Geobios 45 (2012) 29–39

Available online at
SciVerse ScienceDirect
www.sciencedirect.com

Elsevier Masson France
EM|consulte
www.em-consulte.com

Original article

The "rostrum"-problem in coleoid terminology – an attempt to clarify inconsistencies☆

Dirk Fuchs

Freie Universität Berlin, Institute of Geological Sciences, Branch Palaeontology, Malteserstrasse 74-100, 12249 Berlin, Germany

A R T I C L E I N F O

Article history:
Received 29 November 2010
Accepted 16 November 2011
Available online 26 December 2011

Keywords:
Coleoidea
Rostrum proper
Primordial rostrum
Sheath
Homologue shell formations
Morphogeny
Phylogeny

A B S T R A C T

In the coleoid literature, the terminology of shell elements that are deposited on the external surface of the primary shell wall is inconsistent and confusing. Morpho- and phylogenetic interpretations have been therefore controversial. A strict layer-by-layer comparison of seventeen species from seven coleoid subgroups suggests that the coleoid shell is covered by either one (Diplobelida, Spirulida, Sepiida, Vampyropoda) or two (Aulacocerida, Belemnitida, Belemnoteuthidida) outer shell formations. The confusion has been caused mainly by the often ignored presence of a primordial rostrum in the Aulacocerida, Belemnitida, and Belemnoteuthidida. The primordial rostrum is a secondary shell formation, which covers the entire primary shell and, which is itself enveloped by a tertiary shell formation, the rostrum proper. In the Diplobelida, Spirulida, and Sepiida, the primary shell is invested by a single outer formation, the sheath; a rostrum proper is absent in the latter groups. As a secondary shell formation, the aulacocerid, belemnitid and belemnoteuthidid primordial rostrum on the one hand, and the diplobelid, spirulid and sepiid sheath on the other hand are considered to represent homologues. Accordingly, the rostrum proper of the Aulacocerida, Belemnitida, and Belemnoteuthidida are homologues as tertiary shell formations. Outer shell formations in gladius-bearing vampyropods (and teuthids?) might be represented by a single layer. The clarification of the homology of secondary and tertiary shell formations, however, cannot resolve phylogenetic relationships within the Coleoidea.

1. Introduction

The internalization of the shell is the most important character that delimits the Coleoidea from nautiloid and ammonoid cephalopods. As a consequence of the internal (endocochleate) condition of the shell, coleoids obtained the opportunity to secret additional shell layers from outside on the primary shell wall (conotheca) by using the epithelium of the shell sac (Fig. 1). Among amateurs, students and lecturers, these outer formations are widely known as the "rostrum" (Roger, 1952; Nesis, 1987; Teichert, 1988; Westheide and Rieger, 2007) or "guard" (Donovan, 1977; Clarkson, 1998). Particularly, the stratigraphic, paleogeographic, and geochemical value of the belemnitid "rostrum" is well-known. In more specific papers, e.g. on the shell ultrastructure, one can additionally read terms such as "primordial rostrum", "rostrum proper", "epi- and orthorostrum", "telum", "rostral layers", "outer plate", or "guard-like sheath". But what is exactly meant by these terms? Are they synonyms or do they describe different parts of the "rostrum"? Do they respectively explain modifications of homologous shell elements or do they represent independent developments and are therefore taxon-specific? Jeletzky (1966) tried to readjust this terminological confusion. However, many coleoid workers seem to have misunderstood, misinterpreted or overlooked the presence or absence of at least one of these outer shell formations. Contradictory observations on the crystallographic textures of the "rostrum" moreover seem to have enhanced the confusion. Bandel (1985: p. 238) noted: "*The differential diagenesis of aragonitic shells has caused quite a bit confusion and has given rise to many misinterpretations.*" Probably as a result of these widespread inconsistencies, it seems that mistakes have been propagated in the literature. Ultrastructural comparisons and/or phylogenetic approaches to reconstruct evolutionary pathways that might link the shell elements under discussion are finally more or less vacant. This "rostrum"-problem most notably appears in the long-lasting discussion about the phylogenetic origin of the Sepiida and Spirulida, where the "rostrum" possibly plays a central key-role (Naef, 1922; Dauphin, 1984, 1985a, 1985b; Meyer, 1993; Hewitt and Jagt, 1999; Doguzhaeva, 1996, 2000; Doguzhaeva et al., 1999b; Fuchs, 2006).

In order to get an own picture of external shell formations, I re-investigated the shells of both fossil and recent coleoids. Apart from exemplifying the "rostrum"-problem in the literature, it is the

☆ Corresponding editor: Pascal Neige.
Adresse e-mail : drig@zedat.fu-berlin.de.

0016-6995/$ – see front matter © 2012 Elsevier Masson SAS. All rights reserved.
doi:10.1016/j.geobios.2011.11.014

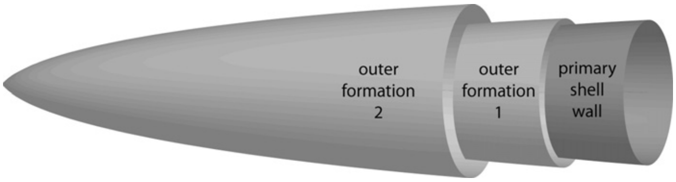

Fig. 1. Schematic drawing of a coleoid phragmocone. The primary shell wall (= conotheca) is enveloped by one or two outer shell formations. The anterior extension of these shell layers are cut away.

purpose of the present contribution to unravel the terminological confusion and to propose a comprehensible and logical framework of homologous shell elements in the coleoid phragmocones.

2. Material and methods

The present study includes fossil and recent specimens of seventeen species from seven systematic orders (Table 1). To investigate the internal cross morphology, the specimens have been fractured or sectioned. Macrostructural details have been photographed with a dhs Microcam 3.3. Shell ultrastructures of some specimens have been additionally analysed with SEM.

My observations exclusively focused on the sequence of shell layers deposited on the external surface of the primary shell wall (conotheca). It is important to note that the conotheca itself will not be considered as it represents a character complex which is morphogenetically and functionally independent from the "rostrum" and therefore of no use in the present context. In order to document the circumstances as simple and neutral as possible, it was moreover reasonable to neglect also some other "rostral" characters. Although their taxonomic-systematic significance is undisputed, the following characters have been considered to be of minor importance in the present context:

- descriptive characters (size, thickness, shape, ornamentation, etc.);
- mineralogy (aragonitic, calcitic, organic);
- crystallographic texture. According to the literature, the crystallographic texture of so-called rostra is inconsistent and contradictory (compare Dauphin, 1984, 1985a, 1985b; Doguzhaeva, 1996, 2000; Doguzhaeva et al., 2002, 2003). Conflicting observations might be due to different preservations and/or preparations;
- sublayers. Outer shell formations in coleoid cephalopods are often lamellar, i.e. they consist of sublayers. The sequence of shell layers (not sublayers) are regarded as morphological units, which are equivalent to formation phases.

All known Mesozoic gladius-bearing coleoids are considered as stem-lineage representatives of the Vampyropoda (Bandel and Leich, 1986; Engeser, 1988; Fuchs, 2006; Fuchs et al., 2007; Fuchs and Weis, 2008, 2010).

3. Previous studies and terminological inconsistencies

3.1. Systematic occurrences of outer shell formations

Hematitida (Early Carboniferous). Doguzhaeva et al. (2002:p. 303, text- 2), Doguzhaeva et al. (2010: p. 175) and Mapes et al. (2010) described a "rostrum" in *Hematites*. Doguzhaeva et al. (2002) distinguished between a "basal part of the rostrum, without ridges" and the overlaying "rostrum". The "rostrum" is described as being ridged and strongly ornamented with a blunt apical tip.

Aulacocerida (Late Carboniferous–Early Jurassic). Aulacocerids are known to possess an aragonitic "rostrum" with a high organic content (Jeletzky, 1966; Dauphin, 1983; Bandel, 1985; Doguzhaeva, 2002; Doguzhaeva et al., 2006). Jeletzky (1966) proposed to use the term "telum" in order to delimit the aulacocerid "rostrum" from the belemnitid "rostrum", but this term could not achieve general acceptance. Additionally, Dauphin (1983 : figs. 7–12, 25–26) referred to a "primordial rostrum" in *Aulacoceras*, but could not adequately illustrate its true nature. Likewise, Bandel (1985: p. 235) cited about *Dictyconites* that "*The conch of the hatching young may have had a short cone-like primordial rostrum*", but without providing appropriate photographs. Doguzhaeva (2002) and Doguzhaeva et al. (2006) did not mention a "primordial rostrum" in *Mutveiconites*.

Phragmoteuthida (Triassic–Early Jurassic). Phragmoteuthids are very poorly represented in the fossil record; information about the existence of a formation (or formations) outside the conotheca is therefore scarce (Jeletzky, 1966; Donovan, 2006; Doguzhaeva et al., 2007). If present (and this is likely), it (they) must have been thin.

Belemnitida (Early Jurassic–Late Cretaceous). The solid "rostrum" (sometimes called holorostrum) of belemnites can be subdivided into orthorostrum and epirostrum (Bandel and Späth, 1988; Doyle, 1990; Schlegelmilch, 1998). The orthorostrum can be

Table 1
Systematic position, origin, age, number of specimens and repository of each taxon investigated in this study.

	Taxon	Origin	Age	Number of specimens studied	Repository
Aulacocerida	*Aulacoceras timorensis*	Timor	Late Triassic	> 100	Institute of Geological Sciences, FU Berlin, Germany
Belemnitida	*Pachyteuthis* sp. 1	Russia	Middle Jurassic	4	Institute of Geological Sciences, FU Berlin, Germany
	Holcobelus trauti	France	Middle Jurassic	> 10	National Museum of Natural History Luxembourg
	Megateuthis gigantea	Luxembourg	Middle Jurassic	> 10	National Museum of Natural History Luxembourg
	Pachyteuthis sp. 2	Russia	Late Jurassic	2	Institute of Geological Sciences, FU Berlin, Germany
	Belemnitella bulbosa	North America	Late Cretaceous	>10	Institute of Geological Sciences, FU Berlin, Germany
Belemnoteuthida	*Belemnotheutis polonica*	Russia	Middle Jurassic	> 10	Institute of Geological Sciences, FU Berlin, Germany
Diplobelida	*Conoteuthis hayakawai*	Japan	Late Cretaceous	3	National Museum of Nature and Science, Tokyo, Japan
Spirulida	*Spirula spirula*	North Atlantic	Recent	> 10	Institute of Geological Sciences, FU Berlin, Germany
	Spirulirostra sp.	France	Eocene	1	Institute of Geological Sciences, FU Berlin, Germany
	Cyrtobelus hornbyense	Canada	Late Cretaceous	> 10	Institute of Geological Sciences, FU Berlin, Germany
Sepiida	*Sepia officinalis*	Mediterranean Sea	Recent	> 10	Institute of Geological Sciences, FU Berlin, Germany
Vampyropoda	*Teudopsis subcostata*	Luxembourg	Early Jurassic	> 10	National Museum of Natural History Luxembourg
	Trachyteuthis sp.	Germany	Late Jurassic	> 100	Institute of Geological Sciences, FU Berlin, Germany
	Plesioteuthis prisca	Germany	Late Jurassic	> 100	Institute of Geological Sciences, FU Berlin, Germany
	Senefelderiteuthis tricarinata	Germany	Late Jurassic	1	Institute of Geological Sciences, FU Berlin, Germany
	Dorateuthis syriaca	Lebanon	Late Cretaceous	> 50	Black Hills Institute, Hill City, USA