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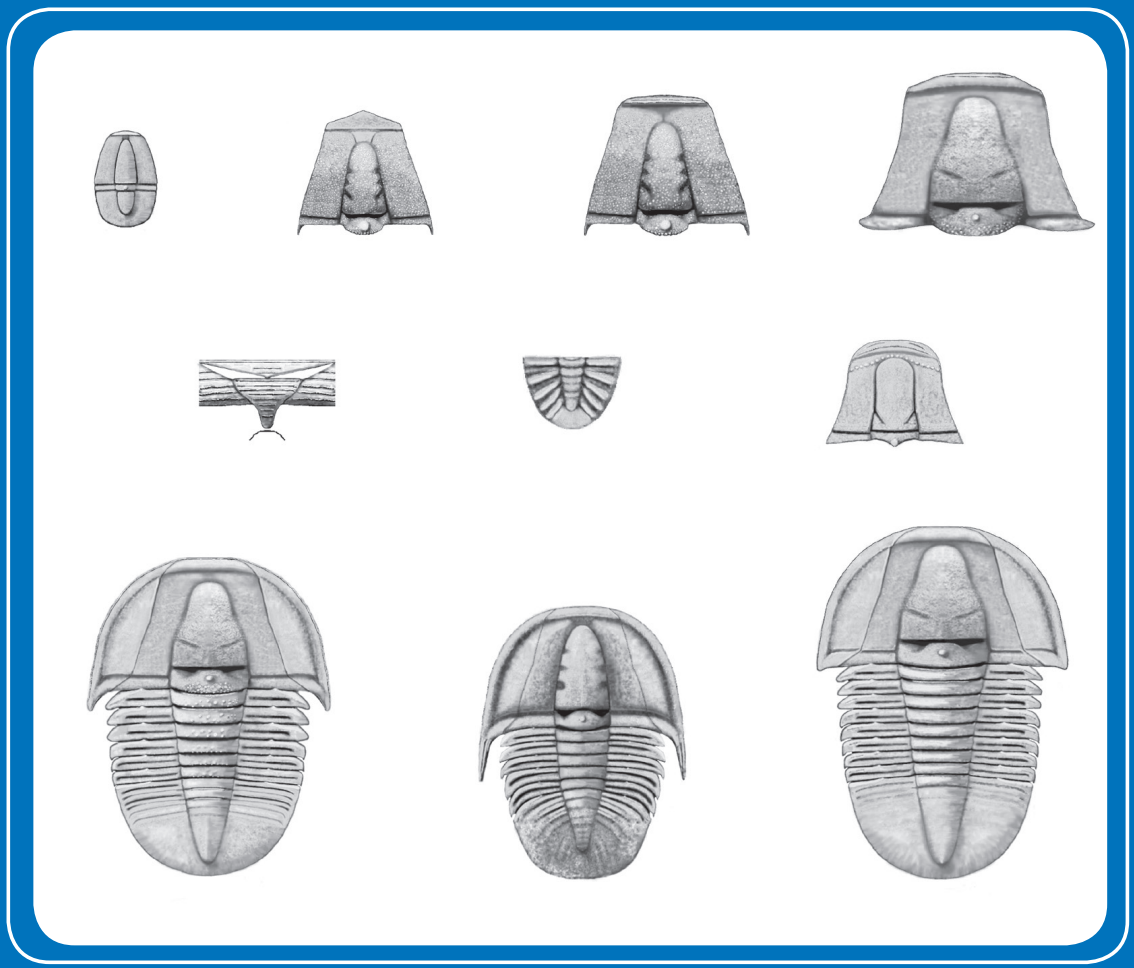

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Cover illustration: Tentative reconstructions of different taxa and ontogenetic stages in the trilobite genus *Drevermannia*, as well as of *Silesiops*? sp. For details, see Basse, M.: Revision und Ontogenie des Trilobiten *Drevermannia schmidti* Richter 1913 aus dem Oberdevon des Bergischen Landes, pp. 9–58 in this issue.
Back cover: Atrium of the Munich Palaeontological Museum, view from the main entrance.

Umschlagbild: Rekonstruktionsversuche für verschiedene Taxa und ontogenetische Stadien der Trilobitengattung *Drevermannia* sowie für *Silesiops*? sp. Für weitere Informationen siehe Basse, M.: Revision und Ontogenie des Trilobiten *Drevermannia schmidti* Richter 1913 aus dem Oberdevon des Bergischen Landes, S. 9–58 in diesem Heft.
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Libanocaris annettae nov. sp. (Crustacea: Dendrobranchiata: Penaeidae) from the Upper Jurassic Solnhofen Lithographic Limestones of Eichstätt

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Abstract

A new species of Penaeidae, *Libanocaris annettae* nov. sp. from the Upper Jurassic Solnhofen Lithographic Limestones (Eichstätt Formation; Lower Tithonian, Hybonotum Zone) is described. In addition, the diagnosis of the genus *Libanocaris* Garassino, 1994 is emended. *Libanocaris annettae* nov. sp. is compared to the type species of the genus *Libanocaris*, *L. rogeri* Garassino, 1994 and the superficially similar *Penaeus meyeri* Oppel, 1862.

Key words: Penaeidae, Solnhofen Lithographic Limestones, new species.

Kurzfassung

Eine neue Art aus der Familie Penaeidae, *Libanocaris annettae* nov. sp., aus den oberjurassischen Solnhofener Plattenkalken (Eichstätt-Formation; Unter-Tithonium, Hybonotum-Zone) wird beschrieben. Zusätzlich wird die Diagnose der Gattung *Libanocaris* Garassino, 1994 erweitert. Unterschiede zwischen *Libanocaris annettae* nov. sp. und der Typusart *Libanocaris rogeri* Garassino, 1994 sowie der flüchtig betrachtet ähnlichen Art *Penaeus meyeri* Oppel, 1862 werden herausgestellt.

Schlüsselwörter: Penaeidae, Solnhofener Plattenkalke, neue Art

1. Introduction

The prawn family Penaeidae is comprised of 216 extant species in 26 genera. Most are inhabitants of tropical and subtropical waters. Of these 216 known species, 166 only occur in the Indo-Pacific (Tavares & Martin 2010). With regard to global shrimp production, some of these species such as *Penaeus monodon* are of great importance.

The Upper Jurassic lithographic limestones of southern Germany represent an important source of information on fossil representatives of the Penaeidae. Apart from the well-known locations such as Solnhofen and Eichstätt there are several other, eminent lithographic limestone locations in southern Germany, including Brunn, Ettling, Painten, Schamhaupten, Zandt, and Nusplingen. In addition to the long since known fossil genera of the Penaeidae, mainly described by Münster (1839) and Oppel (1862), there are several newly described genera or species, e.g., *Albertoppelia* Schweigert & Garassino, 2004, *Pseudodusa* Schweigert & Garassino, 2004, *Bylgia ruedeli* Schweigert & Garassino, 2004, and *Koelga muensteri* Schweigert & Garassino, 2004. This new material has been collected during scientific excavations and by a number of amateur collectors. The new and better preserved specimens document that some of the historical taxa are in need of revision (Schweigert & Garassino 2003).

In this paper, a new species in the genus *Libanocaris, L. annettae* nov. sp. from the Solnhofen Lithographic Limestones (Eichstätt Formation; Lower Tithonian, Hybonotum Zone), is described that represents the hitherto oldest fossil record of the genus *Libanocaris* Garassino, 1994. The two species currently included in this genus are belonging to different geological ages, i.e. *L. annettae* comes from the Upper Jurassic of Solnhofen and *L. rogeri* from the Upper Cretaceous of Lebanon. It is interesting to note, however, that the same is true of the members of the genus *Carpopenaeus* Glaessner, 1945. *Carpopenaeus peterbuergeri* Schweigert & Garassino, 2005 (Schweigert & Garassino 2005) comes from the Upper Jurassic of Solnhofen, while *Carpo-*

penaeus callirostris Glaessner, 1945 and *Carpopenaeus septemspinatus* (Dames, 1886) have been reported from the Upper Cretaceous of Lebanon (Garassino 1994). Moreover, the genus *Cancrinos* also exhibits this pattern, with *Cancrinos claviger* Münster, 1839 (Garassino & Schweigert 2006a) coming from the Upper Jurassic of Solnhofen and *Cancrinos libanensis* Garassino & Schweigert, 2006 from the Upper Cretaceous of Lebanon (Garassino & Schweigert 2006b).

2. Material and methods

The fossil at hand (holotype) comes from the Solnhofen Lithographic Limestones (Eichstätt Formation; Lower Tithonian, Hybonotum Zone) in southern Germany. The specimen occurs on a limestone slab that is 10 mm thick. Specimen preparation was carried out with a vibrograph, and various needles and scrapers. Because the sclerotisation of the exoskeleton of crustaceans preserved in lithographic limestone brightly fluoresces, ultraviolet illumination was used in the study of the fossil. In this way even the most delicate features, which otherwise would have been barely discernible, could be observed and adequately documented photographically. The specimen was photographed with a Canon EOS 450D digital camera equipped with a Canon Macro Photo lens MP-E 65 mm and EF-S 60 mm. Fiber light sources were used for illumination. For enhancement of contrast through autofluorescence, cyan filters were placed over the light sources and a red filter was attached to the camera lens (for details, refer to Haug et al. 2011). A longer excitation wavelength was used since it is often superior to the usually applied UV light because dirt particles do not glow under longer wavelengths (Haug et al. 2009). Digital colour images were captured and then changed to greyscale using Photoshop CS3. As the specimen is too large to be photographed in its entirety with high resolution, several images were taken of different parts of the specimen and then combined into composite images with the ‚Automate' function of Photoshop CS3 (J. Haug, personal commun., 2011).

Abbreviations: BMMS = Museum-Solnhofen, Germany; JME = Jura-Museum Eichstätt, Germany; SMNS = Staatliches Museum für Naturkunde Stuttgart, Germany

3. Systematic palaeontology

Diagnostic characters of the Penaeidae: The classification of Penaeidae follows Tavares & Martin (2010) and McLaughlin (1980), which, however, are largely based on extant taxa. All members of the Penaeidae exhibit the following complement of external features: (1) a laterally compressed body; (2) a well-developed rostrum; (3) a carapace that usually bears an antennal spine; (4) antennules that are biramose (dorsolateral and ventrolateral flagellum); (5) a 3-segmented antennular peduncle; (6) the first three pairs of pereiopods chelate; (7) pereiopods IV and V achelate; (8) the first pair of pereiopods usually short; (9) the third maxillipeds pediform; (10) the second pleomere with pleura that do not overlap those of the first pleomere; and (11) pleopods that are biramose. Mouthpart morphology is usually difficult to assess in fossil prawns from the Solnhofen Limestones due to the mostly lateral embedding of fossils; apart from the third maxillipeds no other mouthparts are typically visible.

Order Decapoda Latreille, 1803
Infraorder Dendrobranchiata Bate, 1888
Superfamily Penaeoidea Rafinesque, 1815
Family Penaeidae Rafinesque, 1815

Genus *Libanocaris* Garassino, 1994

Type species: *Libanocaris rogeri* Garassino, 1994, by original designation.

Species included in genus: *Libanocaris rogeri* Garassino, 1994; *Libanocaris annettae* nov. sp., this paper.

Remarks: Because of the excellent preservation of the fossils described in this paper, additional characters can be identified that are diagnostic for the genus *Libanocaris* Garassino, 1994. As a result, the generic diagnosis is emended.

Emended diagnosis: Small to medium sized penaeid; carapace with anteriorly directed, dorsally dentate rostrum; with epigastric tooth posterior to the rostrum; surface of carapace in the frontal and gastric regions punctate, otherwise smooth; with antennal spine; pereiopods I-III chelate; chelae of pereiopods I and II stronger than those of pereiopods III; pereiopods I shortest; pereiopods III longest and with elongated merus and carpus; pereiopods IV and V achelate; surface of abdomen smooth; abdominal somite VI slightly longer than others; uropodal exopodite with diaeresis.

Libanocaris annettae nov. sp.
Pls 1, 2

Holotype: Specimen illustrated in Pl. 1, Fig. 1, deposited in the BMMS under accession number BMMS/BK101 (as a permanent loan from the collection of N. Winkler).

Paratype: Specimen illustrated in Pl. 2, Fig. 6, deposited in the SMNS under accession number 67900 (ex coll. A. Felthaus).

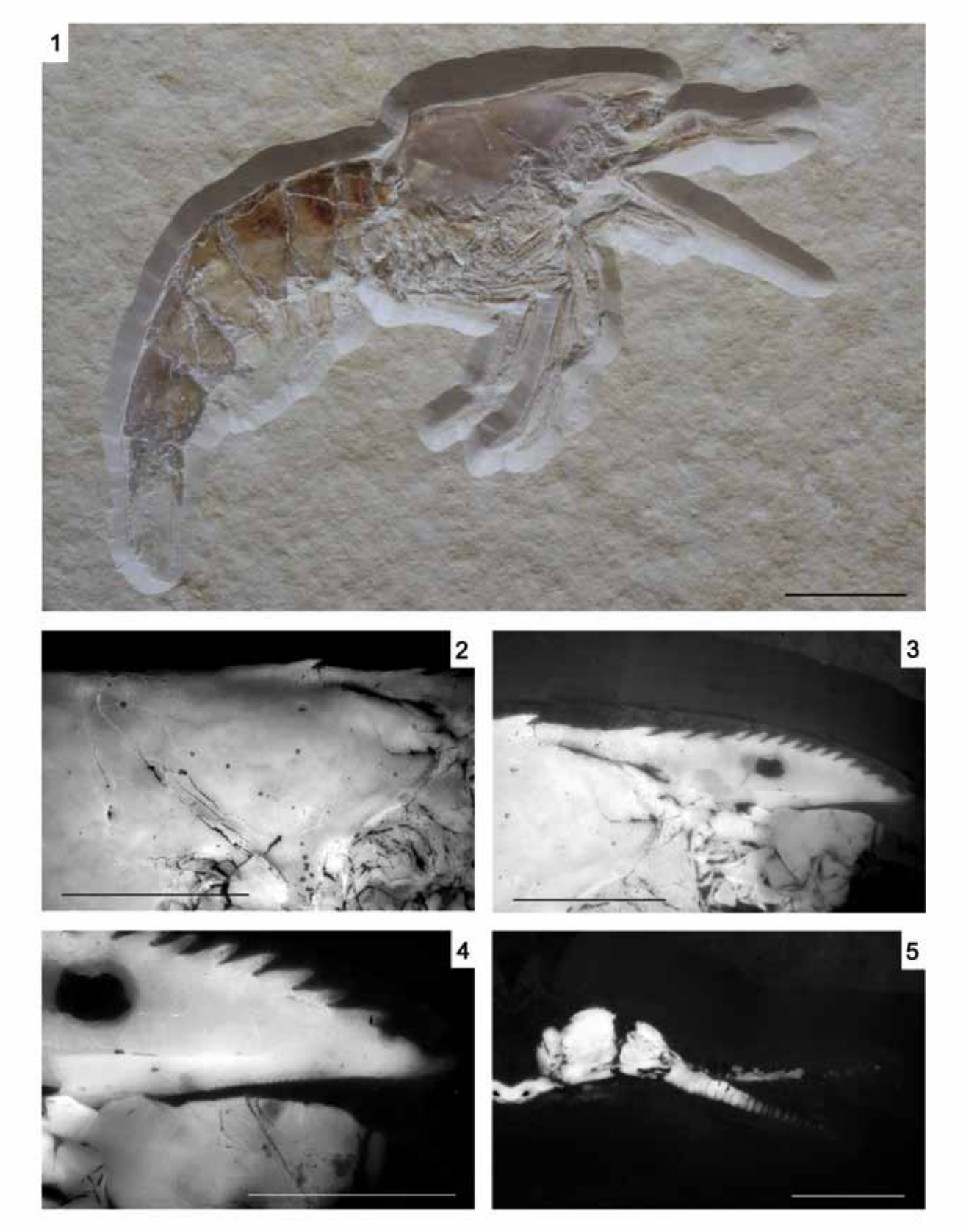


Plate 1: *Libanocaris annettae* nov. sp. Quarry district of Eichstätt (Schernfeld); Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. Holotype, BMMS/BK101. **(1)** Overview; bar 10 mm. **(2)** Punctated surface of carapace and proximal portion of rostrum; bar 5 mm. **(3)** Rostrum; bar 5 mm. **(4)** Microteeth on ventral side of rostrum; bar 2 mm. **(5)** Antennular peduncle and flagella; bar 3 mm.

Etymology: The specific epithet is given in honor of Annette Winkler, who kindly prepared the fossil with great care.

Gender: Feminine.

Type locality: Vicinity of Eichstätt (Schernfeld); S Franconia, Bavaria, southern Germany.

Type horizon and age: Solnhofen Group, Upper Eichstätt Formation, Lower Tithonian, Hybonotum Zone.

Studied material: 2 specimens (holotype; paratype).

Specific diagnosis: Slender penaeid with mostly smooth, partly punctate carapace; rostrum anteriorly directed, bearing 13 dorsal teeth and numerous ventral microteeth; third pereiopods with remarkably elongated carpus and short and slender propodus.

Description (based on the holotype specimen, unless otherwise indicated): The holotype specimen of *Libanocaris annettae* (Pl. 1, Fig. 1) is an excellently preserved moult embedded in lateral view. Its length amounts to 81.9 mm, measured from the tip of the rostrum to the end of the tail fan, along the dorsal axis. The body of the well sklerotized prawn is curved. In the frontal and gastric region of the carapace, as well as in the proximal region of the rostrum, the shell of the body is punctate, otherwise the surface is smooth (Pl. 1, Fig. 2).

In lateral view the carapace is subrectangular in outline and narrows slightly anteriorly. The carapace including the rostrum is 24.5 mm long and 10.4 mm high. The carapace most probably displays a cervical groove. The dorsal midline extends into the forwardly directed rostrum, which is 8.5 mm long (Pl. 1, Fig. 3).

On the dorsal side of the rostrum 13 forwardly directed teeth are recognizable. The anteriorly directed short tip of the rostrum does not reach the end of the scaphocerite. Posterior to the rostrum an epigastric tooth occurs at a distance of 2.0 mm. Ventrally the rostrum bears numerous microteeth (Pl. 1, Fig. 4).

The cephalic appendages are partly preserved. In the anterior part of the carapace remains of the antennal spine are present. Yet another spine, 1.1 mm long, is present, but, however, cannot be assigned precisely. The eyestalk is short, strong, and approximately 2.5 mm long. The second and third segments of the antennular peduncle are preserved intact (Pl. 1, Fig. 5). The third segment exhibits a smooth surface, the second one is punctate. The first proximal segment is incompletely preserved, but its surface seems to be smooth. In the paratype specimen the first segment is preserved and shows a smooth surface. The biflagellate antennules are less than half as long as the antennae; the dorsolateral antennular flagellum is preserved up to 6.7 mm. The portions of the ventrolateral antennular flagellum are considerably stronger than those of the dorsolateral flagellum. The flagella of the antennae seem to be partly preserved and one of them is visible up to a length of 15.8 mm. The carpocerite is notably longer than both the merocerite and ischiocerite. The lanceolate scaphocerite is 8.7 mm long, with a pointed distal extremity. Its tip reaches the distal end of the third segment of the antennular peduncle. The third maxillipeds are pediform (Pl. 2, Fig. 1).

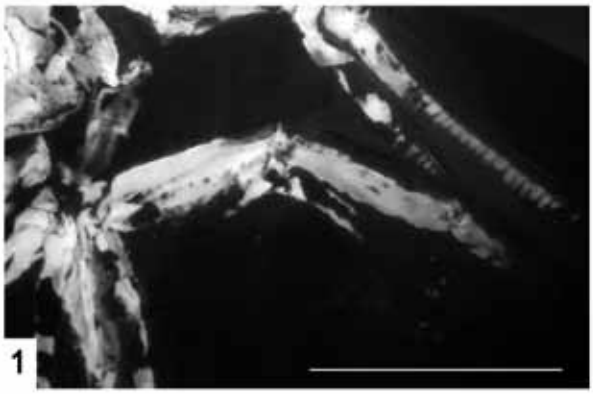
The dorsolateral maxilliped consists of completely preserved merus and carpus, while the propodus is only preserved in its proximal part. The merus shows several strong lateral tubercles. The pereiopods I-III are chelate (Pl. 2, Figs 2, 3). Pereiopods I are the shortest and strongest; the merus of which shows a remarkable row of tubercles. The discernible part of the chela of pereiopod I, mainly its palm and the proximal part of its fingers, is somewhat stocky (Pl. 2, Fig. 5a). In the paratype, in which the chela of pereiopod I is completely preserved, it is stocky too (Pl. 2, Fig. 6). Pereiopods II are longer than pereiopods I because of their longer carpi. The preserved parts of the chela of pereiopods II resemble those of pereiopods I. Pereiopods III are isochelous and the longest of all pereiopods due to their notably elongate, slender carpus. The propodus, including the fixed finger, is thin and relatively short (Pl. 2, Fig. 5b). Both fixed and movable fingers are identical in length. Pereiopods IV and V are achelate, however, the dactylus is hardly discernible. The abdomen shows the typical curvature of penaeids; its surface is smooth (Pl. 2, Fig. 4).

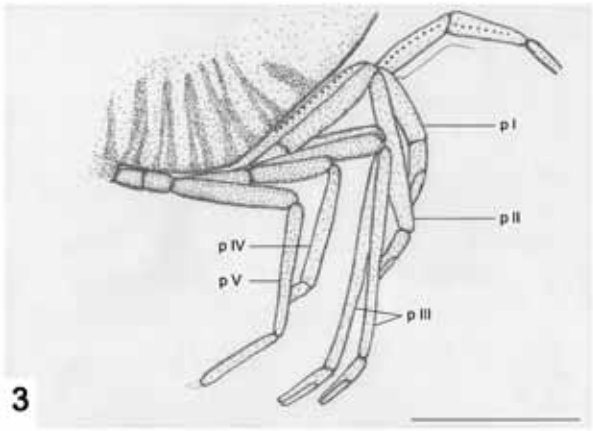
The abdominal somites are subrectangular in outline. The third and sixth somites are slightly longer than the others. The ventral margin of the abdominal somites is smooth. The pleura of the second pleomere do not overlap those of the first pleomere. The telson is partly preserved and does not show any spikes. The biramose pleopods are moderately well preserved. Because of the poor preservation of the uropodal exopodites the diaeresis is hardly discernible. For detailed information of measurements, see Table 1.

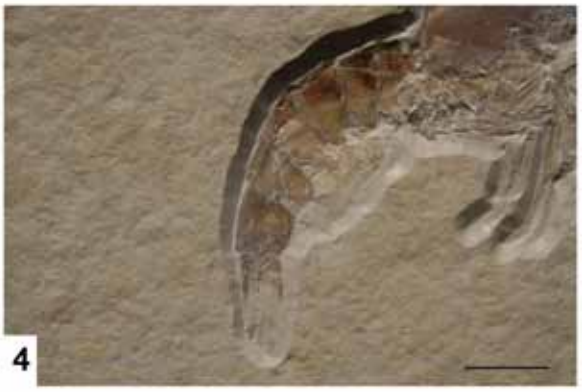
4. Discussion and comparisons

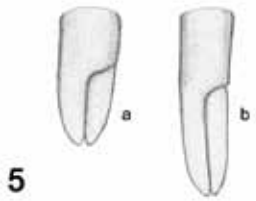
4.1 Differences between *Libanocaris annettae* and *Penaeus meyeri* Oppel, 1862

Libanocaris annettae exhibits several morphological details that discriminate this taxon from the superficially similar species *Penaeus meyeri* from the lithographic limestones at Eichstätt and Solnhofen, first described by Oppel (1862). First, *L. annettae* differs from *P. meyeri* in the shape of the rostrum and in the number of teeth on the dorsal margin of the









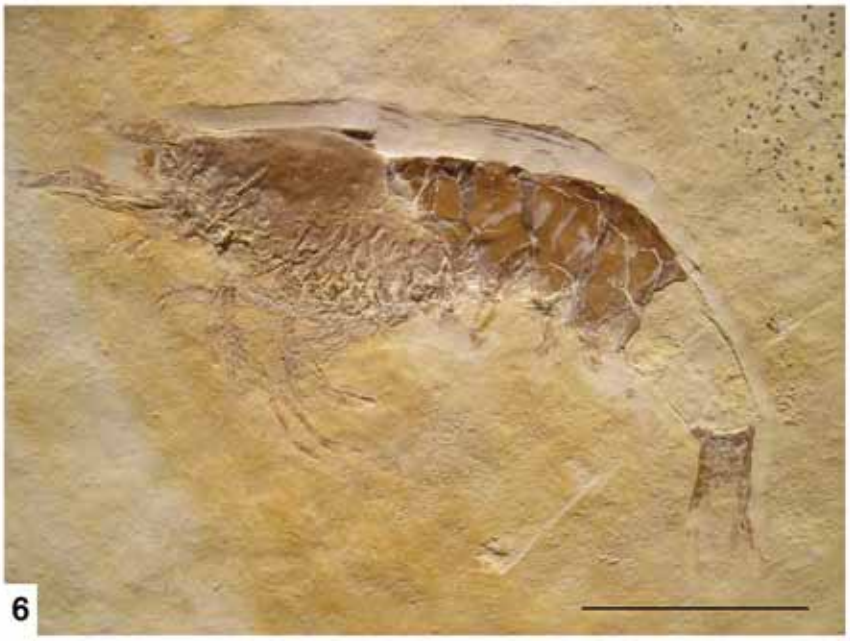


Plate 2: *Libanocaris annettae* nov. sp. Quarry district of Eichstätt (Schernfeld); Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. **(1)** Third maxillipeds of holotype specimen; bar 5 mm. **(2)** Pereiopods of holotype specimen; bar 10 mm. **(3)** Line-drawing of pereiopods I-V; p = pereiopod; bar approximately 10 mm. **(4)** Abdomen of holotype specimen; bar 10 mm. **(5)** Hypothetic reconstruction of chelae of pereiopod I and III of L. annettae; a: pereiopod I; b: pereiopod III, not to scale. **(6)** Paratype, SMNS 67900; bar 10 mm.

Table 1: Measurements (in mm) of *Libanocaris annettae*, holotype specimen; l = left, r = right, d = dorsolateral, P = pereiopod

***Libanocaris annettae* nov. sp.; holotype**	**Length (in mm)**
Antennular peduncle, second	1.7
Antennular peduncle, third	1.5
Carpocerit (r)	2.0
Merocerit (r)	0.8
Ischiocerit (r)	0.6
3. Maxilliped (propodus), visible part (d)	2.5
3. Maxilliped (carpus) (d)	3.7
3. Maxilliped (merus) (d)	4.0
P I carpus	5.7
P I carpus, width	1.1
P I merus	5.8
P II carpus	9.1
P II carpus, width	0.9
P II merus	6.6
P III propodus incl. fixed finger (l)	3.4
P III propodus incl. fixed finger (r)	3.2
P III carpus (l)	12.9
P III carpus, width (l)	0.6
P III carpus (r)	12.6
P III carpus, width (r)	0.6
P III merus (l)	7.4
P IV carpus	7.2
P IV merus	4.5
P IV ischium	2.2
P V propodus	4.8
P V carpus	7.2
P V merus	6.7
P V ischium	1.2
P V basis	1.1
Abdominal somite 1	4.3
Abdominal somite 2	5.0
Abdominal somite 3	7.0
Abdominal somite 4	6.5
Abdominal somite 5	4.9
Abdominal somite 6	7.9
Tail fan	12.0
Telson	9.8

rostrum. Moreover, the shell of the carapace of *P. meyeri* is completely smooth, while there are a few punctae in *L. annettae*. Another important difference is the length of the carpus in pereiopod III, especially with regard to the relation between the length of propodus and length of carpus. The ratio between propodus (incl. fixed finger) and carpus in *L. annettae* (holotype, see Tab. 1) is 1:3.79. The paratype of *L. annettae* is a moult lying on the surface of a limestone slab. It exhibits a body-length of 46 mm, measured from the tip of the rostrum to the end of the telson, along the dorsal axis. It shows propodus (incl. fixed finger):carpus ratio of 1:3.57 (1.9 mm : 6.8 mm). Even though the body-lengths differ considerably between the two specimens, a nearly similar ratio is shown (Pl. 2, Fig. 6). For comparison 11 specimens of *P. meyeri* of different sizes (lengths between 55 and 79 mm) have been measured. *Penaeus meyeri* exhibits a propodus:carpus ratio of approximately 1:1.52 (variations of 1:1.31 to 1:1.66) (see Table 2). The primary reason for this difference is the strongly elongated carpus of *L. annettae*. Based on these morphological differences *L. annettae* is assignable to the genus *Libanocaris*, rather than *Penaeus*.

4.2 Differences between *Libanocaris annettae* and *Libanocaris rogeri* Garassino, 1994

Libanocaris annettae differs from the type species of *Libanocaris*, *L. rogeri*, mainly in the number of dorsal teeth on the rostrum (13 versus 8) and the presence of ventrally situated microteeth, which are absent in *L. rogeri* (according to Garassino´s description). Moreover, the carpus of the third pereiopods is explicitly more elongate in *L. annettae*. In *L. rogeri* the propodus (incl. fixed finger):carpus ratio of the third pereiopods is 1:2.3 (obtained from the holotype, measured from the original illustration). The shape of the third pereiopods and rostrum is regarded as a significant diagnostic feature at species but not generic level. Information on the ontogeny of fossil arthropods of different ages may exhibit developmental patterns (Haug et al. 2010). Conceivably the two species of *Libanocaris* show an evolutionary trend in the form of a reduction of the number of rostral teeth and of the length of the carpus of the third pereiopods.

4.3 Palaeoecology of *Libanocaris annettae*

The strongly elongated third pereiopods of *Libanocaris annettae*, as well as the thin chelae, may represent adaptations to a detritus-feeding lifestyle (Schweigert & Garassino 2004). The well-developed eyes suggest that the species was thriving in well-illuminated shallow water environments (Schweigert & Garassino 2004).

Table 2: Measurements (in mm) of *Penaeus meyeri* (specimens 1–7: coll. N. Winkler; specimen 8: coll. U. Resch; specimens 9–11: JME)

Penaeus meyeri specimen	Length of body	Length of propodus	Length of carpus	Proportion
1	79	6.0	9.0	1:1.50
2	62	4.5	7.5	1:1.66
3	78	6.0	9.2	1:1.53
4	72	6.5	9.8	1:1.51
5	55	4.2	7.0	1:1.66
6	65	4.8	6.5	1:1.35
7	60	4.4	6.9	1:1.57
8	68	5.5	8.6	1:1.56
9	64	5.5	8.0	1:1.45
10	59	5.0	8.0	1:1.60
11	76	7.2	9.5	1:1.31
				Average: 1:1.52

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