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## ***Spirula*—a window to the embryonic development of ammonoids? Morphological and molecular indications for a palaeontological hypothesis**

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**Abstract** *Nautilus* is not suitable as a model organism to infer biological functions, embryonic development, or mode of life in ammonoids. A brief review of the available morphological data is given and molecular data are added to discuss the usefulness of *Spirula* as a biological proxy for ammonoids. Indeed, there are many morphological hints indicating that *Spirula* could be a useful model organism for approaching the embryonic development of ammonoids. The molecular data seem to support this hypothesis. However, a universal model character of *Spirula* cannot be detected as, e.g., the mode of feeding probably differs between *Spirula* and ammonoids.

**Keywords** Coleoid · Ammonoid · *Spirula* · Living model organism · Phylogeny · DNA analysis

### **Introduction**

Ammonoids were a very successful group until they disappeared near the Cretaceous/Tertiary boundary. For a long time the search for a recent model for ammonoids mainly focussed on *Nautilus*. Thus, palaeontologists have often used *Nautilus* as a model organism to infer the biological functions and the behaviour of ammonoids (e.g., Mutvei and Reymont 1973; Reymont 1980), and neontologists have also used *Nautilus* as a proxy for fossil cephalopods (for a discussion see Jacobs and Landman 1993, 1994). This related to the symplesiomorphic ectocochleate shells of ammonoids and *Nautilus*, which show many superficial similarities. Owen (1832), the first western scientist who dissected a well preserved *Nautilus*, indeed placed

ammonoids together with *Nautilus* in the Tetrabranchiata, without knowing the gill number of ammonoids. Gray (1845) already favoured a closer relationship between decabrachian coleoids and ammonoids. Further investigations based on fossil records (Flower 1961; Erben 1966; House 1981; Engeser 1990b) and more recent studies using cladistical analysis (Berthold and Engeser 1987; Engeser 1990a, 1996) supported the hypothesis that coleoids and ammonoids are more closely related than ammonoids and nautiloids. Lehmann (1967) already placed the Ammonoidea and the recent and fossil Coleoidea together in one taxon named Angusteradulata, because of the relatively narrow radula of coleoids and ammonoids. In fact Ammonoidea and Coleoidea have a radula with only 7–9 teeth per row in contrast to 13 teeth per row in the Nautiloidea. The wider radula of the Nautiloidea probably represents the plesiomorphic character state (Berthold and Engeser 1987). Both, ammonoids and coleoids probably were derived in the Lower Devonian from the Bactritoidea (Schindewolf 1933; Erben 1966; House 1981) whereas Nautiloidea already appeared in the Ordovician (e.g., House 1988; Teichert 1988). Doguzhaeva et al. (1999) described early spirulid coleoids from the Late Carboniferous.

The large size of the eggs (approx. 3×2 cm) of recent *Nautilus* (Willey 1902; Mikami and Okutani 1977; Martin et al. 1978) contrasts sharply with the supposedly small egg size of ammonoids. No laid egg masses of ammonoids have been found (e.g., Lehmann 1966), but the diameter of the ammonitella, which is the initial shell of hatchling ammonites, measured between 0.5 and 2 mm (Landman 1988; House 1996; Landman et al. 1996). This size is comparable to the size of the smallest eggs of living coleoids measuring nearly 1 mm (Boletzky 2003).

Jacobs and Landman (1993, 1994) as well as Saunders and Ward (1994) already doubted about the use of *Nautilus* as a model organism for ammonoids in general. Jacobs and Landman (1993) pointed out that for the embryonic development and for the life cycle of ammonoids, the living Coleoidea are of greater significance than *Nautilus*. It is not a new idea to use coleoids for interpretations of fossil cephalopods (e.g., Denton and Gilpin-Brown

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1973; Mutvei 1975; Bandel and Boletzky 1979; Ward and Boletzky 1984), but it is not yet common to use *Spirula* as a model organism instead of *Nautilus*. Within the recent Coleoidea the decabrachian *Spirula* might be an interesting model especially for understanding the embryonic development of ammonoids because it has a well developed internal shell, in contrast to all other living coleoids. The eggs of *Spirula* are about 2 mm in diameter (Chun 1910). The initial shell chamber in *Spirula* and ammonoids is nearly identical (Bandel and Boletzky 1979; Tanabe et al. 1980).

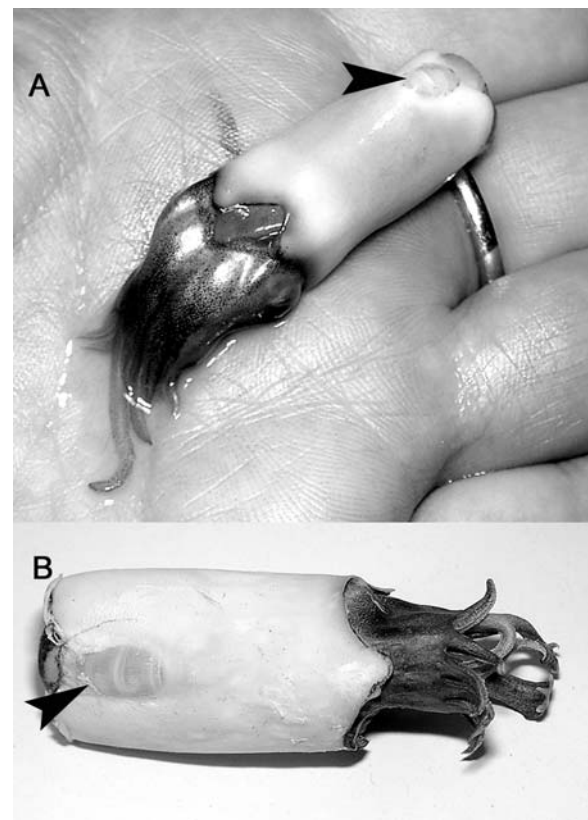
The purpose of this paper is to give a brief review of the available morphological data to discuss the usefulness of *Spirula* as a model organism for approaching embryonic development of ammonoids and to add molecular data to this discussion.

### Morphological and biological data

*Spirula* is supposed to be distributed worldwide in tropical and subtropical waters at temperatures above 10°C (in 1000 m depth) near the continental slope in the neighbourhood of oceanic islands (Bruun 1943; Clarke 1966; Lu et al. 1992). Although Norman (2000) postulated that this small animal is the most common squid found around the Canary Islands there are only a few recent studies on *Spirula*. The material of *Spirula* is ostensibly rare, because the animal has no commercial value. Moreover, it is difficult to catch; only the shells of the animals are cast ashore in large numbers.

*Spirula* is a small (approx. 5 cm mantle length) mesopelagic animal (Fig. 1). Chun (1910, 1915), Naef (1921–1923, 1922) and Nesis (1987) gave detailed descriptions. Besides the remarkable internal shell (Appellöf 1893), which will be discussed later, the animal shows distinctive features, e.g., a unique photophore at the tip of the mantle emitting green light, large eyes of oegopsid type, two greatly modified ventral hectocotyliized arms in the male, a swimming position with the head pointing down. The radula is absent (Nesis 1987) or vestigial (Nixon and Young 2003). A vestigial or totally reduced radula is believed to result from a secondary reduction. Indeed ammonoids developed a strong radula with long lateral brush-like teeth (cf. Lehmann 1967; Nixon 1996; Doguzhaeva et al. 2002). They reduced the jaws particularly in the Mesozoic as a consequence of adopting a mainly microphagous nutrition (Engeser and Keupp 2002).

As stressed above, *Spirula* is a remarkable cephalopod because of its unique internal chambered shell (Fig. 2). This shell is used for osmotic buoyancy control and is similar to a loosely coiled spiral. The shell of *Spirula* was analysed in detail by various authors (Appellöf 1893; Mutvei 1964; Bandel and Boletzky 1979; Bandel 1990). The coiling of the shell in ammonoids is exogastric, in spirulids it is endogastric. Moreover, the structures of the shell wall of *Spirula* and ammonoids (for review see Keupp 2000) are different. Ammonoids have four prismatic layers whereas spirulids have only two prismatic layers (Doyle et



**Fig. 1** *Spirula* caught, in cooperation with the Instituto Canario de Ciencias Marinas (ICCM, Gran Canaria, Spain), in the waters of Fuerteventura. **A** Female. **B** Male (arrow indicates the internal shell)

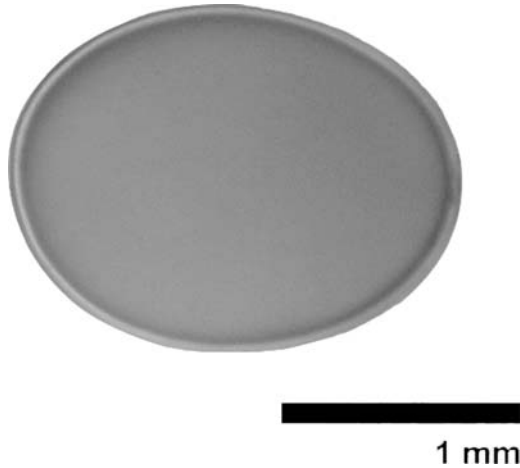
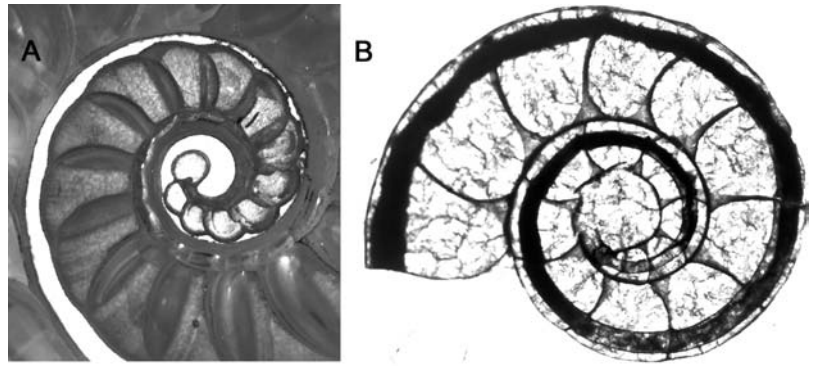
al. 1994; Doguzhaeva 1999). Nevertheless, the shape and composition of the *Spirula* initial chamber, the so-called protoconch, resembles very much that of Ammonoidea, and contrasts with *Nautilus* or *Sepia* (Fig. 2; Bandel and Boletzky 1979). Both the initial chamber of the ammonitella and the protoconch of *Spirula* typically have a more or less spherical form. They have a comparable prosseptum and flange as well as a similar caecum, and both embryonic conchs lack a cicatrix comparable to the structure of the initial shell of nautiloids (further details see Bandel and Boletzky 1979; Bandel 1982). The general mode of mineralization of the embryonic shell of *Spirula* and ammonoids is the same. It does not show growth lines because it was initially entirely organic and then rapidly mineralized (Engeser 1996). Therefore, it should be interesting to analyse the embryonic development of *Spirula*.

The reproductive strategy of ammonoids with many relatively small eggs clearly links them more closely to coleoids than to nautiloids (Engeser 1990b; Jacobs and Landman 1993; Tanabe et al. 1993; Keupp 2000). Landman et al. (1996) postulated that: "... This relationship between ammonoids and coleoids needs to be more fully explored by explicit studies comparing embryonic development and posthatching mode of life in both of these groups."

Unfortunately, at present nothing is known about spawning in *Spirula*. Mature ovarian eggs measure between 1.7 mm (Chun 1910) and 1.9 mm (our own observations;



**Fig. 2** The internal shell of *Spirula* **A** and the shell of the ammonite *Dorsetensia* sp. **B** Bajocian, Middle Jurassic, material coll. Schindewolf



**Fig. 3** A *Spirula* egg dissected from a freshly dead adult female

Fig. 3). However, no laid *Spirula* eggs have ever been observed. Therefore, it is not clear how the spawned egg masses look or where spawning takes place in the water column (Nesis pers. comm.). It is assumed that the eggs are laid near the bottom (Bruun 1943; Nesis 1987). These estimates correlate well with those based on first analysis of oxygen isotope composition of the first few septa (pers. comm. H. Erlenkeuser, Kiel). The shell of the first chamber seems to be built with a lower ambient temperature (around 4°C lower) than those of the following chambers. Clarke (1970) reported that the youngest individuals of *Spirula* with less than 0.5 cm in length are concentrated at water depths of 1000–1750 m while larger ones are found at about 600–700 m. These observations support the hypothesis that *Spirula* spawns near the bottom. However, because of the small egg size Bandel (1982) supposed for ammonoids and *Spirula* the same mode of hatching with small shells and fully functional buoyancy control. Because of the high firmness of the conch of the first stage of the postembryonic ammonites, Hewitt (1996) proposed that they lived in deeper water probably below the euphotic zone.

### Molecular data

If *Spirula* is a useful model organism for a partial reconstruction of the embryonic development of ammonoids,

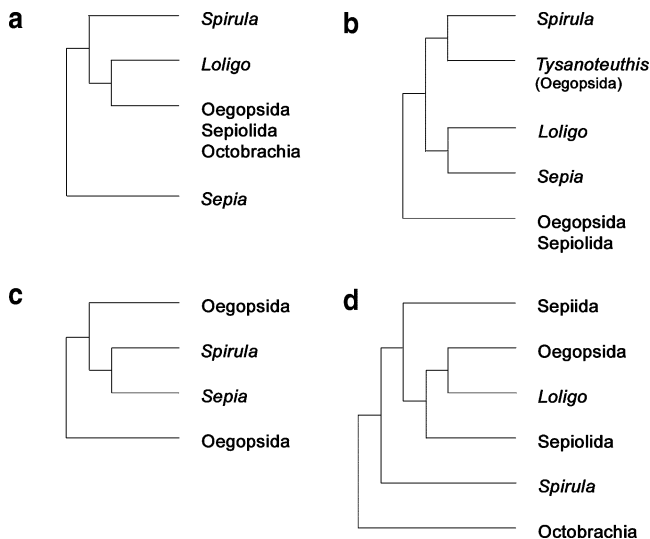
and if one considers the similar structure of the initial chamber in ammonites and spirulids as a synapomorphic feature within the Angusteradulata (Lehmann 1967), one can expect to find the Spirulida in a relatively basal position among the recent Coleoidea. Engeser and Bandel (1988) regard *Spirula* as the most ancient form of Decabrachia. However, it may also be that the proposed similar embryonic development in ammonites and spirulids represents the plesiomorphic character state of a wider group. Probably many other character states of *Spirula* are apomorphic. Depending on the set of characters used for phylogenetic analysis the phylogenetic position of *Spirula* changes (see Naef 1921–1923; Donovan 1977; Nesis 1987; Boletzky 1999). Therefore, it is still difficult to position *Spirula* in systematic studies using morphological characters.

Only few molecular data concerning the higher level taxa within the Cephalopoda were so far published. Moreover, they were not focussing on the phylogenetic position of *Spirula*, and thus there remain problems in the definitive classification of spirulids.

An example are the investigations into the relationships among coleoids (Bonnaud et al. 1994, 1996; Carlini and Graves 1999) using fragments of the mitochondrial genes 16S rRNA, COI and COIII. *Spirula* was found in these studies in different positions. Because these genes are relatively fast evolving genes all examined sequences indicated a high amount of saturation, which is regarded as an indication for homoplasy (Carlini et al. 2000). Therefore, Carlini et al. (2000) re-examined the higher level relationships within the Coleoidea using the highly conserved actin gene family (Fig. 4). But each actin gene analysed suggested a different phylogenetic position for *Spirula* and a different sister group. Using the actin gene I, *Spirula* turns out basal to all other coleoids (except *Sepia*). In actin gene II or III *Spirula* is either considered more closely related to *Thysanoteuthis* (Teuthida, Oegopsida), or to *Sepia*.

To clarify the phylogenetic position of *Spirula* within the Coleoidea, we analysed the relatively slow-evolving nuclear 18S rRNA gene (Warnke et al. 2003). This gene is used quite often and its suitability for the resolution of higher level taxa within the Mollusca was shown by various authors (e.g., Harasewych et al. 1997; Winnepeninckx et al. 1998; Wollscheid and Wägele 1999; Dreyer et al. 2003).





**Fig. 4** Summaries of molecular-based hypotheses of the phylogenetic position of *Spirula* compared with the results of our molecular study. **a** Strict consensus of 50 equally parsimonious trees on the basis of sequences from actin gene I (after Carlini et al. 2000). **b** Strict consensus of 50 equally parsimonious trees on the basis of sequences from actin gene II (after Carlini et al. 2000). **c** Strict consensus of 50 equally parsimonious trees on the basis of sequences from actin gene III (after Carlini et al. 2000). **d** Most parsimonious tree on the basis of sequences from 18S ribosomal RNA gene (after Warnke et al. 2003)

Nearly the complete gene, which is about 2500 base pairs in length, from seven different Decabrachia and one representative of the Octobranchia were investigated. Using parsimony analysis *Spirula* and the other Decabrachia were well supported by a high bootstrap value and a high decay index. The decay index indicates the robustness of the tree. In conclusion, our molecular data tend to support the hypothesis that *Spirula* is in a basal position within the recent Decabrachia. But the methods of analysis showed a strong influence on the topology of the tree, therefore these results remain preliminary.

## Discussion

Certainly *Spirula* should not be considered a universal model because features such as the mode of feeding probably differ between *Spirula* and the ammonoids.

However, as to the question whether *Spirula* could serve as an appropriate recent model organism for understanding the embryonic development of ammonoids, there are many morphological as well as molecular data which argue for this hypothesis. The main morphological indications are the similar form and composition of the embryonic shell of *Spirula* and ammonoids. If this similar structure is considered a synapomorphic feature within the Angusteradulata, Spirulida should be found in a very basal position within the Decabrachia. On the basis of the results of Young (1977), considering the brain and the statoliths of *Spirula*, Engeser and Bandel (1988) already regarded *Spirula* as the most primitive form of the recent Decabrachia. This result was

supported by molecular data (Warnke et al. 2003). Nevertheless, much more morphological and molecular data are needed to support that hypothesis. Additionally, embryonic developmental stages would provide helpful comparative and evolutionary information to further clarify the phylogenetic position of *Spirula* within the Decabrachia.

Moreover, a further worthwhile approach could be the investigation of the embryonic development of *Spirula* with regard to shell sac differentiation and development of the embryonic shell. If *Spirula* eggs will not be found in the sea, the outcome of artificial fertilization could fill the gaps in our knowledge (Boletzky 1989, 1998). For example Arnold and O'Dor (1990) obtained interesting data on the embryonic development of rare oceanic squids using artificial fertilization under semi-sterile conditions.

To catch adult animals and to study the embryonic development of *Spirula* using artificial fertilization is a complex task, but in association with studies focusing on ammonites it can provide many valuable hints.

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