NAEFIA WETZEL 1930 FROM THE QUIRIQUINA FORMATION (LATE MAASTRICHTIAN, CHILE): RELATIONSHIP TO MODERN *SPIRULA* AND ANCIENT COLEOIDEA (CEPHALOPODA)

KLAUS BANDEL[1] and WOLFGANG STINNESBECK[2]

[1] *Universität Hamburg, Geologisch-Paläontologisches Institut und Museum, Bundesstraße 55, D-20146 Hamburg, Germany*
bandel@geowiss.uni-hamburg.de
[2] *Geologisches Institut der Universität, Kaiserstraße 12, D-76131 Karlsruhe, Germany*
wolfgang.stinnesbeck@bio-geo.uni-karlsruhe.de

Abstract: The shell of *Naefia neogaeia* Wetzel, 1930 from the Maastrichtian of Chile is revised and compared with other Cretaceous taxa placed in the Groenlandibelidae. *Naefia* differs from these species by the absence of a rostrum and other external layers of the shell, and a rectangular tissue attachment scar. The thorn-like dorsal proostracum is another distinctive feature of *Naefia*. Shell characters found in *Spirula* and *Sepia* do not favor a relation with *Naefia*, which would then not fit any group proposed in literature. *Naefia,* as well as *Groenlandibelus,* remain isolated regarding their taxonomic position among fossil coleoids.

Key words: Mollusca, Coleoidea, evolution, shell construction, cretaceous

INTRODUCTION

The cephalopod genus *Naefia* Wetzel, 1930 is based on *Naefia neogaeia* Wetzel, 1930 from Quiriquina Formation, Maastrichtian of Quiriquina Island, southern Central Chile. The genus *Naefia* has been established by Wetzel, in 1930, and thus prior to *Groenlandibelus* Birkelund, 1956. Both *Naefia* and *Groenlandibelus* are Late Cretaceous in age and have been interpreted to represent relatives of *Spirula,* but with a straight orientation of their shell (Haas 1997, 2003). They were assigned to the Groenlandibelidae by Jeletzky, 1966. Their relationship to modern *Spirula* is primarily based on the presence of a siphuncular tube in the first chamber (Jeletzky 1966). In Aulacocerida and Belemnitida, the first chamber of the phragmocone is closed by an organic septum and no siphuncular tube crosses through it (Grandjean 1910, Jeletzky 1966). In *Spirula* and *Groenlandibelus,* in contrast, the siphuncular tube initiates within the first chamber and is here attached to its inner wall by a prosiphon (Appellöff 1893), similar to embryonic shells (ammonitellas) of the ammonites.

All recent cephalopods with the exception of *Nautilus* have an internal shell covered by muscular mantle. Only *Nautilus* is able to withdraw into its shell and close the aperture with a hood. This basic construction of the cephalopod shell is long known. Ehrhardt (1727) considered the chambered portion of *Nautilus* homologous to the phragmocones of belemnites, ammonites, and *Spirula*. Erhardt knew *Spirula* from the study of Rumpf (1704) (the genus was described as "Posthoorentje") and considered it closely related to the ammonites.

The shell of coleoid cephalopods is entirely enclosed by soft tissue (Endocochleata). According to authors such as Schindewolf (1933), Erben (1964) or Jeletzky (1966), endocochleat conditions established progressively when skin folds of the mantle edge gradually covered more and more of the shell of adult individuals. In contrast to the above hypothesis, Naef (1922), argued that this process initiated within the egg capsule and that the early ontogenetic shell was progressively covered by the embryo.

This latter view has since become more plausible. Muscular mantle covers the shell of embryos of many different mollusks that have a sheltered yolk-rich development (Bandel 1982). It connects to the shell from the outside and enables the embryo to concentrate on the manipulation of yolk and to retard the formation and attachment of retractor muscles. This is also the case in *Nautilus* (Tanabe 1989, Arnold 1987, Arnold & Carlson 1986). Recent squids have a hatching gland where the margins of the muscle meet in a position at the base of the fins. When the young is ready to hatch it lies attached to a special spot of the egg capsule and enzymes released by the hatching gland locally dissolve egg-envelopes. The embryo creeps through the hole with the aid of cilia that cover the body (Boletzky 1979, 1989, 1999).

This mode of hatching could well have developed during Late Silurian times, among the small and slender embryos of a group of michelinoceratid ectocochleates (Bandel et al., 1983, Bandel & Boletzky 1988). With embryonic endocochleat conditions carried into adult life, only muscular folds of the mantle had to evolve into fins and these cephalopods would have functioned as squid-like aulacoceratids.

Abel (1916), Naef (1922) and Jeletzky (1966) interpreted the belemnite rostrum to cover most or all of the phragmocone which was considered similar to the shell of

Orthoceras. They interpreted the rostrum to represent part of the periostracum. However, in all conchiferan mollusks the periostracum is produced by special cells on the edge of the mantle. In belemnites, the periostracum consequently lies below the rostrum and covers both the phragmocone and proostracum (Bandel et al., 1984). It is segregated by the cells of a gland at the margin of the mantle. The periostracum thus forms a basal layer onto which the mantle that lies behind that zone segregates additional layers of calcareous biominerals, such as nacre in the case of the class Cephalopoda.

Construction of the siphuncular tube is variable in belemnite-like cephalopods and may help to distinguish different groups (Naef 1922). For instance, belemnites from the Jurassic and Cretaceous have a simple organic tube (Jeletzky 1966), while Triassic Aulacoceratidae are characterized by a double-walled tube that resembles that of modern *Spirula* (Bandel 1985). Abel (1916) was the first to assume a buoyancy control in chambered cephalopods, long before the fundamental discussions on this function by Denton & Gilpin Brown (1961, 1971). He stated (translated): It appears to be likely that belemnites were deliberately able to fill the chambers of the phragmocone with gas or liquid to dive up or down. Abel's correct assumption was rejected by Naef (1922) who saw "no reason" for such a process. Finally, Denton & Gilpin Brown (1961, 1971), Denton et al. (1967) and Denton (1974) explained the function of the chambered shell and buoyancy control of the cephalopods became apparent.

The basic design of Coleoidea has been presented by Naef (1922). Their origin lies in the Ectocochleata of Late Silurian to Early Devonian age as documented by Bandel et al. (1983) and further discussed by Bandel & Boletzky (1988). Coleoidea are characterized by a functional siphuncular tube with a construction as found in Orthoceratida. They may well have had ten arms and a buccal apparatus resembling that of modern squids. Their hallmark is the internal shell whereas shell additions to the outside of the phragmocone such as a rostrum are possible but not necessarily present. The distinction from Ectocochleata is, therefore, difficult (Bandel 1982, Bandel & Stanley, 1988) because it is not always evident in fossil material whether a phragmocone was covered by mantle or not. In case no additional shell material is added to the outside of a phragmocone, the presence of muscle mantle can not be reconstructed with certainty.

REDESCRIPTION OF *NAEFIA*

The genus *Naefia* has been described by Wetzel (1930), 36 years before *Groenlandibelus* became known (Birkelund 1956, Jeletzky 1966). Both genera have a shell that has been interpreted to resemble that of modern *Spirula* but with a straight orientation of the phragmocone. *Naefia* is based on its type *Naefia neogaeia* Wetzel, 1930 from the Quiriquina Formation, Maastrichtian of Quiriquina Island, in the bay of Talcahuano near Concepción, southern Central Chile.

For the present research we have revised the five specimens housed in the collections of the Geological Department of the University of Concepciòn, Chile, in addition to new material collected by one of us (Wolfgang Stinnesbeck) in the type localities of the Quiriquina Formation. These specimens will also be housed in the University of Concepción.

The best preserved specimen consists of a straight phragmocone with an apical angle of about 14°. It is about 20 mm long and 4.5 mm wide and consists of 13 chambers, with the earliest chambers broken off. Septa are simple watch glass-like and round to oval. The teleoconch in other specimen studied has a width of more than 12 mm. Other shell fragments indicate that the shell may have grown to at least 100 mm in length and 15 mm in width.

Growth lines demonstrate the presence of a straight apertural margin on the ventral side of the shell, as is also indicated by the position of the siphuncular tube within the shell. A narrow projection is present on the dorsal side of the apertural margin. It consists of two narrow zones with sharply forward curving growth increments on both sides. This proostracum forms a double keeled dorsal ribbon seen on the outer layer of the phragmocone. It thus represents a narrow dorsal projection of the shell margin, with dense lateral growth lines which are steeply inclined and disconnected from the margin. The proostracum was narrow, elongate and relatively long, although its actual length can not be determined.

On the dorsal inner shell wall, a rectangular scar of tissue attachment is present on the anterior dorsal part of each chamber (Plate 1). It was imprinted by tissue to that posterior position of the shell tube next to last formed septum of the chambered shell (phragmocone). The rectangular scar is surrounded by a groove, which therefore corresponds to a thickening of the shell. The scar is about one third of chamber in height.

The initial chamber is globular in shape, about 4 mm wide, and attached to the shell tube with an inclination towards the ventral side (Plate 2). No remains of the siphuncular tube are preserved in the initial chamber. In polished section, an elongate sausage-like structure is present. It contains sediment of different composition than the remainder of the chamber. This suggests that a siphuncular tube of originally organic composition may have existed which disappeared due to the activity of microbial organisms.

Later chambers are about three times wider than high. The siphuncular tube is in a marginal position and consists of a single organic layer with very short mineralized septal necks (Plate 2). Each mineral neck ends at a short distance posterior to the septum to which it belongs. These mineralized portions of the siphuncular tube continue only for about one fourth of the height of a chamber. The tube extends for one chamber height and individual segments are attached to the interior of the septal neck of the chamber formed before. The septal necks are also mineralized and the siphuncular tube ends within the septal neck of the previous chamber. The tube diameter is about 3 mm in a chamber that measures 10 mm in diameter.

Remarks

Wetzel (1930) extracted his type material of *Naefia neogaia*, two small phragmocones, from concretions containing abundant *Eubaculites carinatus* which occur commonly in the upper portion of Quiriquina Formation. The age of this formation was determined by ammonites (Stinnesbeck 1986, 1996) to represent the Late Maastrichtian. According

to Wetzel (1930) the chambered conical fossils have an apical angle of about 13°. The diameter is round and the siphuncular tube lies marginal. The septa are simple, with an even convex-concave curving and a distance between each other of about 0.6 mm from each other in the juvenile shell, and up to 4 mm in later shell portions. Wetzel's (1930, Pl. 14, Fig. 3) illustration shows two fragments of chambered cones, one of which is reproduced by Haas (1997). There is no trace of a rostrum, as has been suggested by Haas (2003).

Biro-Bogoskoy (1982) added new specimens and new information on *Naefia* from Quiriquina Island and the mainland villages of Lirquén and Cocholgue, both at the sea shore to the north of Concepción. His specimens are up to 14 mm in length, with an apical angle of 15°. Biro noted some deposits on the outside of the phragmocone, which he considered transitional to *Belemnoteuthis*. He also suggested that *Naefia* should best be placed in the proximity of *Groenlandibelus rosenkrantzi* (Birkelund 1956). Stinnesbeck (1986) added several new specimens from Lirquén and Tomé and identified dorsal lines on the phragmocone which represent the projecting narrow proostracum.

Filled chambers resembling *Naefia neogaeia* were described from the Maastrichtian of northeastern Mexico (Ifrim et al., 2004, Text-fig. 2A–B). These steinkerns of single chambers of a phragmocone with a marginal siphuncular tube neither show remnants of a dorsal proostracum, nor imprints of a tissue attachment scar. Only a longitudinal striation on the dorsal side may indicate the former presence of a proostracum. In consequence, this fossil could just as well represent the phragmocone of a belemnite. They remain enigmatic. If they were to belong to belemnites these would be the only ones known from the Late Cretaceous of that region.

Haas (1997, Fig. 1, 4) illustrated a dorsal view of the phragmocone of *Naefia neogaeia* from the Quiriquina Formation, demonstrating the presence of slender narrow proostracum. Haas (1997, Fig. 2) considered an evolutionary reduction of the proostracum to represent one of the important characters of *Groenlandibelus* and *Naefia*. In his idealized reconstruction of a groenlandibelid cephalopod, he united characters of both genera and the resulting animal has a relatively short proostracum, a ventrally open body chamber and a short rostrum. The whole shell is reconstructed as resting in the dorsal portion of a *Sepia*-like animal.

Special characters of *Naefia*

1. The protoconch is spherical, quite large in comparison to that of *Spirula* (more than four times); it contains the beginning of the organic siphuncular tube.

2. The phragmocone is slender, with a narrow apical angle of about 14°, and without a cover of external shell material added from the outside.

3. The septa are simple and evenly rounded. The siphuncular tube resembles that of belemnites. It corresponds to an organic continuation of the short calcareous septal neck.

4. The living chamber (camera terminalis) has a narrow proostracum on its dorsal side and was open in unknown length at its ventral side. The median dorsal ribbon represents a projection of the aperture and very narrow marginal zone. The aperture of the phragmocone was therefore connected to a narrow spine-like projection with unknown dimension and an otherwise simple margin. This projection was already present in young individuals.

5. A rectangular attachment scar of the body is identified internally, in a posterior position on the dorsal side.

DISCUSSION OF OTHER SPECIES THAT HAVE BEEN PROPOSED TO BELONG TO *NAEFIA*

A single phragmocone considered to represent a *Naefia* was described by Doyle (1986) from the Campanian-Maastrichtian Ariyaloor Group of Pondicherry, southern India. It belongs to the fossils collected in the Tiruchirappalli area by Forbes (1846), obviously with unknown exact locality and stratigraphic position. This area of Tamil Nadu exposes fossil bearing strata that range from Aptian to Maastrichtian (Bandel 2000).

The apical angle of the phragmocone is about 8.5°. The largest fragment is 24.5 mm long and has 7 chambers preserved. The dorsal wall of the phragmocone bears a median keel. This structure is interpreted to represent the proostracum and resembles the one found in *Naefia neogaeia* but differs in details. According to Doyle (1986, Fig. 1d, Fig. 4) the Indian material differs from *Naefia neogaeia* from Chile by having a double keel. *Naefia neogaeia* is characterized by dorsal ribbon growth lines that strongly curve forwards. This zone appears to be narrower than that described from *Naefia* aff. *neogaeia* from India.

A siphuncular tube is present at the ventral side and a median dorsal line was noted on mould that reflects the presence of an internal furrow on the phragmocone (Doyle 1986, Fig. 2b). Such a dorsal line is not present in *Naefia neogaeia* from Chile but resembles features noted in *Naefia kabonovi* from Russia (see below). Doyle (1986) noted that the Indian fossil differs from *Groenlandibelus* by the shape of the "proostracum". The south Indian phragmocone could possibly be derived from a belemnite.

Naefia kabanovi from the Aptian of Russia was described by Doguzhaeva (1996, Text-fig. 4, Pl. 6, Figs. 1–5, Pl. 7, Figs. 1, 2, Pl. 8, Figs. 1–4, Pl. 9, Figs. 1–3). It consists of a phragmocone that reaches an apical angle of 14° when younger and later may be as narrow as 7°. The chambers are about three times wider than high. Septa are simple and reported to be constructed of lamello-fibrillar nacre, as is found in the septa of *Spirula*. The siphuncular tube lies ventral and continues into the septa with short septal necks. It is described as consisting of two spherulitic-prismatic layers. The final chamber (body chamber) is reported to be short. The shell wall shows a prismatic structure, coated by an outer layer which is thicker ventrally than dorsally. No nacre is reported from the walls of the conotheca. On the inner mould of the phragmocone, body attachment scars are found. They are longitudinal, slender, spindle-like and thus differ strongly from the rectangular attachment scar of *Naefia neogaeia*. Instead, they may correspond to the "Normallinie" which is noted in many cephalopods and is not specific to Coleoidea (in case of the orthoceratids see discussion by Bandel & Stanley 1988).

According to Doguzhaeva (1996) the suture line is normal to the shell axis in *Naefia kabanovi* and oblique in *Naefia neogaeia*. However, this difference does not exist and septa in *Naefia neogaeia* are also oriented normal to the shell axis as well. Doguzhaeva (1996) further suggested that the outline of the proostracum of the two species is identical. However, this character is not preserved in *Naefia kabanovi,* and its first chamber is also unknown.

Hewitt & Jagt (1999, Fig. 3D) illustrated a fragment of a Campanian *Naefia* derived from the collection of the Royal Ontario Museum. The specimen preserves sheets of a nacreous microstructure. They consequently suggested that the Aptian *Naefia kabanovi* Doguzhaeva 1996 should also have presented nacre, composing its septa, similar to the modern *Spirula.* This nacre should have been of lamellar-fibrillar type as defined by Mutvei (1964, 1970). Both, the outer and the inner shell layer of *Naefia kabanovi* are described as prismatic in structure. Hewitt et al. (1991) suggested that in *Naefia* the shell wall could be nacreous on the outside and prismatic on the inner side and that the nacreous construction of septa are of *Spirula*-type.

The attachment scar distinguishes the Chilean *Naefia neogaeia* from the Russian *Naefia kabanovi* and *Naefia* aff. *neogaeia* from India. The Chilean *Naefia* is characterized by rectangular attachment scars surrounded by a furrow. The scar is positioned in the anterior part of each chamber. It is as wide as the dorsal outer ribbon and as high as one third of each chamber. In contrast, attachment scars of *Naefia kabanovi* Doguzhaeva, 1996 are elongate and cross the entire chamber in height, as is noted in the phragmocone of belemnites.

The two species described as *Naefia* aff. *neogaeia,* from the Cretaceous of India, and *Naefia kabanovi,* from Russia do not fit the characters of *Naefia* sufficiently to include them in the same genus as *Naefia neogaeia* from Chile. The "Normallinie" seen in *Naefia* aff. *neogaeia* from India indicates its resemblance to the Russian fossil. While the Indian fossil had a proostracum, the Russian fossil did apparently not preserve one or had none. The proostracum of the Indian coleoid is a little wider and of different ornament to that of *Naefia neogaeia*. Both these fossils should not be included in the genus *Naefia*, but rather be placed with belemnite-like endocochleates.

A *Naefia* described from Mexico by Ifrim et al. (2004) may belong here or not. The fossil consists only of internal chamber-fills which present no features that would allow a decision that this was a phragmocone of a belemnite or of *Naefia*.

Comparison of *Naefia* with *Groenlandibelus*, evaluation of the family Groenlandibelidae

The family Groenlandibelidae has been erected by Jeletzky (1966) around *Belemnoteuthis rosenkrantzi* Birkelund 1956. Jeletzky (1966) later excluded the genus *Belemnoteuthis* from the group based on differences in the first chamber. Even though the phragmocone of *Naefia* and *Groenlandibelus* may be similar to belemnites in shape, Jeletzky (1966) noted that differences exist with regard to the beginning of the siphuncular tube. While belemnites are characterized by an organic first septum, the siphuncular tube of *Groenlandibelus* begins with a blind sack extending into the first chamber of the phragmocone, as is the case in modern *Spirula*.

The shell is essentially straight in both *Naefia* and *Groenlandibelus*, and apical angles are narrow, between 12°–15°. Watch-glass-like septa and simple sutures characterize the phragmocone in the two genera and chambers are about three times wider than high. Birkelund & Hansen (1974) found these septa to resemble those of belemnites. In *Groenlandibelus*, however, the apical part of the phragmocone walls is covered by a short, wrinkled cone forming a short rostrum. *Naefia,* on the other hand, does not present a rostrum, even though the phragmocone grew longer and wider.

The dorsal side of *Groenlandibelus* carries a ridged elongate structure that is reconstructed as proostracum (see also Doyle 1986 for schematic drawing). This ribbon is narrow and presents sharp margins. It was apparently unconnected to growth lines (Birkelund 1956). A dorsal keel may also be present, which according to Jeletzky (1966) resembles the one found in the belemnite *Diplobelina*, and is similar to the proostracum of *Naefia*.

The ventral siphuncular tube is relatively wide, not mineralized, but may have been double-walled (Jeletzky 1966, Pl. 20–22). Even then, both walls were of organic composition. The septal necks are relatively long in early chambers and gradually shorten. Their mineral composition ends on the margin of the siphuncular tube. It initiates in the first globular chamber. It is of sausage-like shape and continues for three-quarters of the height of the first chamber. It consists of organic material and is attached to the inside of the chamber by a sheet (prosiphon) (Jeletzky 1966, Pl. 20, Figs. 1A, B). The siphuncular tube could have been similar in *Naefia*, but the first chamber of *Groenlandibelus* as documented by Jeletzky (1966, Pl. 20, Fig. 1A) is much smaller, with only about 0.5 mm, contrasting to 4 mm in *Naefia*.

According to Jeletzky (1966) the Groenlandibelidae represent members of the order Sepiida. In *Groenlandibelus,* Jeletzky (1966) noted a "prismatic structure" of the phragmocone wall and a double walled siphonal tube. In a thin section, Jeletzky (1966, Pl. 23, Fig. 1A) documented vertical structures in both the phragmocone wall and the septum. They could represent remnants of columnar nacre. His interpretation of the original structure of the outer shell wall as prismatic is thus doubtful.

Doguzhaeva (1996) suggested that the structure of the siphon of *Naefia* resembles *Groenlandibelus,* based on information gathered from *Naefia kabanovi.* Since this species is not a member of the genus *Naefia,* the Russian phragmocone can not be assigned properly. Doguzhaeva (1996) interpreted the outer layer of the siphon to represent a structurally modified continuation of the septal neck, whereas the inner layer would represent the remains of a slightly calcified wall, or a wall of organic composition.

According to Jeletzky (1966, Pl. 23, Figs. 1D, 1E) and Birkelund & Hansen (1974, Pls. 13–15). the siphuncular tubes of *Groenlandibelus* and *Spirula* differ. In both genera, the septum apparently did not continue into an outer calcareous tube, but mineralized layers ended right next to the hole through which the siphuncular tube passed. This tube is predominantly of organic composition. *Naefia*, in contrast, has mineralized septal necks, similar to those found in belemnites.

Jeletzky (1966) suggested that both *Groenlandibelus* and *Naefia* represent members of the Groenlandibelidae. However important differences exist between *Groenlandibelus rosenkrantzi* and *Naefia neogaeia* regarding the presence of a rostrum (Jeletzky 1966, Pl. 20, Fig. 1A), the shape of the transition of the septum into the siphuncular tube, and the size of the first chamber. Haas (1997, Fig. 2, 2003) provided a model in which *Groenlandibelus* and *Naefia* both present a short proostracum and a rostrum. Both features could serve for a reconstruction of *Groenlandibelus* as described by Birkelund (1956), Birkelund & Hansen (1974) and Jeletzky (1966). For *Naefia*, however, they can not be confirmed. According to our restudy, *Naefia neogaeia* may have had a slender narrow elongate proostracum and no rostrum.

Comparison of *Naefia* with *Spirula*

Spirula is characterized by an internal open coiled shell with smooth apertural margin. The shell is calcareous, located in the posterior end of the animal and contains over 30 chambers in adults, connected by a siphuncular tube. *Spirula spirula* (Linné 1758), a member of the Spirulidae Orbigny, 1826, corresponds to an animal without a radula (Kerr 1931). It lives at about 600–700 m depth during the day and rises to about 300 m during night. The initial chamber of its shell is globular and the siphuncular tube has a double wall (Bandel & Boletzky, 1979). Naef (1922) noted that the external layer of the siphuncular tube is the continuation of the septum. This mineralized tube is coated on the inside by an organic tube.

Gregoire (1961) was the first to note that the nacre observed in septa of *Spirula* differs from the nacre seen in other mollusks, including that of *Nautilus*. The ultra-structure of the shell of *Spirula* was described by Mutvei (1970), and by Dauphin (1976). The latter author noted that the calcareous sipho begins with an organic tube that initiates in an organic attachment sheet (prosiphon) (Dauphin 1976, Fig. 23). In *Spirula,* the nacre of the septum and the outer siphuncular tube consists of needles of about 0.2 micron in diameter arranged in layers oriented along the growth surface and not in platelets. This structure was called lamello-fibrillar by Erben (1972). Between the outer calcareous and the inner organic layer of the siphuncular tube, a porous intermediary layer exists of prismatic needles (Dauphin 1976, Figs. 18–21). The detailed three-layered construction of the siphuncular tube of *Spirula* was first described by Bandel & Boletzky (1979). A similar tube but with shorter fully calcified outer wall has been present in the late Triassic aulacoceratidid *Dictyoconites,* analyzed by Bandel (1985).

The permeable zone within the siphuncular tube of *Spirula* is as long as one chamber is high. In consequence, much of the chamber liquid is in contact with the living siphuncle. Liquid is actively moved in and out of the buoyancy system by a salt pump of the siphuncular mantle. While much of the vertical movements of *Spirula* may simply relate to its weight, – the animal is heavier when well fed and lighter when digestion is completed –, the buoyancy of the shell may also change fairly rapidly (Bandel & Boletzky, 1979).

The siphonal system is responsible for buoyancy regulation and thus represents an important feature in shell construction. It is therefore important to note that the siphuncular tube of *Naefia* differs considerably from that of *Spirula*. In *Spirula*, the septal neck is continuous through the entire chamber, forming a solid outer wall, whereas in *Naefia* only a part of the siphuncular tube forms a solid outer wall. The initial chamber of *Naefia* is about five times larger than that of *Spirula*, and there is a shell layer in *Spirula* added from the outside to the phragmocone that is not found on the *Naefia* shell. Visceral mass is connected to the shell of *Spirula* along a dorsal ribbon. On both sides of this ribbon retractor muscles end in the tissue of the mantle (Bandel 1982).

Hypothesis of a transition from a *Spirula*-like shell to the cuttlebone of *Sepia*

Modern *Sepia* has a characteristic internal shell, the cuttlebone. It varies quite a lot in shape and size among the living species, but is always of similar construction. *Sepia* is not found in the Americas and most of the Central and Eastern Pacific. About 120 species exit of the genus and the similar *Sepiella* (Adam & Rees, 1966, Voss & Williamson, 1971, Roeleveld 1972). The cuttlebone of *Sepia* has been described by Appellöff (1823) and his terminology has largely been utilized and adopted by Bandel & Boletzky (1979). Accordingly, the cuttlebone consists of a dorsal shield and the ventral chamber zone. The mid-dorsal line close to the posterior end of the dorsal shield bears a more or less well developed spine or rostrum. The ventral surface the chamber zone has the siphuncular zone anterior and the last formed chamber posterior. This chamber zone is embraced by the fork. The cuttlebone serves as backbone with solid lateral attachment to the large marginal fins and as buoyancy regulator due to ventral chambers.

The construction of the *Spirula* shell was compared to that of *Sepia* by Bandel & Boletzky (1979). The authors found that the phragmocone wall and the septa are built of a specific nacre, but that the prismatic shell walls are otherwise similar to the ones found in *Sepia*. While the shell structure is similar, the embryonic shell of *Spirula* and *Sepia* differs very strongly. While *Spirula* has a rounded initial chamber that of *Sepia* is an open cup-like structure. The first chamber of *Spirula* is closed by the first septum, while the initial shell of *Sepia* grows on its anterior edge and chambers are added to it in consecutive layers on top of each other. It was suggested by Appellöf (1893), Bandel & Boletzky (1979), Haas (1997), Hewitt & Jagt (1999) that the septa as in *Spirula* developed into the inner plate of the cuttlebone of *Sepia*, and that the siphuncular tube as in *Spirula* was opened to form the *Sepia* septa and supporting walls. The siphuncular tube is, therefore, interpreted to be homologous to the flat chambers of the cuttlebone of *Sepia*.

Squires (1983) described a cuttlebone of a sepiid from the Eocene of California. Transitional species should therefore be older. They should present chambers not connected to a flat ventral chamber zone on one side and a globular initial chamber on the other, thus resembling neither *Sepia* nor *Spirula*. *Groenlandibelus* or *Naefia* do not provide any similarity regarding their siphuncular tube, which rather resembles that of belemnites instead.

Bonnard et al. (1997) and Carlini & Graves (1999) carried out a molecular phylogenetic analysis comparing *Spirula*

with other coleoids and noted neither a link to *Sepia* nor to teuthoids. The results of Warnke et al. (2003) also support this analysis. Woodward (1856) placed the Sepiidae on equal level to the Belemnitidae and the Spirulidae. This interpretation has in principle been confirmed by the molecular data, as the distance stated by Young et al. (1998) between Sepiidae and Spirulidae.

Coleoids with ten arms (Decabrachia Boettger, 1952 (= Decapoda)) according to Haas (1997, 2003) are considered to form the two sister groups Uniductia Berthold & Engeser, 1987 and Oegopsida. The first have lost their calcified shell and are considered to have had ancestors similar to the Groenlandibelidae which are interpreted to be representatives of the stem group of the Uniductia by Berthold & Engeser (1987, Fig. 8). *Groenlandibelus,* on the other hand, is considered close to the stem group to the Spirulida by Haas (2003). According to that interpretation it was a member of the Uniductia which have the ventral living chamber open, as in the belemnites but convergent to them. The Uniductia, thus, remain to be an rather artificial construct, and the resemblance of a stem group represented by *Groenlandibelus* is only assumed. This construct has not been improved by creating a reconstruction of an animal that unites the features of *Groenlandibelus* and *Naefia* (Haas 1997, Fig. 2).

SHELL CHARACTERS THAT CAN BE UTILIZED IN THE ANALYSIS OF CEPHALOPOD EVOLUTION AND IN DISCRIMINATION OF NAEFIA FROM OTHER COLEOIDS

The shell is interpreted in terms used with Ectocochleata and Mollusca in general.

a. The organic shell is formed by the mantle edge and its special glandular cells (periostracum gland). It is usually organic in construction and is also present in cases where the shell is formed covered by mantle, as is the case among coleoids. Periostracum is present in all conchiferan mollusks including the cephalopods, at least at some stage of their ontogeny. In case of the Endocochleata the periostracum is secreted below the cover of the muscular mantle. In this group the shell secreting epithelium is progressively covered by muscular mantle during embryonic development. The shell is formed below this muscular mantle, that in ectocochleate cephalopods is found in front of the periostracal gland zone. In *Naefia* the periostracum is not covered by additional shell (Pl. 1 and 2), in contrast to *Spirula*, *Groenlandibelus* and *Sepia*.

b. The mineralized shell is produced by the mantle behind the periostracal gland zone and is formed within and by the extrapallial liquid secreted by the mantle. The characteristic biomineral of the shell is nacre which is found in all phragmocone-bearing cephalopods. Nacre can be organized as platelets forming pillars (*Nautilus*-nacre), or as lamellar structures composed of needles (*Spirula* – nacre). *Spirula*-nacre is also called lamellar prismatic nacre and is only found in the phragmocone of Endocochleata. Among these it helps to distinguish such groups that also have *Nautilus*-nacre as dominant biomineral of the inner layer in the phragmocone wall, and *Spirula*- nacre in the septa and other taxa, where only *Spirula*-nacre is present. This latter case is present in *Spirula* and *Sepia,* and the former in belemnites and aulacoceratids. Nacre is aragonitic and, thus, commonly replaced diagenetically by calcite or other substances. During this process crystal morphology changes, as in case of all individuals of *Naefia* and *Groenlandibelus* that have been studied.

c. A more simple construction is present in the mineral shell that is produced outside the shell mantle behind the periostracal gland by the cells of the muscular mantle. It does not consist of nacre or other characteristic molluskan biominerals. An outer shell layer secreted by the muscle mantle can be organic, calcitic, or aragonitic or all three, but it may also be totally absent, as is the case in *Naefia*. Deposits formed in the shell sac by the cells of the muscular mantle may be calcitic or aragonitic with organic material added to it. In either case, characteristic textures are developed. Aragonitic morphologies are commonly spherulitic or consist of spherulite sectors, as on the cuttlebone of *Sepia* and the rostrum of many aulacoceratids. Calcitic structure is regularly prismatic on a base of spherulites as is the case in the rostrum of belemnites. The composition of the rostrum may change from calcitic to aragonitic or vice versa during shell growth. In *Spirula,* the aragonitic outer layers are spherulitic and prismatic (Pl. 3). The latter structure was likely developed in the rostrum of *Groenlandibelus* before its transformation into calcite.

d. The siphuncular tube may resemble that of *Nautilus* with a calcareous and porous outer layer and an organic inner layer, but it may also be a single organic tube as in belemnites where it grades into the mineralized septa at the septum – tube contact. In advanced ammonites the siphuncular tube may be distinct from the septa, and it may be double walled as in *Spirula* and *Aturia*. In case of some of the Paleozoic Ectocochleata even more complex structures are known to exist. In case of *Spirula* the tube may occasionally have been sealed and filled with organic shell. The siphuncular tube of *Naefia* is like that of belemnites (Pl. 2), while that of *Groenlandibelus* appears to differ in regard to its attachment to the septum.

e. The first shell developed, or embryonic shell may reflect eggs rich in yolk, such as in *Sepia* or *Nautilus.* In these organisms, it is larger than 0.5 mm in diameter. Eggs that are relatively poor in yolk exist in the Recent *Spirula,* in ammonites, belemnites and aulacoceratids, among fossil forms. The shape of this first shell is quite stable within the groups. Ammonites always develop an “Ammonitella” that remains similar in shape and size from the Devonian to the end of the Cretaceous. Similar conditions can be expected in other groups with external or internal shell. Apparently, Belemnitida and Aulacoceratida form another large unit. They are closely connected to their common stem group, the Bactritida. The first shell of *Naefia* and *Groenlandibelus,* in contrast, resembles that of those bactritids that developed into the ammonites and present a siphuncular tube entering the first chamber (Pl. 3).

f. Anterior of the last septum, the shell is more or less tubular in *Spirula*, and short. It is elongate in Aulacocerida, closely resembling that of the Bactritida. In Belemnitida, it is short on the ventral side and extended into a more or less elongated dorsal lobe or spine, the proostracum. In this respect, *Naefia* and *Groenlandibelus* resemble the belemnites.

g. The visceral mass of that part of the body that enters the "living chamber" leaves a scar on the dorsal side. This scar reflects the shape of attachment of the soft tissue to the shell. It is elongate in the Belemnitida and Aulacocerida and also in *Spirula* (Pl. 3), and short and rectangular in *Naefia* (Pl. 1).

In conclusion *Naefia* differs from *Groenlandibelus* in regard to its tissue attachment scar, the connection of the septum to the organic siphuncular tube, the size of the first globular chamber of the phragmocone and the absence of a rostrum. It is distinguishes from belemnites by the shape of the attachment scar, the composition of the siphuncular tube in the initial chamber of the phragmocone and the absence of a rostrum. *Naefia* differs from *Spirula* by the shape of the tissue attachment scar, the composition of the siphuncular tube, and the presence of a proostracum, besides not having a coiled shell. *Naefia* differs from the aulacoceratid *Dictyoconites* in regard to the tissue attachment scar, the composition of the siphuncular tube in the initial chamber of the phragmocone, the presence of a proostracum and the absence of a rostrum. If *Naefia* would have been found in strata of the Late Paleozoic it could be connected to Bactritidae and would then differ from this group by the attachment scar to the interior of the protoconch, as well as by the presence of a proostracum. In conclusion, *Naefia* represents a Late Cretaceous coeleoid that does not fit into the Groenlandibelidae, the Spirulidae, the Belemnitidae, the Aulacoceratidae, and the Bactrididae.

Acknowledgments. Prof. Dr. Luis Arturo Quinzio-Sinn (Concepción) provided us with his help and friendship. The plates were assembled by Eva Vinx (Hamburg). Financial support for the study and the field work in Chile came from the DFG in the projects Sti 128/6 and Ba 675/25. We express our sincere thanks to these persons and the Deutsche Forschungsgemeinschaft.

REFERENCES

Abel O., 1916: Paläobiologie der Cephalopoda aus der Gruppe der Dibranchiaten. Verlag Gustav Fischer, Jena 281 pp.

Adam W., Rees W. J., 1966: A review of the cephalopod family Sepiidae. Scientific Reports. John Murray Expedition, 11, 165 pp.

Appellöf A., 1893: Die Schalen von *Sepia*, *Spirula* und *Nautilus*. Studien über den Bau und das Wachsthum. Kongl. Svenska Vt. Akad., Handl. 25: 1–106.

Arnold J. M., 1987: Reproduction and embryology of *Nautilus*. In: Saunders W. B. and Landman N. H. (eds.), *Nautilus*. The Biology and Paleontology of a Living fossil (in Plemum Press), New York, pp. 353–372.

Arnold J. M., Carlson B. A., 1986: Living *Nautilus* embryos: Preliminary observations. Science 232: 73–76.

Bandel K., 1982: Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. Facies 7: 1–198.

Bandel K., 1985: Composition and ontogeny of *Dictyoconites* (Aulacocerida, Cephalopoda). Paläontologische Zeitschrift 59: 223–244.

Bandel K., 2000: Some gastropods from the Trichinopoly Group Tamil Nadu, India and their relation to those from the American Gulf Coast. Memoir Geological Society of India 46: 65–111, Bangalore.

Bandel K., Boletzky S. von, 1979: A comparative study of the structure, development and morphological relationship of chambered Cephalopod shells. The Veliger 21: 313–354.

Bandel K., Boletzky S. von, 1988: Features of development and functional morphology required in the reconstruction of early coleoid cephalopods. In: Wiedmann J. and Kullmann J. (eds.), Cephalopods – Present and Past, Stuttgart, 229–246.

Bandel K., Engeser T., Reitner J., 1984: Die Embryonalentwicklung von *Hibolithes* (Belemnitida, Cephalopoda) (The embryonic development of *Hibolithes*, Belemnitida, Cephalopoda). Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 167: 275–303.

Bandel K., Reitner J., Stürmer W., 1983: Coleoids from the Lower Devonian Black Slate („Hunsrück-Schiefer") of the Hunsrück (West Germany). Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 185: 397–417.

Bandel K., Stanley G. D., 1988: Reconstruction and biostratinomy (Lamellorthoceratidae) of Devonian Cephalopods with unique cameral deposits. Senckenbergiana Lethaea 69: 391–437.

Berthold T., Engeser T., 1987: Phylogenetic analysis and systematization of the Cephalopoda (Mollusca). Verhandlungen naturwissenschaftlicher Verein Hamburg. (NF) 29: 187–220.

Birkelund, T., 1956: Upper Cretaceous belemnites from West Greenland. Meddelelser om Groenland 137: 1–28.

Birkelund T., Hansen H. J., 1974: Shell ultrastructures of some Maastrichtian Ammonoidea and Coleoidea and their taxonomic implications. Det Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter 20, Kobenhavn.

Biro-Bogoczky L., 1982: Contribucion al concimiento de *Naefia neogaeia* Wetzel, Coleoidea, en la Formation Quiriquina, Campaniano-Maastrichtiano, Region des Bio-Bio, Chile, Sudamerica (36°30'–36°45' Lar.Sur). III Congreso Geologico Chileno, Concepción, Chile: A17-A28.

Boletzky S. von, 1979: Nos connaissances actuelles sur développement des octopodes. Vie Milieu 28–29: 85–120.

Boletzky S. von, 1989: Recent studies on spawning, embryonic development, and hatching in the Cephalopoda. Advances in Marine Biology 25: 85–115.

Boletzky, S. von, 1999: Cephalopod development and evolution. In: Oloriz F. & Rodriguez-Tovar F. J. (eds.), Advancing Research on Living and Fossil Cephalopods, 3–11. Kluwer Academic/ Plenum Publishers, New York.

Bonnaud L., Bouchere-Rodoni R., and Monnerot M., 1997: Phylogeny of cephalopods inferred from mitrochondrial DNA sequences. Mol. Phyl. Evol. 7: 44–54.

Carlini D. B., Graves, J. E., 1999: Phylogenetic analysis of cyochrome oxidase I sequences to determine higher-level relationships within the coleoid cephalopods. Bull. Mar. Sci. 64: 57–76.

Dauphin Y., 1976: Microstructure des coquilles de cephalopods, I. *Spirula spirula* L. (Dibranchiata, Decapoda). Bulletin du Muséum National D'Histoire Naturelle 3rd ser. 382: 197–238.

Dauphin Y., 1982: Analyse microstructurale d'un *Aulacoceras* (Mollusca- Coleoidea) juvenile du Trias de Turquie. Paläontologische Zeitschrift 56: 53–75.

Denton E. J., 1974: On buoyancy an lives of modern and fossil cephalopods. Proceedings of the Royal Society of London B 185: 273–299.

Denton E. J., Gilpin Brown J. B., 1961: The buoyancy the cuttlefish *Sepia officinalis* (L.). – Journal of the Marine Biological Association of the United Kingdom 41: 319–342.

Denton E. J., Gilpin Brown J. B., Howarth J. V., 1967: On the buoyancy of *Spirula spirula*. – Journal of the Marine Biological Association of the United Kingdom 47: 181–191.

Denton E. J., Gilpin Brown J. B., 1971: Further observations on the buoyancy of *Spirula*. – Journal of the Marine Biological Association of the United Kingdom 51: 363–373.

Doguzhaeva L. A., 1996: Two Early Cretaceous spirulid coleoids of the north-western Caucasus: Their shell ultrastructure and evolutionary implications. Palaeontology 39: 681–707.

Doyle P., 1986: *Naefia* (Coleoidea) from the late Cretaceous of southern India. Bull. Br. Mus. Nat. Hist. (Geol.) 40: 133–139.

Ehrhart B., 1727: De Belemnitis Suevicis. Augsburg.

Erben H. K., 1964: Die Evolution der ältesten Ammonoidea. Neues Jahrbuch für Geologie und Paläontologie 120: 107–212.

Grandjean F., (1910): Le siphon des ammonites et des belemnites. Soc. Geol. France Bull. Sér. 4 (10): 496–519.

Gregoire C., 1961: Sur la structure de nacre septal des Spirulidae, etudiee au microscop electronique. Archives Intern. Pysilogie et Biochimie 69: 374–377.

Haas W., 1997: Der Ablauf der Entwickungsgeschichte der Decabrachia (Cephalopoda, Coleoidea). Palaeontographica (a) 245: 63–81.

Haas W., 2003: Trends in the evolution of the Decabrachia. Berliner Paläobiol. Abh. 3: 113–129

Hewitt R. A., Jagt, J. W. M., 1999: Maastrichtian *Ceratisepia* and Mesozoic cuttlebone homeomorphs. Acta Palaeontologica Polonica, 44: 305–326.

Hewitt R. A., Yoshiike T., Westermann G. E., 1991: Shell microstructure and ecology of the Cretaceous coleoid cephalopod *Naefia* from the Santonian of Japan. Cretaceous Research 12: 47–54.

Ifrim C., Stinnesbeck W., Lopez-Oliva J. G., 2004: Maastrichtian cephalopods from Cerralvo, North-Eastern Mexico. Palaeontology 47: 1575–1627.

Jeletzky J. A., 1966: Comparative morphology, phylogeny, and classification of fossil Coleoidea. – Univ. Kansas Palaeontological Contributions to Mollusca, Art: 7: 1–162. Lawrence, Kansas.

Kerr J. G., 1931: Notes upon the Dana specimens of *Spirula spirula* and upon certain problems of cephalopod morphology. Danish "Dana" Exp. 1920–1922 in North Atlantic and Gulf of Panama, No. 8, Kopenhagen.

Mutvei H., 1964: On the shell of *Nautilus* and *Spirula* with notes on shell secretion in non- cephalopod molluscs. Ark. Zool. 16: 221–278.

Mutvei H., 1970: Ultrastructure of the mineral and organic components of molluscan nacreous layers. Biomineralisation Research Reports 2: 48–72.

Naef A., 1922: Die fossilen Tintenfische. Gustav Fischer Verl., Jena, 322 pp.

Naef A., 1928: Die Cephalopoden, Embryologie. Fauna Flora Golfo Napoli, 35. Monogr. 1–2, Tafelband Neapel.

Schindewolf O. H., 1933: Vergleichende Morphologie und Phylogonie der Anfangskammern tetrabranchiater Cephalopoden. Preuss. Geol. Landesanst. Abh. N. S. 148: 1–115.

Squires R. L., 1983: New mollusks from the Lower Middle Eocene Llajas Formation, Southern California. Journal of Paleontology 57: 354–362.

Stinnesbeck W., 1986: Faunistic and paleoecological contributions of the Quriquina Formation (Maastrichtian) of Central Chile. Palaeontographica A, 194: 99–237.

Stinnesbeck W., 1996: Ammonite extinctions and environmental changes across the Cretaceous- Tertiary boundary in Central Chile. In: MacLeod N. and Keller, G. (eds.), The Cretaceous-Tertiary boundary mass extinction: Biotic and environmental events. Norton Press, New York, pp. 289–302.

Tanabe K., 1989: Endocochleate embryo model in the Mesozoic Ammonitida. Hist. Biol. 2, 183–196.

Voltz, 1830: Observations sur les belemnites. Mem. Soc. Mus. d'Hist. Nat. Strasburg 1: 1–70.

Voss G., Williamson G., 1971: Cephalopods of Hong Kong. Hong Kong Government Press, 138 pp.

Warnke K., Plötner J., Rueda M. J., Santana I., Llindas O., 2003: Reflections on the phylogenetic position of *Spirula* (Cephalopoda): Preliminary evidence from the 18S ribosomal RNA gene. Berliner Paläobiologische Abhandlungen 3: 253–260.

Wetzel W., 1930: Die Quiriquina – Schichten als Sediment und paläontologisches Archiv. Palaeontographica A, 73: 49–106.

Woodward S. P., 1856: On the occurrence of the fossil genus *Conotheuthis* d'Orb. in England. Ann. Mag. Nat. Hist. 17. London.

Young R. E., Vecchione M., Donovan D. T., 1998: The evolution of coleoid cephalopods and their present biodiversity and ecology. – Cephalopod Biodiversity; Ecology and Evolution, in: Paynbe A. I. L., Lipinski M. R., Clarke M. R., Roelefeld M. A. C., (eds.), South African Journal mar. Sci. 20: 393–420.

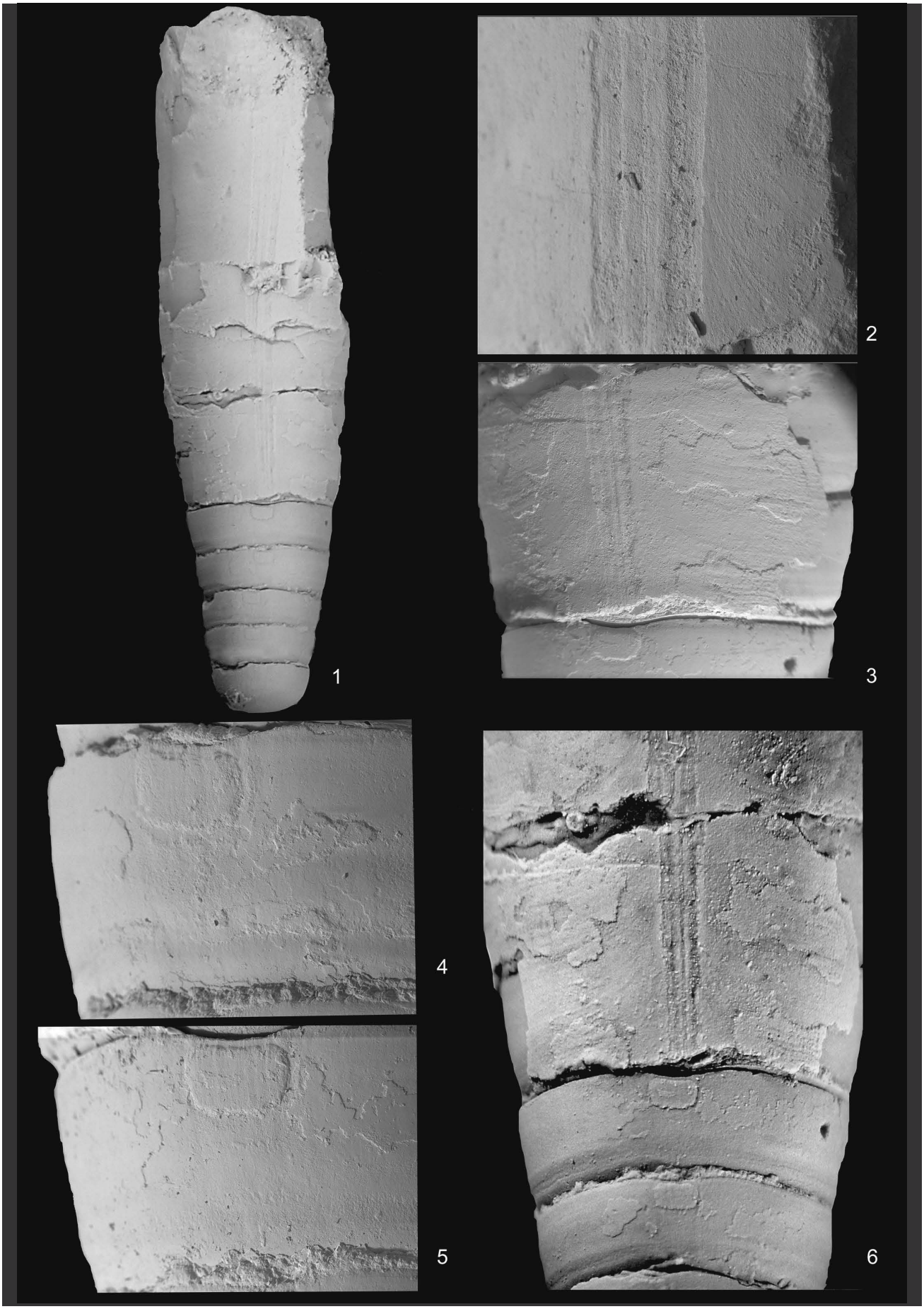

Plate 1. Fig. 1 Dorsal view of 20 mm long phragmocone of *Naefia neogaeia.* Details are present in figures 2–6. Fig. 2 Proostracum with two keels and growth lines at its margin. Fig. 3 Part of the shell with proostracum and with internal chamber filling. Fig. 4 and 5 Attachment scars of the body to the shell in consecutive chambers with rectangular shape preserved on sediment of the filled chamber.

Plate 2. Fig. 1 Ventral side of the shell of *Naefia neogaeia*. The 20 mm long shell is seen in dorsal view on Plate 1. Fig. 2 Polished section of the globular first chamber of 4 m in width and 4.5 mm in greatest diameter with traces of the rounded blind end of the siphuncular tube in the sediment filling the chamber. Fig. 3 Suture line of the fifth septum in detail with traces of the attachment lamellae of the siphuncular canal to the inner side of the shell wall. Fig. 4 and 5 Sections of the siphuncular tube on the 8 mm long cambered part representing the mineralized septal necks and the succeeding organic tube. The whole specimen is 20 mm long and composed of 11 chambers.

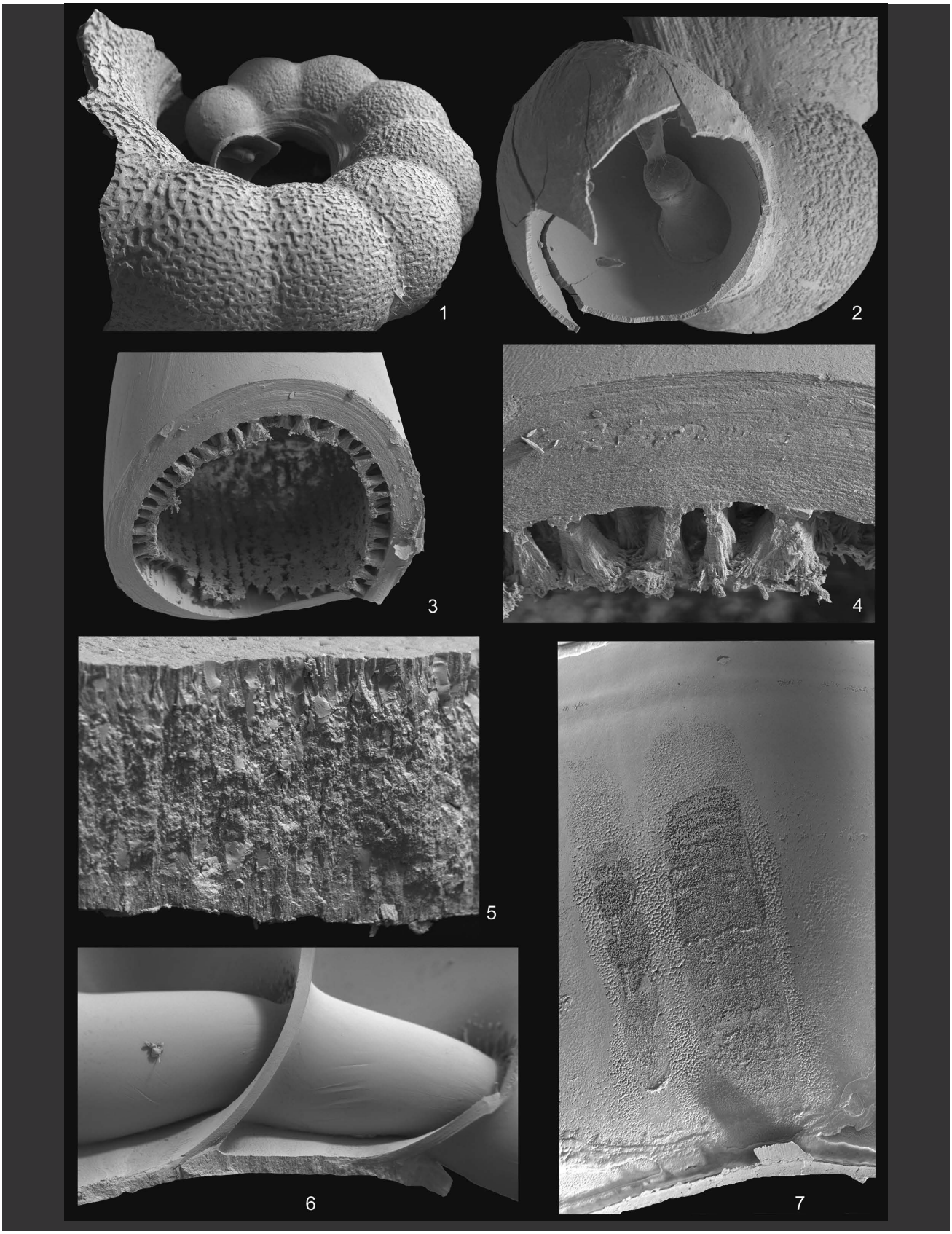

Plate 3. All figures are from *Spirula* from the Indo Pacific of Western Australia. Fig. 1 Shell with about 3 mm in diameter with opened first chamber and outer side of phragmocone covered by external calcareous deposits. Fig. 2 Opened first chamber of about 0.5 mm width with the beginning of the siphuncular tube. An organic sheet (prosiphon) connects the initial organic layer of the tube to the shell. This organic cap continues in a mineralized elongate septal neck. Fig. 3 Siphuncular tube with nacreous outer wall, porous pillar zone and thin organic inner tube here dissolved. Fig. 4 Detail to Fig. 3 with laminated nacre of outer tube and prismatic structure of pillar zone. Fig. 5 Section of outer wall (detail to Fig. 6) with fine grained central shell layer and inner and outer prismatic structure. Fig. 6 Shell opened to expose siphuncular tube and two fractured septa. Fig. 7 Elongate attachment scar of the body to the interior of the shell opposite to the siphuncular tube. The septa cover it, so it forms a continuous dorsal scar on the shell interior.

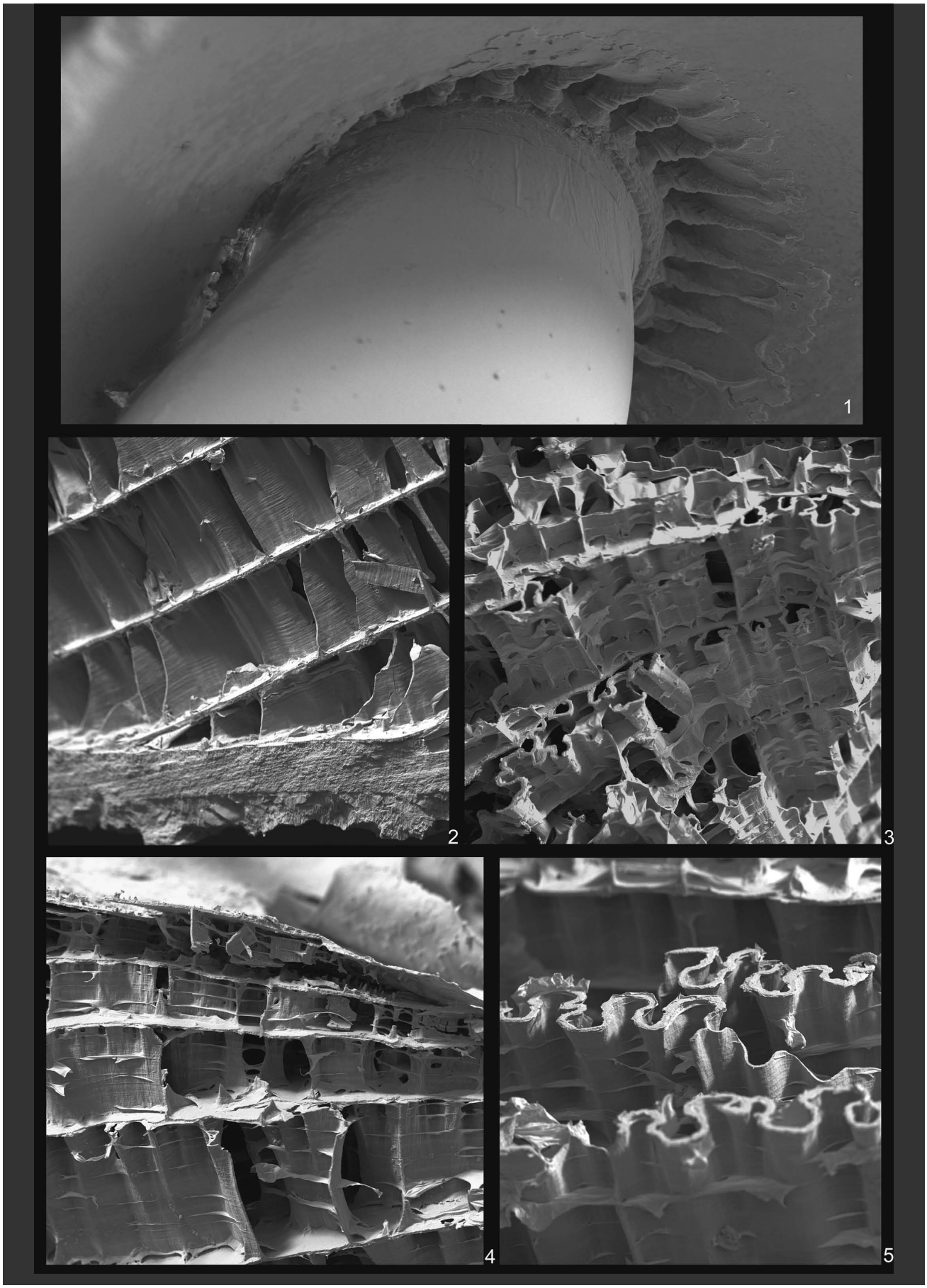

Plate 4. Fig. 1 Siphuncular tube of *Spirula.* Entrance from the chamber to the space between nacreous and organic layer. Note that pillars are not unlike those found in the cuttlebone of *Sepia*. Figures 2–4: *Sepia pharaonis* from the Red Sea. Fig. 2. Fractured cuttlebone with attachment of the septa to the outer wall. Fig. 3. Central fracture of consecutive chambers. Fig. 4. Outermost chambers and zone of chambers next to the pumping epithelium. Fig. 5. Attachment suture of chamber pillar walls to the septum. About three chambers above each other amount to 1 mm in height.