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NEW RECORDS OF SOFT PARTS OF *MUENSTERELLA SCUTELLARIS* MUENSTER, 1842 (COLEOIDEA) FROM THE LATE JURASSIC PLATTENKALKS OF EICHSTÄTT AND THEIR SIGNIFICANCE FOR OCTOBRACHIAN RELATIONSHIPS

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ABSTRACT

The systematic position of Jurassic Vampyromorpha among the octobrachiate cephalopods is not without doubts. The present paper deals with the significance of soft part preservation in reconstructing vampyromorph morphology and consequently their phylogenetic relationships. The investigation is based on the reexamination of four specimens of *Muensterella scutellaris* including the counterpart of Muenster´s lost holotype. Ultra-violet light revealed unknown details of muscle organization. Due to very well preserved remains of soft parts including arms, web, suckers and marginal fins, the octobrachian nature of *Muensterella scutellaris* has been confirmed.

INTRODUCTION

On the basis of morphological and molecular data the sister-group relationship between the Vampyromorpha - with its only extant representative *Vampyroteuthis infernalis* - and the Octopoda (Cirrata and Incirrata), is now almost accepted (Bonnaud *et al.* 1996, Carlini & Graves 1999, Vecchione *et al.* 2000, Young *et al.* 1998). They are grouped together as Octobrachia (Doyle *et al.* 1994) or, in other classifications, as Octopodiformes (Young *et al.* 1996) or as Vampyropoda (Boletzky 1999).

But the phylogenetical relationships of the so-called "Fossil Teuthids" – whether they are Decabrachia or Octobrachia – have been controversially discussed in numerous publications for many years (Naef 1922, Jeletzky 1966, Donovan 1977, Bandel & Leich 1986, Berthold & Engeser 1987, Doyle *et al.* 1994, Young *et al.* 1998). Taxa which are now included in the catchall "Fossil Teuthids" bear both decabrachian and octobrachian characters. The divisions are made solely on the basis of gladii and the arm crown. But at the moment it is impossible to decide on the homology or homoplasy of the different gladii. Furthermore, until now we only have evidence of 8 arms in this group. According to Bandel and Leich (1986) most theories of ten-armed individuals were based on the misinterpretation of drag marks. Although the museums have accumulated a huge number of "Fossil Teuthids" like *Plesioteuthis, Trachyteuthis* or *Leptoteuthis*, there are no observations of 10 arms. Young and co-workers (1998) stated that the affinity of the "Fossil Teuthids" remains unsolved since no more details are known about their morphological features.

In order to meet this demand we will consider the type species of the vampyromorph genus *Muensterella* (MÜNSTER, 1842). Since Naef (1922) nobody has dealt with *Muensterella scutellaris* in detail.

We had the opportunity to investigate 4 new specimens of *M. scutellaris*, including the negative plate of Muenster´s holotype, with exceptionally well preserved soft parts.

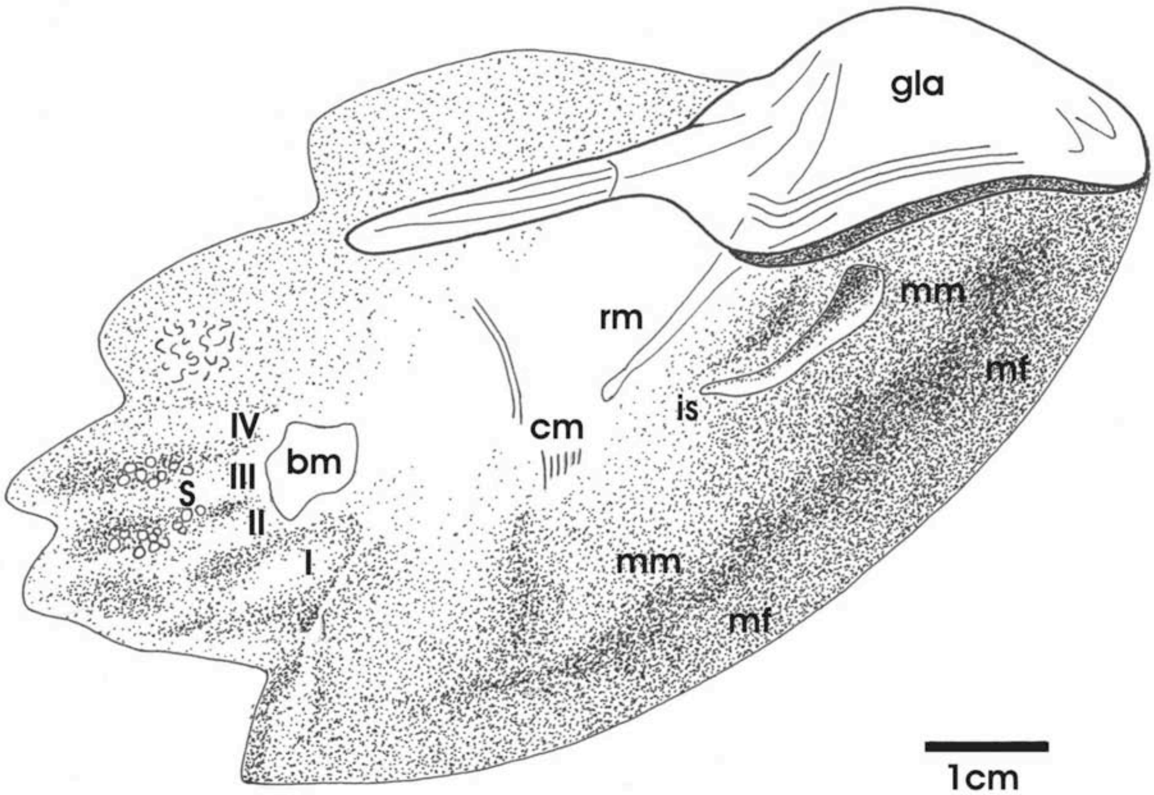

Fig. 1 Drawing of specimen MC-21. Abbreviations: I, ventral arm; II, ventrolateral arm; III, dorsolateral arm; IV, dorsal arm; bm, buccal mass; cm, circular muscles; gla, gladius; is, inc sac; mf, marginal fins; mm, mantle margin; rm, retractor muscle; s, suckers

MATERIAL AND METHODS

We studied 3 specimens (MC-21, MC-18, MC-51) from the collection of Prof. Dr. H. Keupp and one specimen from the Museum of Natural History in Berlin (invent.-no. MB.-C. 1023). Specimen M.B.-C.1023 surprisingly proved to be the negative counterpart of Muenster´s lost holotype. With the exception of the latter the present material has not been illustrated previously.

All specimens descended from the Solnhofen plattenkalks of Eichstätt (Southwest Germany), Lower Tithonian, Malm 2b.

The specimens were investigated in detail with a binocular. Oblique light should reveal faint structures which were not recognized under vertical light conditions. Ultra-violet light was used to indicate phosphatized soft-tissues.

We paid particular attention to the morphology of the soft parts and disregarded gladius characteristics.

MC-21 (Fig. 1, Pl. 1/1) is a prepared upper slab which contains the very best preserved specimen, showing the patella-like gladius, the body outline, ink sac, viscera and head with arm bases. The animal was embedded laterally on its left flank because all structures of the viscera lie beyond the gladius. The whole fossil is 10.3 cm in length and max. 5.5 cm in width.

MC-18 (Pl. 2/1) is an unprepared lower slab which moulds some important structures. The animal is seen from the left side. From the end of the conus to the most distal imprint of the head the fossil measures 12.5 cm in length and 7 cm in width.

MC-51 (Pl. 2/3) is a prepared upper slab in which the animal was again embedded laterally on its right side. At the first view gladius, ink sac, body outline and head region are visible. The fossil is 11.4 cm in length and 6.5 cm in width.

Muenster´s lost holotype (Pl. 2/7) was presumably the upper slab. Muenster did not mention whether he described a lower or an upper slab. But, in accordance with the common fossil taphonomy of the Solnhofen plattenkalks, the so called “Sockelerhaltung” (the fact that the fossils themselves appear elevated above the surrounding bedding plane), showed us that we have the lower slab, the counterpart of Muenster´s holotype (Seilacher *et al.* 1976). Our specimen is not prepared. As in the previous specimen the animal was embedded laterally.

SYSTEMATIC PALAEONTOLOGY

Subclass COLEOIDEA Bather, 1888
Order VAMPYROMORPHA Robson, 1929
Suborder KELAENINA Starobogatov. 1983
Family MUENSTERELLIDAE Roger, 1952
Genus MUENSTERELLA Schevill, 1950

Muensterella scutellaris Muenster, 1842
1842 *Kelaeno scutellaris,* Muenster, p. 96, Pl. 1, fig. 1
1842 *Kelaeno arquata,* Muenster, p.96, Pl. 1. fig. 2
1848 *Kelaeno arquata,* Bronn, p. 621
1848 *Kelaeno scutellaris*, Bronn, p. 621
1849 *Kelaeno arquata*, Quenstedt, p. 522, Pl. 35, figs 7, 8
1849 *Acanthoteuthis scutellaris*, Bronn, p. 539
1849 *Acanthoteuthis arquata*, Bronn, p. 539
1851 *Kelaeno arquata,* Quenstedt, p. 332
1859 *Celaeno scutellaris*, Wagner, p. 276
1860 *Celaeno scutellaris*, Wagner, p. 780
1863 *Kelaeno scutellaris*, Winkler, p. 391
1863 *Kelaeno arquata*, Winkler, p. 391
1863 *Kelaeno spec.*, Winkler, p. 391
1865 *Kelaeno arquata,* Quenstedt, p. 395
1883 *Kelaeno arquata*, Quenstedt, p. 509
1884 *Kelaeno scutellaris*, Zittel, p. 519
1887 *Celaeno*, Fischer, p. 354
1904 *Kelaena scutellaris*, Walther, p. 171
1920 *Celaeno arcuata,* Bülow-Trummer, p. 266
1920 *Celaeno scutellaris*, Bülow-Trummer, p. 266
1922 *Celaeno scutellaris*, Naef, p. 151, Fig. 56b, c
1942 *Listroteuthis*, Kretzoi, p. 125, Fig. 1.20
1949 *Kelaeno scutellaris*, Van Regteren Altena, p. 60
1949 *Kelaeno spec.*, Van Regteren Altena, p. 60, Figs 1, 2
1950 *Münsterella scutellaris*, Schevill, p. 117
1952 *Münsterella scutellaris*, Roger, p. 742, Fig. 96.2
1961 *Celaeno scutellaris*, Kuhn, p. 19
1965 *Münsterella scutellaris*, Müller, p. 317, Fig. 445b
1966 *Kelaeno*, Jeletzky, p. 45
1977 *Kelaeno sp.*, Donovan, p. 40, Fig. 14
1981 *Kelaeno scutellaris*, Müller, p. 344, Fig. 457b
1988 *Celaenoteuthis scutellaris*, Bandel & Boletzky, p.233, Fig. 3f
1988 *Muensterella scutellaris*, Engeser, p. 94
1993 *Muensterella scutellaris,* Wade, p. 361
1995 *Muensterella scutellaris*, Riegraf, p. 155
1998 *Muensterella* scutellaris, Riegraf, p. 309

Holotypus: Muenster (1842: Plate 1, fig. 1), destroyed during World War II
Locus typicus: Eichstätt, Bavaria (Germany)
Stratum typicum: Lower Tithonian, Malm □2b, "Solnhofener Plattenkalk"
Stratigraphical and geographical distribution: Franconia (southern Germany)
Remarks: There has been a long nomenclatural confusion about this taxon.
Description: All fossils examined belong without doubt to *M. scutellaris*.

Body outline, mantle outline and fins

Muenster (1842) wrote in his description of the holotype: "Der Sack eiförmig, oben abgestutzt, ohne Schwimmflossen…". Naef (1922) and other authors agreed with Muenster.

Indeed, in all studied specimens the squat-like body outline is obvious. But as it is seen in our specimen MC-21 (Fig. 1, Pl. 1/1 and 7), MC-51 (Pl. 2/1 and 6) and in the "holotype" (Pl. 2/7) a slight ridge running from anterior to posterior has led us to assume marginal fins (fin-seam). Oblique light makes these structures visible. The ridge commences at the posterior ventral part of the conus and runs up to the head region.

Ultraviolet light reveals that except in our "holotype" the mantle musculature is always well preserved (more about the musculature in the next section). Especially in MC-18 (Pl. 2/2) and MC-51 (Pl. 2/4) the postero-ventral mantle margin is very well defined. The mantle margin seen under ultraviolet light (in MC-18 and MC-51) and the ridge (in MC-21 and "holotype") are congruent and fit together. In MC-51 both details, the phosphatizing mantle margin and the ridge, are even combined. We interpret these observations as marginal (fringing) fins. Thus the "squat-like" habitus mentioned by previous authors resulted from the presence of marginal fins which were compressed dorsoventrally (in contrast to the gladii). Until now this fact was unknown and we can no longer agree with the idea of a "squat-like" *Muensterella scutellaris*.

Apparently the musculature of the fins has not been developed as much as the mantle musculature, so that it was not strong enough to withstand the process of decay and to have the same preservational potential as the mantle musculature.

Musculature

As mentioned above, musculature is very well preserved. In specimen MC-21 (Fig. 1, Pl. 1/2, 4, 6 and 8), MC-18 (Pl. 2/2) and MC-51 (Pl. 2/4) presumed bundles of muscle fibres of the circular mantle and retractor muscles are clearly visible. Usually they are replaced by phosphatized bacteria (Wilby & Briggs 1997).

In specimen MC-21 and MC-51 these three-dimensional "striations" of the circular mantle musculature are continuously 100µm thick and the gaps between them are of almost similar size (Pl. 1/6). In MC-21 they appear beyond the visceral mass (Fig. 1).

In MC-51 almost the complete mantle musculature is preserved. It covers the outer surface of the gladius and extends all along the gladius from the posterior end up to the anterior head region. As it is seen in Pl. 2/5 especially the posterior ventral end of the mantle is very well defined (as well as in MC-18). In both specimens, MC-51 and MC-18, it is located about 1 cm away from the end of the conus. In MC-21 preservation is faint but presumed (Fig. 1).

Apart from the circular mantle musculature preservation of the retractor muscles are widely distributed (Fig. 1, Pl. 1/8, Pl. 2/5). In all specimens the retractor muscles are arranged in the same way as Naef (1922, p. 151) illustrated his specimen. They appear to have been attached exactly to the surface of the lateral asymptotes of the gladius and run forward up to the region where the funnel has been situated. Although the longitudinal striations of these retractor muscles are weak we can easily distinguish between the orientation of both circular and longitudinal musculatures.

In MC-21 (Pl. 1/4) even the arm musculature is preserved. Here only longitudinal striations are preserved. Transversal or helical striations as described from recent forms are not visible (Kier 1985).

Number of arms

The number of arms is probably the most important feature. In at least two specimens we can count four arm bases. Oblique light makes them distinct.

In our "holotype" we can count four ridges which correspond (from dorsal to ventral) to the outer surface of the dorsal, the dorsolateral, the ventrolateral and to the ventral left arm (Pl. 2/8). MC-21 also shows four ridges (Fig. 1, Pl. 1/3). As in the "holotype" they represent the left arms. As already mentioned above, ultraviolet-light confirms this assumption, because here even musculature has been preserved (Pl. 1/4). Additionally, between the dorsolateral and ventrolateral as well as between the dorsolateral and dorsal arms appear the inner surface of the corresponding right arms. It is presumably the dorso- and ventrolateral right arms which appear as sucker imprints (more about suckers below) and the presumably ventral right arm appears as faint phosphatized musculature (Pl. 1/4)

It seems unlikely that a fifth arm pair (e.g. tentacles) is hidden somewhere or has been retracted into pouches. We postulate that there are no indications of a fifth pair of arms.

We guess that only the tips of the arms are missing so that the arms must have been comparatively short.

It is difficult to demonstrate but we also presume a short arm web nearly 1 cm beyond the arm bases (Pl. 1/5).

Suckers

Only in MC-21 are sucker imprints visible (Fig. 1, Pl. 1/5). They appear between the dorso- and ventrolateral and the ventrolateral and ventral left arms. As mentioned above they belong to the inner surface of the right ventrolateral and dorsolateral arms.

The diameter of the biggest and most distinctive sucker is remarkably wide (~ 5 mm) and radial in shape. The more distal suckers become smaller and less distinguished. The last recognizable sucker is ~ 1 mm wide. Proximally they are arranged in a single row, more distally probably in a zigzag pattern.

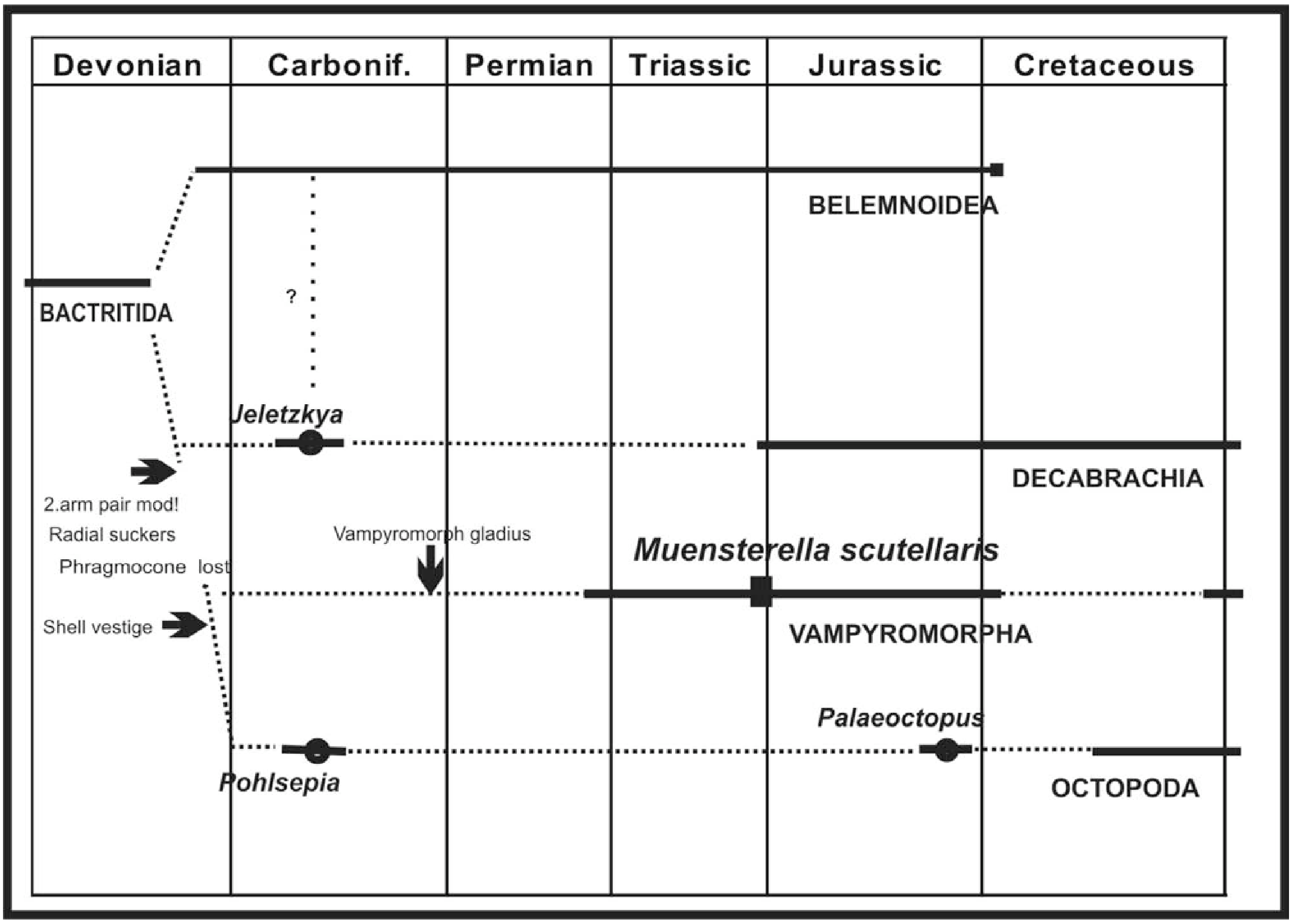

Fig. 2 Phylogenetic tree of the Coleoida with the supposed position of *Muensterella scutellaris*

Head

In the Solnhofen Plattenkalks the head region is mostly easily preserved as drusy calcite (Seilacher *et al.* 1976). So we have no morphological details about head characteristics. However in all specimens investigated the anterior mantle margin is distinct. Thus the mantle margin always protrudes from the head region and it seems that the head is retracted (Pl. 1/1, Pl. 2/1, 3 and 7). Unfortunately it cannot be decided whether or not the head and mantle are fused. Nevertheless it is evident that the head is not clearly demarcated.

DISCUSSION

It is not necessary to compare the gladius of the present specimens of *M. scutellaris* with other members of the family. Their gladius characteristics are unambiguous and well known. Additionally Vecchione *et al.* 2000 also refer to the difficulties of using only the gladius for phylogenetical implications.

On the other hand, until now nobody has considered the grade of mineralization of the gladius of *M. scutellaris*. We suppose that it must have been at least partly mineralised. In the Lithographic Limestones of Solnhofen completely chitinous structures like beaks, radulae or belemnite onychites are mostly preserved as imprints - not substantially. So it is unlikely that the gladius was composed of pure chitin (like the gladius of *Vampyroteuthis infernalis*). Thus a partly mineralised vampyromorph gladius would imply a progressive loss of mineralization from the late Jurassic forms up to the recent *Vampyroteuthis*. The plesiomorphic character “mineralised gladius” is common in octobrachian and decabrachian groups and therefore not useful for phylogenetic argumentations.

Phylogenetically relevant characters of muensterellid soft-parts are rare and a comprehensive description is still lacking. In the following we want to concentrate the discussion on the presence of more informative soft-parts.

In the “holotype” and in MC-21 we recognized the left arms of the four pairs. We suggest that these laterally embedded animals had 8 arms. The visible arms cover the arms beneath them. On the assumption that specimens of *M. scutellaris* possessed four pairs of arms we consider at least this "Fossil Teuthid" genus *Muensterella* as an ancestral member of the Octobrachia (Fig. 2).

The first discovery of marginal fins in *M. scutellaris* as well as the musculature is an extraordinary palaeobiological step forward but of no further phylogenetical aid. Although Vecchione *et al.* (2000) used the character "presence of fins", the "shape of fins" is useless because of homoplasy. Actually preservation of fin musculature is common. Donovan (1995) described a second pair of fins in *Trachyteuthis*. Unfortunately only the impressions have been preserved. However, the impressions of thick muscle bundles are visible. In our specimens neither musculature nor the impressions are preserved, which is not surprising if one compares *Sepia* and its faint marginal fins. Consequently we suggest a similar mode of locomotion and thus a similar life habitat for *M. scutellaris*.

Detailed knowledge about structure and arrangement of retractor musculature even of extant forms is poor, so that it is impossible to draw any conclusions, although the completely preserved retractor muscles might give rise to a comparison with other forms.

Young and Vecchione (1996) tried to determine the sister-taxon relationships of Coleoids. They found that the radial sucker symmetry is an unambiguous character of the Octopoda/Vampyromorpha. Character no. 11 "arm III armature series" and character no. 15 "well-developed interbrachial web" were considered as plesiomorphic features. Nevertheless, the uniserial rows of suckers and the arm web in the present study suggest an octobrachian affinity. Whether the imprints of the suckers in specimen MC-21 had a cuticular lining (an autapomorphy of the Octopoda) could not be established. However, there are no signs of typically decabrachian stalked suckers or "horny rings".

Cirri are missing. This is probably no artefact because cirri are known in the "Fossil Teuthid" *Leptotheuthis* and *Trachyteuthis* (Bandel & Leich 1986). In the Carboniferous octopod *Pohlsepia mazonensis* Kluessendorf and Doyle (2000) have not found any signs of cirri. This shows that the occurrence of cirri in the fossil record and consequently their character state are questionable and need further observations.

The character "indistinctly demarcarted head" is weak and it is not considered by Young and Vecchione (1996) but Kluessendorf and Doyle (2000) placed *Pohlsepia mazonensis* into the stem group of the Octopoda on the basis that "… it does not possess a well-defined head".

According to Young and Vecchione (1996) the "…Octopoda had eight unambiguous character changes that support its monophyly". Unfortunately these characters are completely useless in palaeontological studies because they concern very fine internal structures which have absolutely no preservational potential. Nevertheless the decision to assign *M. scutellaris* to the Octobrachia rests on the presence of a clearly differentiated gladius similar to the vampire-squid and on their eight arms. Since the finding of *Pohlsepia mazonensis* which is determined as a very early Octopod without any shell remnants (but this postulation must be proven) it is likely that *M. scutellaris* is really a vampyromorph representative (see the clearly differentiated gladius). Regarding the recently published revision of Haas (2000) about the evolutionary history of the eight-armed Coleoidea we would assign *M. scutellaris* to his paraphylum "Trachyteuthimorpha".

If *M. scutellaris* really had five pairs of arms we would have had great difficulties to find any other decabrachian similarities so that it is impossible for us to present an alternative approach.

CONCLUSIONS

We have considered several soft-part characters (body, fins, musculature, arms, suckers, web, head) of *M. scutellaris* which were until now completely new or poorly understood. The repeated presence of four arm pairs is the most important feature and phylogenetically applicable. In this context we have found no further helpful soft-part characters. Nevertheless we have enhanced the morphological knowledge of *Muensterella scutellaris*.

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Plate 1

1 Specimen MC-21. Lateral view. Showing gladius, body outline, ink sac, viscera, head, and arms. Scale bar = 1 cm.

2 Same specimen photographed with ultra-violet light. The white shining spots indicate phosphatized soft tissues like gladius and musculature. Scale bar = 1 cm

3 Specimen MC-21. Enlargement of the arm crown. Scale bar = 0.75 cm

4 Same arm crown photographed with ultra-violet light. Longitudial arm musculature is visible. Scale bar = 0.75 cm

5 Enlargement of Fig. 3 showing the imprints of the suckers. The arrows indicate the presumed position of the arm web. Scale bar = 1 mm

6 Specimen MC-21. Circular mantle musculature photographed with ultra-violet light showing the “striations” of bundles of fibres. Scale bar = 1 mm

7 Specimen MC-21. The slight elevation extending from SW to NE representing the boundary between mantle margin (above this elevation) and the seam of fins (below). Scale bar = 1 cm

8 Specimen MC-21. Phosphatized retractor muscle. Scale bar = 5.0 cm plate 1

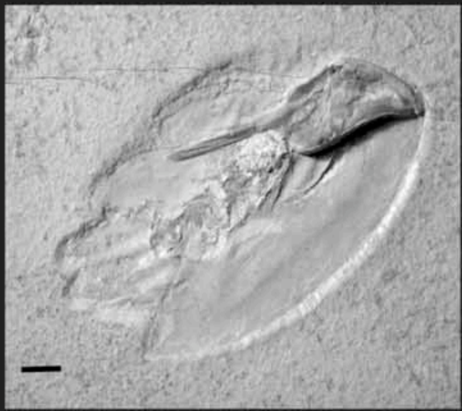

fig.1

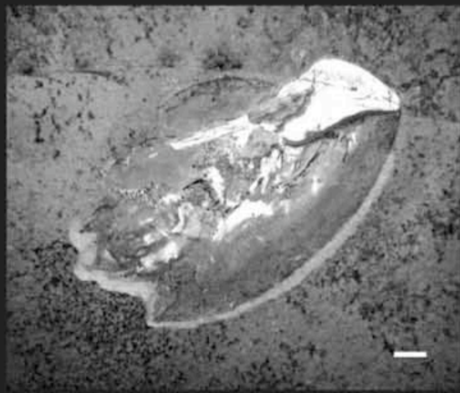

fig.2

fig.3

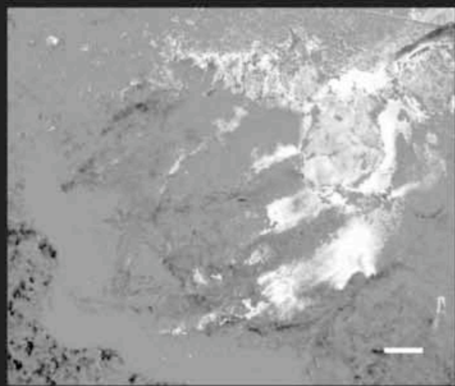

fig.4

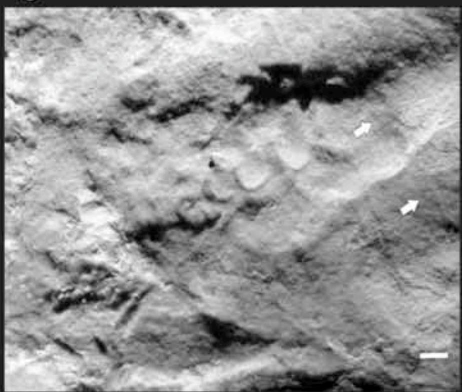

fig. 5

fig. 6

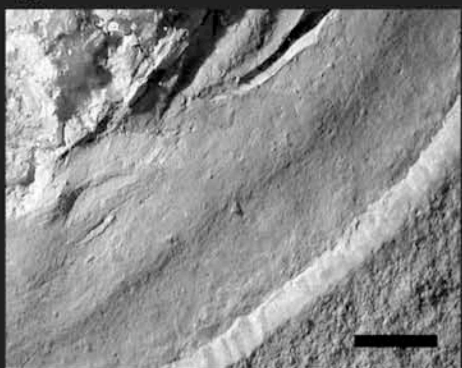

fig. 7

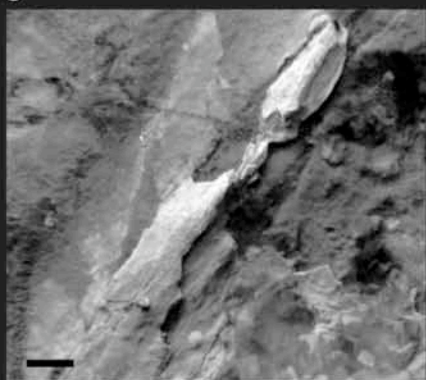

fig. 8

Plate 2

1 Specimen MC-18. Lateral view. Scale bar = 1 cm
2 Same specimen photographed with ultra-violet light
3 Specimen MC-51. Lateral view. Scale bar = 1 cm
4 Same specimen photographed with ultra-violet light
5 Specimen MC-51. Phosphatized circular mantle musculature covering the gladius. The arrow marks the well defined posterior mantle margin. Scale bar = 1 cm
6 Specimen MC-51. The posterior mantle margin seen in Fig.5 fits together with the more anterior elevation (arrow) indicating marginal fins. Scale bar = 1 cm
7 "Holotype". Museum of Natural History, Berlin. Invent. no.: M.B.-C.1023. Lateral view. Scale bar = 1 cm
8 Enlargement of Fig.7. Four arm bases are visible. Scale bar = 1 cm

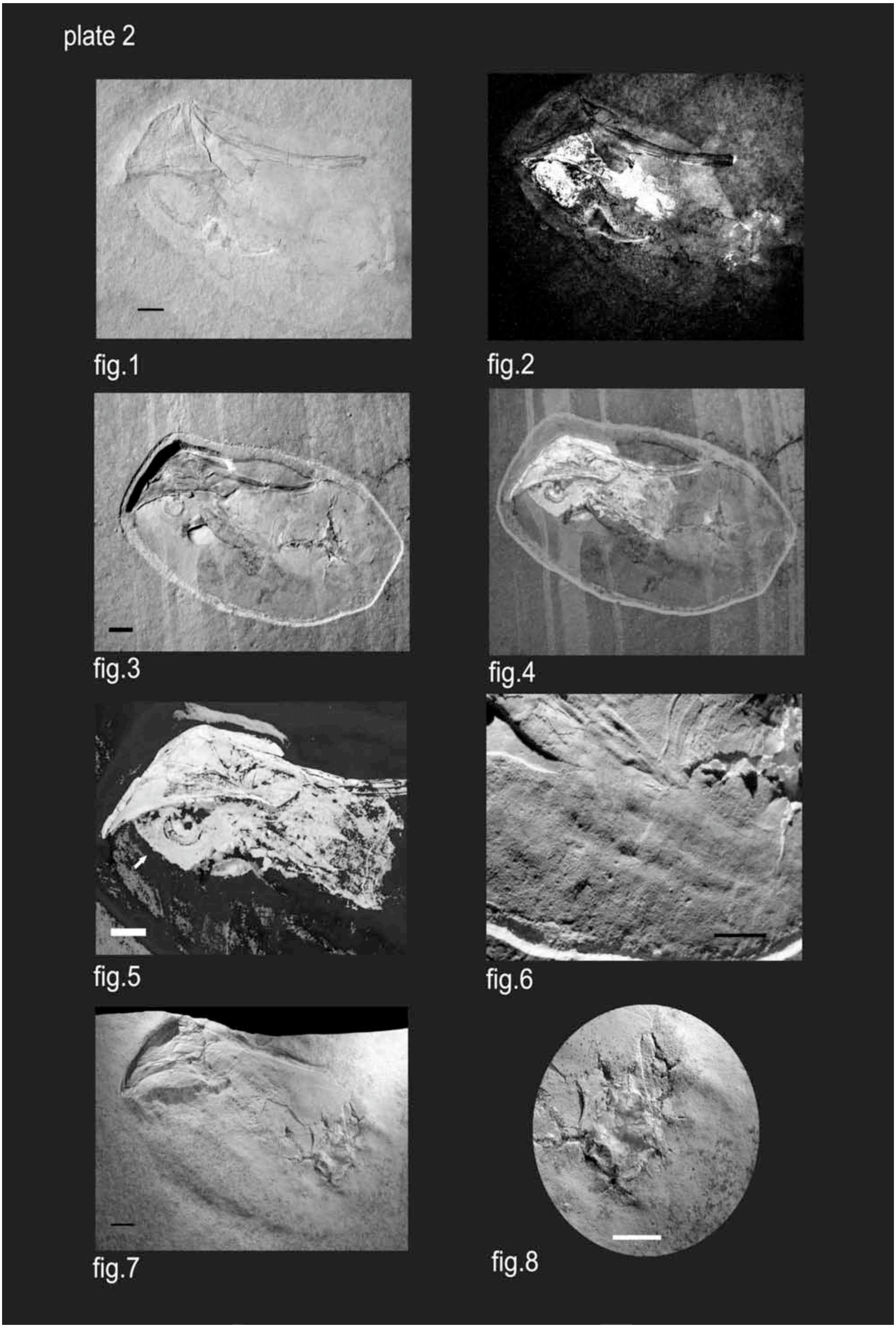
plate 2
fig.1
fig.2
fig.3
fig.4
fig.5
fig.6
fig.7
fig.8