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

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Although the calcitic hard parts of belemnites (extinct Coleoidea) are very abundant fossils, their soft parts are hardly known and their mode of life is debated. New fossils of the Jurassic belemnite *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 Belemnitida in the stem of Decabrachia (Decapodiformes).

1. Introduction

In Jurassic and Cretaceous (201–66 Ma) sediments of middle and high latitudes, remains of belemnitids (extinct squids with chambered internal shells, ‘belemnites’ *sensu lato*) can be extremely abundant [1]. Here, we describe exceptionally preserved specimens of *Acanthoteuthis*, assigned by most authors to the suborder Belemniteuthina of the order Belemnitida [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 nektonic habitat [12,13].

In contrast to the supposed nektonic habit, the stream lined hard parts of belemnitids 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 or the Octobrachia (eight arms; Octopodiformes). Both the five arm-pairs and the phragmocone with prostracum are long known [15,16], but some character states remained unknown for the Belemnitida. 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 belemnite material and discuss implications for belemnite locomotion and phylogeny.

2. Material

Almost a century ago [10], it was postulated that belemnites 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 belemnites 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 *Belemnitina* 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 1*b,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 Fossilagerstätten [16,20,21]. By contrast, the funnel is rarely preserved and was unknown in belemnites. In a UV-light photo (figure 1*f*), 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 belemnite radula was discovered in specimen SMNS 67751 (figure 1*c,d*). Similar to other coleoids, it contains rows of seven teeth and two marginal plates (nine elements/row). The radular 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 hyponome 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 belemnites, 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 2*a–c*) suggests a nektonic habit. Several other characters corroborate the ability to swim rapidly, such as the statocysts. The statocysts of fast-swimming buoyant squids are commonly larger than those of non-buoyant ones [14]. We used published measurements of statocyst and statolith dimensions of modern octobranchians 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 stiffen the connection from the hyponome–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 belemnites 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 belemnites has been widely discussed (electronic supplementary material, figure S6). The new anatomical information is here used to test hypotheses that belemnites are stemgroup Coleoidea, Decabrachia or Octobranchia. The clade Coleoidea contains all living squids and octopuses (electronic supplementary material, figure S6). They derive from the Bactritida, the stemgroup of both Coleoidea and Ammonoidea [3,27,28]. Crowngroup Coleoidea comprise the Octobranchia and the Decabrachia. A number of extinct groups (Aulacoceratida, Belemnitida, Diplobelida, Donovaniconida, Hematitida Phragmoteuthida) were positioned phylogenetically in the Coleoidea [3,28]; *Acanthoteuthis*

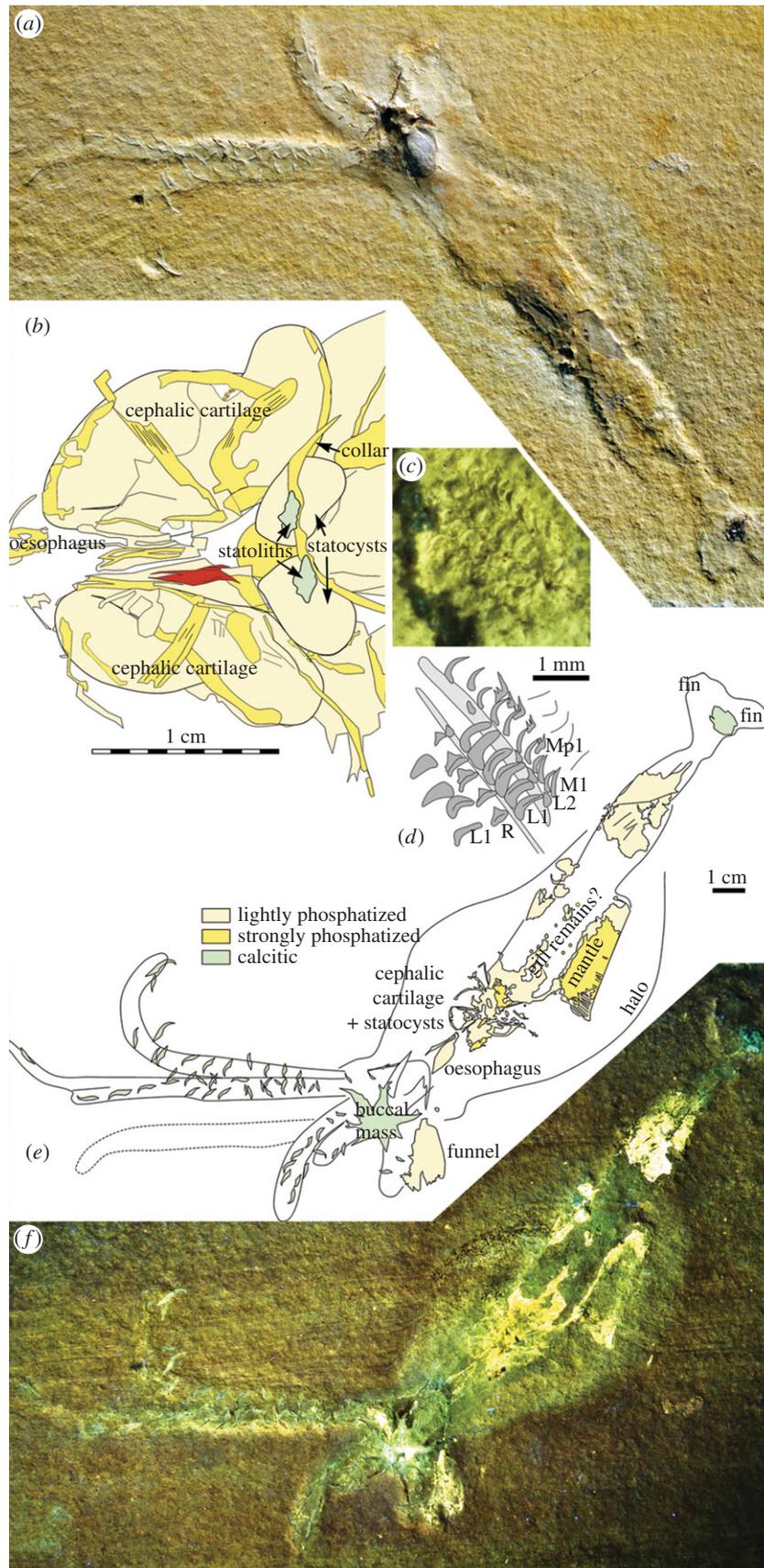


Figure 1. Key specimen of *Acanthoteuthis speciosus* Münster 1839, Tithonian, Solnhofen, Germany, SMNS 67751. (a) Specimen under white light, counter slab with radula. Phosphatized buccal mass and fins well visible. (b) Drawing of cephalic cartilage, statocysts with statoliths and oesophagus. (c) UV-image of phosphatized radula. (d) Drawing of the radula (counter slab) after the photos in (c). (e) Drawing of the complete specimen. (f) UV-image of the specimen (slab); the brightest luminescence is produced by phosphatized parts, the slightly bluish luminescence by calcitic parts (arm hooks, buccal mass, statoliths). R, rhachidian tooth; L, lateral tooth (1, 2); M, marginal tooth; Mp, marginal plate.

is normally assigned to the suborder Belemnotherutina 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 prostracum-bearing groups was

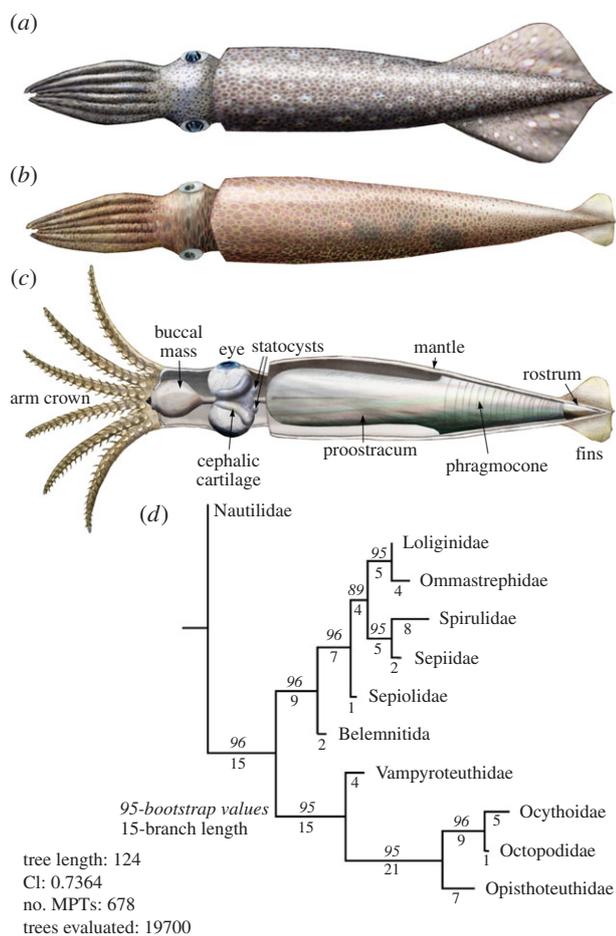


Figure 2. Reconstruction of *Acanthoteuthis*. Length of animal between 250 and 400 mm; mantle length 100–250 mm. (a) Reconstruction with large fins as in specimen HT 76/122 (electronic supplementary material, figure S3). (b) Reconstruction with small fins corresponding to the extent of the rostrum as in specimen SMNS 67751 (figure 1). (c) Anatomy of *Acanthoteuthis* focusing on the parts preserved in SMNS 67751 (figure 1). (d) Phylogram of the shortest tree obtained by a heuristic search (tree bisection and reconstruction), 500 bootstraps [17]. Character matrix based on [18] with own data including the information obtained from our new specimens (see the electronic supplementary material, table S1). Outgroup: Nautilidae. Note the position of the Belemnitida in the stem of Decapodiformes. no. MPTs, number of most parsimonious trees.

suggested to lie in the stem of Octobranchia 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 belemnitids (Phragmoteuthida, Diplobelida) were also stemgroup Decabrachians and the Octobranchia 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 Belemnitida and Belemnopseina [2,27] also supported fins. The presence of one as compared with two fin-pairs in some stem-octobranchians 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 Octobranchia branch was specialized for a demersal habitat. Belemnitids were fast-swimming predators with a buoyant body that inhabited the water column. This information is important for the interpretation of ^{18}O -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 belemnitids 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.

Authors' contributions. C.K and G.S. conceived the project. H.T. took the UV-images and provided two of the specimens. D.F. contributed palaeobiological implications of the fins and statocysts, and the phylogenetic discussion. I.K. contributed the text on the radula. All authors contributed to the interpretation of the material, the writing of the manuscript, and its revision, and approved its final version. All the authors agree to be accountable for the content.

Competing interests. We have no competing interests.

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