N. Jb. Geol. Paläont. Abh.	164	1/2	3—305	Stuttgart, Oktober 1982

Contents

additional steering impulse. In terms of hydromechanics, this additional force can be described as an asymmetrical lift that results from a circular motion of potential, superimposed on a symmetric flow (Fig. 2). The circular motion of the fluid builds up during the first instance of flow around the disk; in the ammonite case it can be related to the angular jet propulsion used for steering.

If we assume that maneuverability, rather than fast swimming, is the main factor, physiological and hydrodynamical constraints do not invalidate the functional significance of ammonite shell geometry. Furthermore, this view allows us to integrate into the model minor morphological features, such as sculpture, apophyses, and keels. Certain types of keels, for instance, may have functioned as trailing edges separating fluid layers of different velocities. Similarly, apophyses could have supplied an elongated support for the hyponome and thus have improved directional control.

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J. REITNER & T. ENGESER

Phylogenetic trends in phragmocone-bearing coleoids (Belemnomorpha)

Classification

Traditionally coleoids comprise all endocochlean cephalopods. The classification of fossil coleoids is difficult because of their lack of distinctive features and their low fossilization potential. Three groups (supraorders), however, can be easily distinguished: phragmocone-bearing coleoids (Belemnomorpha), Sepiomorpha and coleoids without phragmocone (Teuthomorpha). JELETZKY (1966) classified the orders of Belemnomorpha according to the proostraca. DONOVAN (1977) tried to use the arm-crown and

protoconch apart from the proostracum. ENGESER & REITNER (1981) propose to use only the protoconch for classification at the level of orders. According to the four types of protoconchs (Fig. 1) observed within the group Belemnomorpha, four orders are distinguished: Aulacocerida, Belemnitida, Belemnoteuthida and Spirulida.

1. **"Aulacocerid type"** (Fig. 1b)

The protoconch is egg-like and sealed by a closing membrane. Protoconch and phragmocone have the same longitudinal axis. The siphuncle grows on the closing membrane; therefore caecum and prosipho are missing.

2. **"Belemnitid type"** (Fig. 1d)

The protoconch is spherical and closed. The longitudinal axes of Protoconch and phragmocone do not coincide. The other features correspond to those of the aulacocerid type.

3. **"Belemnoteuthid type** (Fig. 1c)

The protoconch is cup-like and sealed. Both phragmocone and protoconch have the same longitudinal axis. (Other features see under point 1).

4. **"Spirulid type"** (Fig. 1a)

The protoconch is spherical and has no closing membrane; thus there is a caecum and a prosipho.

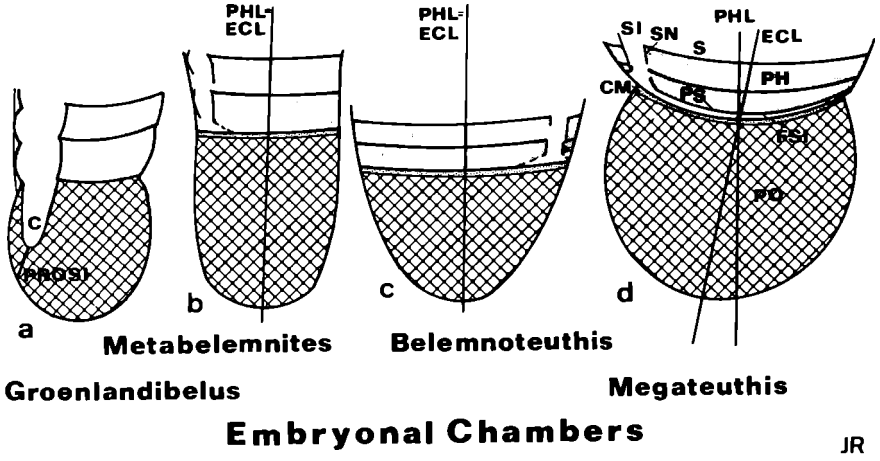

Fig. 1. The four different embryonal chambers of the Belemnomorpha (Partly based on JELETZKY, 1966 and DONOVAN, 1977). a. "spirulid type"; b. "aulacocerid type"; c. "belemnoteuthid type"; d. "belemnitid type". (Abbreviations: PH = phragmocone, PHL = length axis of phragmocone, C = caecum, PROSI = prosipho, ECL = length axis of embryonal chamber, SI = sipho, SN = septal necks, CM = closing membrane, PS = primairy septum, S = septum, FSI = foot of the siphuncle, PO = protoconch).

Order Aulacocerida

The most important representatives among the Aulacocerida include the Lower Carboniferous genus *Hematites*, the Middle Triassic genus *Aulacoceras*, the Triassic and Liassic *Atractites*, and the Pliensbachian *Chitinoteuthis*. The oldest representatives have recently been found by STÜRMER & REITNER (unpubl.) in the Hunsrückschiefer (Lower Devonian) (Fig. 2).

Apart from the characteristic embryonic chamber, the Aulacocerida show a closed body chamber which may contain a short dorsal flap (JELETZKY 1966, a. o.). The phragmocone is acutely conical in shape; septal spacings being wide. Known species have a rostrum which may differ in structural and chemical composition (aragonitic, calcitic and organic rostrum; JELETZKY & ZAPFE 1967; MÜLLER-STOLL 1936).

Order Belemnitida

After the discovery that the originally described "soft-part belemnites" are forgeries (RIEGRAF & REITNER 1979), the organisation of the soft parts of the belemnites was unclear again. New specimens of true "soft-part belemnites" will make it possible to answer some of the open questions (URLICHS, in prep.).

So far the proostracum was known only from growth lines in the conotheca and some incomplete specimens. The only complete specimen from Solnhofen (QUENSTEDT 1882—85) was rediscovered and interpreted (ENGESER & REITNER 1981). Its proostracum is short relative to the phragmocone and shows no obvious median keel. The lateral fields are a lot more distinctive than the median field.

Whether the genus *Chitinobelus* FISCHER, 1981 belongs to a different order other than the Aulacocerida and Spirulida, remains uncertain because *Chitinobelus* shows an organic (?aragonitic) epirostrum, while all other Belemnitida have a purely calcitic rostrum.

The Belemnitida range from Hettangian to Maastrichtian (Fig. 2). The taxonomic position of the belemnite-like *Bayanoteuthis* from the Eocene is unclear.

Order Belemnoteuthida

The order Belemnoteuthida ranges from the Callovian (*B. antiqua* PEARCE) to the Lower Tithonian (*B. mayri* ENGESER & REITNER, *Acanthoteuthis speciosa* MÜNSTER) (Fig. 2). Their rostrum (guard), being small and only coating the tip of the phragmocone, was probably aragonitic (DONOVAN 1977). The short phragmocone is a broad cone; septal spacings are short. The proostracum is composed of only one part and situated in a dorsal position. Ten equal arms are equipped with undifferentiated double

rows of hooks belonging to the conservative type. Ink bag and mantle muscle are present.

The genus *Acanthoteuthis* from the Lower Tithonian was formerly interpreted as part of the belemnite *Hibolithes hastatus* DE BLAINVILLE (JELETZKY 1966 and others). On the base of new complete specimens, ENGESER & REITNER (1981) placed the genus *Acanthoteuthis* as an independent taxon in the family Belemnoteuthididae of the order Belemnoteuthida.

Order Spirulida

The order Spirulida is known since the Upper Campanian with the genus *Groenlandibelus* (Fig. 2). Its phragmocone has an orthocone, narrow conical shape and widely spaced septae. The guard is thin with a deep alveole. The proostracum is reduced to a rodlike structure. Significant is an open embryonic chamber, indicating close phylogenetic relationships to the Ammonoidea.

Forms of uncertain taxonomic position

Apart from the four orders of Belemnomorpha, which are well defined by their protoconch, there are other forms whose embryonic chamber is unknown. A common feature among all of them is an undifferentiated arm crown. *Jeletzkya,* which probably still had a ventrally closed living chamber (SAUNDERS & RICHARDSON 1979), belongs to this type. The radula is similar to that of recent Coleoids as well as of the Ammonoidea.

The specimens ? *Jeletzkya douglassae* JOHNSON & RICHARDSON (SAUNDERS & RICHARDSON 1979: 354, Fig. 10) are early Teuthomorpha.

Another group, the Phragmoteuthididae is known from the Permian to the Toarcian. Characteristic is a three-fold, ventrally open proostracum (SUESS, 1865; REITNER, 1978, a. o.). The Diplobelina from the Tithonian and the Middle Cretaceous show a rod-like, reduced proostracum (JELETZKY 1966) and belong partly to the Belemnitida (JELETZKY 1981).

The family Suevitheuthididae, established by REITNER & ENGESER (1981), has a proostracum differing from all other groups. The proostracum consists of four "sticks", two of which are dorsal and two ventral. Mantle muscle, ink sac, and ten equal arms are documented. The arms have double rows of undifferenciated, very slim and densely spaced hooks. Since the protoconch is unknown, it remains uncertain to which order it should be assigned (Belemnoteuthida ?).

Palecology and phylogenetic trends

The transition from ectocochleans to endocochleans already took place during a very early phase of cephalopod radiation (early Paleozoic ?).

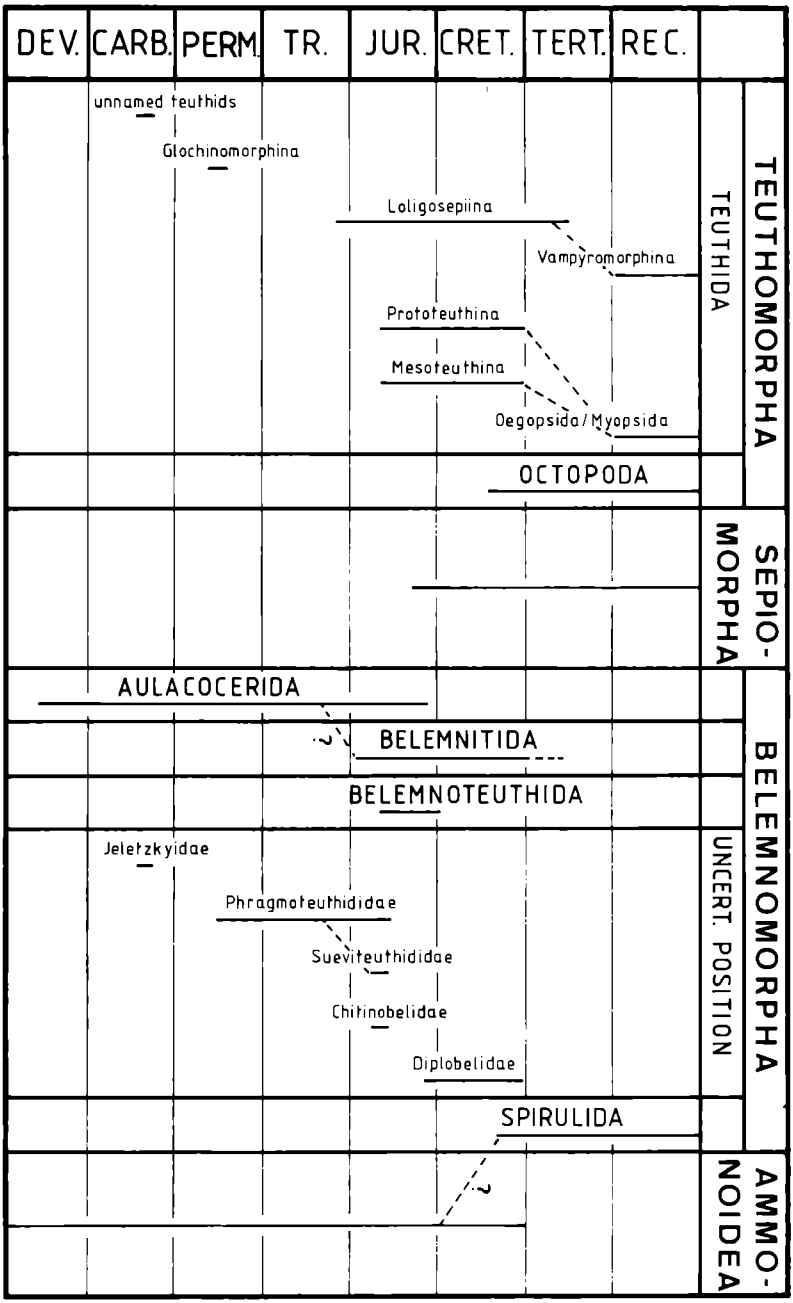

Fig. 2. Stratigraphic distribution of the different groups of Coleoidea.

This transition opened the way to a new mode of locomotion, i. e. from a vagile-benthonic resp. slow nectonic to a more rapid nectonic movement and also to new modes of nutrition (SEILACHER & WIESENAUER 1978). The internal position of the shell offers the possibility to develop fins which allow a forward movement. Furthermore a mantle ring muscle is formed within this group enabling to escape faster (backwards). With this it is efficient to develop an inc bag.

An additional advantage is provided by shifting the mantle to an external position, for it is then possible to cure injuries of the shell. The altered mode of life and nutrition also requires a foot being formed into an arm crown. Ten strong and muscular arms are developed, on which hooks or suckers are located. All this improves the ability to catch prey. Shifting the shell towards the interior also makes a reduction of the shell possible, which happened to occur in two directions and possibly indicates a polyphyletic origin. One line reduced the phragmocone (Sepiomorpha) and in most cases retained the proostracum (Teuthomorpha), the other reduced the proostracum and retained the phragmocone (Belemnomorpha). Since the ectocochlean stock remained slow-swimming and largely microphagous, they did not develop the distinctive "coleoid" features (shell reduction, inc bag, catching apparatus).

The Belemnomorpha show a coninuous transition from a ventrally closed to a totally reduced living chamber. In contrast to this phylogenetic trend coleoids without phragmocone (Teuthida) evolve a tripartite proostracum comparable to the Phragmoteuthida.

All known Belemnomorpha with the exception of *Spirula* have a arm crown with 10 arms with double rows of hooks. In the Spirulida, the arms are equipped with suckers. All Belemnomorpha have an ink bag and mantle muscles (not known from the Aulacocerida), which do not extend over the phragmocone. Nor have fins been observed in any fossil Belemnomorpha. In some forms, radular and jaw structures are also preserved.

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A new terminology of aquatic propulsion in vertebrates

In order to name different modes of propulsion in fishes, BREDER (1926) developed a terminology. He chose certain genera as types for certain propulsives modes (i. e. anguilliform after *Anguilla*, carangiform after *Caranx* etc.). Since then numerous authors have used and refined this terminology (e. g. GRAY, 1968; LIGHTHILL, 1969; ALEEF, 1977; WEBB, 1975). Substantial progress in the study of fish propulsion was published by LINDSEY (1978). However, BREDER's terminology was used differently by different authors. Also, in certain cases the terms were wrongly assigned to various propulsion methods. For example, *Manta* (our Fig. 1, nr. 36) is considered by LINDSEY (1978, Fig. 6) as a rajiform swimmer, even though his figure shows clearly that it is a subaqueous flier. Thus a more comprehensive terminology is needed.

Presented below is a new terminology which incorporates for the first time the locomotory patterns of both living and fossil fish and aquatic tetrapods. Its advantage is that it consists of a few basic terms which do not burden the memory and that newly discovered modes of propulsion can

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