. The siphuncle is central in position.

The writer follows Mojsisovics (1902, p. 206) in deriving *Proclydonautilus* from *Styrionautilus.* The only essential difference between these two genera is that the ventral saddle of *Styrionautilus* passes over the venter in a straight line. *Styrionautilus sauperi* develops a small lobe on the ventral saddle in the very late septa and seems to be a form transitional to typical *Proclydonautilus.*

Closely related to *Proclydonautilus* are *Cosmonautilus* Hyatt and Smith and *Callaionautilus* Kieslinger. Kieslinger (1924, p. 63) suppressed *Cosmonautilus* and placed all the species assigned to it in *Clydonautilus* and *Proclydonautilus.* He also suppressed *Callaionautilus* (Kieslinger, 1924, p. 133–138). The writer considers *Callaionautilus* and *Cosmonautilus* valid genera closely related to *Proclydonautilus.* These three closely related taxonomic groups show a great diversity in the form of the conch.

Distribution of species of the genus Proclydonautilus

Species	Stratigraphic distribution	Geographic distribution
Proclydonautilus angustus Kieslinger 1924	Triassic (upper)	Timor.
P. buddhaicus Diener 1908	Triassic (Karnian)	Alps, Himalayas, Timor.
P.? ermolli Diener 1919	do	Alps, Timor.
P. gasteroptychus (Dittmar) 1866	Triassic (Norian)	Alps.
P. gasteroptychus timorensis Welter 1914	Triassic (upper)	Timor.
P. goniatites (Hauer) 1849	Triassic (Karnian)	Alps, Timor.
P. griesbachi Mojsisovics 1896	Triassic (Karnian, Norian)	Alps, India, Timor.
P. hessi (Smith) 1927	Triassic (Karnian)	California.
P. inflatus Welter 1914	Triassic (upper)	Timor.
P. mandevillei (Marschall) 1909	do	New Zealand.
P. natosini McLearn 1946	Triassic (Norian)	British Columbia.
P. singularis Welter 1914	Triassic (upper)	Timor.
B. spirolobus (Dittmar) 1866	Triassic (Karnian, Norian)	Alps, Timor, California.
P. squawensis Kummel n. sp	Triassic (Karnian)	California.
P. stantoni Smith 1927	do	Do.
P. triadicus (Mojsisovics) 1873	do	Alps, India, Timor, California.
P. tuvalicus Diener 1919	do	Alps.
P. ursensis Smith 1927	do	California.

Proclydonautilus triadicus Mojsisovics

Plate 9, figures 1–20

1873. *Nautilus triadicus* Mojsisovics, K.-k. geol. Reichsanstalt Wien Abh., Band 6, Hälfte 1, p. 27, pl. 14, figs. 1–4.

1882. *Clydonautilus triadicus* Mojsisovics, K.-k. geol. Reichsanstalt Wien Abh., Band 10, p. 281.

1891. *Clydonautilus triadicus* Mojsisovics, Foord, Catalogue of fossil Cephalopoda, Part 2, p. 182.

1902. *Clydonautilus* (*Proclydonautilus*) *triadicus* Mojsisovics, K.-k. geol. Reichsanstalt Wien Abh., Band 6, Hälfte 1, Supplement Heft, p. 209.

1904. *Clydonautilus* (*Proclydonautilus*) *triadicus* Mojsisovics, Gemmellaro, I Cefalopodi del Trias Superiore della Regione Occidentale della Sicilia, p. 7, tav. 1, figs. 14, 15, Palermo.

1904. *Proclydonautilus triadicus* Mojsisovics, Smith, Proc. California Acad. Sci. 3rd Series, vol. 1, no. 10, p. 401–402, pl. 46, fig. 2, pl. 47, fig. 2.

1905. *Proclydonautilus triadicus* Mojsisovics, Hyatt and Smith, U. S. Geol. Survey Prof. Paper 40, p. 206–207, pl. 49, figs. 1–3, pl. 50, figs. 1–17.

1908. *Proclydonautilus triadicus* Mojsisovics, Diener, Mem. Geol. Survey India, vol. 1, series 15, p. 50, taf. 1, fig. 1.

1914. *Proclydonautilus triadicus* Mojsisovics, Welter, Paläontologie von Timor, I. Lieferung, p. 207–208, figs. 78, 79.

1919. *Clydonautilus* (*Proclydonautilus*) *triadicus* Mojsisovics, Diener, Akad. der Wiss. Wien, Denkschriften, Band 97, p. 766–768, figs. 6, 7.

1924. *Proclydonautilus triadicus* Mojsisovics, Kieslinger, Jaarboek Van Het Mijnwezen in Nederlandsch Oost-Indië, Verhandelungen 3, p. 131.

1927. *Proclydonautilus triadicus* Mojsisovics. Smith, U. S. Geol. Survey Prof. Paper 141, p. 102–103, pl. 49 figs. 1–3, pl. 50, figs. 1–17.

This is one of the most common and widespread Upper Triassic nautiloids. The seven plesiotypes described and figured by Smith (1927, p. 102) are available for study. Smith's original description of these specimens is quoted here in part.

> Involute, somewhat compressed laterally, high-whorled, with broadly rounded flanks and venter without any angle on either. Umbilicus completely closed; broadly rounded umbilical shoulders. The whorl is slightly broader than it is high, and the greatest breadth is even with the projection of the top of the inner whorl. The height of the whorl is two-thirds of the total diameter. The

> siphuncle lies a little below the center. The surface is smooth and has no ornamentation except the exceedingly fine radial striae of growth, which bend backward on the venter, forming a broad hyponomic sinus.
>
> The septa are sinuous, showing both lobes and saddles; the broad and deep ventral saddle is divided by a narrow and shallow abdominal lobe; the lateral lobe is long and rather broad; on the umbilicus there is a second lateral lobe, shallow and broad. There is no internal lobe.

The measurements (in millimeters) of the specimens illustrated are as follows:

U.S.N.M. No.	Diameter	Height of last whorl	Width of last whorl
74027	97	62	72
74027a	71	40	46
74027b	37	23	25
74027c	13	7	10
74027d	12	7	10
74027e	7	3. 3	4. 5
74027f	3. 5	2	3. 5

Occurrence.—Upper Triassic Hosselkus limestone, in both subzones of the zone of *Tropites subbullatus*, on the divide between Squaw Creek and Pit River, 3 miles east of Madison's ranch and half mile north of the trail to Brock's ranch, in Shasta County, Calif.

Plesiotypes.—U.S.N.M. 74027, 74027a-f.

Proclydonautilus spirolobus (Dittmar)

Plate 7, figures 10–19

1866. *Nautilus spirolobus* Dittmar, Geognostische palaeontologische Beitrage, Band I, p. 352, pl. 13, figs. 1, 2.
1873. *Nautilus spirolobus* (Dittmar). Mojsisovics, K.-k. geol. Reichsanstalt Wien Abh., Band 6, Hälfte 1, p. 28.
1882. *Clydonautilus spirolobus* (Dittmar). Mojsisovics, K.-k. geol. Reichsanstalt Wien Abh., Band 10, p. 281.
1891. *Nautilus* (*Clydonautilus*) *spirolobus* Dittmar. Foord, Catalogue of fossil Cephalopoda, Part 2, p. 187–188, fig. 33.
1902. *Clydonautilus* (*Proclydonautilus*) *spirolobus* (Dittmar). Mojsisovics, K.-k. geol. Reichsanstalt Wien Abh., Band 6, Hälfte 1, Supplement Heft, p. 211–212, pl. 10, fig. 3, pl. 11, fig. 1.
1914. *Proclydonautilus spirolobus* (Dittmar). Welter, Palaontologie von Timor, 1 Lieferung, p. 209–210, pl. 32, figs. 2, 3.
1924. *Proclydonautilus spirolobus* (Dittmar). Kieslinger, Jaarboek Van Het Mijnwezen in Nederlandsch Oost-Indië, Verhandelungen 3, p. 76, fig. 10.
1927. *Proclydonautilus spirolobus* (Dittmar). Smith, U. S. Geol. Survey Prof. Paper 141, pl. 88, figs. 6–14.
1939. *Proclydonautilus spirolobus* (Dittmar). Muller and Ferguson, Bull. Geol. Soc. America vol. 50, p. 1605.

This Alpine Triassic species is represented in the collection by five specimens, four of which are the specimens described and figured by Smith (1927). This species has been recorded from California, Nevada, the Alps, and Timor. The most diagnostic features are the ridgelike growth lines which are prominent even on the internal mold. Conch is globose and involute with a well-rounded venter and no distinct ventrolateral shoulders. One of the paratypes with a diameter of 13 mm has a smooth internal mold with delicate growth lines on the shell. One of the specimens has a portion of the aperture preserved and shows a shallow hyponomic sinus on the venter. Measurements (in millimeters) of the plesiotypes are as follows:

	14128	14128a	14128b	14128c
Diameter	54	45	13	6. 5
Height of last whorl	32	27	7	3. 5
Width of last whorl	35	32	10. 5	4. 5

Ornamentation is in general uncommon in the Clydonautilidae. *Proclydonautilus spirolobus* is very easily distinguished from all other species of *Proclydonautilus* by its surface markings.

Occurrence.—Upper Triassic Hosselkus limestone, in the *Tropites subbullatus*, *Juvavites* subzone, at the north end of Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.

Plesiotypes.—U.S.N.M. 14128, 14128a, 14128b, 14128c.

Proclydonautilus stantoni Smith

Plate 10, figures 1–6

1927. *Proclydonautilus stantoni* Smith, U. S. Geol. Survey Prof. Paper 141, p. 103, pl. 85, figs. 6–11.

Smith's original description is as follows:

> Robust, involute, subspherical, with rounded flanks, subangular shoulders, and narrow flattened band on the venter. Surface with sinuous growth lines, making a broad, shallow backward-curving sinus on the venter. Septa with short narrow ventral lobe and deep lateral.

Measurements (in millimeters) of the specimens are as follows:

	Holotype	Paratype
Diameter	75	30
Width of last whorl	59	23
Height of last whorl	45	18

Proclydonautilus stantoni is most similar to *P. triadicus*, which, however, lacks the flattened venter.

Occurrence.—Upper Triassic Hosselkus limestone, at the lower horizon (*Trachyceras* subzone) of the *Tropites subbullatus* zone, 3 miles east of Madison's ranch, on Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.

Types.—Holotype, U.S.N.M. 74123; paratype, U.S.N.M. 74123a.

Proclydonautilus ursensis Smith

Plate 11, figures 1–8

1927. *Proclydonautilus ursensis* Smith, U. S. Geol. Survey Prof. Paper 141, p. 103, pl. 84, figs. 1–3, pl. 85, figs. 1–5.

The holotype and two small paratypes are available for study. The conch of the holotype is large, robust, globular, and nautiliconic. The venter is broadly rounded, passing onto the flanks with no distinct ventral shoulders. The flanks are broadly convex and converge towards the venter. The umbilicus is completely closed. The living chamber appears to be nearly complete and is one-third volution in length. The shell is smooth except for conspicuous growth lines.

The two small paratypes agree in most features with the holotype. There is no ventral lobe in the smallest paratype at a diameter of 8 mm. The larger paratype has a small ventral lobe. The measurements (in millimeters) of the specimens are as follows:

	Holotype	Paratype	Paratype
Diameter	125	21	5
Width of last whorl	75	18	6
Height of last whorl	69	13	5

The large robust globular conch of this species is uncommon in *Proclydonautilus* and direct comparison with other species is unnecessary.

Occurrence.—Upper Triassic Hosselkus limestone, in the upper part (*Juvavites* subzone) of the *Tropites subbullatus* zone, at Bear Cover, at the north end and east side of Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.

Types.—Holotype, U.S.N.M. 74122; paratypes, U.S.N.M. 74122a and 74122b.

Proclydonautilus hessi (Smith)

Plate 15, figures 12–15

1927. *Clydonautilus hessi* Smith, U. S. Geol. Survey Prof. Paper 141, p. 107–108, pl. 88, figs. 15–19.

Conch small, involute, and compressed. The venter is flattened and rather broad, passing on to very distinct ventrolateral shoulders. At the maximum diameter of the conch the venter is 22 mm wide. The flanks are broadly rounded on the phragmocone but become more rounded on the living chamber. The umbilical shoulders are broadly rounded. On the phragmocone the venter is well rounded and the ventral shoulders are not distinct. No part of the shell is preserved but the surface of the internal mold contains impressions of the growth lines on the living chamber that clearly indicate the presence of a deep hyponomic sinus. The suture has a ventral saddle divided by a small bluntly pointed lobe, passing to a broad, deep lateral lobe, and then to a narrow rounded lateral saddle just above the umbilical shoulder.

Smith placed this species in *Clydonautilus* on the characters of its shape and septation. The shape of the conch in the Clydonautilidae is highly variable and *Proclydonautilus* and *Clydonautilus* cannot be distinguished on this basis. The sutures of *Proclydonautilus hessi* are typical of the genus, having only a small ventral lobe. In *Clydonautilus* there is a small saddle in the middle of the ventral lobe. This species is most closely related to *Proclydonautilus squawensis* Kummel, n. sp., differing in features of the ventral shoulders, and in having a more inflated conch.

Occurrence.—Upper Triassic Hosselkus limestone, at the lower horizon (*Trachyceras* subzone) of the *Tropites subbullatus* zone, 3 miles east of Madison's ranch, on Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.

Types.—Holotype, U.S.N.M. 74129; paratype, U.S.N.M. 74129a.

Proclydonautilus squawensis n. sp.

Plate 8, figures 1–7, text figure 42

1927. *Styrionautilus sauperi* Smith, U. S. Geol. Survey, Prof. Paper 141, p. 107, pl. 85, figs. 12–18.

The original assignment of the species to *Styrionautilus* cannot be followed. *Styrionautilus* is characterized by a suture that passes over the venter in a straight line. *Styrionautilus sauperi* develops a narrow ventral lobe on the last few septa of a mature individual (Mojsisovics, p. 206, 1902). The present species has a distinct ventral lobe at a diameter of 13 mm. On this basis it seems advisable to place this species in *Proclydonautilus.*

The conch is involute, somewhat compressed, and smooth. The venter is broadly arched, terminating at sharply rounded ventral shoulders. The distinct ventral shoulders first develop at a diameter of approximately 15 mm. The flanks converge toward the venter and are concave on the ventral half, passing to a well-rounded umbilical shoulder (text fig. 42). The surface of the conch is smooth except for growth lines that form a deep rounded hyponomic sinus on the venter. The suture has a small bluntly pointed ventral lobe, a deep lateral lobe, and a lateral saddle on the umbilical shoulder. The suture at a conch diameter of 13 mm has a shallow broad ventral lobe. Measurements (in millimeters) of the holotype and paratypes are as follows:

	Holotype 74124	Paratype 74124a	Paratype 74124b
Diameter	52	18	7
Height of last whorl	32	11	4. 5
Width of last whorl	35	14	5. 5

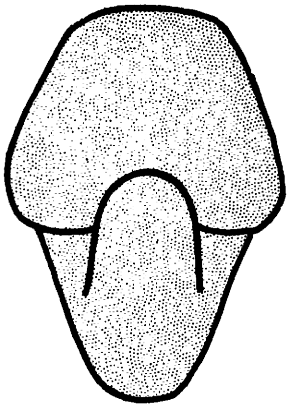

FIGURE 42.—Diagrammatic cross section of holotype of *Proclydonautilus squawensis* n. sp. (U.S.N.M. 74124) from Hosselkus limestone Brock Mountain, Shasta County California, ×1.

The form of the conch in the Clydonautilidae is extremely varied. The general conch pattern of *Proclydonautilus squawensis* is similar to that of *Proclydonautilus griesbachi*, *Styrionautilus sauperi*, and *Clydonautilus biangularis*, but its suture pattern is different. It is also similar in conch pattern to some species of *Cosmonautilus* but lacks the nodose ornamentation, and differs in suture pattern.

This species is named for Squaw Creek, which is near the outcrop area where the specimens were collected.

Occurrence.—Upper Triassic Hosselkus limestone, at the upper horizon (*Juvavites* subzone) of the *Tropites subbullatus* zone, at Bear Cove, at the north end and east side of Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.

Types.—Holotype, U.S.N.M. 74124; paratypes 74124a and 74124b.

Proclydonautilus natosini McLearn

1946. *Proclydonautilus natosini* McLearn, Geol. Survey Canada, Paper 46–25, Appendix, p. 1, pl. 2, figs. 1, 2.
1947. *Proclydonautilus natosini* McLearn, Geol. Survey Canada, Paper 47–14, p. 5, 6.

The writer has not had the opportunity to study representatives of this species but McLearn's original description is quoted here.

> The holotype is an incomplete shell of 90 mm in diameter; robust, involute, thicker than high whorls, with almost flat, converging sides, well-rounded ventral shoulder, low, rounded venter and nearly central siphuncle. Surface has fine, transverse, costae, nearly straight on sides, but bending back in a broad curve on venter; also longitudinal, short, low, closely spaced costae, forming with the transverse costae a delicate, textural ornament. Some specimens are larger than the holotype. Largest known specimen 200 mm in diameter, at which stage venter is wide and flat * * * Suture line like those of *P. spirolobus* Dittmar, *P. goniatites* Hauer and *P. angustus* Kieslinger; the ornament is different from these species, however, in having longitudinal as well as transverse ornament.

Occurrence.—Upper Triassic along Sikanni Chief River below Chicken Creek, northeastern British Columbia; from beds 'd' and 'e' of measured section in McLearn (1946, p. 2, 3).

Types.—Geol. Survey Canada, holotype 9257, paratype 9260.

Genus COSMONAUTILUS Hyatt and Smith, 1905

Genotype: *Cosmonautilus dilleri* Hyatt and Smith

Hyatt and Smith (1905, p. 207) described the genus as follows:

> Form involute, high whorled, laterally compressed, with narrow flattened venter and distinct abdominal shoulders. Surface at maturity smooth with only the striae of growth. Septa very sinuous, with broad rounded ventral lobe, long principal lateral, and a shallow small lobe outside of the umbilicus. The internal septum has no lobe. Siphuncle above the center.
>
> In the adolescent stage this genus resembles *Metacoceras* (*M.*) *cavatiforme* Hyatt, Geol. Survey Texas, Second Ann. Rept., 1890, p. 334, figs. 30–33). In these stages the whorl is broad, much lower than at maturity, with simple septa, and a strong row of tubercles on the angular abdominal shoulders. The phylogeny of this group seems to be as follows: *Temnocheilus-Metacoceras-Cosmonautilus.*

Welter (1914, p. 218) followed Hyatt and Smith in according *Cosmonautilus* full generic rank. Diener (1919, p. 770–771) pointing to the close similarity between *Cosmonautilus dilleri* and *Proclydonautilus buddhaicus* came to the conlusion that the former could at best be only considered a subgenus of *Proclydonautilus*. Kieslinger (1924, p. 63 etc.) completely suppressed *Cosmonautilus* and placed its species in *Proclydonautilus*. Smith (1927, p. 104) in his monograph on the Upper Triassic Faunas of North America, merely repeated the description by Hyatt and Smith (1905, p. 207) and made no reference to the work of Welter, Diener, or Kieslinger. The rather involved discussion of *Cosmonautilus* and *Proclydonautilus* by Kieslinger, and the wide latitude he allows *Proclydonautilus* does not appear to be the correct or simplest approach to this problem.

The only essential difference between *Cosmonautilus* and *Proclydonautilus* rests in the presence of ventrolateral nodes on the early whorls of the former. These nodes, however, have no relationship whatsoever with a "*Metacoceras*" ancestry as believed by Hyatt and Smith. The present writer believes that *Cosmonautilus* is derived from *Proclydonautilus*, and that the Clydonautilidae have their ancestry in the Paranautilidae (probably *Paranautilus*). In neither of these families are nodes of any form a dominant morphological feature, on the contrary both families are characterized by involute smooth forms generally lacking ornamentation. The development of nodes in *Cosmonautilus* is a coenogenetic character developed as a new feature and un-

Distribution of species of the genus Cosmonautilus

Species	Stratigraphic distribution	Geographic distribution
Cosmonautilus dilleri, Hyatt and Smith 1905	Triassic (Karnian)	California; Sonora, Mexico.
C. dilleri var. spiralis Kieslinger 1924	Triassic (upper)	Timor.
C. hersheyi Smith 1927	Triassic (Karnian)	California.
C. jonkeri Kieslinger 1925	Triassic (Norian)	Timor.
C. malayicus Welter 1914	Triassic (upper)	Do.
C. pacificus Smith 1927	Triassic (Karnian)	California.
C. shastensis Smith 1927	do	Do.

related to the ancestral form. A similar feature is found in another smooth stock, that of the Gryposeratidae. In some species of *Domatoceras* and *Plummeroceras,* low ventrolateral and dorsolateral nodes are developed in late maturity. *Gryponautilus* also includes species that develop ventrolateral nodes. This genus is very similar in some respects to *Proclydonautilus* and has an annular lobe. It thus appears that the nodes on the early whorls of *Cosmonautilus* have no phylogenetic significance but are rather a new modification that developed on a proclydonautilid stock.

Cosmonautilus dilleri Hyatt and Smith

Plate 12, figures 1–4; pl. 13, figs. 1–7; pl. 14, figs. 1–6.

1905. *Cosmonautilus dilleri* Hyatt and Smith, U. S. Geol. Survey Prof. Paper 40, p. 207–208, pl. 51, fig. 1; pl. 52, fig. 1; pl. 53, figs. 1, 2; pl. 54, figs. 1–4; pl. 55, figs. 1–11.

1914. *Cosmonautilus* cf. *dilleri* Hyatt and Smith. Welter, Palaontologie von Timor, 1, Lieferung, p. 128–220, figs. 93–98; pl. 33, figs. 1–3.

1919. *Cosmonautilus dilleri* Hyatt and Smith. Diener, Akad. Wiss. Wien, Denkschriften, Band 96, p. 770–771.

1924. *Proclydonautilus* (*Cosmonautilus*) cf. *dilleri* Hyatt and Smith. Kieslinger, Jaarboek Van Het Mijnwezen in Nederlandsch Oost-Indie, Verhandelungen 3, p. 87, pl. 3, figs. 3a, b; text fig. 17, 18; p. 90, fig. 19.

1924. *Proclydonautilus* (*Cosmonautilus*) *dilleri* var. *spiralis* Kieslinger, Jaarboek Van Het Mujnwezen in Nederlandsch Oost-Indie, Verhandelungen 3, p. 90, pl. 6, figs. 1a, b.

1927. *Cosmonautilus dilleri* Hyatt and Smith. Smith, U. S. Geol. Survey Prof. Paper 141, p. 104, pl. 51, fig. 1; pl. 52, fig. 1; pl. 53, figs. 1, 2; pl. 54, figs. 1–4; pl. 55, figs. 1–11; pl. 90, fig. 1; pl. 91, figs. 1, 2; pl. 92, figs. 1, 2.

The original description of this species is as follows:

Form involute, high whorled, somewhat compressed laterally, deeply embracing, and deeply indented by the inner volutions. Greatest breadth of the whorl at a point even with the projection of the inner volution. The height of the whorl is two-thirds of the total diameter of the shell, the width is six-sevenths of the height, and the indentation by the inner volution is less than one-third of the height. The whorl is broadly convex, and slopes up from the widest point to the abruptly rounded abdominal shoulders; the venter is flattened and its width between the shoulders is less than one-third of the greatest breadth of the whorl. The siphuncle is above the center of the chamber.

The septa are sinuous, divided externally into complex lobes and saddles. The long ventral saddle is divided by a broad U-shaped ventral lobe, forming two very narrow tongue-shaped saddles on the abdominal shoulders; there is a deep and broad principal lateral lobe, with rounded extremity, and a small shallow lateral on the umbilical slope. The internal septum has no lobe nor saddles. The surface of the shell is smooth at maturity, having only fine cross striae of growth.

In youth, up to the diameter of 8 mm, the whorl is subglobose and perfectly smooth, with simple straight septa. At this size the abdominal shoulders begin to develop, and very soon faint tubercles begin to appear on the shoulders; this sculpture rapidly grows strong, until the shape, sculpture, and septa are very like those of *Metacoceras* Hyatt. But by the time a diameter of 12 mm is reached the septa already show the sinuous lobes and saddles characteristic of the mature form, except that they are not so complex. We thus find *Metacoceras* characters and those belonging to *Cosmonautilus* occurring simultaneously in the same individual, which may mean either that the Paleozoic characters are retarded in the development or that the Mesozoic characteristics are unduly accelerated in their appearance.

At the diameter of 35 mm the tubercles become obsolete and the shoulders lose their angularity. The shell is then entering on maturity, and from this time onward does not change in any essential characters, the whorls becoming proportionally higher and more compressed laterally, but retaining their general characters. J. P. Smith has found a specimen of 280 mm diameter that agreed in all essentials with those of about 100 mm.

Occurrence.—Upper Triassic Hosselkus limestone, in the *Juvavites* subzone of the zone of *Tropites subbullatus,* on the divide between Squaw Creek and Pit River, 3 miles east of Madison's ranch and half a mile north of the trail to Brock's ranch, in Shasta County, California. At the same horizon at Terrup Chetta (Cottonwood Flat), near Squaw Creek, about 6 miles north of the locality just mentioned. Cerro Colorado (or Cerro de la Cruz) about 150 meters east of El Antimonio Sonora, Mexico; in red shale and platy limestone, probably zone described by Burchardt (1930) as red argillaceous shale with fossils of Karnic age.

Types.—Holotype and paratypes, U.S.N.M. 74028; plesiotypes 74463, 108003.

Cosmonautilus pacificus Smith

Plate 16, figures 1–14

1927 *Cosmonautilus pacificus* Smith, U. S. Geol. Survey Prof. Paper 141, pl. 86. figs. 1–15.

The holotype of this species is incomplete. The conch is compressed and involute. The venter is flattened, grading to sharply rounded ventral shoulders. At the maximum diameter of the conch, the venter is 18 mm wide; where the phragmocone and living chamber meet, the venter is slightly arched and 12 mm wide. The most adoral part of the living chamber shows a trace of the apertural margin, which on the venter defines a shallow sinus. The living chamber is about one-third of a volution in length.

The flanks converge towards the venter, and are flattened, with broadly rounded umbilical shoulders. The surface of the conch has very fine closely set ribs from the umbilicus to the venter. On the internal mold of the living chamber the ribs are visible only to the midpoint of the flanks and absent on the umbilical shoulders. The suture forms a deep U-shaped ventral lobe adjoined by a rounded saddle on the flanks adjacent to the ventral shoulders. The lateral lobe is deep and asymmetrical, and there is a lateral saddle on the umbilical shoulder. The siphuncle is centrally located.

The largest paratype, with a diameter of 56 mm, has indistinct ventral shoulders and a well-arched venter. The flanks converge strongly towards the venter. The ribbing is especially prominent on the ventral shoulders. The second largest paratype has a flattened venter and distinct ventral shoulders. The flanks are also flattened and converge towards the venter. The adapical portion of the conch small nodes are present on the ventral shoulders. The third largest paratype, with a diameter of 18 mm, has a more compressed conch and a flattened venter. The pattern of ornamentation is similar to that of larger paratypes and consists of both nodes and ribs. The siphuncle is central. The smallest paratype, with a diameter of 12 mm, has a slight ventral lobe on the adoral half whorl but adapically, the suture is straight and conch smooth and rounded. The siphuncle is below the center.

A weathered but complete topotype plus three fragmentary topotypes are also available. All of these specimens agree perfectly with the primary types. The measurements (in millimeters) of the type specimens are as follows:

	Holotype 74125	Paratype 74125a	Paratype 74125b	Paratype 74125c	Paratype 74125d
Diameter	95	56	31	18	12
Width of last whorl	60	39.5	24	14	9
Height of last whorl	61	36	21.5	11	7.5

Occurrence.—Upper Triassic Hosselkus limestone, in the upper horizon (*Juvavites* subzone) of the *Tropites subbullatus* zone, at the north end of Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.

Types.—Holotype, U.S.N.M. 74125; paratypes, U.S.N.M. 74125a, 74125b, 74125c, 74125d; topotypes, U.S.N.M. 108002.

Cosmonautilus shastensis Smith

Plate 15, figures 1–11

1927. *Cosmonautilus shastensis* Smith, U. S. Geol. Survey Prof. Paper 141, pl. 87, figs. 1–11.

The holotype and three small paratypes are available for study. The holotype is a fragment of a large, robust phragmocone. The conch is very involute, with its greatest width in the vicinity of the umbilical shoulders. The venter is broadly arched, measuring up to 25 mm in width on the most adoral part of the conch. The ventral shoulders are acutely rounded. The flanks adjacent to the ventral shoulders are concave, but where the shell is preserved this concavity is less pronounced. The central and dorsal part of the flanks is arched. The flanks converge strongly towards the venter.

The sutures have a rounded ventral lobe and a deep lateral lobe with a lateral saddle adjacent to the umbilical shoulder. The position of the siphuncle is not observable on the holotype. The shell is preserved in a few places on the conch of the holotype. The shell is 3.5 mm thick on the venter and is 1.5 mm thick on the midpoint of the flanks. Strong growth lines are visible on the shell. The ventral shoulders bear long, high nodes 15 to 20 mm apart.

The largest paratype is an immature individual that is 31 mm in diameter, 26 mm wide at the most adoral part and 19 mm high. The shell has a broad, flattened venter and sharp ventral shoulders. The flanks are flattened and converge strongly towards the venter. The ventrolateral nodes are very weakly developed. The second largest paratype is 15.5 mm in diameter, and has only a faint indication of flattening of the venter on its most adoral part. The preserved adapical part of the conch has a rounded venter and flanks with no prominent ventral shoulders. The surface is marked by conspicuous growth lines that show a shallow hyponomic sinus. The siphuncle is central. The smallest paratype is 7 mm in diameter, has a broadly rounded venter, and flanks with no ventrolateral shoulders. The conch is involute, and has whorls 6 mm wide, 4 mm high. The siphuncle is below the center.

The various species of *Cosmonautilus* are so distinctive that direct comparisons are not necessary.

Occurrence.—Upper Triassic Hosselkus limestone, at the upper horizon (*Juvavites* subzone) of the *Tropites subbullatus* zone, at Bear Cove, at the north end and rast side of Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.

Types.—Holotype, U.S.N.M. 74126; paratypes, U.S.N.M. 74126a, 74126b, 74126c.

Cosmonautilus hersheyi Smith

Plate 10, figures 7–15

1927. *Cosmonautilus hersheyi* Smith, U. S. Geol. Survey Prof. Paper 141 pl. 89, figs. 1–9.

This species is the smallest American species of *Cosmonautilus*. The holotype and two small paratypes are available for study. The conch is involute, smooth, and has a narrow, arched venter. The ventral shoulders are subangular, and there is a groove just dorsad of the ventral shoulder. There are slight nodes on the ventral shoulder on the adapical half of the last whorl of the holotype. The flanks are convex and converge towards the venter. The greatest width of the conch is at the umbilical shoulders. The shell is smooth with delicate growth lines which form a sinus on the venter. The siphuncle is central.

The largest paratype measures 33 mm in diameter, 22 mm in height of the last whorl and 22 mm in width of the last whorl. There is no groove on the ventral portion of the flank. The venter is more arched and the ventral shoulders not as distinct as on the holotype. The smallest paratype has a diameter of 19.5 mm, a height at the last whorl of 13 mm, and a width of 12.5 mm. Distinct ventral shoulders develop at a diameter of 12 mm. Adapically the whorls are rounded, and have no distinct ventral shoulders. The growth lines are very conspicuous. The septa on this small paratype are like those on the mature specimens.

Occurrence.—Upper Triassic Hosselkus limestone, at the upper (*Juvavites* subzone) of the *Tropites subbullatus* zone, at the north end of Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.

Types.—Holotype, U.S.N.M. 74130; paratypes, U.S.N.M. 74130a, 74130b.

Genus CALLAIONAUTILUS Kieslinger, 1924

Genotype: *Callaionautilus turgidus* Kieslinger

Kieslinger (1924, pp. 93–95) described the type species of his new genus as follows:

> Die neue Gattung gehört in die Nähe der von Hyatt und Smith unter dem Namen *Cosmonautilus* zusamengefassten Formen.
>
> Die inneren Windungen, bis zu einem Durchmesser von etwa 70 mm, stimmen vollständig mit *Proclydonautilus* (*Cosmonautilus*) *Dilleri* überein: Eine gedrungene, fast vollkommen involute Form, die Flanken kräftig aufgebläht, jedoch gegen die Schultern hin ebenso stark komprimiert; mit scharfen Kanten setzt der flache Externteil an. Diese Kanten tragen im inneren Teile der Windungen, bei Durchmessern von durchschnittlich 35 mm, Knoten, die bald scharf und deutlich ausgeprägt sind, bald kaum merklich hervortreten.
>
> Zwei Exemplare zeigen eine etwas abweichende Externskulptur in diesem Stadium, nämlich flache Quewülste auf den Externteil wie bei *Proclydonautilus inflatus*, andere Formen erscheinen wieder ganz glatt; die Variationsbreite dieser Formen ist also auszerordentlich grosz. Ein Bild von diesem Stadium gibt Text fig. 20 [fig. 43 of this report]. Einige Maszzahlen sollen es näher ergänzen:
>
> | | *Millimeters* | | |
> |---|---|---|---|
> | Durchmesser | 77 | 57 | 69 |
> | Windungshöhe | 45 | 34 | 42 |
> | Lichte Höhe | 31 | 20 | 30 |
> | Breite | 52 | 45 | 43(?) |
>
> Das von Welter (Timor, S. 225, Taf. 34, Fig. 4, 5) als *Gryposeras* cf. *Suessiforme* (Diener) beschriebene Exemplar scheint eine solche Jugendform eines *Callaionautilus turgidus* zu sein.
>
> Bei einem Durchmesser von durchschnittlich 70 mm beginnt nun eine eigentümliche Änderung: Die scharfen Kanten verschwinden, der Externteil wölbt sich auf, die Zone der gröszten Breite rückt von der Nabelgegend gegen die Externseite bis in die Projektion des vorhergehenden Umganges. Der Querschnitt bildet nun ein fast einheitliches Oval. Nun beginnt sich in der Medianlinie des Externteiles ein plumper Kiel herauszuheben, der sich bald in eine Reihe groszer, länglicher, stumpfer Knoten auflöst [pl. 19, figs. 6, 7, of this report]. Diese eigentümliche Skulptur läszt sich etwa mit einem Hahnenkamm vergleichen. Beiderseits dieser Knotenkielreihe liegt eine flache Einsenkung, die durch ganz gerundete Schultern mit den Flanken zusammenhängt.
>
> Die Schale aller Exemplare ist auffallend dick, auch bei ganz kleinen Formen. Gewissermaszen im Widerspruch hiezu sind die Kammerscheidewande bei fast allen Stücken zerstört, nur zwei zeigen schlecht erhaltene Fragmente, zwischen einem Gewirr von *Serpuliden*, welche das leere Gehäuse besiedelt hatten.
>
> Die Lobenlinie bleibt—ähnlich wie bei *Proclydonautilus singularis* Walter—lange Zeit in dem primitiven Stadium etwa eines *Paranautilus:* ein einfacher Laterallobus, ein ebenso flacher, stumpfwinkeliger Externlobus (das Gehäuse zeigt in diesem Stadium eine deutliche Normallinie). Erst nach einem Durchmesser von 40 mm beginnt sich der Laterallobus zu vertiefen, bzw. der Externsattel höher zu werden. So entsteht eine *Proclydonautilus*-Sutur. Ein gröszeres Exemplar zeigt (bei einem Durchmesser von ca. 70 mm) einem spitzen Laterallobus, der etwa an *Proclydonautilus Dilleri* erinnert.
>
> Der Sipho konnte infolge des ungünstigen Erhaltungszustandes nirgends beobachtet werden.
>
> Dimensionen (am Steinkern gemessen):
>
> | | *Millimeters* |
> |---|---|
> | Durchmesser | 106 |
> | Windungshöhe | 60 |
> | Lichte Höhe | 39 |
> | Breite | 58 |
> | Nabelweite | 11 |

Kieslinger's description of *Callaionautilus turgidus* can be summarized as follows:

> This new genus is similar to *Cosmonautilus* Hyatt and Smith. The inner whorls, up to a diameter of approximately 70 mm, agrees completely with *Proclydonautilus* (*Cosmonautilus*) *dilleri.* Conch almost completely involute, whorl sides strongly inflated, but compressed towards the shoulders, venter flattened, shoulders angular. The ventral shoulders up to a diameter of the conch of 35 mm bears nodes which adorally disappear. The extent of variation in this species is very great. *Grypoceras* cf. *suessiforme*

(Welter, 1914, p. 225, pl. 34, figs. 4, 5) appears to be a young form of *Callaionautilus turgidus*.

At a diameter of 70 mm the whorl section begins to become oval and the angular ventral shoulders disappear. A median keel is formed on the benter on which soon develop large nodes. This peculiar sculpture is similar to a cock's comb. On both sides of the median nodose keel is a shallow furrow. The suture is similar to that of *Proclydonautilus dilleri*. The siphuncle was not observed.

In a supplement to his main article Kieslinger (1924) discussed *Callaionautilus turgidus* in greater detail and came to the conclusion that his new genus fell within the sphere of variation of *Proclydonautilus* and suppressed it. Whereas the early whorls show remarkable similarity to *Cosmonautilus* and *Proclydonautilus*, the transformation of the conch to a smooth oval whorl with a central nodose keel appears to be a definite evolutionary change (or advancement) over these other two genera. *Callaionautilus* can better be considered as another evolutionary development (similar to *Cosmonautilus*) out of a proclydonautilid stock and taxonomically ranked as a genus. It is, however, true that we are dealing with a monotypic genus in which all of the few specimens known came from the Upper Triassic of Timor. Probably when more material is available the relationships of *Callaionautilus* will be better understood. Spath (1927b, p. 24) believes that *Callaionautilus* probably does not belong in the Clydonautilidae, but gave no reasons for his opinion.

Genus CLYDONAUTILUS Mojsisovics, 1882

Genotype: *Nautilus noricus* Mojsisovics

Mojsisovics' description of the genus is as follows:

> Aus der ziemlich beträchtlichen Anzahl der triadischen Formen scheiden wir vorläufig blos die auf die juvavische Provinz beschränkte Gruppe des *Nautilus noricus* als besondere Gattung unter der Bezeichnung *Clydonautilus* aus. Es gehören dahin involute, hochmundige Formen mit geschlossenem oder sehr kleinem Nabel und drei ausserhalb des Nabels liegenden, tiefen, spitzgerundeten Loben, von welchen zwei ausserhalb der Projection der vorhergehenden Windung liegen. In höherem Alter theilt sich der Externlobus durch einen grossen, sattelförmigen Medianhöcker in zwei getrennte, auf die Seitenflanken abgedrängte Partien. Ein Interlobus ist nicht vorhanden. Der Sipho steht unter oder uber der halben Mundhöhe. Schalenoberfläche entweder reticulirt oder quer gestreift oder mit schwachen Lateralfalten versehen.

A summary of Mojsisovics' description is as follows:

> Conch involute, compressed, with a closed or very small umbilicus. Suture with deep sharply rounded lobes. The ventral lobe has a small median saddle. No annular lobe is present. The siphuncle lies either above or below the center of the whorl section. Shell reticulate, with cross striae, or with weak folds.

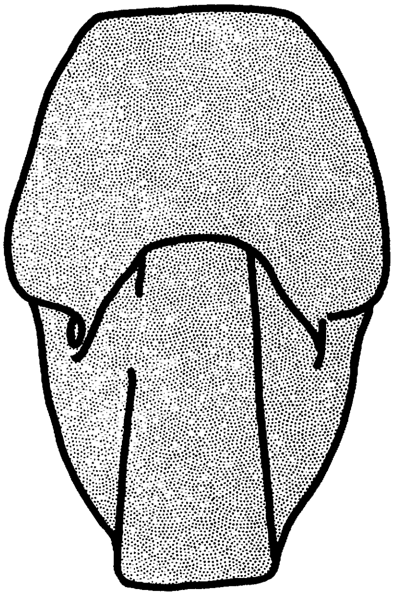

FIGURE 43.—Diagrammatic cross section of young form of *Callaionautilus turgidus* Kieslinger, ×1. (After Kieslinger, 1924, fig. 20).

The conch of *Clydonautilus* is involute and of the same pattern as in *Proclydonautilus*, which was separated by Mojsisovics (1902) as a subgenus of *Clydonautilus*, but the shell is generally more compressed. Generally the venter is flattened, at least during some stage of growth. The division of the ventral lobe by a small saddle ("Medianhocker") is most highly developed in *Clydonautilus noricus* (see text fig. 41), in which the saddle is very deep and somewhat quadrangular in shape. In *Clydonautilus salisburgensis* and *C. biangularis* the dividing saddle of the ventral lobe is very slightly developed (text fig. 41). Other species such as *Clydonautilus quenstedti* have a small saddle intermediate between that found in *C. noricus* and *C. biangularis;* it is, however, still rounded and not angular as in *C. noricus*.

Most species of *Clydonautilus* are smooth, but a few species show ornamentation. *Clydonautilus cicatricosus* Kieslinger has nodes developed on the ventral shoulders, as in typical representatives of *Cosmonautilus*, but it has a clydonautilid suture. Other species, as *C. biangularis*, have low flat folds on the flanks that extend in lesser degree over the venter.

The only essential difference between *Clydonautilus* and *Proclydonautilus* is the former has a median saddle dividing the ventral lobe. As pointed out by Kieslinger (1924) the median saddle does not develop until a late stage of growth in some species. The oldest known species of *Clydonautilus* seems to be *C. kieslingeri* Pakuckas from the Ladinian of Timor. These two genera, differing in only one feature, probably represent independent but closely related lines developing out of *Styrionautilus*. *Cosmonautilus* is thought to stem from *Proclydonautilus* but does show affinities to *Clydonautilus* through *Clydonautilus cicatricosus*.

Distribution of species of the genus Clydonautilus

Species	Stratigraphic distribution	Geographic distribution
Clydonautilus acutilobatus Diener 1908	Triassic (Karnian)	Himalayas, India.
C. biangularis Mojsisovics 1896	Triassic (Norian)	Himalayas, India; Timor.
C. cicatricosus Kieslinger 1924	do	Timor.
C. compressus Welter 1914	do	Do.
C. glaber Kieslinger 1924	Triassic (upper)	Do.
C. kieslingeri Pakuckas 1928	Triassic (Ladinian)	Do.
C. noricus (Mojsisovics) 1873	Triassic (Norian)	Alps.
C. noricus var. *timorensis* Welter 1914	Triassic (upper)	Timor.
C. quenstedti (Hauer) 1849	Triassic (Norian)	Alps.
C. salisburgensis (Hauer) 1849	do	Alps, Timor.
C. salisburgensis timorensis (Welter) 1914	Triassic (upper)	Timor.

Family GONIONAUTILIDAE Kummel, 1950

Genus GONIONAUTILUS Mojsisovics, 1902

Genotype: *Nautilus securis* Dittmar

This monotypic genus includes one of the most specialized of Triassic nautiloids (pl. 19, figs. 4, 5). Mojsisovics considered *Gonionautilus* to be the end form in an evolutionary development beginning with *Paranautilus* through *Clydonautilus*. The genus has been recorded from Norian rocks of the Alpine region and from the *Pinacoceras metternichi* zone (Norian) of the Gabbs formation, southwestern Nevada (Muller and Ferguson, 1939, p. 1605).

Mojsisovics' original description of this genus is quoted here in full (1902, p. 207).

> Die hochmündigen involuten Gehäuse sind mit einem schmalen, biangularen Externtheil versehen und stimmen in allen wesentlichen Merkmalen mit den typischen Clydonautilen mit zweispitzigem Externlobus überein. Es uterscheidet sie blos ein, meines Wissens, bei Nautilen bisher noch neimals beobachtetes Merkmal, ein zwei spitziger Internlobus. Dem zweispitzigem Externlobus entspricht bei *Gonionautilus* auch ein zweispitziger Internlobus. Es ist sehr bemerkenswert, dass *Gonionautilus* ohne Passirung eines Zwischestadiums mit einspitzigem Internlobus sich aus einer Gattungsreihe herausgebildet hat, welche überhaupt keinen Internlobus besass.
>
> Die Position des Sipho schwankt um die halbe Mündungshöhe; bei der typischen Art steht der Sipho oberhalb der halben Mündungshöhe.

Mojsisovics' description can be summarized as follows:

> Conch compressed with a narrow, angular ventral area and similar to *Clydonautilus* in its double pointed ventral lobe. It is mainly characterized by its double pointed annular lobe. It is remarkable that *Gonionautilus*, belonging to a stock which possesses no annular lobe, attained a double annular lobe without an intermediate stage of a singular annular lobe. Siphuncle is in the upper half of the whorl section.

The shape of the conch, and the external suture place this genus close to the Clydonautilidae. However, the peculiar double annular lobe sets this form apart from other Triassic nautiloids. The Clydonautilidae do not have annular lobes.

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Zimmermann, Ernst, 1892, Ein neuer Nautilus aus dem Grenzdolomit des thuringischen Keupers (*Trematodiscus jugatonodosus*): Jahrb. preuss. geol. Landesanst., 1889, pp. 322–327, pl. 27.

ERRATA

Page 10, col. 1, line 31—for *mesodiscus* read *mesodicum*

Page 19, table—take out *F. wynnei* (Waagen) 1879

col. 2, line 8—for *cavatiformis* read *cavatiforme*

Page 21, col. 2, line 9—for *aureculatum* read *auriculatum*

Page 26, col. 2, line 53—for *goliathus* read *goliathum*

Page 33, col. 2, line 38—for *Encoiloseras* read *Encoiloceras*

Page 44. col. 1, line 40—for *Trachynatilus* read *Trachynautilus*

Page 51, col. 1, line 27 (second table)—for *gumbeli* read *gümbeli*

Page 53, table—for *guembeli* read *gümbeli*

col. 2, line 3—for *hunicus* read *hunicum*

Page 55, table—for *parallelus* read *parallelum*

Page 59, col. 1, lines 4, 12—for *convolutus* read *convolutum*

Page 60, col. 2, line 38—for *granulosostriatus* read *granulosostriatum*

Page 61, col. 1, line 27—for *evolutus* read *evolutum*

col. 1, line 27—for *eugyrus* read *eugyrum*

Plate 1—for *sangamonensis* read *sangamonense*

INDEX

[Italic numbers indicate descriptions]

PLATES 1–19

PLATE 1

[All figures natural size]

FIGURES 1, 2. *Temnocheilus latus* (Meek and Worthen) (p. 17).
Holotype, University of Illinois, X–438A. From a formation of Pennsylvanian age, Carbon Cliff, Rock Island County, Illinois.

3, 4, 5. *Metacoceras sangamonensis* (Meek and Worthen) (p. 19).
Holotype, University of Illinois, X–291 (11074). From the McLeansboro formation, Sangamon County, Illinois.

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TEMNOCHEILUS AND METACOCERAS


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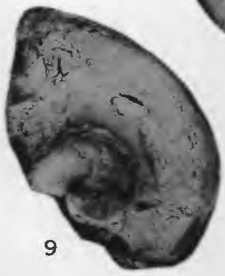
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METACOCERAS

PLATE 2

[All figures natural size]

FIGURES 1–10. *Metacoceras* (*Mojsvaroceras*) *frenchi* Kummel, n. sp. (p. 23).

1. Holotype, U.S.N.M. 107069; 2, paratype, U.S.N.M 107070; 3, paratype, U.S.N.M. 107071; 4, 5, paratype, U.S.N.M. 107072; 6, paratype, U.S.N.M. 107073; 7, paratype, U.S.N.M. 107074; 8, paratype, U.S.N.M. 107075; 9, paratype, U.S.N.M. 107076; 10, paratype, U.S.N.M. 107077. Figures 1–9, from upper shale member (*Columbites* zone) of the Thaynes formation, Montpelier Canyon, Idaho, sec. 31, T. 12 S., R. 45 E. Figure 10 from same horizon of Thaynes formation, Hot Springs, Idaho, sec. 18, T. 15 S., R. 45 E.

11–14. *Metacoceras* (*Mojsvaroceras*) *turneri* Hyatt and Smith (p. 23).

11, 12. Holotype, U.S.N.M. 74026; 13, 14, paratype, U.S.N.M. 74026a. From Upper Triassic Hosselkus limestone, in the *Juvavites* subzone of the *Tropites subbullatus* zone, 3 miles east of Madison's ranch, between Squaw Creek and Pit River, Shasta County, California.

PLATE 3

[All figures natural size]

FIGURES 1–10. *Germanonautilus brooksi* Smith (p. 29).

1, 2, Holotype, U.S.N.M. 74206; 3, 4, 5, paratype, U.S.N.M. 74206; 6, 7, 8, topotype, U.S.N.M. 107087; from U.S.G.S. locality 9384, south bank of Yukon River opposite mouth of Nation River, Alaska; 9, 10, Plesiotype, U.S.N.M. 107086. From U.S.G.S. locality 9385, Nation River, hillside one third mile northeast of mouth of Yukon Valley, Alaska.

11. *Germanonautilus montpelierensis* Kummel, n. sp. (p. 30).

Holotype, U.S.N.M. 107089. From upper shale member (*Columbites* zone) of the Thaynes formation, Hot Springs, Idaho, sec. 18, T. 15 S., R. 45 E.

12, 13. *Germanonautilus furlongi* Smith (p. 29).

Holotype, U.S.N.M. 74444. From the *Daonella dubia* zone of the Star Peak formation, Fossil Hill, West Humboldt Range, Nevada.

14, 15. *Germanonautilus johnstoni* Kummel, n. sp. (p. 30).

Holotype, U.S.N.M. 107088. From Star Peak formation, South Canyon, New Pass, Desatoya Range, Nevada.


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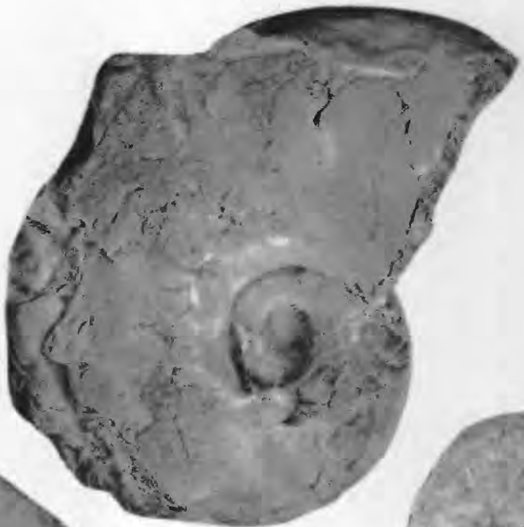
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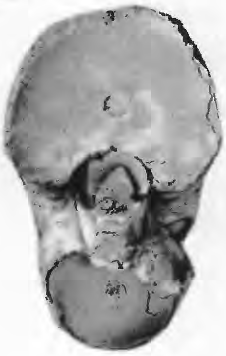
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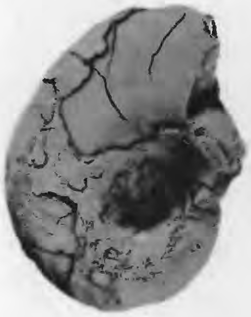
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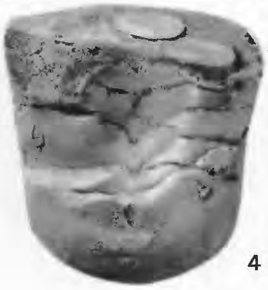
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GERMANONAUTILUS


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PLEURONAUTILUS

PLATE 4

[Figures natural size except as indicated

FIGURE 1. *Pleuronautilus* (*Enoploceras*) *newelli* Kummel, n. sp. (p. 41).
1. Holotype, U.S.N.M. 107085. From upper shale member (*Columbites* zone) of the Thaynes formation, Montpelier Canyon, Idaho, sec. 31, T. 12 S., R. 45 E.

2, 3, 4. *Pleuronautilus idahoensis* Kummel, n. sp. (p. 37).
2. Holotype, U.S.N.M. 107079. From upper shale member (*Columbites* zone) of the Thaynes formation, Hot Springs, Idaho, sec. 18, T. 15 S., R. 45 E; 3, 4. Paratype, U.S.N.M. 107080. From same locality and horizon as figure 1.

5, 6. *Pleuronautilus alaskensis* Kummel, n. sp. (p. 34).
Holotype, U.S.N.M. 107082. From U.S.G.S. locality 13749, Chitistone limestone (Upper Triassic, Karnian) from the flats at base of Kennicott glacier, 5 miles north of Kennicott, Chitna Valley, Alaska.

7. *Phloioceras* sp. (p. 44).
Ventral view. U.S.N.M. 107094. From point at north entrance to Herring Bay, Admiralty Islands, Alaska.

8, 9, 10. *Metacoceras* (*Mojsvaroceras*) *frenchi* Kummel, n. sp. (p. 23).
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11, 12. *Paranautilus smithi* Kummel, n. sp. (p. 71).
Plesiotype, U.S.N.M. 32644. From Middle Triassic, Fossil Hill, Nevada.

PLATE 5

[Figures natural size except as indicated]

FIGURE 1. *Grypoceras (Grypoceras) whitneyi* (Gabb) (p. 53).
Holotype from Buena Vista District, Humboldt Mining region, Nevada. (after Gabb, 1863, pl 3, fig. 2).
2, 3. *Grypoceras (Grypoceras) mesodicum* (Hauer) (p. 53).
After Mojsisovics, 1873, pl. 8, fig. 1a, b). × 0.5.
4. *Grypoceras (Plummeroceras) plummeri* Kummel, n. sp. (p. 54).
Holotype, Bureau of Economic Geology 7173, from Belle Plains formation, 2½ miles west of Baird, Callahan County, Texas. × 0.83.

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DOMATOCERAS

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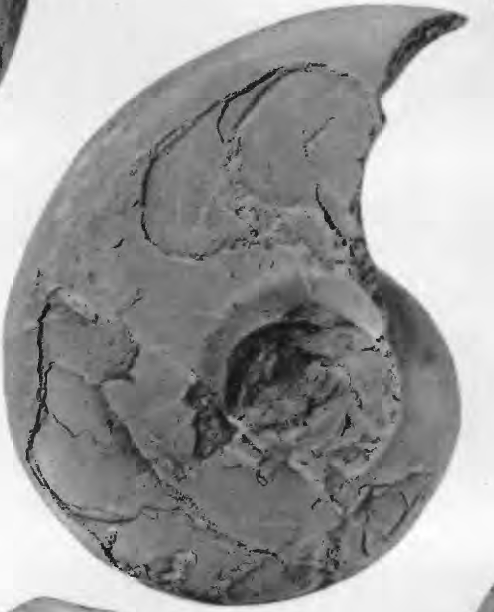

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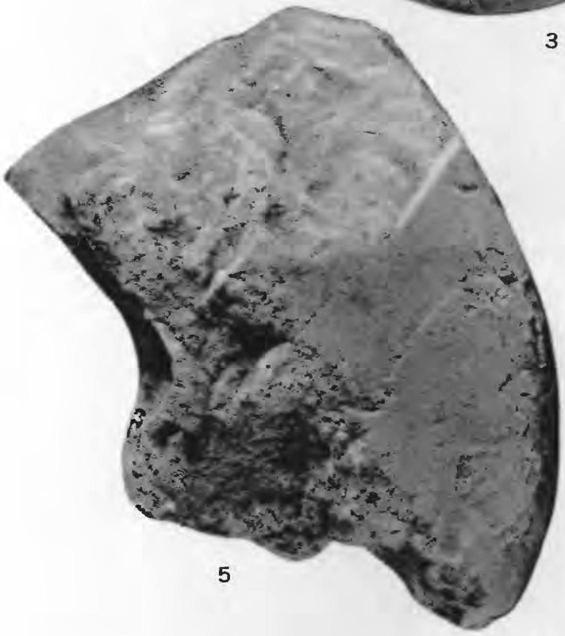

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DOMATOCERAS

PLATE 6

[All figures natural size]

FIGURES 1–4. *Grypoceras* (*Grypoceras*) whitneyi (Gabb) (p. 53).
Plesiotype, U.S.N.M. 74459, from Middle Triassic, zone of *Ceratites trinodosus*, Wheeler mine, Buena Vista Canyon, near Unionville, West Humboldt Range, Nevada.

5, 6. *Grypoceras* (*Grypoceras*) milleri Kummel, n. sp. (p. 53).
Holotype, U.S.N.M. 107095, from Dinwoody formation, Slight Canyon, Paris-Bloomington region, southeastern Idaho.

PLATE 7

[Figures natural size except as indicated]

FIGURES 1–5. *Gryponautilus cooperi* Smith (p. 56).
1, 2, 3. Holotype, U.S.N.M. 74127; 5, 6, paratype, U.S.N.M. 74127a. From the Upper Triassic Hosselkus limestone, upper or *Juvavites* subzone of the zone of *Tropites subbullatus*, Bear Cove, north end and east side of Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.

6, 7. *Syringoceras spurri* Smith (p. 63).
Holotype, U.S.N.M. 74219. From *Pseudomonitis* zone of Star Peak formation, Muttleberry Canyon, West Humboldt Range, Nevada.

8, 9. *Clymenonautilus ehrlichi* (Mojsisovics) (p. 65).
After Mojsisovics 1873, pl. 6, fig. 9a, b.

10–19. *Proclydonautilus spirolobus* (Dittmar) (p. 82).
10–11. Plesiotype, U.S.N.M. 14128; 12, 13, plesiotype, U.S.N.M. 14128a; 14, 15, 16, plesiotype, U.S.N.M. 14128b; 17, 18, 19, plesiotype, U.S.N.M. 14128c. All specimens from same locality as figures 1–5.


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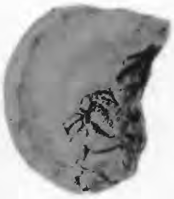
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GRYPONAUTILUS, SYRINGOCERAS, CLYMENONAUTILUS, AND PROCLYDONAUTILUS


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PROCLYDONAUTILUS, PARANAUTILUS, AND SIBYLLONAUTILUS

PLATE 8

[Figures natural size except as indicated]

FIGURES 1–7. *Proclydonautilus squawensis* Kummel, n. sp. (p. 83).
1, 2. Holotype, U.S.N.M. 74124; 3, 4, paratype, U.S.N.M. 74124a; 5, 6, 7, paratype, U.S.N.M. 74124b. From Upper Triassic Hosselkus limestone, in the upper or *Juvavites* subzone of the zone of *Tropites subbullatus*, at the north end of Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.

8, 9. *Paranautilus* sp. (p. 72).
Plesiotype, U.S.N.M. 107098. From north side of Union Canyon about 1½ miles above its mouth, from Triassic limestone (Luning (?) formation) above contact with volcanic rocks, Shoshone Range, Tonopah Quadrangle, Nevada.

10, 11. *Sibyllonautilus fergusoni* Kummel, n. sp. (p. 74).
Holotype, U.S.N.M. 107099. From U.S.G.S. locality 13420, Gabbs formation, 2½ miles north of mouth of New York Canyon, Gabbs Valley Range, Nevada.

12, 13. *Paranautilus smithi* Kummel, n. sp. (p. 71).
Holotype, U.S.N.M. 74445. From Middle Triassic *Daonella dubia* zone, Fossil Hill, south Fork of American Canyon, 4 miles south of Fitting post office (formerly Foltz), West Humboldt Range, Nevada.

PLATE 9

[Figures natural size except as indicated]

FIGURES 1–20. *Proclydonautilus triadicus* Mojsisovics (p. 81).

1, 2. Plesiotype, U.S.N.M. 74027; 3, 4, 5, Plesiotype, U.S.N.M. 74027a; 6, 7, 8, plesiotype, U.S.N.M. 74027b; 9, 10, 11, plesiotype, U.S.N.M. 74027c; 12, 13, 14, plesiotype, U.S.N.M. 74027d; 15, 16, 17, plesiotype, 74027e, 18, 19, 20, plesiotype, U.S.N.M. 74027f. From Upper Triassic Hosselkus limestone, in both subzones of the *Tropites subbullatus* zone, 3 miles east of Madison's ranch, between Squaw Creek and Pit River, Shasta County, California.


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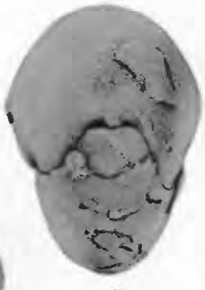
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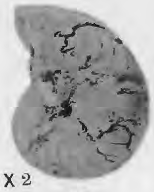
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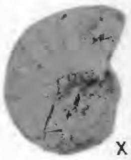
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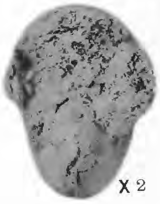
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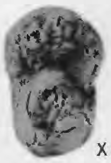
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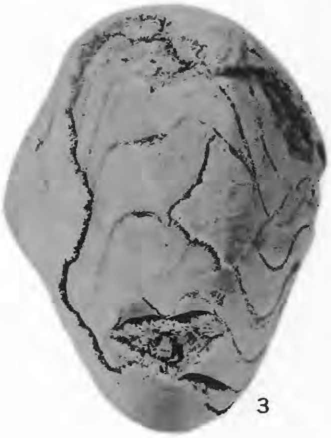
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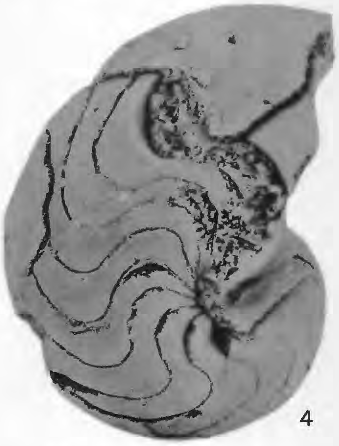
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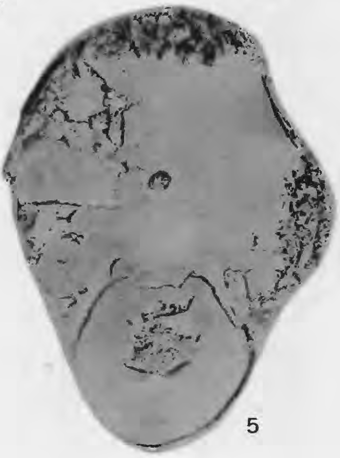
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PROCLYDONAUTILUS


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PROCLYDONAUTILUS AND COSMONAUTILUS

PLATE 10

Figures natural size except as indicated]

FIGURES 1–6. *Proclydonautilus stantoni* Smith (p. 82).

1, 2, 3. Holotype, U.S.N.M. 74123; 4, 5, 6, paratype, U.S.N.M. 74123a. From the Upper Triassic Hosselkus limestone, in the upper or *Juvavites* subzone of the zone of *Tropites subbullatus*, at the north end and west side of Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.

7–15. *Cosmonautilus hersheyi* Smith (p. 87).

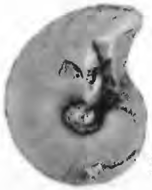
7, 8, 9. Holotype, U.S.N.M. 74130; 10, 11, 12, paratype, U.S.N.M. 74130a; 13, 14, 15, paratype, U.S.N.M. 74130b. All from same *Juvavites* subzone as figures 1–6, at north end and east side of Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.

PLATE 11

[Figures natural size except as indicated]

FIGURES 1–8. *Proclydonautilus ursensis* Smith (p. 83).

1, 2. Holotype, U.S.N.M. 74122; 3, 4, 5, paratype, U.S.N.M. 74122a; 6, 7, 8, paratype, U.S.N.M. 74122b. From the Upper Triassic Hosselkus limestone, upper or *Juvavites* subzone of the zone of *Tropites subbullatus*, north end and east side of Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.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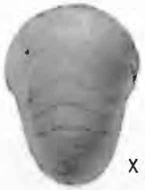
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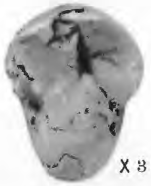
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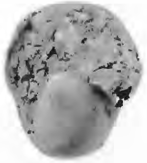
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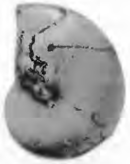
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PROCLYDONAUTILUS

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COSMONAUTILUS

PLATE 12

[Figures natural size except as indicated]

FIGURES 1–4. *Cosmonautilus dilleri* Hyatt and Smith (p. 85).

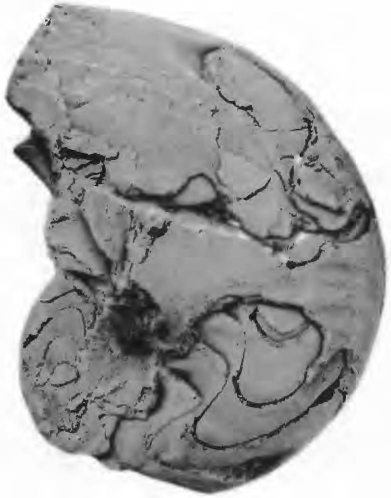
1, 2. Plesiotype, U.S.N.M. 74463a, front and rear views of specimen shown on plate 13, figure 1, × 0.87; 3, 4, plesiotype, U.S.N.M. 74463c. From Upper Triassic Hosselkus limestone, upper or *Juvavites* subzone of the zone of *Tropites subbullatus*, north end and west side of Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.

PLATE 13

[Figures natural size except as indicated]

FIGURES 1–7. *Cosmonautilus dilleri* Hyatt and Smith (p. 85).

1. Plesiotype, U.S.N.M. 74463, side view of specimen shown on plate 12, figures 1, 2, × 0.87; 2, 3, 4. Plesiotype, U.S.N.M. 74028; 5, 6, 7, plesiotype, U.S.N.M. 74028a. From Upper Triassic Hosselkus limestone, in the *Juvavites* subzone of the zone of *Tropites subbullatus* zone, 3 miles east of Madison's ranch, between Squaw Creek and Pit River, Shasta County, California.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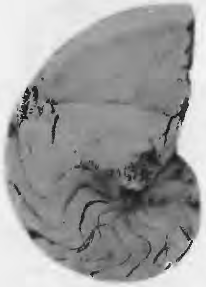
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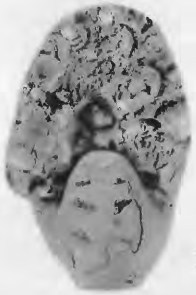
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COSMONAUTILUS


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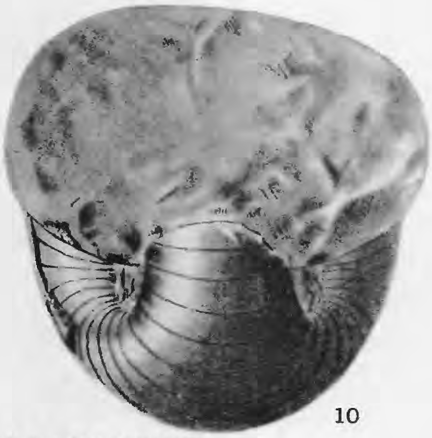
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COSMONAUTILUS, PARANAUTILUS, AND SIBYLLONAUTILUS

PLATE 14

Figures natural size except as indicated]

FIGURES 1–6. *Cosmonautilus dilleri* Hyatt and Smith (p. 85).

1, 2, 3. Cotype; 4, 5, 6, cotype, U.S.N.M. 74028. From Upper Triassic Hosselkus limestone, in the *Juvavites* subzone of the *Tropites subbullatus* zone, 3 miles east of Madison's ranch, between Squaw Creek and Pit River, Shasta County, California. (After Smith, 1927, pl. 55, figs. 6–11).

7, 8. *Paranautilus multicameratus* (Gabb) (p. 71).

Holotype from near the Auld Lang Syne Mine, Sierra district, Humboldt County, Nevada. (After Gabb, 1864, pl. 3, fig. 4, 5).

9, 10. *Sibyllonautilus liardensis* (Whiteaves) (p. 75).

Holotype from Upper Triassic on Liard River, 25 miles below Devils Portage, British Columbia, at horizon of *Dawsonites canadensis*. (After Whiteaves, 1889, pl. 18, figs. 1, 1a).

PLATE 15

[Figures natural size except as indicated]

FIGURES 1–11. *Cosmonautilus shastensis* Smith (p. 86).

1, 2. Holotype, U.S.N.M. 74126; 3, 4, 5, paratype, U.S.N.M. 74126a; 6, 7, 8, paratype, U.S.N.M. 74126b; 9, 10, 11, paratype, U.S.N.M. 74126c. From the Upper Triassic Hosselkus limestone, upper or *Juvavites* subzone of the zone of *Tropites subbullatus*, Bear Cove, north end and east side of Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.

12–15. *Proclydonautilus hessi* (Smith) (p. 83).

12, 13. Holotype, U.S.N.M. 74129; 14, 15, paratype, U.S.N.M. 74129a. From same locality as figures 1–11.

16. *Styrionautilus* sp. (p. 80).

U.S.N.M. 108001. From Middle Triassic (Anisian), South Canyon, New Pass, Desatoya Range, Nevada.

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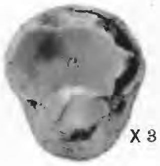

9 X 3

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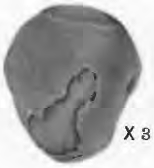

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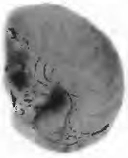

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COSMONAUTILUS, PROCLYDONAUTILUS, AND STYRIONAUTILUS


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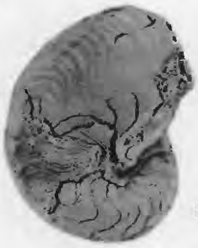
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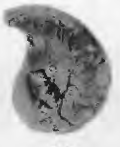
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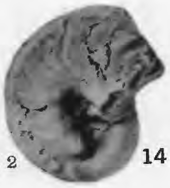
X 2

14

COSMONAUTILUS

PLATE 16

[Figures natural size except as indicated]

FIGURES 1–14. *Cosmonautilus pacificus* Smith (p. 85).

1, 2. Holotype, U.S.N.M. 74125; 3, 4, 5, paratype, U.S.N.M. 74125a; 6, 7, 8, paratype, U.S.N.M. 74125b; 9, 10, 11, paratype, U.S.N.M. 74125c; 12, 13, 14, paratype, U.S.N.M. 74125d. From the Upper Triassic Hosselkus limestone, *Juvavites* subzone of the zone of *Tropites subbullatus*, at the north end of Brock Mountain, between Squaw Creek and Pit River, Shasta County, California.

PLATE 17

[Figures natural size except as indicated]

FIGURES 1, 2. *Pleuronautilus* (*Anoploceras*) *ampezzanus* (Loretz) (p. 43).
From the Karnian of the Alps (after Mojsisovics, 1882, pl. 84, figs. 1a, b). × 0.66.
3, 4. *Pleuronautilus* (*Holconautilus*) *semicostatus* (Beyrich) (p. 42).
From the Anisian of the Alps (after Mojsisovics, 1882, pl. 86, figs. 1a, b). × 0.7.
5, 6. *Phloioceras gemmatum* (Mojsisovics) (p. 44).
From the Karnian of the Alps (after Mojsisovics, 1837, pl. 3, figs. 1a, b). × 0.5
7, 8. *Pleuronautilus* (*Trachynautilus*) *subgemmatus* Mojsisovics (p. 44).
From the Anisian of the Alps (after Mojsisovics, 1882, pl. 85, figs. 2a, b).
9, 10. *Pleuronautilus* (*Encoiloceras*) *superbus* (Mojsisovics) (p. 42).
From the Karnian of the Alps (after Mojsisovics, 1873, pl. 4, figs. 1a, b). × 0.65.


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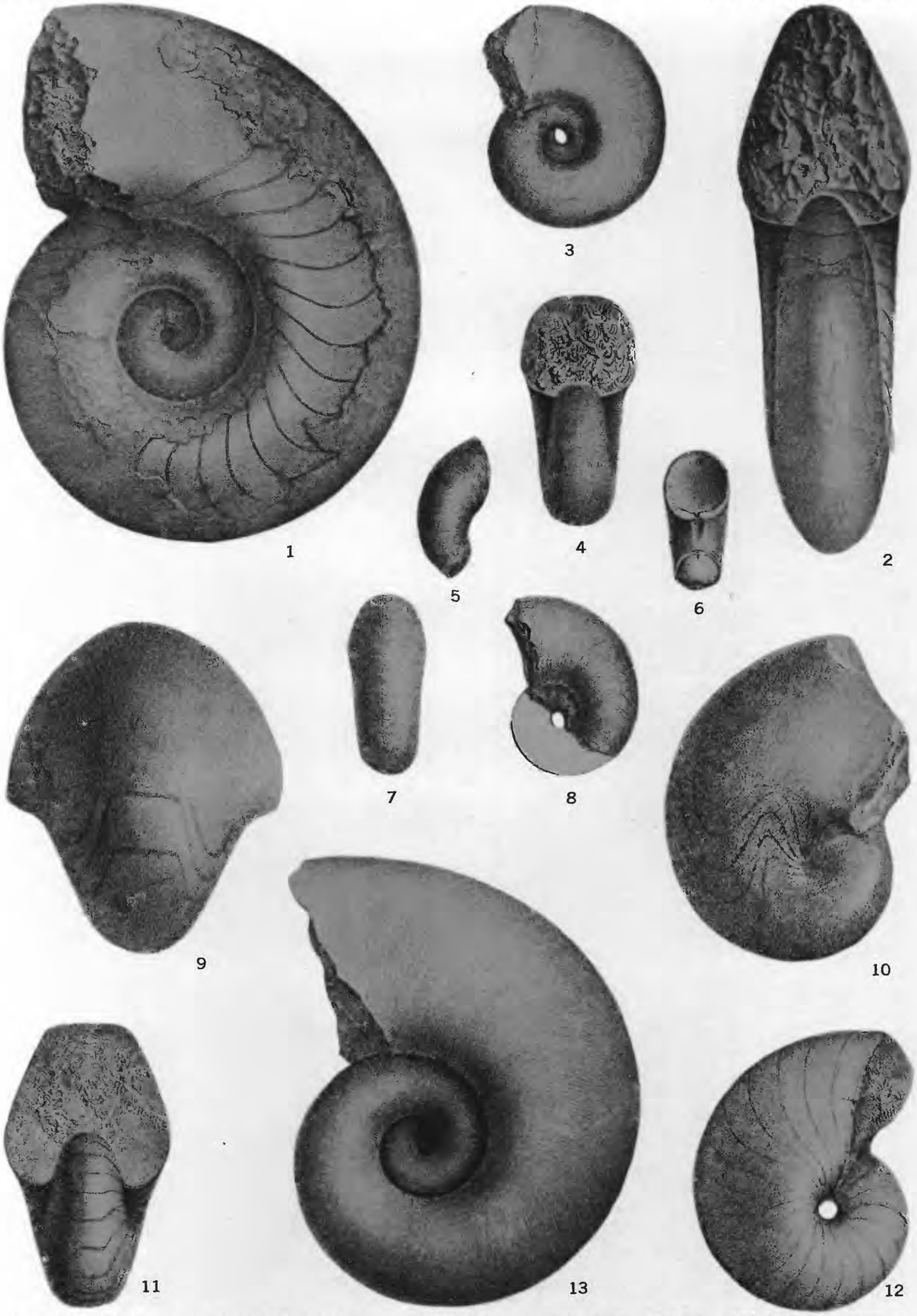
PLEURONAUTILUS AND PHLOIOCERAS



JUVAVIONAUTILUS, SYRINGONAUTILUS, SYRINGOCERAS, STYRIONAUTILUS, AND INDONAUTILUS

PLATE 18

[Figures natural size except as indicated]

FIGURES 1, 2. *Juvavionautilus heterophyllus* (Hauer) (p. 63).
From the Norian of the Alps (after Mojsisovics, 1902, pl. 4, figs. 2a, b). × 0.75.

3, 4. *Syringonautilus lilianus* (Mojsisovics) (p. 60).
From the Anisian of the Alps (after Mojsisovics, 1882, pl. 82, figs. 3a, b).

5, 6, 7, 8. *Syringoceras granulosostriatum* (Klipstein) (p. 60).
From the Karnian of the Alps (after Mojsisovics, 1882, pl. 82, figs. 8a, b; 9a, b).

9, 10. *Styrionautilus styriacus* (Mojsisovics) (p. 80).
From the Karnian of the Alps (after Mojsisovics, 1873, pl. 14, figs. 7a, c).

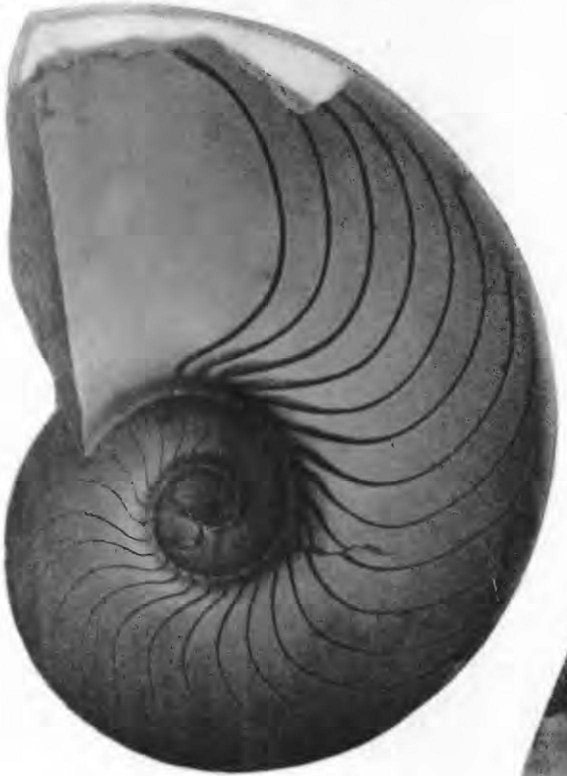
11, 12. *Indonautilus kraffti* Mojsisovics (p. 72).
From the Norian of the Himalayas, India (after Mojsisovics, 1896, pl. 21, figs. 2a, b).

13. *Syringoceras barrandei* (Hauer) (p. 60).
From the Karnian of the Alps (after Mojsisovics, 1902, pl. 5, fig. 2a).

PLATE 19

[Figures natural size except as indicated]

FIGURES 1, 2. *Oxynautilus acutus* (Hauer) (p. 63).
From the Norian of the Alps (after Mojsisovics, 1902, pl. 3, figs. 1a, b). × 0.75.
3. *Tainionautilus trachyceras* Frech (p. 27).
From the Scythian of the Salt Range, India (after Frech, 1905, pl. 26, fig. 2). × 0.6.
4, 5. *Gonionautilus securis* (Dittmar) (p. 89).
From the Norian of the Alps (after Mojsisovics, 1902, pl. 1, figs. 1a, b). × 0.66.
6, 7. *Callaionautilus turgidus* Kieslinger (p. 87).
From the Norian of Timor (after Kieslinger, 1924, pl. 5, figs. 1a, b). × 0.66.



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OXYNAUTILUS, TAINIONAUTILUS, GONIONAUTILUS, AND CALLAIONAUTILUS