

## RESEARCH NOTE

### New evidence of functional suckers in belemnoid coleoids (Cephalopoda) weakens support for the ‘Neocoleoidea’ concept

Dirk Fuchs<sup>1</sup>, Sigurd von Boletzky<sup>2</sup> and Helmut Tischlinger<sup>3</sup>

<sup>1</sup>Freie Universität Berlin, Institute of Geological Sciences, Malteserstr. 74-100, 12249 Berlin, Germany;

<sup>2</sup>Laboratoire Arago, 66650 Banyuls-sur-Mer, France; and

<sup>3</sup>Tannenweg 16, 85134 Stammham, Germany

Correspondence: D. Fuchs; e-mail: drig@zedat.fu-berlin.de

The idea of a sister-group relationship between the cephalopod superorders Decabrachia (squids and cuttlefishes) and Vampyropoda (octopods, cirrotopods and vampire squid) has been widely accepted since Jeletzky (1966: fig. 2). In their phylogenetic analyses, Berthold & Engeser (1987) and Engeser & Bandel (1988) regarded the presence of suckers as a character state that supports the monophyly of what they called the ‘sucker-bearing Coleoidea’. In 1997, Haas introduced the terms ‘Neocoleoidea’ for coleoid groups with living representatives and ‘Palaeocoleoidea’ for a group of hook-bearing coleoids also known as ‘Belemnoidea’, which was thought to have disappeared at the end of the Cretaceous.

Like Berthold & Engeser (1987) and Engeser & Bandel (1988), Haas (1989: 166; 1997: 64, fig. 9; 2002: 341, text-fig. 1; 2003: 114, fig. 1) detected only one character state uniting the ‘Neocoleoidea’, the ‘presence of suckers’. Although von Boletzky (1992) found strong arguments against the monophyletic origin of the group later called ‘Neocoleoidea’, Young, Vecchione & Donovan (1998: fig. 1) followed Haas (1997) and adopted the ‘Neocoleoidea’ concept. Phylogenetic analyses including morphological and/or molecular data sets have subsequently assumed that the ‘Neocoleoidea’ are a monophyletic group and that the ‘Belemnoidea’ represent its extinct sister-group (e.g. Young & Vecchione, 1996; Vecchione, Young & Carlini, 2000; Lindgren, Giribet & Nishiguchi, 2004; Strugnell & Nishiguchi, 2007).

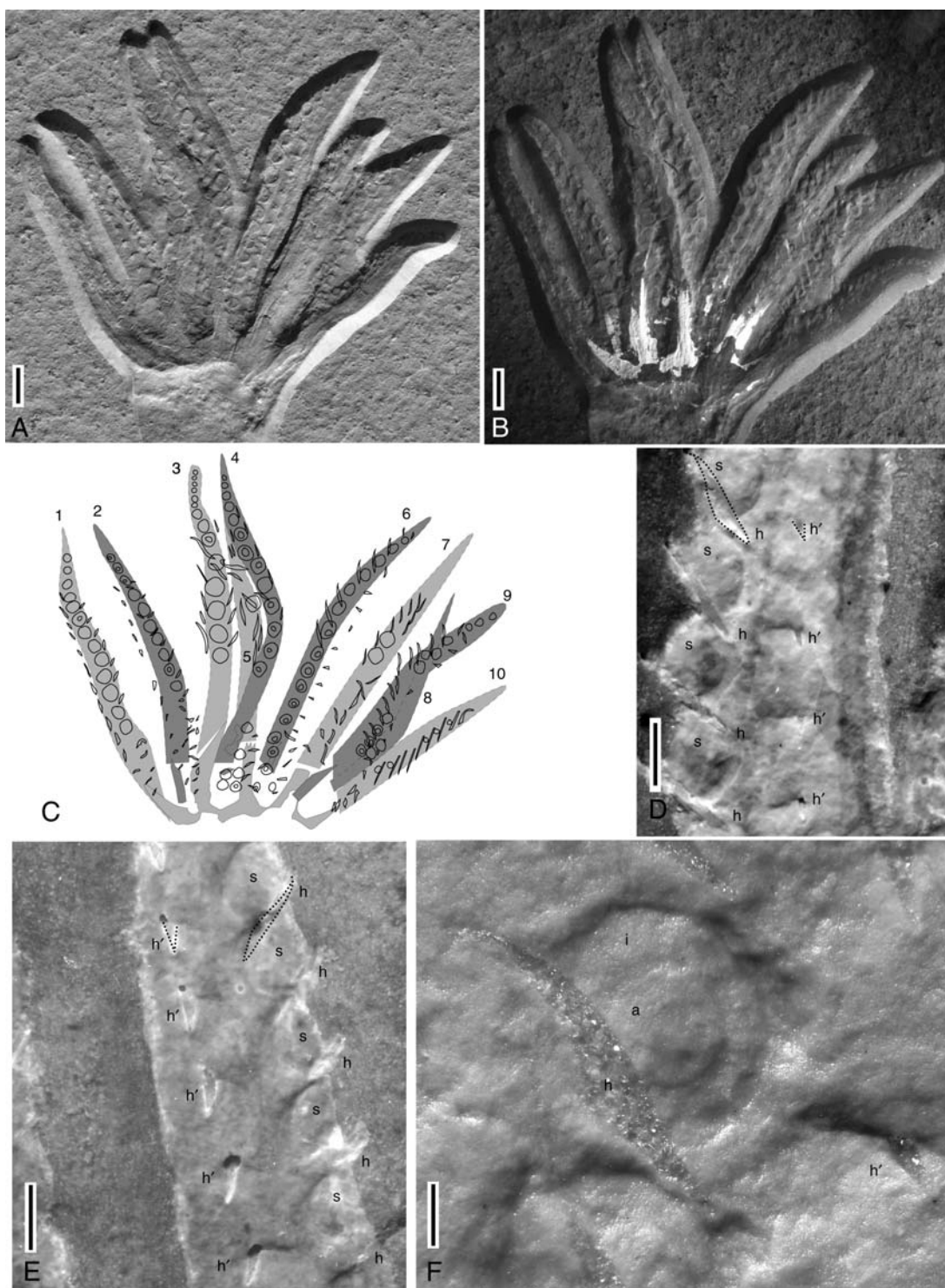
Thus, the ‘Neocoleoidea’ concept is chiefly based on the presumed absence of suckers in belemnoids, although equivocal evidence for their presence has existed for some time. Mantell (1852: 19, fig. 4) probably observed suckers in *Belemnotheutis antiquus* Pearce, 1847, a belemnoid from the middle Jurassic (Callovian; 164 Ma) Oxford Clay of Christian Malford (UK). Engeser & Clarke (1988: 139) suggested that these structures instead represented muscles that moved the hooks and that they were unlikely to be functional suckers. In their redescription of the type material of *B. antiquus*, Donovan & Crane (1992: 286), however, recorded sucker-like structures in a second specimen from the same area and described them as follows: “Where suckers are preserved there are the same number of pairs of hooks as suckers, but it is not clear whether the hooks are rooted in the suckers, as they sometimes appear to be (Pl. 2 fig. 2). There could have been only one row of suckers per arm. Distal suckers are smaller than proximal ones, the largest being about 2 mm in diameter. Several suckers show what could have been a chitinous ring around the outside (Pl. 2 fig. 4)”. Their observations led them to conclude that “...the presence of suckers in *Belemnotheutis* shows that suckers are not autapomorphic for Dibranchiata *sensu* Berthold and Engeser...” and that “...it is likely that suckers were already present in the common ancestors of the Belemnitida

and the living forms”. Both Young *et al.* (1998: 395) and Fuchs (2006: 71, 77, fig. 3.7–3) later expressed doubts about the existence of functional suckers in belemnoids. We report here a new record of a belemnoid arm crown with exceptionally preserved soft parts including apparent suckers, which again question the monophyly of the ‘Neocoleoidea’.

The isolated arm crown comes from the late Jurassic (Tithonian; 150 Ma) limestones of Eichstätt (southern Germany). The specimen (Coll. H. Tischlinger, catalogue no. 98/3) is flattened and consists of slab and counter slab. Most probably, the arm crown belongs to the genus *Acanthoteuthis* Wagner in Münster, 1839, a common belemnoid genus in the Eichstätt limestones and close relative of *Belemnotheutis* Pearce, 1842. It consists of 10 equal arms (maximum arm length 12 cm), each of which shows well-preserved imprints of hooks and suckers (Fig. 1A–F). Observations under UV light indicate that the proximal arm musculature is preserved as calcium phosphate and that five arms cover the remaining arms (Fig. 1B). The plane in which the arm crown has been embedded is unclear; identification of ventral and dorsal arms is therefore impossible. Although distal arm musculature is not preserved, the position of each arm can be reconstructed through the arrangement of hook and sucker imprints (Fig. 1C).

Hook imprints, which are generally filled with calcite, suggest a biserial arrangement as is typical for belemnoids (Fig. 1D–F). Only few hooks are visible as brownish staining. The shape of the paired hooks is variable along each arm as described by Engeser & Reitner (1992) for *Acanthoteuthis* from the Eichstätt region.

Apart from the hooks, each arm is equipped with one series (= longitudinal row) of circular suckers (because the arm crown consists of part and counterpart, upper as well as lower arms left sucker imprints). The suckers appear very close to the arm bases. The sucker diameter increases gradually from proximal to one half the arm length and then decreases distally. The largest sucker imprints are 5 mm in diameter, the smallest 2 mm. We counted a maximum number of 19 suckers per arm. The best preserved sucker imprints exhibit another circular imprint in their centre (Fig. 1F). This inner circle can be interpreted as the opening of a suction chamber of the acetabulum; this would strongly suggest that this is, indeed, a sucker. If so, the periphery would correspond to the imprints of the infundibulum. It is important to note that there is no evidence of horny rings as are typical for decabrachian suckers. The present suckers seem to be identical to those illustrated and described in Donovan & Crane (1992: pl. 2) but, in contrast to their specimen, our new record unambiguously shows that the hooks are not rooted within the suckers (Fig. 1D–F). Instead, the paired hooks clearly alternate with the unpaired suckers. In particular, the latter observation demonstrates the



**Figure 1.** Arm crown of *Acanthoteuthis* sp. (Belemnoidea), Eichstätt, Late Jurassic (Tithonian), Coll. H. Tischlinger (specimen 98/3). **A.** Overview. Scale bar = 10 mm. **B.** Overview photographed under UV-light. Phosphatized arm bases appear white. Scale bar = 10 mm. **C.** Sketch to show the position of arms 1–10. Arms 5 and 8 are partly overlain by other arms, but detectable through hook imprints. **D.** Middle part of arm 6. Four uniserial sucker imprints (s) alternate with pairs of hooks (h, h'). Photographed under UV-light to enhance the visibility of the hooks. The hooks (h) on the left are seen in lateral view, while corresponding hooks (h') on the right just exhibit their bases. Scale bar = 3 mm. **E.** Middle part of arm 2. Five uniserial sucker imprints (s) alternate with pairs of hooks (h, h'). Photographed under UV light to enhance the visibility of the hooks. The hooks (h) on the right are seen in lateral view, while corresponding hooks (h') on the left just exhibit their bases. Scale bar = 3 mm. **F.** Detail of a circular sucker imprint from the proximal part of arm 9. The inner circle might be imprinted by the acetabulum (a); the periphery by the infundibulum (i). The associated hook imprint (h) is filled with calcite. Scale bar = 1 mm.

morphological and functional independence of suckers and hooks. The present specimen therefore confirms earlier reports of Mantell (1852) and Donovan & Crane (1992) about presumed suckers in belemnoids and further indicates the weakness of the ‘Neocoleoidea’ concept.

Moreover, our observation contributes to the still unsolved discussion about the homology of suckers, hooks, cirri and trabeculae. Naef (1921–1923) regarded belemnoid hooks as homologous with decabrachian hooks. However, as several authors later explained, belemnoid hooks cannot result from secondary modification of a sucker ring as observed in decabrachian hooks (Engeser & Bandel, 1988: 113; Engeser & Clarke, 1988: 135; Young *et al.*, 1998: 395). The apparent absence of horny rings in the *Acanthoteuthis* suckers supports this assumption. Haas (1989: 182) tried to correlate the arrangement of belemnoid hooks with the arrangement of suckers in vampyropods and decabrachians. However, the arm crown described above clearly shows that the arrangement of hooks and suckers cannot be correlated, because these characters represent two independent morphological and functional units. Haas (1989: 183) concluded further that belemnoid hooks and cirri cannot be homologues. In contrast, Engeser & Bandel (1988: 113) derived belemnoid hooks from cirri and also Young *et al.* (1998: 395) remarked that “...belemnoid hooks could be homologous with cirri...”. Engeser & Clarke (1988: 135, fig. 1) suggested that most of the hook shaft was covered with soft tissue and that only the terminal claw was naked. Thus, the reduction of hooks without the reduction in the associated soft tissues would have produced flap-like innervated structures very similar to cirri or trabeculae.

Our specimen clearly supports the ideas of Engeser & Bandel (1988), Engeser & Clarke (1988) and Young *et al.* (1998). Because vampyropod cirri are thought to be homologous with decabrachian trabeculae (Young & Vecchione, 1996: 98; Young *et al.*, 1998: 395), belemnoid hooks may be homologous with both cirri and trabeculae. Each of the three coleoid superorders (‘Belemnoidea’, Vampyropoda and Decabrachia) exhibits pairs of supposedly tactile organs in close association with suckers. This conclusion is clearly in accordance with Naef’s hypothetic ‘*Protodibranchus*’. Naef (1921–1923: 97, fig. 23) postulated one series of suckers with a series of ‘small, movable processes or palps’ on each side of the suckers to be the ancestral character state of the Coleoidea.

#### ACKNOWLEDGEMENTS

We are grateful to Hans-Joachim Himßler (Schlüchtern, Germany), one of the most widely acknowledged preparators of fossils from Eichstätt and Solnhofen, who cautiously prepared the arm crown. We are furthermore indebted to Richard Young, Michael Vecchione and Janet Voight for fruitful discussions. Thanks to their comments, the manuscript has been considerably improved.

#### REFERENCES

- BERTHOLD, T. & ENGESER, T. 1987. Phylogenetic analysis and systematization of the Cephalopoda (Mollusca). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg*, **29**: 187–220.
- DONOVAN, D.T. & CRANE, M.D. 1992. The type material of the Jurassic cephalopod *Belemnotheutis*. *Palaeontology*, **35**: 273–296.
- ENGESER, T. & BANDEL, K. 1988. Phylogenetic classification of cephalopods. In: *Cephalopods – present and past* (J. Wiedmann & J. Kullmann, eds), pp. 105–115. Schweizerbart’sche Verlagsbuchhandlung, Stuttgart.
- ENGESER, T. & CLARKE, M.R. 1988. Cephalopod hooks, both recent and fossil. In: *The mollusca, palaeontology and neontology of cephalopods*. Vol. 12 (M.R. Clarke & E.R. Trueman, eds), pp. 133–151. Academic Press, San Diego.
- ENGESER, T. & REITNER, J. 1992. Ein neues Exemplar von *Belemnotheutis mayri* Engeser & Reitner, 1981 (Coleoidea, Cephalopoda) aus dem Solnhofener Plattenkalk (Untertithonium) von Wintershof (Bayern). *Archaeopteryx*, **10**: 13–17.
- FUGHS, D. 2006. Fossil erhaltungsfähige Merkmalskomplexe der Coleoidea (Cephalopoda) und ihre phylogenetische Bedeutung. *Berliner Paläobiologische Abhandlungen*, **8**: 1–115.
- HAAS, W. 1989. Suckers and arm hooks in Coleoidea (Cephalopoda, Mollusca) and their bearing for Phylogenetic Systematics. *Abhandlungen des naturwissenschaftlichen Vereins in Hamburg*, **28**: 165–185.
- HAAS, W. 1997. Der Ablauf der Entwicklungsgeschichte der Decabrachia (Cephalopoda, Coleoidea). *Paleontographica, Abteilung A*, **245**: 63–81.
- HAAS, W. 2002. The evolutionary history of the eight-armed Coleoidea. *Abhandlungen der Geologischen Bundesanstalt*, **57**: 341–351.
- HAAS, W. 2003. Trends in the evolution of the Decabrachia. *Berliner Paläobiologische Abhandlungen*, **3**: 113–129.
- JELETZKY, J.A. 1966. Comparative morphology, phylogeny and classification of fossil Coleoidea. *Paleontological contributions, University of Kansas, Mollusca* **7**: 1–166.
- LINDGREN, A.R., GIRIBET, G. & NISHIGUCHI, M.K. 2004. A combined approach to the phylogeny of Cephalopoda (Mollusca). *Cladistics*, **20**: 454–486.
- MANTELL, G.A. 1852. A few notes on the structure of the belemnite. *Annals of the Magazine of Natural History*, **10**: 14–19.
- NAEF, A. 1921–1923. *Fauna e Flora del Golfo di Napoli. 917. Cephalopoda*. Friedlaender und Sohn, Jerusalem.
- STRUGNELL, J. & NISHIGUCHI, M.K. 2007. Molecular phylogeny of coleoid cephalopods (Mollusca: Cephalopoda) inferred from three mitochondrial and six nuclear loci: a comparison of alignment, implied alignment and analysis methods. *Journal of Molluscan Studies*, **73**: 399–410.
- VECCHIONE, M., YOUNG, R.E. & CARLINI, D.B. 2000. Reconstruction of ancestral character states in neocoleoid cephalopods based on parsimony. *American Malacological Bulletin*, **15**: 179–193.
- VON BOLETZKY, S. 1992. Evolutionary aspects of development, life style, and reproduction mode in incirrate octopods (Mollusca, Cephalopoda). *Revue de Suisse Zoologie*, **4**: 755–770.
- YOUNG, R.E. & VECCHIONE, M. 1996. Analysis of morphology to determine primary sister-taxon relationships within coleoid cephalopods. *American Malacological Bulletin*, **12**: 91–112.
- YOUNG, R.E., VECCHIONE, M. & DONOVAN, D.T. 1998. The evolution of cephalopods and their present biodiversity and ecology. *South African Journal of Marine Science*, **20**: 393–420.