Berliner paläobiologische Abhandlungen	10	289-295	Berlin	2009-11-11

Preserved gill remains in *Phragmoteuthis conocauda (*Quenstedt, 1846-49) (Toarcian, Southern Western Germany)

Joachim Reitner

Abstract: Preserved gill remains in coleoid endocochleate cephalopods are extremely rare and only known from the Toarcian belemnoid *Phragmoteuthis conocauda* from the Holzmaden area in south western Germany, Tithonian vampyromorph *Plesioteuthis prisca* of the Solnhofen Lithographic Limestone, and late Cenomanian octopods from the Lebanon. The gill remains of *Phragmoteuthis conocauda* resemble strongly the gills of octopod and vampyromorph coleoids. However, the gill type has no significant phylogenetic importance. The different gill types are dependent on the life style of the various cephalopods.

Zusammenfassung: Erhaltene Kiemenskelette von endocochleaten Cephalopoden sind extrem selten und bis dato nur bekannt von *Phragmoteuthis conocauda* aus dem Toarcium von Holzmaden, von vampyroteuthiden Cephalopoden (*Plesioteuthis prisca*) aus den oberjurassischen Plattenkalken des Fränkischen Jura und von Octopoden aus dem Cenoman des Libanon. Die Kiemenskelette von *Phragmoteuthis conocaud*a sind kurz und breit und erinnern an die von *Octopus* und *Vampyroteuthis*, die von *Plesioteuthis* sind langgezogen und haben eher Ähnlichkeiten mit modernen Teuthiden. Die Form des Kiemenapparates hat jedoch keine signifikante phylogenetische Bedeutung, sondern ist abhängig von der Größe der Mantelhöhle und somit der Lebensweise der unterschiedlichen Cephalopoden.

Address of the author: Universität Göttingen, Göttinger Zentrum Geowissenschaften GZG Abt. Geobiologie, Goldschmidtstr. 3, D-37077 Göttingen. E-mail: jreitne@gwdg.de

Introduction

The first publication dealing with preserved gill remains was published by F. Klinghardt in 1932. He described gill remains from a specimen of *Plesioteuthis prisca* (Rüppel 1829) from the Solnhofen Lithographic Limestone (lower Tithonian). This paper had been forgotten or ignored for a long time until W. Haas recovered this publication in 2002. K. Bandel & H. Leich were the next paleontological investigators in 1986 who described also preserved gill remains in *Plesioteuthis prisca*. This paper is a milestone in fossil coleoid research, because these authors have recognised in this paper that most of the fossil teuthids are vampyromorph cephalods. Mehl (1990) has described gills from *Plesioteuthis prisca* again and likewise W. Haas in 2002. The first record of gill remains in belemnomorph cephalopods was represented by Reitner & Mehl (1989) who show the gill type in *Phragmoteuthis conocauda*. This specimen is the best preserved one and topic of the here presented investigation. Gill remains are also known from fossil octopod forms of the late Cenomanian fossil lagerstätte of Hakel and Hadjoula in the Lebanon (e.g. Fuchs et al. 2009). Gill remains are also know from ectocochleate coleoids (ammonites) described by Lehmann & Weitschat (1973).

Material and Methods

The here presented specimen of *Phragmoteuthis conocauda* Quenstedt was found within Liassic epsilon (Toarcian) “Koblenzer” bed near the small village Ohmden (Fig. 1a, b). The specimen is deposited within the “Staatliches Museum für Naturkunde Stuttgart” no. 61129, coll. Weber. The x-ray micrographs were carried out by Dr. J. Mehl within the former Institute for Interdisciplinary Paleontology at the University of Erlangen. The specimen was prepared by Ellen Drescher of the Institute of Paleontology of the Freie Universität Berlin. The recent coleoid material was collected at the marine research station of Banyuls-sur-Mer (Southern France) under the supervision of Dr. Sigurd von Boletzky. The material was histologically prepared by the author of this paper. Some of the material is housed in the collection of the geoscience museum of the University of Göttingen.

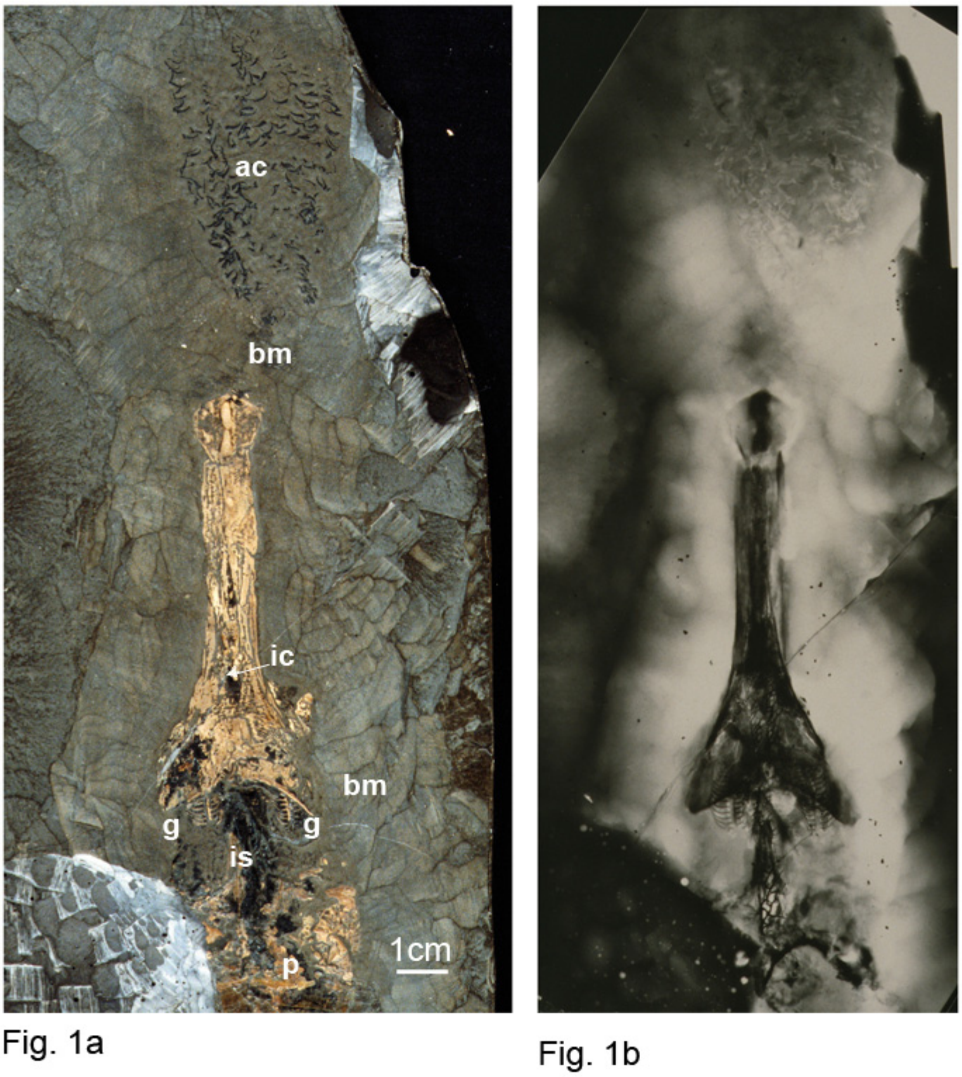

Fig. 1a: *Phragmoteuthis conocauda* (Quenstedt, 1846-49) with preserved arm crown (ac), remains of buccal mass (bm), muscle sack (ms), pair of gills (g), ink channel (ic), destroyed ink sack (is), and phragmocone (p). **1b:** X-ray micrograph of the specimen. Francolite-rich soft parts are dark

Results

The *P. conocauda* specimen with the gill remains is nearly completely preserved and has a length of 21 cm (Fig. 1a, b). The specimen has a well preserved arm crown with ten arms with double rows of simple hooks, typical of this genus (Riegraf & Reitner 1979). No strong difference in the hook types is visible except in hook sizes, also no (sexual) dimorphism is observed, which is known from real belemnites with special hooks (onychites) Riegraf & Hauff (1983). At the base of the arm crown a centimetre-sized black spot is visible which is interpreted as remains of the beaks resp. buccal mass. The very characteristic strong muscle sack of *P. conocauda* exhibits a specific cross pattern, remains of muscle structures. Muscle sack with a length of ca. 9 cm exhibits a taphonomic shrinkage pattern which causes the opening of the mantle cavity on the dorsal side. The central part of the mantle cavity is filled with a black substance which is probably melanin of the damaged ink sack. Remain of the ink channel is visible in the centre of shrunken muscle sack as a dark pattern. Clearly visible within the mantle cavity is the pair of gills (Fig. 2a, b). Behind the gill remains remain of the ink sack is recognisable. This part of the specimen is heavily damaged and the mantle and muscle tissue is disrupted from the phragmocone (Figs. 1a, b; 2a, b). The wide angle phragmocone is partly broken and exhibits typical bite deformation which is common in the “Koblenzer”-bed of the Holzmaden black shale. Most of the well-preserved belemnoid cephalopods exhibit this type of deformation (e.g. Reitner & Urlichs 1983) that means a destruction of the buoyancy function of the phragmocon probably due to fish or ichthyosaur attacks. The dead specimens of belemnoid cephalopods had sunken fast into the anaerobic zone of the Toarcian “Black Sea”. Normally phragmocone-bearing cephalopods drift for long time till the phragmocone loses its buoyancy gas. In this case soft part preservation is not possible.

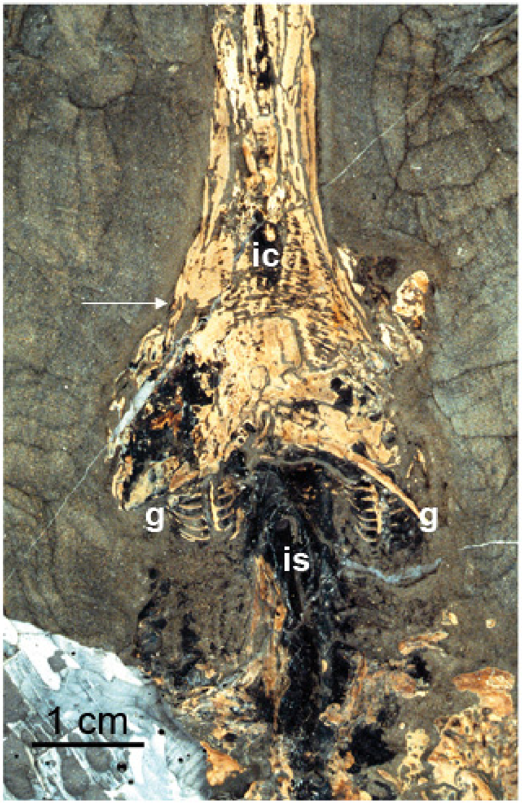

Fig. 2a

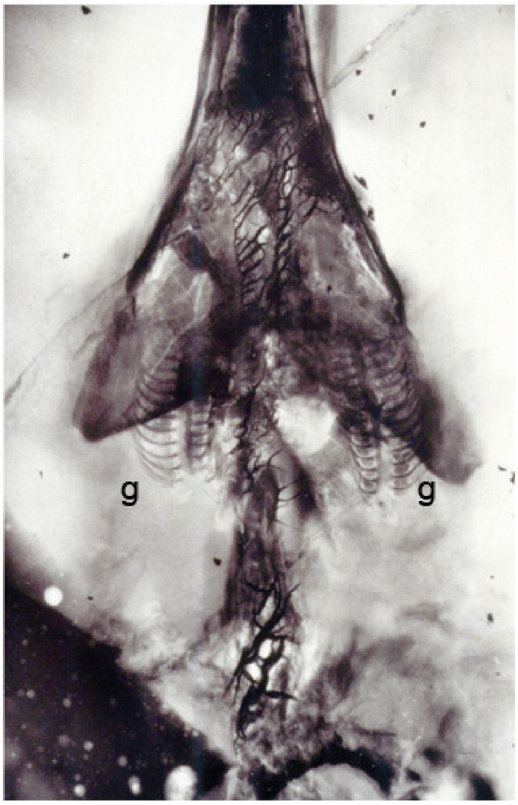

Fig. 2b

Fig. 2a: Detail of the disrupted mantle cavity. The mantle cavity ends with the heavy shrinkage of the muscle tissue (arrow). In the centre of the shrunken areas remains of the ink channel are visible (ic). The dark mass between the gills (g) is the remain of the ink sack (is). The phragmocone is partly broken (p). **2b:** X-ray micrograph clearly exhibits the size of the gill apparatus (g) which is partly covered by the muscle and mantle tissue

Description of the gills

The gills have a preserved length of ca. 1.5 cm and a width of 9 mm (Figs. 2a, b; 3a, b). The gills are partly covered by the strong muscle sack of the mantle cavity. Using x-ray analysis the gill structures under the covered portions are clearly visible. Due to the disruption of the mantle cavity the gill hearts are destroyed. The anterior front of the gills is also preserved and visible. Mainly the cartilage skeleton of the gill body is preserved of the gill apparatus and also remains of the very prominent main efferent vessel. The branches represent the skeleton of the second order vessels. In the x-ray graphs the efferent vessel exhibits dark shadows. The space between the gill lamellae cartilage is filled up with grey unstructured matter which is interpreted as remains of the gill tissue (Fig. 3a, b). The portion of the right gill covered by the mantle possibly exhibits well-preserved remains of the second order gill vessels (Fig. 3b). However, it is not possible to decide if it is part of the efferent or afferent vessel system. It is possible to count 15 gill lamellae. Some of the heart-orientated lamellae are missing, also the front parts are not preserved. Due to the size of the mantle cavity possibly not more than three or four additional gill lamellae are missing. Muscle tissue and gill cartilage are preserved in francolite a complex Ca-phosphate mineral (for details see Mehl 1990 and Kear et al. 1995).

Discussion

The overall shape and size of the gill skeleton is comparable with those of the octopodiform coleoids including *Vampyroteuthis infernalis*. Very characteristic is the compact structure of the entire gill body with ca. 15 gill blades, which is close to the octopodiform coleoids which exhibit ca. 12 gill blades (Fig. 4a, b, c). This observation is in contrast to the preserved gill remains in *Plesioteuthis prisca* which show up to 24 gill blades (Fig. 5). *Plesioteuthis prisca* is definitely a vampyromorph coleoid (Bandel & Leich 1986).

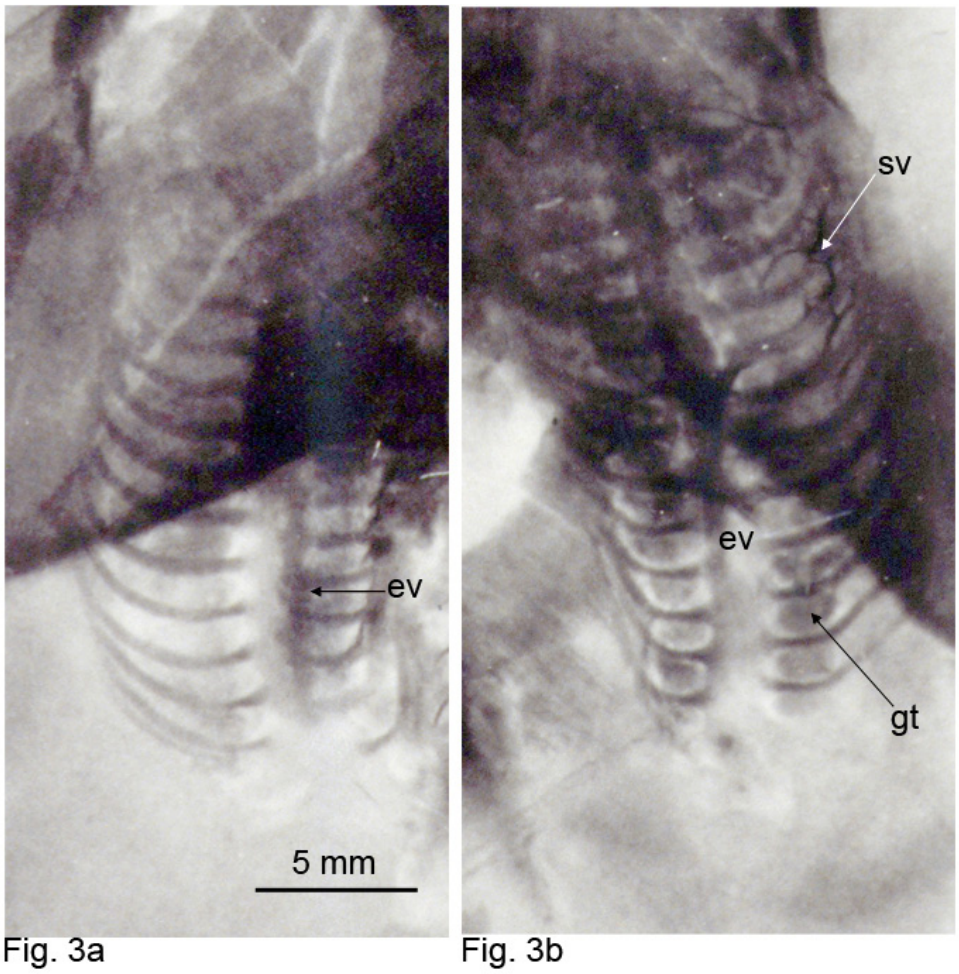

Fig. 3a: Left gill with remains of the efferent vessel (ev). The gill lamellae represent the gill cartilage skeleton. **3b:** Right gill with remains of the gill tissue (gt), efferent vessel (ev), and second order vessel system (sv).

However, the modern representative *Vampyroteuthis infernalis* Chun has a comparable gill body as known from the octopods (Young & Vecchione 2002, 2004) (Fig. 4c). The gill character of *P. prisca* is more comparable with those observed in modern myopsid and oegopsid teuthids (Fig. 6a, b). Since the fossil material does not allow the detailed analysis of the gill histology, it is not possible to make a direct comparison. Most likely the size of the gills depends on the space of the mantle cavity. Phragmoteuthid cephalopods exhibit a short mantle cavity in contrast to the long non-phragmocone bearing vampyromorph squids like *Plesioteuthis prisca*. On the other hand it could also be possible that the gill body in *Plesioteuthis prisca* is an apomorphic character especially for this group. The phragmoteuthid coleoids are representatives of the stem group of the modern coleoids (Lindgren et al. 2004). The gill apparatus in the octopodiform cephalopods could therefore be plesiomorphic. However, the functional morphological interpretation of the gill size is more convincing. The fast swimming squid-like vampyromorphs probably lived in the same ecological niche of open oceanic conditions like the modern teuthids. Modern octopodiform cephalopods have a different lifestyle in contrast to the early vampyromorphs. The entire shape and proportions of the mantle cavity of *Phragmoteuthis conocauda* is somewhat comparable with *Vampyroteuthis infernalis* and also with modern *Octopus*. This assumption is probably not valid for the true belemnites which probably had a lifestyle comparable to *Plesioteuthis prisca* and may-be also modern squids. Unfortunately up to now no preserved gill remains are known in belemnites.

As a résumé the fossil remains of the different gill types do not have convincing phylogenetic character. However, the observed different gill types are probably good anatomical indicators for different cephalopod life styles in related ecological niches.

Fig. 4a

Fig. 4b

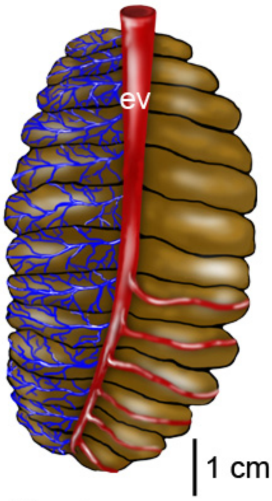

Fig. 4c

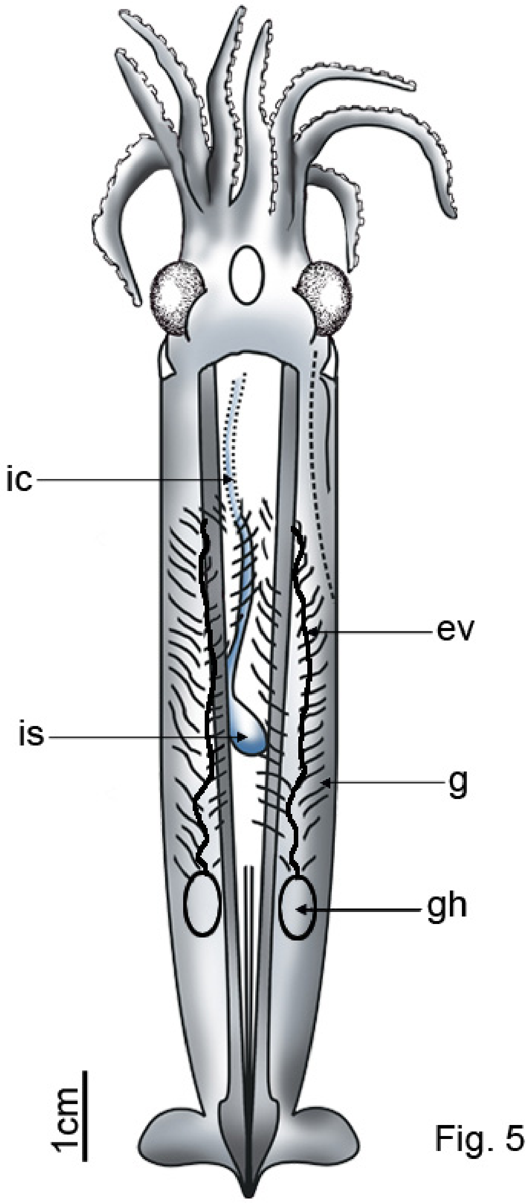

Fig. 5

Fig. 4a: Gill-pair of *Octopus vulgaris* Cuvier, 1797 with gill hearts (gh). Collected in the Mediterranean Sea near Banyuls-sur-Mer (France). **4b:** Right gill of fig. 4a exhibiting the efferent vessel (ev) and the linked gill heart (gh). **4c:** Gill of *Vampyroteuthis infernalis* Chun exhibiting the blood circulation. Efferent main vessel (ev) and second order efferent vessel are red coloured and second order afferent vessel is blue coloured (redrawn and modified from Young & Vecchione 2004). Note the similarity with the *Octopus* gills.

Fig. 5: Reconstruction of the gill-pair position in *Plesioteuthis prisca* (modified after J. Mehl 1990, fig. 5). Up to 25 gill blades are known. The modern octopodiform cephalopods have only 12-15 gill blades. The ancient vampyromorph *Plesioteuthis* has a type of gill skeleton comparable with modern oegopsid and myopsid teuthids.

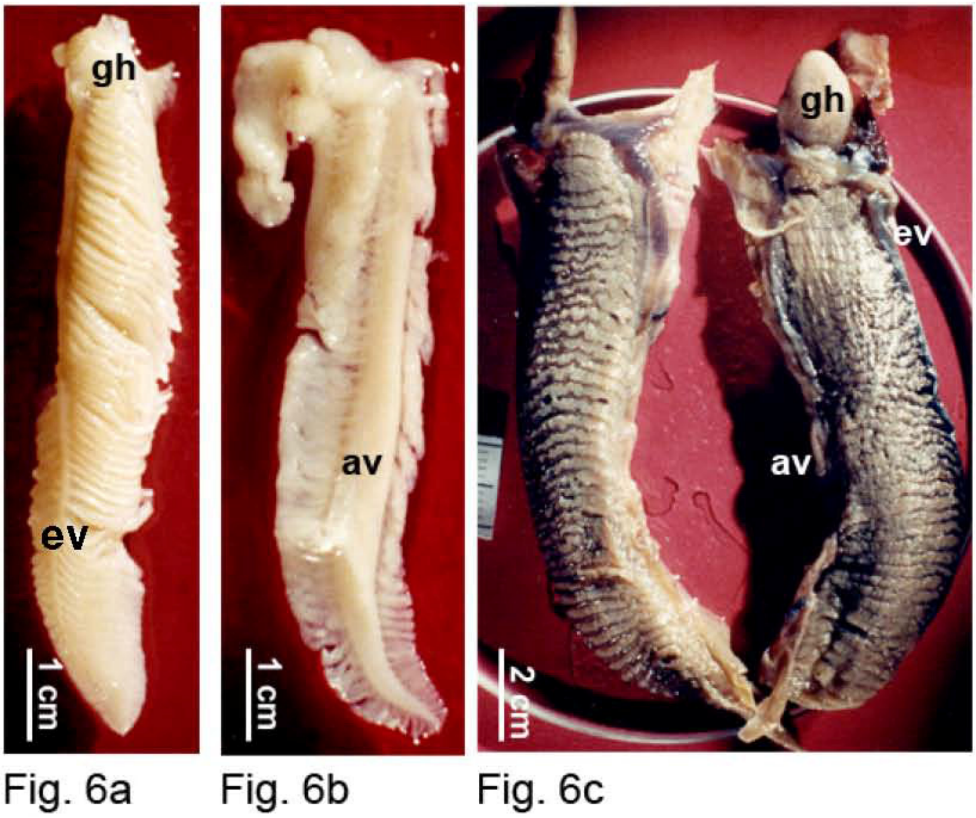

Fig. 6a: Single gill from the myopsid *Alloteuthis* sp.. Dorsal view with gill heart (gh), efferent main vessel (ev) and numerous gill blades. Ventral view of the gill with a very prominent afferent vessel (av). Collected in the Mediterranean Sea near Banyuls-sur-Mer (France). **6b:** Gill pair of the oegopsid *Todadores saggitatus* (Lamarck, 1799) with gill heart (gh), efferent and afferent vessel (ev, av). Collected in the Mediterranean Sea near Banyuls sur Mer (France).

Acknowledgements

The author thanks the Staatliches Museum für Naturkunde Stuttgart for the possibility to investigate this specimen and Dr. J. Mehl who carried out some x-ray micrographs. Conny Kaubisch of the Geobiology group of the University of Göttingen carefully improved some of figures.

Excellence Initiative FL3 Courant Research Centre Geobiology Göttingen publication no. 32.

References

Bandel, K. & Leich, H. (1986): Jurassic Vampyromorpha (dibranchiante cephalopod).- Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **1986:** 129-148.

Fuchs, D., Bracchi, G. & Weis, N. (2009): New Octopods (Cephalopoda: Coleoidea) from the Late Cretaceous (Upper Cenomanian) of Hakel and Hadjoula, Lebanon.- Palaeontology, **52:** 65-81.

Haas, W. (2002): The Evolutionary History of the Eight-armed Coleoidea.- Abhandlungen der Geologischen Bundesanstalt, **57:** 341-351.

Kear, A.J., Briggs, D.E.G. & Donovan, D.T. (1995): Decay and fossilization of non-mineralized tissue in coleoid cephalopods.- Palaeontology, **38:** 105-131.

Klinghardt, F. (1932): Über den methodischen Nachweis der Eingeweide bei fossilen Tintenfischen.- Paläontologische Zeitschrift, **14:** 160-164.

Lehmann, U. & Weitschat, W. (1973): Zur Anatomie und Ökologie von Ammoniten. Funde von Kropf und Kiemen.- Paläontologische Zeitschrift, **47:** 69-76.

Lindgren, A.R., Giribet, G. & Nishiguchi, M.K. (2004): A combined approach to the phylogeny of the Cephalopoda (Mollusca).- Cladistics, **20:** 454-486.

Mehl, J. (1990): Fossilerhaltung von Kiemen bei Plesioteuthis prisca (Rüppel 1829) (Vampyromorpha, Cephalopoda) aus untertithonen Plattenkalken der Altmühlalb.- Archaeopteryx, **8:** 77-91.

Reitner, J. & Mehl, J. (1989): Ein besonderes Fossil.- Paläontologische Zeitschrift, **63:** 3-4.

Reitner, J. & Urlichs, M. (1983): Echte Weichteilbelemniten aus dem Untertoarcium (Posidonienschiefer) Südwestdeutschlands.- Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, **165:** 450-465.

Riegraf, W. & Hauff, R. (1983): Belemnitenfunde mit Weichkörper, Fangarmen und Gladius aus dem Untertoarcium (Posidonienschiefer) und Unteraalenium (Opalinuston) Südwestdeutschlands.- Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, **165:** 466-483.

Riegraf, W. & Reitner, J. (1979): Die „Weichteilbelemniten“ des Posidonienschiefers (Untertoarcium) von Holzmaden (Baden-Württemberg) sind Fälschungen.- Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **1979:** 291-304.

Young, R.E. & Vecchione, M. (2002): Evolution of the gills in the Octopodiformis.- Bulletin of Marine Science, **71:** 1003-1018.

Young, R.E. & Vecchione, M. (2004): Cephalopod Gills.- Tree of Life Web Project: http://to/web.org