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THE MORPHOLOGY, SYSTEMATICS AND EVOLUTION OF THE CLYDONAUTILACEANS (NAUTILOIDEA)

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Abstract: The superfamily Clydonautilaceae is revised. It is proposed that this group of Triassic nautiloids be raised to the rank of the suborder Clydonautilina on the basis of the following distinctive morphological features: their complexly dissected suture, which is unique in the nautiloids; their siphuncle with annular intrasiphonal deposits; and their unusually small "embryonic" shell that occupies the entire first whorl.

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The clydonautilaceans are the dominant group among the Upper Triassic nautiloids. With the ammonoids and the pelagic bivalves, they are an essential element of the biocoenoses in all paleogeographic regions. But the classification of this group remains unstable and unclear, like their position in the systematics of the superorder Nautiloidea.

While studying the Triassic nautiloids of Northeast Asia, I obtained new data that permitted definite corrections for the existing system and for clarification of the history of the Clydonautilaceae. My study took into account the revision of the main sections through the Triassic in Europe and Asia by a group of Austrian geologists and paleontologists [12-21, 30, 31]. These data in some cases substantially changed the prevailing ideas of the stratigraphic ranges of many species belonging to their group.

The original specimens used for this work are in the monographic section of the geological museum of the Institute of Geology and Geophysics, Siberian Branch, USSR Academy of Sciences, as Collection Nos. 759 and 935. A number of the views developed in this article were discussed with A. S. Dagys and V. N. Shimansky, whom I wish to thank.

HISTORY OF THE CLASSIFICATION OF THE CLYDONAUTILACEAE

The current systematics of the nautiloids was worked out chiefly by Flower and Kummel [10]. In this system, the taxa now assigned to the clydonautilaceans are combined into two families, the Clydonautilidae and Gonionautilidae, which belong to the order Nautilida. Besides the Clydonautilidae, this order also contains certain Upper Paleozoic (the Liroceratidae and Ephippioceratidae) and Triassic (Paranautilidae) families, and also all the post-Triassic nautiloids

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(Nautilidae, Paracenoceratidae, Cymatoceratidae, Hercoglossidae and Aturiidae). According to Flower and Kummel, the clydonautilaceans probably originated from the paranautilids and were a highly specialized deviant branch. The derivation of the clydonautilids from the paranautilids was based chiefly on the absence, in most taxa of both families, of an annular lobe in the suture line, as well as the similarity of their shells. The classification of the clydonautilaceans was founded on the structure of their suture. The first family combined the genera *Styrionautilus, Proclydonautilus, Cosmonautilus, Callaionautilus* and *Clydonautilus,* characterized by a complexly dissected suture line of the *Clydonautilus* type with deep lobes on the ventral and lateral sides. In the second family, represented only by the genus *Gonionautilus*, the suture line attained its greatest degree of complexity, as manifested in the doubling of the dorsal lobe. The complication of the suture line in the clydonautilaceans reached its culmination in the family Siberionautilidae, first described by Popov [2] from the Upper Triassic of Northeast Asia. In this family, which includes *Siberionautilus* and *Yakutionautilus*, the suture is of the *Clydonautilus* type, but with additional lobes between the ventral and lateral lobes. The *Yakutionautilus* also differed in the denticulation of their saddles. Popov proposed that all the coiled nautiloids with complexly dissected suture lines be set apart in the large group of Anguloceratidae, but this was not supported by other investigators.

In reconsidering the classification of the nautiloids, Shimansky [5] concluded that all the related groups of Late Paleozoic, Mesozoic and Cenozoic coiled nautiloids should be regarded as belonging to the single order Nautilida, with the major branches being distinguished as independent suborders and superfamilies. In his scheme the clydonautilaceans were assigned to the superfamily Clydonautilaceae, which together with the liroceratacеans were included in the suborder Liroceratina. The main distinctive characteristics of the clydonautilaceans consisted in the presence of a complexly dissected suture and an "embryonic" shell occupying the whole first whorl. The clydonautilaceans were increased by the addition of two families: the Late Triassic Siberionautilidae and the Jurassic-Early Cretaceous Pseudonautilidae. In contrast to the ideas of Flower and Kummel, in Shimansky's scheme the clydonautilaceans are derived from Permian representatives of the family Liroceratidae and they continued to develop in the Late Jurassic and Early Cretaceous, represented by the Pseudonautilidae. The nautiloid classification proposed by Shimansky is reflected almost unchanged in the basic Soviet reference guide to paleontology, the *Principles of Paleontology* [1].

Kummel's classification, which was published somewhat later in the analogous American guide [23], has no suborders. The clydonautiloid and liroceratid families are here combined into the superfamily Clydonautilaceae. The pseudonautiloids were removed from the superfamily since, in Kummel's opinion, they originated from the highly variable Liassic genus *Cenoceras* of the superfamily Nautilaceae.

In his 1967 classification Shimansky [7] retained the principles underlying his 1957 system of the clydonautilaceans, while agreeing with Kummel, however, on including the pseudonautiloids in the superfamily Nautilaceae.

A different view of the classification of the clydonautilaceans was advanced relatively recently by Dzik [9], who, on the basis of the ontogeny of the shell and the transverse section through the whorls, divided the clydonautilacean taxa between two families: the Clydonautilidae and the Liroceratidae, which he included in the suborder Tainoceratina that formally combines all the Late Paleozoic and Triassic nautiloids. To the first family he assigned the genera *Callaionautilus, Proclydonautilus* and *Clydonautilus*, considering *Cosmonautilus* and *Gonionautilus*

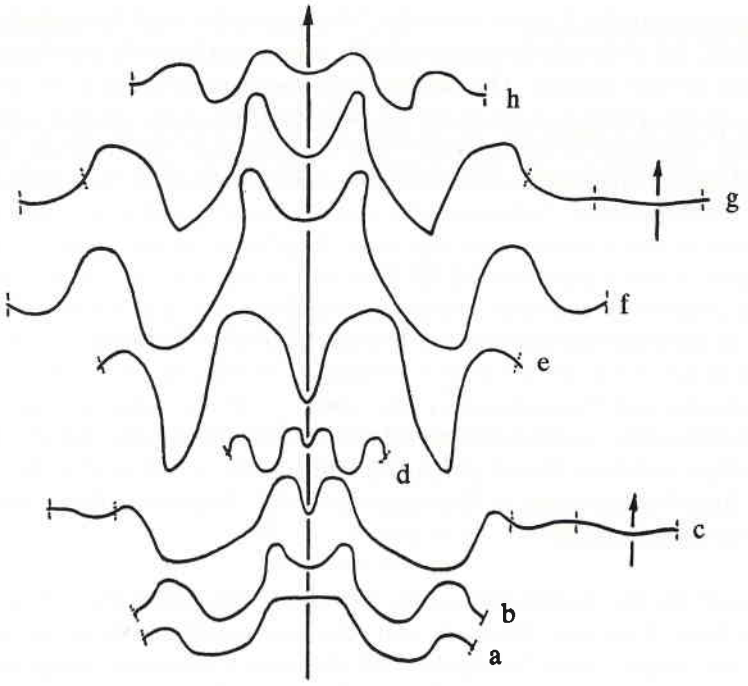

Fig. 1. Suture lines of clydonautilids: *a* - *Styrionautilus discoidalis* (Welter); Timor Island, Carnian [22]; *b* - *Proclydonautilus griesbachi* (Mojsisovics); Central Himalayas, Kumaon, Norian [27]; *c* - *P. anianiensis* (Shimansky), Spec. No. 759/243 at H = 66 mm, W = 54 mm, eastern Taymyr, Cape Tsvetkova, USSR, Lower Carnian; *d* - *P. spirolobus* (Dittmar), Austria, Upper Norian [28]; *e* - *P. natosini* McLearn, Spec. No. 759/215 at H = 70 mm, W = 75 mm, eastern Yakutia, Baky River, Upper Norian; *f* - *Cosmonautilus dilleri* Hyatt et Smith, California, Upper Carnian [22]; *g* - *C. polaris* Sovolev, Spec. No. 759/207 at H = 68 mm, W = 61 mm, eastern Taymyr, Cape Tsvetkova, Lower Carnian; *h* - *Callaionautilus turgidus* Kieslinger; Timor Island, Norian [11].

to be synonyms of the last two genera. To the second family he assigned *Styrionautilus* and *Siberionautilus.*

It can be seen from this brief survey of the most important publications on the nautiloids that the system and phylogeny of the clydonautilaceans are still subjects of dispute.

PROBLEMS OF MORPHOLOGY

This article will consider the clydonautilaceans as understood by Kummel [23] and Shimansky [7]. This group includes genera close in shell form, involuteness of their whorls, character of sculpture, structure of suture line and of the "embryonic" shell. The structure of the siphuncle has recently also come to be regarded as a highly important morphological criterion.

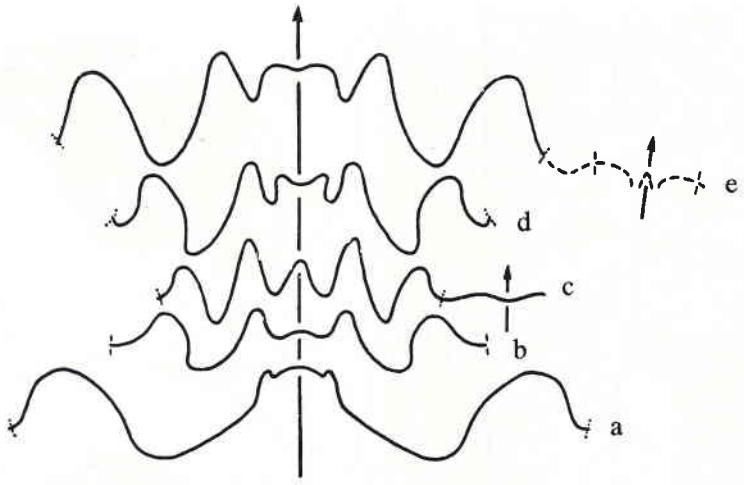

Fig. 2. Sutures of clydonautilids and gonionautilids: *a* - *Clydonautilus ermollii* Diener, Timor Island, Upper Carnian [11]; *b* - *C. biangularis* Mojsisovics; Central Himalayas, Kumaon, Norian [27]; *c* - *Clydonautilus* sp., Nevada, Upper Carnian [29]; *d* - *C. noricus* Mojsisovics; Austria, Norian [26]; *e* - *Gonionautilus securis* (Dittmar), Austria, Upper Norian [26].

The clydonautilaceans are characterized by involute (often with closed umbilicus), discoidal, lenticular, subspherical and spherical shells, with trapezial, semielliptical, semioval and semicircular transverse sections through the whorls. *Clydonautilus* and *Gonionautilus* are represented mainly by discoidal, *Proclydonautiuus* and *Styrionautilus* by both discoidal and subspherical or spherical, *Cosmonautilus* and *Callaionautilus* by discoidal and lenticular, *Siberionautilus* by spherical, and *Yakutionautilus* mainly by lenticular shells. The shell surface may be smooth *(Styrionautilus, Clydonautilus, Gonionautilus* and many species of *Proclydonautilus)*, with tubercles along the ventral turns in the early whorls (*Cosmonautilus*), with circumventral tubercles in the early whorls and a median keel on the ventral side in the later whorls (*Callaionautilus*), with transverse folds (*Proclydonautilus gasteroptychus* Dittmar, *P. gasteroptychus timorensis* Kieslinger), with frequent transverse costulae (*Proclydonautilus spirolobus* (Dittmar), *P. goniatites* (Hauer)), with transverse and longitudinal costulae forming a reticular ornamentation (*Proclydonautilus natosini* McLearn, *P. seimkanense* Bytschkov, etc., and also *Siberionautilus* and *Yakutionautilus*).

The suture lines of the clydonautilaceans are characterized by the greatest degree of dissection among all the nautiloids. In the combination of lobes and saddles, and also in their configuration and depth, the sutures of this group are of the *Clydonautilus* type [6]. The basic features of this type of suture line are the following: the ventral lobe is subdivided on the central saddle into two, or one narrow and deep. The lateral lobe is deep and often pointed apically; between the ventral and lateral lobes, there may be additional lobes.

The simplest suture is that of *Styrionautilus.* It is characterized by a deep and wide lateral and a shallower umbilical lobe. The dorsal lobe is wide and fairly shallow. On the ventral side the suture forms a wide saddle (fig. 1*a*); but in some species of this genus, for example, in

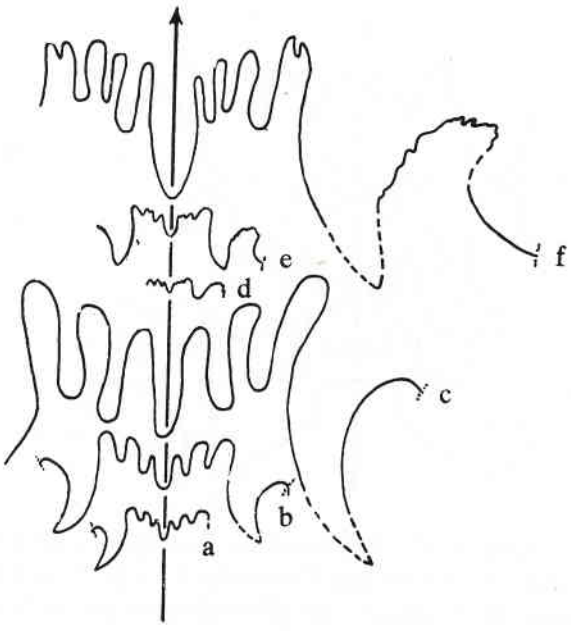

Fig. 3. Suture lines of siberionautilids: *a-c* - *Siberionautilus multilobatus* Popov: *a, b* - Spec. No. 759/232: *a* - at H = 20 mm, W = 25 mm, *b* - at H = 33 mm, W = 33 mm; northern part of Central Siberia, Karadan Creek, Middle Norian; *c* - Spec. No. 392/6399 (TsNIGR Museum, Leningrad) at H = 72 mm, W = 81 mm; Northern Circumokhotsk region, Bozhekchan River, same age; *d-f* - *Yakutionautilus kavalerovae* Arkhipov et Barskov, Spec. No. 759/228, *d* - at H = 15 mm, W = 15 mm, *e* - at H = 25 mm, W = 30 mm, *f* - at H = 110 mm, W = 115 mm; eastern Yakutia, Nel'-gekhe River; same age.

S. sauperi (Hauer), in the concluding stages of ontogenesis a fairly shallow lobe may appear on the ventral side [28, p. 209, fig. 6]. The suture of *Proclydonautilus*, in contrast to the preceding genus, has a clearly manifested ventral lobe. The configuration of the lobes and saddles in the species of this genus may vary (fig. 1*b-e*). The ventral and lateral lobes in some cases are deep and narrow (*P. natosini* McLearn, *P. seimkanensis* Bytschkov, *P. goniatites* (Hauer)), in others wide and shallow (*P. griesbachi* Mojsisovcs, *P. singularis* Welter). One often finds a deep and narrow ventral lobe combined with wide lateral lobes (*P. anianiensis* Shimansky, *P. ursensis* Smith). *Callaionautilus* has a suture line close to the second type (fig. 1*h*). The suture of *Cosmonautilus* resembles that of *Proclydonautilus* in its number of lobes, but differs in their configuration (fig. 1*f-g*). As a rule, in *Cosmonautilus* the ventral lobe is wide and uniformly concave, and the lateral lobe also wide and often pointed. The saddles between the ventral and lateral lobes are narrow and apparently turned sideward.

Some species of *Clydonautilus* show a new element in the suture line—a central saddle, which divides or only indicates the division of the ventral lobe into two parts (fig. 2*a-d*). A wide and fairly shallow lobe often appears in it. Kieslinger [11] noted that in some species a ventral saddle appears only in the later stages of ontogenesis. A similar suture line on the ventral and lateral sides characterizes the genus *Gonionautilus*. The essential difference of this genus from

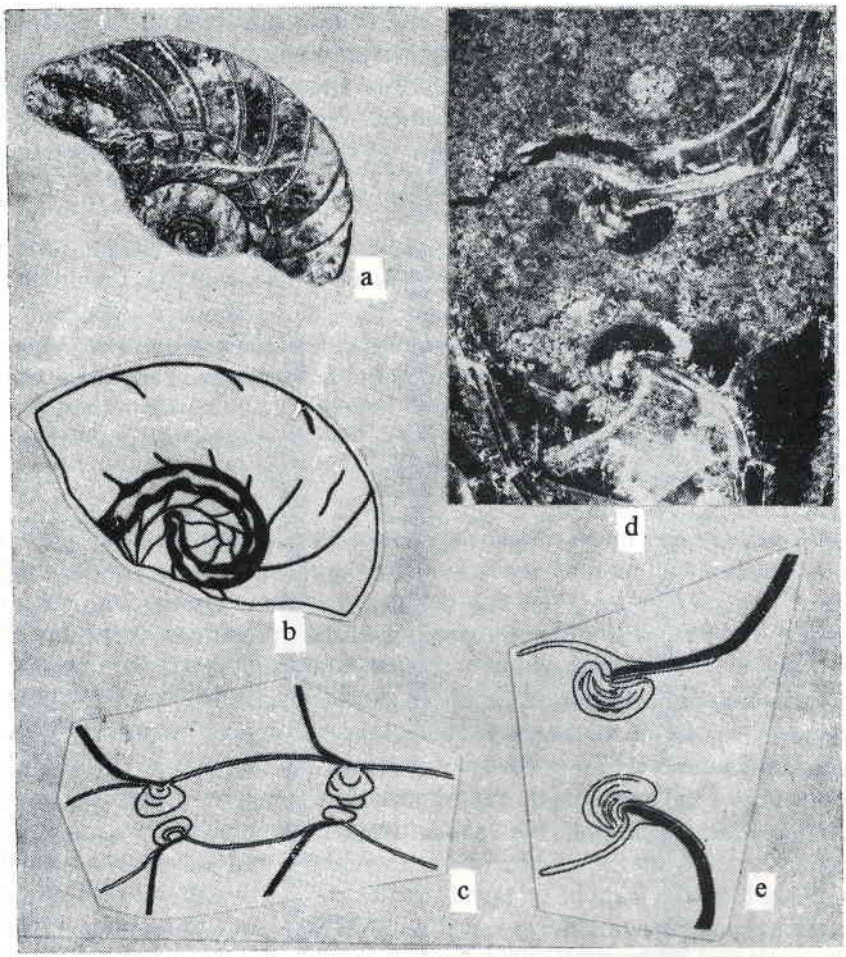

Fig. 4. Structure of siphuncle in clydonautilaceans (polished sections): *a-c* - *Proclydonautilus seimkanensis* Bytschkov, Spec. No. 759/234: *a* - phragmocone (×3), *b* - first whorl (×9), *c* - second whorl (×18); eastern Yakutia, Nel'gekhe River; Middle Norian; *d-e* - *P. anianiensis* (Shimansky), Spec. No. 935/1, beginning of third whorl: *d* - ×11, *e* - ×9; eastern Taymyr, Cape Tsvetkova; Lower Carnian.

Clydonautilus and all the other clydonautilids is the presence of a dorsal lobe divided into two by a median saddle (fig. 2*e*).

As mentioned above, the most complicated suture lines have been described in

Siberionautilus and *Yakutionautilus* from the Norian of Siberia. Its main features are the presence of one to three additional lobes between the narrow pointed ventral and lateral lobes, and also the denticulation of the saddles in *Yakutionautilus* (fig. 3). During the ontogeny of the siberionautilids, the first to form is a suture of proclydonautilid appearance, but this is followed by the division of a saddle between the ventral and lateral lobes. This fact indicates that *Proclydonautilus* is related to the siberionautilids.

The character of the suture line is unquestionably the main systematic criterion of the clydonautilaceans. But my study of their siphuncles has shown that this feature too is of very great significance in the systematics of this group. The chief distinctive feature of morphology of the siphuncles in the Siberian species studied is the presence of annular intrasiphonal deposits. These formations, which are unique in this order, were first described in detail by Silberling [29] in the genus *Proclydonautilus* from the Upper Carnian of Nevada and California. Similar formations were later described by Schastlivtseva [4] in *Proclydonautilus spirolobus* from the Lower Carnian of Afghanistan and in *P. altus* from the Upper Norian of the Pamir.

I have found annular intrasiphonal deposits in Siberian *Proclydonautilus (P. anianiensis* (Shimansky), *P. natosini* McLearn, *P. seimkanensis* Bytschkov, *P. pseudoseimkanensis* Sobolev), *Cosmonautilus (C. polaris* Sobolev) and *Yakutionautilus (Y. kavalerovae* Arkhipov et Barskov). In the above species of *Proclydonautilus*, the position of the siphuncle is subdorsal. The siphonal structure has been most fully studied in *P. seimkanensis* from the Lower Norian of eastern Yakutia. In this species the siphuncle begins in the first chamber as a slightly wider closed segment—a caecum (fig. 4*a, b*). In the second and at the beginning of the third whorls, the septal necks are relatively short, narrowing toward the center of the siphon (loxochoanitic). The connecting rings are of medium length, subcylindrical, with round contours. In this stage of ontogenesis, intrasiphonal deposits of the annular type are developed on the inner surface of the septal necks (fig. 4*c*). In form these deposits are ring-shaped and convex into the siphon; in the medial section they have the form of semioval structures. In the first whorl the annulosiphonal rings become thicker adapically and form a continuous lining within the connecting rings. In this stage of ontogenesis and in the subsequent deposits they do not fully close the septal aperture, leaving a narrow canal free. In the medial sections through *P. anianiensis* from the Lower Carnian of the Taymyr, the intrasiphonal deposits show a distinctly laminar structure (fig. 4*d-e*).

In *Cosmonautilus polaris* from the Lower Carnian of Siberia, the position of the siphuncle during ontogenesis changes from dorsal in the first to dorsocentral at the end of the third whorl. In the second whorl the septal necks are short and loxochoanitic. The connecting rings are of medium length and subcylindrical, with round outlines. The inner surfaces of the septal necks clearly show intrasiphonal deposits of the annular type like those described in species of *Proclydonautilus.* Similar intrasiphonal deposits have also been found in *Yakutionautilus kavalerovae* from the Middle Norian of eastern Yakutia.

Finally, intrasiphonal deposits of the annular type were, probably, seen in the medial section through the shell of *Clydonautilus salisburgensis* (Hauer) from the Upper Norian in the Alps [28, pl. 11, fig. 4].

Among the distinctive features of shell structure in the clydonautilaceans, in addition, is the extremely small size of the first whorl or, more precisely, the "embryonic" shell, since the embryonic shell in this group occupied the entire first whorl. The Siberian species of *Proclydonautilus (P. seimkanensis* and *P. pseudoseimkanensis)* had a first whorl 5 and 6 mm in size.

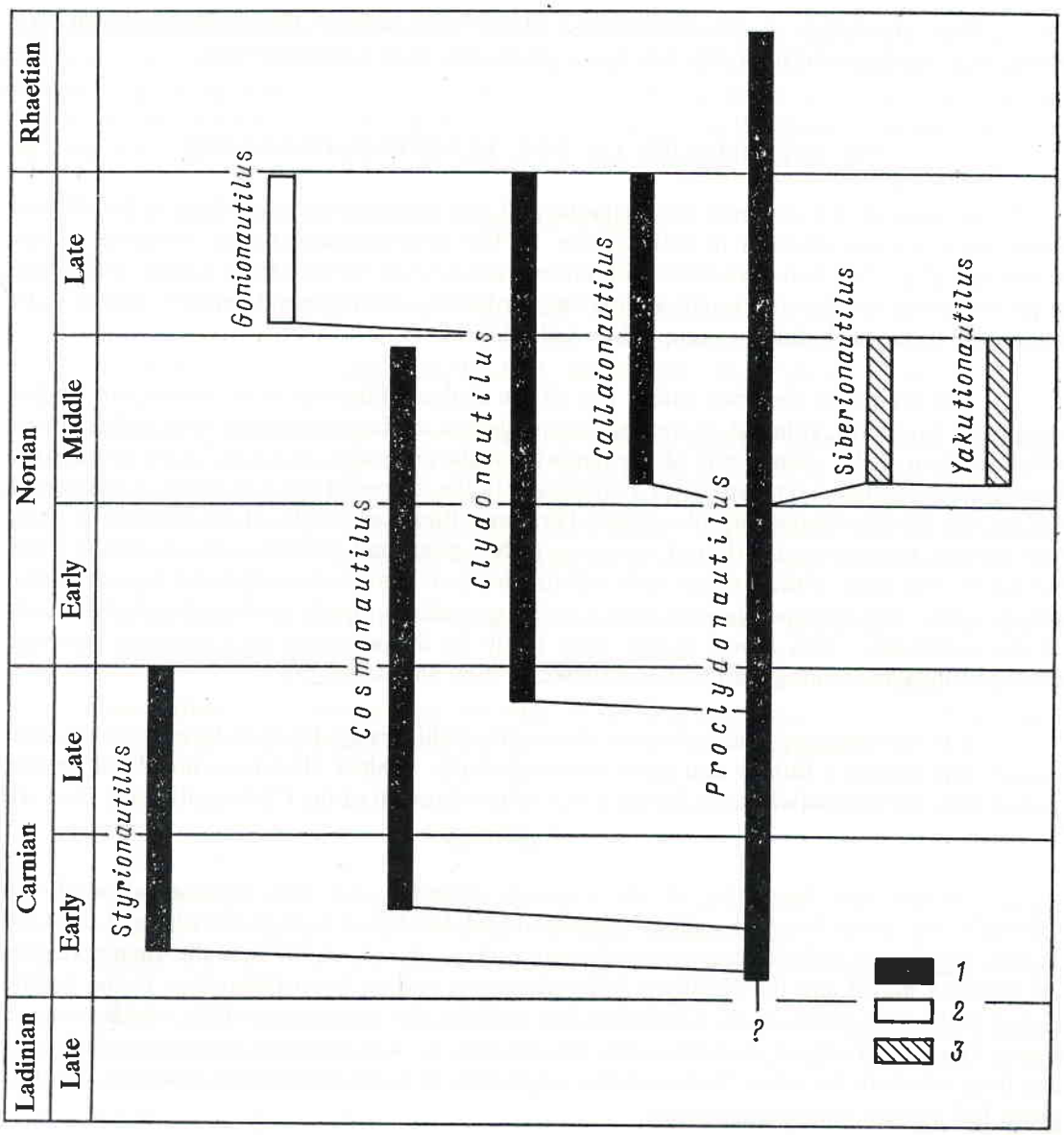

Fig. 5. Phylogeny of suborder Clydonautilina: 1 - Clydonautilidae, 2 - Gonionautilidae, 3 - Siberionautilidae.

In the North American representatives of this same genus (*P. triadicus* and *P. spirolobus*) the diameters of the first whorls reached 3.5 and 6.0 mm, respectively [22]. The size of the first whorl in *Cosmonautilus polaris* was from 8.4 to 8.8 mm, and in the North American species from 7 to 8 mm. For a comparison, it should be said that the diameters of the first whorls in most Permian nautilids were in the range of 12-40 mm [3], in the Triassic nautilids 12-24 mm, and in the post-Triassic representatives 10-25 mm [8, 24].

Thus an analysis of the external and internal structures of the clydonautilacean shell shows their fundamental similarity, which is explained by their common origin.

THE SYSTEMATICS OF THE CLYDONAUTILACEANS

In view of the common shell structure of the clydonautilaceans, there is hardly any justification for the division in which some of the clydonautilaceans are assigned to the liroceratids [9]. The Late Paleozoic and Triassic liroceratids, despite their similar shell form, differ in having an almost straight suture line, in lacking intrasiphonal deposits and in their embryonic shell, which did not occupy the whole first whorl.

The complexly dissected suture line of the clydonautilaceans is, of course, not unique among the nautiloids, although it does have a number of distinctive features, such as the strong differentiation of the ventral part of the line with slight dissection, as a rule, of its dorsal part. Complications of the suture line arose periodically in the history of the nautiloids. Examples of this are the families Permoceratidae (Early Permian), Pseudonautilidae (Late Jurassic to Early Cretaceous), Hercoglossidae (Late Cretaceous to Neogene) and Aturiidae (Paleogene to Early Neogene). But none of these shows such a distinctive feature as the intrasiphonal deposits of the annular type. The clydonautilaceans were a highly specialized, rapidly evolving blind-end branch of the nautiloids. This group should most likely be distinguished as a separate suborder Clydonautilina, containing the families assigned to it by Shimansky [7].

The currently prevailing views on the origin of this group, it seems to me, are far from correct and require a further and more thorough study. I shall, therefore, not dwell on this matter here, but instead will consider the paths of development of the Clydonautilina in the Late Triassic.

At the very beginning of the Carnian, probably, the first representative of the suborder—the genus *Proclydonautilus*—appeared, and developed through the whole of the Late Triassic (fig. 5). Its earliest occurrences (the *tenuis* phase) have been found in the Taymyr region, the Omolon massif and the Northern Okhotsk region, and its latest (Rhaetian) in the Alpine region [25]. This genus of the Clydonautilina contains the most species (25), which occur in Upper Triassic virtually all over the world. *Proclydonautilus* was, probably, the main evolutionary line from which all the other Clydonautilina originated. It is at least possible, however, that this genus had a heterogeneous character.

At the beginning of the Carnian age in the Tethys region (the Alps and Himalayas), *Styrionautilus* first appeared and continued to exist to the end of the age. At almost the same time, the genus *Cosmonautilus* branched off from *Proclydonautilus*; it appeared first in the Boreal region (Siberia) and then during the Late Carnian spread out into North America, the Himalayas, and also to the island of Timor, where it continued to develop in the Norian. At the very end of the Carnian, *Clydonautilus* appeared in the Tethyan region and became widespread in this paleobiochore until the beginning of the Rhaetian. In the Late Norian (the *suessi* phase) this genus probably gave rise to the family Gonionautilidae with the single genus *Gonionautilus*. *Proclydonautilus* in the Middle Norian also gave rise to *Callaionautilus*, which is known only from Timor Island and existed until the end of the Norian. The evolution of the clydonautilaceans in the Boreal region had its own specific features. Here, through the entire Late Triassic (to the beginning of the *efimovae* phase), the representatives of only the one genus *Proclydonautilus*

developed virtually without interruption. Only at the beginning of the Middle Norian (the *ussuriensis* phase) did some species of *Proclydonautilus* with a reticular ornament (perhaps *P. natosini* or *P. seimkanensis*) give rise to the family Siberionautilidae, which developed in the Middle Norian only within the region of present-day Siberia. At the Triassic-Jurassic boundary the Clydonautilina ceased to exist in all paleogeographic regions of the world.

A system of the Clydonautilina is presented below.

ORDER NAUTILIDA AGASSIZ, 1847

SUBORDER CLYDONAUTILIDA SOBOLEV, SUBORDO NOV.

Diagnosis. Shell nautiliconic, involute, discoidal, lenticular, or spherical, smooth or with sculpture of transverse and longitudinal costulae, more rarely of tubercles on ventral side or of transverse folds. Suture line of *Clydonautilus* type. Siphon central or located between center and dorsal side. Septal necks short and, as a rule, loxochoanitic. Intrasiphonal deposits of annular type present. Very small embryonic shell occupying whole whorl. Upper Triassic.

Composition. Three families: Clydonautilidae Hyatt, 1900; Gonionautilidae Kummel, 1950; Siberionautilidae Popov, 1951.

Comparison. Differs from other suborders of nautilids in complexly dissected suture line, presence of intrasiphonal deposits of annular type and small embryonic shell.

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