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THE ANCESTRY OF THE FAMILY NAUTILIDAE

BY BERNHARD KUMMEL

The evolutionary history of the ammonoids and nautiloids is quite parallel. The nautiloids had their greatest radiation in the early stages of their history — in the Ordovician and Silurian — and declined rapidly in numbers of genera per period until the Recent. The ammonoids, however, displayed a slow start in the middle Paleozoic but reached a peak of development in the Upper Triassic and again in the Jurassic and Cretaceous. Both groups experienced periods of mass extinctions with few surviving lines which formed the starting point for new and generally even greater radiations. The transition from the Permian to the Triassic witnessed wholesale extinctions among the ammonoids with only the Xenodiscidae and Pronotitidae giving rise to the early Triassic stocks (Spath, 1934). The nautiloids at this critical boundary did not undergo such radical changes. A number of late Paleozoic families did become extinct but three major stocks continued uninterrupted into the Triassic.

The Triassic-Jurassic boundary was, however, a time of crisis for both the ammonoids and the nautiloids. Only a single stock of ammonoids survived the Rhaetic to give rise to the vast numbers of Jurassic and Cretaceous forms (Spath, 1934). The Triassic families of nautiloids became extinct by the Norian. No Rhaetic nautiloids have as yet been described. The general character of Triassic nautiloids is quite distinct from those of the Jurassic.

Spath (1927) was the first to present a comprehensive summary of post-Triassic nautiloids. He placed all the post-Triassic nautiloids in 5 families and 28 genera, many of which were established by him. On the problem of origin of these post-Triassic nautiloids Spath (1927, p. 23) discussed "*Grypoceras* cf. *mesodicum*" (Hauer) recorded by Trechmann (1918, p. 181) from the Upper Triassic (Carnian, bed C) of the Hokonui Hills, New Zealand. Spath considered this species a

Bisiphytes and stated that "... there is more probability of *Bisiphytes* being an involute, globose, development of the family Syringonaulitidae Mojsisovics, with annular lobe."

Neither Trechmann (1918) nor Spath (1927) illustrated this species and Trechmann's description is inadequate. The purpose of this paper is to illustrate this species and discuss its affinities, and review the problem of ancestry of post-Triassic nautiloids. The author is indebted to Dr. L. F. Spath and Dr. W. N. Edwards for many courtesies during his visit to the British Museum (Natural History) and for permission to study Trechmann's specimen. The photographs were taken in the British Museum by its staff photographer.

The uniqueness of this species (here named *Bisiphytes trechmanni* n. sp.) lies in the fact that it is the only tangible clue we have to deciphering the evolutionary patterns of the nautiloids across the Triassic-Jurassic boundary. Spath (1927, p. 23) recognized that Trechmann's specimen was not a *Grypoceras* and goes on to mention it as "... indistinguishable from typical *Bisiphytes*, with their strong strigations, especially on larger whorls, annular lobe and only slightly sinuous septa." With this statement I am in complete agreement.

The evolutionary patterns of Triassic nautiloids can be summarized as those of culminating trends which began in the Carboniferous. Three distinct lines of development are represented. One includes the Paranautilidae, Clydonautilidae, and Gonionautilidae characterized by globular, occluded conchs and tendency towards sinuosity of the suture. The second major group consists of the Tainoceratidae including most of the "ornamented" Triassic nautiloids. This stock is generally evolute and with nodes and ribs. The Tainoceratidae includes Pennsylvanian, Permian, and Triassic genera. The third major group comprises the Grypoceratidae and Syringonaulitidae. The Grypoceratidae include evolute to involute, generally smooth, compressed nautiloids with tendency for modification of the venter. This family also includes Pennsylvanian, Permian, and Triassic genera. The Upper-Triassic developments of this family, *Grypoceras* and *Gryponautilus*, are completely unlike *Bisiphytes trechmanni*. Within the Syringonaulitidae there are forms which are very similar in conch patterns to *Bisiphytes trechmanni*. *Syringoceras* and *Syringonautilus* are the most similar to the species described here. These two genera include evolute nautiloids with rounded whorl sections in the early volutions that become more quadrate in outline adorally. The outer whorls have distinct umbilical and ventral shoulders and steep

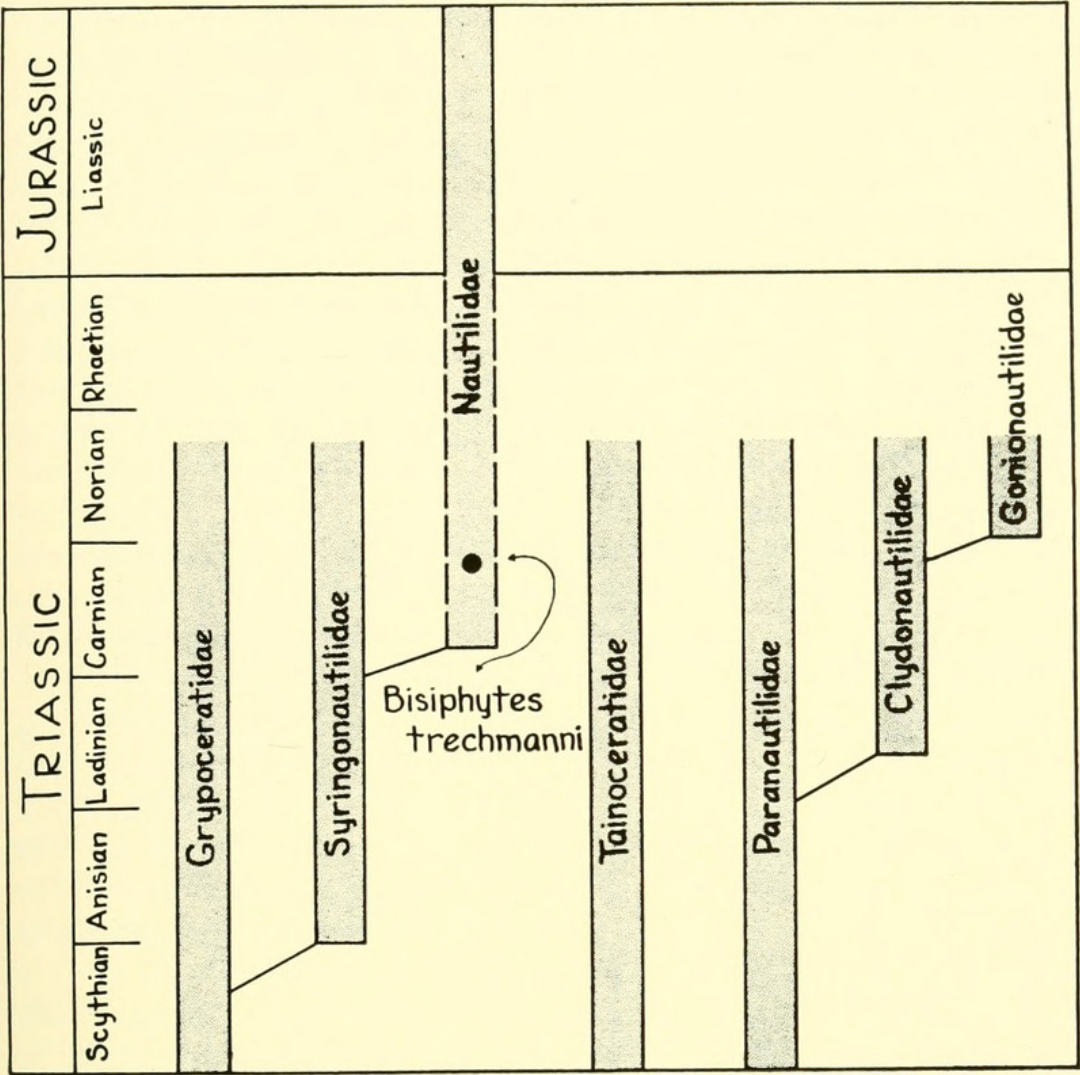


Fig. 1. Phylogenetic diagram illustrating the relationships of the Liassic Nautilidae with the Triassic nautiloid families. The columns representing the Triassic families have been terminated at an arbitrary even line in the Norian. The exact relative extinction dates of these families in the Norian are not known.

umbilical walls. The shell bears fine radial and longitudinal lines. These two genera differ only in the position of the siphuncle; *Syringoceras* has the siphuncle very near but not at the venter, *Syringonutilus* has its siphuncle in a more central position. There are about 14 species of *Syringonutilus*, with 9 species in the Anisian, 5 in the Ladinian, 3 in the Carnian, and 1 indeterminate species in the Norian (Some of these species occur in more than one epoch.) Of *Syringoceras*

there are 17 species recorded, 1 from the Anisian, 3 from the Ladinian 1² from the Carnian, and 1 from the Norian. The pattern of development of these two genera is markedly different in that *Syringonautilus* had a large radiation soon after its appearance and then declined rapidly; *Syringoceras* had its maximum radiation in the Carnian, after a slow development in the Anisian and Ladinian. Both stocks are represented by a single species in the Norian.

The Syringonautilidae also include three aberrant genera of Norian age, namely *Clymenonautilus*, *Juravionautilus*, and *Oxynautilus*. *Clymenonautilus* has a conch pattern like that of *Syringonautilus*, but has a very sinuous suture convergent to the type of suture present in the Clydonautilidae. *Juravionautilus*, in its conch shape, is a heterochronus homeomorph of *Domatoceras* of the Pennsylvanian and Permian. *Oxynautilus* is an involute oxycone similar in its conch pattern to *Stenopoceras* of the Pennsylvanian and Permian. *Clymenonautilus* and *Oxynautilus* are monotypic and only 6 species are known of *Juravionautilus*.

On the basis of the prominent peripheral strigations this species is placed in *Bisiphytes* and not in *Syringoceras* or *Syringonautilus*. The latter two genera are more evolute than *Bisiphytes*, the umbilicus approximating 25 to 30 per cent of the diameter of the conch. The umbilicus of *B. trechmanni* is about 19 per cent of the diameter of the conch. Among typical Liassic *Bisiphytes* the width of the umbilicus ranges from around 20 per cent to completely occluded conches as in *B. simillimus* Foord and Crick. A general evolutionary trend among the coiled cephalopods, except the heteromorph ammonoids, is towards greater involution. Among Triassic nautiloids this trend is very apparent in the *Domatoceras-Crypoceras* line in the Grypoceratidae and the *Metacoceras-Mojsvaroceras* line in the Tainoceratidae. The shape of the whorl section and suture of *B. trechmanni* is quite similar to such species of *Syringoceras* as *S. credneri* Mojsisovics, *S. evolutus* Mojsisovics or species of *Syringonautilus* as *S. lilianus* (Mojsisovics), and *S. longobardicus* (Mojsisovics).

Early Jurassic Nautilidae are accommodated in 5 genera including *Bisiphytes* Montfort, 1808, *Cenoceras* Hyatt, 1883, *Sphaeronautilus* Spath, 1927, *Digonioceras* Hyatt, 1894, *Ophionautilus* Spath, 1927. *Sphaeronautilus* is monotypic, *Digonioceras* has 4 species, and *Ophionautilus* only 5 species. The remaining species of early Jurassic Nautilidae belong to *Bisiphytes* and *Cenoceras*. The Paracenoceratidae, Hercoglossidae, and Cymatoceratidae are derived from the

Nautilidae.

Liassic nautiloids have received rather thorough treatment by Prinz (1906) and Pia (1914). Pia considered the attempt at a phylogenetic arrangement of Liassic nautiloids by Prinz as unsuccessful and premature. Spath (1927) came to the same conclusion. Although Pia (1914, p. 45) was not prepared to offer a detailed phylogenetic arrangement of Liassic nautiloids, he made the following tentative thesis on the evolution of the great majority of Liassic nautiloids:

- 1.) The conch was probably originally rounded without angular shoulders (perhaps broader than high).
- 2.) The primitive sculpture consisted of radial and longitudinal striae of equal strength. A smooth shell is a secondary development.
- 3.) The reduction of the longitudinal striae took place first on the whorl sides, afterwards on the venter.
- 4.) The siphuncle was originally round.
- 5.) The annular lobe is a primitive character, its absence a specialization.
- 6.) The umbilicus was originally open.

Pia considered *Nautilus striatus* as being morphologically very similar to the primitive original stock of Liassic nautiloids.

Of the known Upper Triassic nautiloid stocks, only the *Syringonaulitidae* appear to be possible ancestors to the post-Triassic forms; the remaining Triassic stocks are specialized developments morphologically unsuited to be potential ancestors to the known Liassic nautiloids. *Bisiphytes* is thus considered a late Triassic off-shoot of the Syringonaulitidae, as first suggested by Spath (1927, p. 23), and in the direct line of ancestry of all later nautiloids.

SYSTEMATIC DESCRIPTION

Family NAUTILIDAE d'Orbigny, 1840

Genus BISIPHYTES Montfort, 1808

BISIPHYTES TRECHMANNI n. sp.

Plate 1, figures 1, 2, 3; text figure 2

Grypoceras cf. *mesodicum* (Hauer). Trechmann, Quart. Jour. Geol. Soc. London, vol. 73, pp. 181-182, 1918.

The single specimen upon which this species is based is a moderately large phragmocone. It measures 71 mm. in diameter, 38 mm. in height of the last whorl, and approximately 50 mm. in width of the

most adoral part of the last whorl. The conch is evolute, the umbilicus measuring 13.5 mm. in diameter. The venter is broadly rounded, as are the ventral shoulders. The whorl sides are somewhat flattened and convergent. The widest part of the whorl is just above the umbilical shoulders which are more sharply rounded than the ventral shoulders. The umbilical wall is steep and convex.

Only fragmentary portions of the shell are preserved. The conch bears fine strigations which are present both on the whorl sides and the venter of the inner whorls. On the most adoral volution the strigations are present only on the venter. On this region there are about 7 lines in a width of 5 mm.

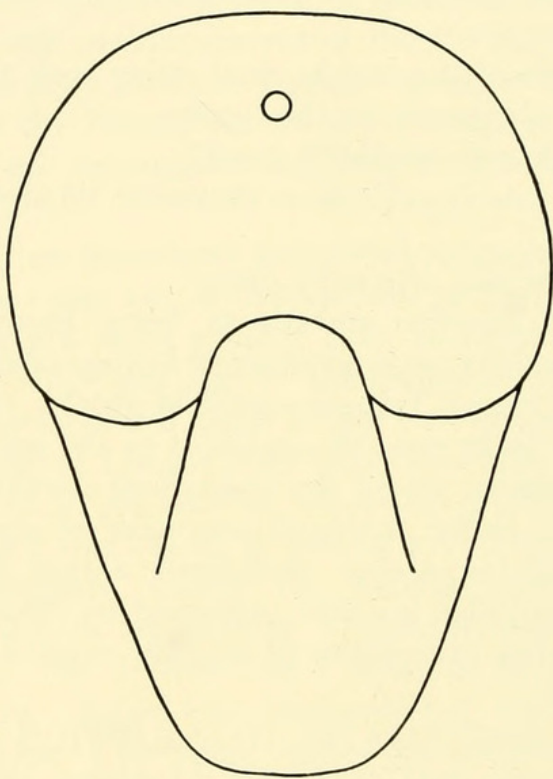


Fig. 2. Diagrammatic cross section of *Bisiphytes trechmanni* n. sp.

The suture forms a broad, very shallow ventral lobe and a slightly deeper lateral lobe. There is an annular lobe. The siphuncle is sub-ventral in position. It is 2 mm. in diameter and lies 7 mm. from the venter.

Occurrence. Upper Triassic, Carnian, Bed C, Otamita, Hokonui Hills, New Zealand.

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