Evolutionary biology

Adaptations to squid-style high-speed swimming in Jurassic belemnoids

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Although the calcitic hard parts of belemnoids (extinct coleoids) are very abundant fossils, their soft parts are hardly known and their mode of life is debated. New fossils of the Jurassic belemnoid Acanthoteuthis provided supplementary anatomical data on the fins, nuchal cartilage, collar complex, statoliths, hyponome and radula. These data yielded evidence of their pelagic habitat, their nektonic habit and high swimming velocities. The new morphological characters were included in a cladistic analysis, which confirms the position of the Belemnoida in the stem of Decabrachia (Decapodiformes).

1. Introduction

In Jurassic and Cretaceous (201–66 Ma) sediments of middle and high latitudes, remains of belemnoids (extinct squids with chambered internal shells, 'belemnites' sensu lato) can be extremely abundant [1]. Here, we describe exceptionally preserved specimens of Acantothoeuthis, assigned by most authors to the suborder Belemnotheriina of the order Belemnida [2,3]. Their calcitic or aragonitic rostra (bullet-shaped hard parts capping the chambered phragmocone, fin-attachment) are widely used to measure the isotopic signature of seawater [4–6], yielding information on palaeoclimate, habitat and the carbon cycle [7–9]. Although assumptions on their pelagic–nektonic (open marine, free-swimming) mode of life have been made based on comparisons with living remote relatives [10,11], the evidence was poor in spite of their great abundance. Some studies on stable isotopes seemed to support a nektobenthic habitat [12,13].

In contrast to the supposed nektobenthic habit, the stream lined hard parts of belemnoids like Acanthoteuthis are suggestive of a nektonic mode of life with high swimming speeds, which is difficult to test because direct observations are impossible.

We present new anatomical information from three exceptionally preserved specimens of Acanthoteuthis from Solnhofen (Germany). For the first time, some specimens prove the presence of fins, and reveal the morphology of the cephalic cartilage and remains of the statocysts [14] (angular acceleration sense); additionally, the nuchal cartilage with the collar, the hyponome and the radula are preserved.

These findings also provide new data to reconstruct coleoid phylogeny. The new specimens reveal a pattern of morphological traits that support a closer affinity to decabrachians (10 arms; Decapodiformes), whereas other traits seem to corroborate a position in the stem of all Coleoidea (eight arms; Octopodiformes). Both the five arm-pairs and the phragmocone with proostracum are long known [15,16], but some character states remained unknown for the Belemnoida. This is interesting, because the decabrachian lineage evolved several adaptations to rapid swimming [2,10,11]. Here, we describe the novel...
anatomical information of the new belemnitid material and discuss implications for belemnitid locomotion and phylogeny.

2. Material

Almost a century ago [10], it was postulated that belemnitids had a pair of fins because of the presence of furrows in the rostra [2,16]. Based on two specimens (SMNS 67751, HT 02/02), we can now confirm that belemnitids possessed fins (figure 1; electronic supplementary material, figures S1–S3), indicating that this species had a rostrum, which is often not or poorly visible [15] (aragonitic, unlike the calcitic rostrum of Belemninita and Belemnopseina); also, the rostrum is preserved in specimen HT 02/02 (electronic supplementary material, figures S4 and S5). The fins of these specimens have a rhomboid shape, and are positioned posteriorly, but differ in size (10% of mantle length in figure 1; electronic supplementary material, figure S2; 30% of mantle length in figure 2; electronic supplementary material, figure S3). Owing to the low number of specimens, we cannot determine yet whether these differences relate to distinct species, sexual dimorphism, allometry or a different taphonomic history [19]. In decay experiments, coleoid fins deteriorated already after a week [19], highlighting their exceptional preservation and the possibility of decay altering their appearance.

UV-examination revealed the preservation of cephalic cartilages and statoliths in all specimens (figure 1b;f, electronic supplementary material, figure S1–S5) and vague imprints of the statocysts in two specimens (SMNS 67751, HT 02/2; figure 1; electronic supplementary material, figures S1–S6). The poor preservation of statoliths in SMNS 67751 precludes a detailed morphological description but it helped in locating the statocysts and estimating statocyst size (electronic supplementary material, figure S2).

A strongly developed mantle is needed for swimming, but this organ is long known in fossil squids from several Fossil Lagerstätten [16,20,21]. By contrast, the funnel is rarely preserved and was unknown in belemnitids. In a UV-light photo (figure 1f), the strong funnel is visible. Furthermore, specimen HT 02/2 shows the nuchal cartilage and the collar (electronic supplementary material, figures S4 and S5).

Additionally, the first evidence of a belemnitid radula was discovered in specimen SMNS 67751 (figure 1c,d). Similar to other coleoids, it contains rows of seven teeth and two marginal plates (nine elements/row). The radial ribbon is preserved from below (cusps pointing into the matrix); therefore, the tooth morphology cannot be reconstructed. Nevertheless, this radula is characteristic for squids with a normal predatory habit.

3. Methods

For the visualization of phosphatized soft parts, we used UV-lamps and special filters [22]. Synchrotron- and CT-examinations yielded no details of the radula or other organs owing to absent density contrast.

We carried out cladistic analyses using the software PAST [17]. Most of the information on character states was obtained from the literature [18]. We added three characters (see the electronic supplementary material, text) and a dataset for the Belemnitida in order to test their hypothetical Decabrachian stemgroup-position. We tried different kinds of heuristic searches, including nearest neighbour and tree bisection and reconnection with different optimization methods (Wagner, Fitch) and various bootstrap values (500, 1000).

4. Results

We were able to detect the presence of several organs in the new material of Acanthoteuthis that had never been documented before. We list these organs here with their properties: (i) the radula is embedded in the phosphatized buccal mass; it is typical for a predatory pelagic cephalopod. (ii) The hyponomoe is strongly developed. (iii) Two specimens display the fins, which differ strongly in size. (iv) The nuchal cartilage and collar complex are preserved in phosphate at the anterior mantle edge. (v) The cephalic cartilage and the associated statocysts with statoliths are preserved in several specimens; in relation to body size, the statocysts are rather large. See the electronic supplementary material for detailed descriptions.

5. Discussion

(a) Mode of life

For belemnitids, a nektonic or a nektobenthic mode of life has been hypothesized [12,13]. Additionally, good swimming abilities were suggested [10]. With the new materials, we provide new evidence to test these hypotheses. Most obviously, the presence of fins (figure 2a–c) suggests a nektic habit. Several other characters corroborate the ability to swim rapidly, such as the statocysts. The statocysts of fast-swimming buoant squids are commonly larger than those of non-buoyant ones [14]. We used published measurements of statocyst and statolith dimensions of modern octobrachians and decabrachians [14] (electronic supplementary material, figure S2 and table S2) to compare them with those of Acanthoteuthis. The size of these structures in Acanthoteuthis corresponds to the sizes of fast-swimming buoyant decabrachians. If the shape of the statolith’s rostrum is correctly interpreted as narrow, this would indicate a midwater habitat [23,24].

Specimen HT 02/2 displays two additional characters important for rapid swimming in squids (electronic supplementary material, figures S4 and S5). The nuchal cartilage and collar stiffer the connection from the hyponomoe-head complex to the mantle, enhancing the effect of the water jet for fast swimming [25,26].

It is impossible to confidently reconstruct the actual swimming speed of a prehistoric animal. The evidence for adaptations to rapid locomotion in Acanthoteuthis similar to those of modern decabrachians points at similar maximum swimming speeds; we thus speculate that belemnitids reached velocities between 0.3 and 0.5 m s⁻¹ like, for example, today’s Todarodes during migration [25,26].

(b) Phylogeny

The phylogenetic affinity of belemnitids has been widely discussed (electronic supplementary material, figure S6). The new anatomical information is here used to test hypotheses that belemnitids are stemgroup Coleoidea, Decabrachia or Octobrachia. The clade Coleoidea contains all living squids and octopuses (electronic supplementary material, figure S2) to compare them with those of Acanthoteuthis. The size of these structures in Acanthoteuthis corresponds to the sizes of fast-swimming buoyant decabrachians. If the shape of the statolith’s rostrum is correctly interpreted as narrow, this would indicate a midwater habitat [23,24]. Specimen HT 02/2 displays two additional characters important for rapid swimming in squids (electronic supplementary material, figures S4 and S5). The nuchal cartilage and collar stiffer the connection from the hyponomoe-head complex to the mantle, enhancing the effect of the water jet for fast swimming [25,26]. It is impossible to confidently reconstruct the actual swimming speed of a prehistoric animal. The evidence for adaptations to rapid locomotion in Acanthoteuthis similar to those of modern decabrachians points at similar maximum swimming speeds; we thus speculate that belemnitids reached velocities between 0.3 and 0.5 m s⁻¹ like, for example, today’s Todarodes during migration [25,26].
is normally assigned to the suborder Belemnotheutina within the order Belemnitida [15,27,28]. These groups share a mineralized internal shell with a conical chambered part. Except for the Aulacoceratida, Hematitida and Donovaniconida, they have a ventrally open body chamber [2,27–30]. The phylogenetic position of these proostracum-bearing groups was
suggested to lie in the stem of Octobrachia by some [27] and of Decabrachia by others [3]. There is little doubt that the Aulacoceratida are stemgroup representatives of the entire crown of the Coleoidea [3].

Overall, the previously unknown anatomical details provide the following new information on character states in the Belemnitida: like Decabrachia, Acanthoteuthis had one pair of fins, a nuchal cartilage, and comparatively large statocysts and statoliths. The radula does not provide useful information for phylogenetic reconstructions. We used these new characters to test the hypothesis that Belemnitida were stem-decabrachians. The shortest trees resulting from cladistic analyses using the new information support this hypothesis (figure 2d; electronic supplementary material, figure S6). It thus appears likely that the proostracum-bearing relatives of belemnids (Phragmoteuthida, Diplobelida) were also stemgroup Decabrachians and the Octobrachia split off before the evolution of Belemnitida and their kin.

The presence of one pair of fins in Acanthoteuthis suggests that the calcitic rostra of the sister suborders Belemnitina and Belemnopseina [2,27] also supported fins. The presence of one as compared with two fin-pairs in some stem-octobrachians is another argument favouring a phylogenetic position of the Belemnitida in the decabrachian stem. Further support for the affinity to decabrachians comes from the preservation of the nuchal cartilage, the large size of statocysts and the strong hyponome. Accordingly, several important decabrachian crown-group characters can now be extended to the stemgroup Belemnitida.

6. Conclusion

We suggest that a nektonic mode of life with high swimming velocities is apomorphic in the Decabrachia, including several stemgroups such as the Belemnitida (phylogenetic position was confirmed by a cladistic analysis); much of the Octobrachia branch was specialized for a demersal habitat. Belemnites were fast-swimming predators with a buoyant body that inhabited the water column. This information is important for the interpretation of 18O-isotope data from belemnite rostra [31,32], because it would indicate that the temperature measured from calcitic belemnite rostra would be from the water column rather than from the bottom water, casting doubt on the temperature interpretation of stable isotope values of other studies, which suggested that belemnids were nektobenthonic [5,6].

Ethics. The work conducted complies with the ethical regulations of European countries.
Data accessibility. Raw data were uploaded as the electronic supplementary material.


29. Bandel K. 1985 Composition and ontogeny of Dictyococes (Aulacocerida, Cephalopoda) and their phylogenetic meaning. Berliner Paläobiol. Abh. 8, 1 – 122. [In German.]


