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New genera and species of shrimps (Crustacea: Decapoda: Dendrobranchiata, Caridea) from the Upper Jurassic lithographic limestones of S Germany

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In memoriam KARL ALBERT FRICKHINGER (1924–2003)

Abstract

From the Upper Jurassic Solnhofen Lithographic Limestones of Eichstätt and Zandt (S Franconia) and from the Nusplingen Lithographic Limestone (Swabia) 4 new genera and 8 new species of natant decapod crustaceans are recorded and described: *Albertoppelia kuempeli* n. gen. n. sp., *Pseudodusa frattigianii* n. gen. n. sp., *Bylgia ruedeli* n. sp., *Koelga muensteri* n. sp., *Udora koschnyi* n. sp., *Buergerocaris psittacoides* n. gen. n. sp., *Pleopteryx kuempeli* n. gen. n. sp., and *Hefriga proboscideawulfi* n. sp. The reasons for their scarcity are briefly outlined. We assume that they mostly had an epibenthic lifestyle in various shallow marine habitats in the more distant surroundings of the lagoons where the lithographic limestones were deposited.

Keywords: decapods, lithographic limestones, taxonomy, diversity, Upper Jurassic, Solnhofen.

Zusammenfassung

Aus den oberjurassischen Solnhofener Plattenkalken der südlichen Frankenalb (Eichstätt, Zandt) und dem Nusplinger Plattenkalk der südwestlichen Schwäbischen Alb werden 4 neue Gattungen und 8 neue Arten von Garnelen vorgestellt und beschrieben: *Albertoppelia kuempeli* n. gen. n. sp., *Buergerocaris psittacoides* n. gen. n. sp., *Pseudodusa frattigianii* n. gen. n. sp., *Bylgia ruedeli* n. sp., *Koelga muensteri* n. sp., *Pleopteryx kuempeli* n. gen. n. sp., *Hefriga proboscideawulfi* n. sp. und *Udora koschnyi* n. sp. Die Gründe für ihre Seltenheit werden kurz ausgeführt. Die beschriebenen Arten dürften meistens eine bodenbezogene Lebensweise in verschiedenartigen Flachwasserbiotopen im weiteren Umfeld der Plattenkalk-Lagunen besessen haben.

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1. Introduction

The Upper Jurassic lithographic limestones of S Germany provide an outstanding resource of otherwise unknown fossil decapods. Without this material, the fossil record of Jurassic decapods would be quite poor, mainly restricted to isolated chelae of anomurans and astacideans or carapaces of astacideans and prosopids. During the last decades, a large number of undescribed rare taxa of decapods from the Upper Jurassic of S Franconia accumulated in various widespread private collections. Some of them were figured in the monographs of FRICKHINGER (1994, 1999), whereas others came to light after further intensive research in these collections. Other interesting specimens come from current scientific excavations in Swabia (Nusplingen, see DIETL & SCHWEIGERT 1999), from E Bavaria (Brunn near Regensburg, see RÖPER et al. 1996), or from newly opened quarries in S Franconia.

In addition to the ongoing review of the type material of decapod crustaceans mainly described in the 19th century by SCHLOTHEIM (1820, 1822), MÜNSTER (1839), OPPEL (1861, 1862), and a few others, the new material is to be described continuously (SCHWEIGERT 2001, 2002, 2003; SCHWEIGERT et al. 2000; SCHWEIGERT & GARASSINO 2003a, 2003b; SCHWEIGERT & RÖPER 2001; this paper). Despite the fact that fossil decapod crustaceans were collected over the centuries when quarrying extensively for lithographic limestones or roof tiles, precise data on their exact provenance are often missing or even incorrect. It must be kept in mind that these “Solnhofen” fossils come from an area of several thousands of square kilometres, where the quarries and exposures widely differ both in age and, to some degree, in lithology. The focus of this study is the description of the newly discovered rare decapod crustaceans from the Upper Jurassic lithographic limestones of Eichstätt, Zandt, and Nusplingen (for localities see SCHWEIGERT & GARASSINO 2003b, fig. 1).

For the documentation and reconstruction of the specimens ultraviolet illumination was successfully used in most cases (for methodology of using ultraviolet illumination see TISCHLINGER 2002). Total lengths of specimens mentioned in the descriptions are measured in dorsal line from the tip of the rostrum to the end of the telson. The terminology of carapace features follows PÉREZ FARFANTE & KENSLEY (1997).

Abbreviations

- BSPM Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.
- JME Juramuseum Eichstätt, Germany.
- SMNS Staatliches Museum für Naturkunde Stuttgart, Germany.

Acknowledgements

The excellent and extremely rare material on which this study is based was kindly provided by courtesy of several private collectors: P. BÜRGER (Bad Hersfeld), R. FRATTIGIANI (Laichingen), K. HENNE (Stuttgart), G. KOSCHNY (Bad Soden), D. KÜMPEL (Wuppertal), P. RÜDEL (Gröbenzell), and M. WULF (Rödelsee). K. A. FRICKHINGER (†, Emmering) strongly encouraged this study and contributed several photographs. C. SCHWEITZER (Kent, Ohio) and an anonymous referee kindly suggested several improvements. R. BÖTTCHER (SMNS,

Stuttgart) is thanked for his carefully proof-reading of the manuscript. Mrs. R. HARLING (SMNS, Stuttgart) kindly prepared most of the photographs, partly using ultraviolet illumination.

2. Systematic palaeontology

For the classification of higher taxa of decapods we follow the classification of MARTIN & DAVIS (2001), although it is mainly based on the Recent taxa, and there exist some alternative classifications subdividing the ‘carideans’ (BURKENROAD 1981, SCHRAM 1986). Of course, the preservation of fossil decapods does not allow studying all features that are present in Recent ones. Within the shrimp genera and species of this study, we distinguished penaeids and carideans. The latter exhibit a wide range of differentiations of pereopods I–III developed chelate or achelate. They mainly share the pleura of somite II expanded to overlap the preceding and following ones. This feature, however, is also developed (? independently) in some primitive Astacidea (e.g. SCHWEIGERT & GARASSINO 2003a).

Order Decapoda LATREILLE, 1803
 Infraorder Dendrobranchiata BATE, 1888
 Superfamily Penaeoidea RAFINESQUE, 1815
 Family Penaeidae RAFINESQUE, 1815

Genus *Albertoppelia* n. gen.

Type species: *Albertoppelia kuempeli* n. sp.

Derivation of name: After ALBERT OPPEL (1831–1865), first reviser of Jurassic decapod crustaceans from SW Germany and adjacent areas, whose monograph is still the most comprehensive essay on this matter.

Diagnosis: See diagnosis of the type species.

Albertoppelia kuempeli n. sp.

Figs. 1–2

v 2003b Penaeid (n. gen., n. sp.). – SCHWEIGERT & GARASSINO, p. 178, figs. 2 d, 3 d.

Holotype: Specimen figured as Fig. 1, housed in the collection of the SMNS, no. 64945 (ex coll. D. KÜMPEL).

Derivation of name: After DIETER KÜMPEL, Wuppertal, who prepared and kindly donated the holotype of this species for description.

Type locality: Eichstätt, S Franconia, Bavaria, S Germany.

Type horizon: Solnhofen Group, Upper Eichstätt Formation (see ZEISS 1977, fig. 8; Lower Tithonian, Hybonotum Zone).

Studied Material: 6 specimens (holotype; 5 additional specimens in private collections of P. BÜRGER, Bad Hersfeld, G. KOSCHNY, Bad Soden, and R. FRATTIGIANI, Laichingen).

Occurrence: Lower Tithonian (Hybonotum Zone) of Eichstätt.

Diagnosis. – Small penaeid with smooth carapace; rostrum high, serrate both dorsally and ventrally; pereopods I–III chelate; pereopods I strongest; pereopods III longest; other pereopods achelate.

Description. – The holotype is a moult lying little below the lower bedding plane of a very hard limestone plate. Its length is about 81 mm. The carapace and the abdomen are smooth. The carapace is relatively long, with its largest height in the

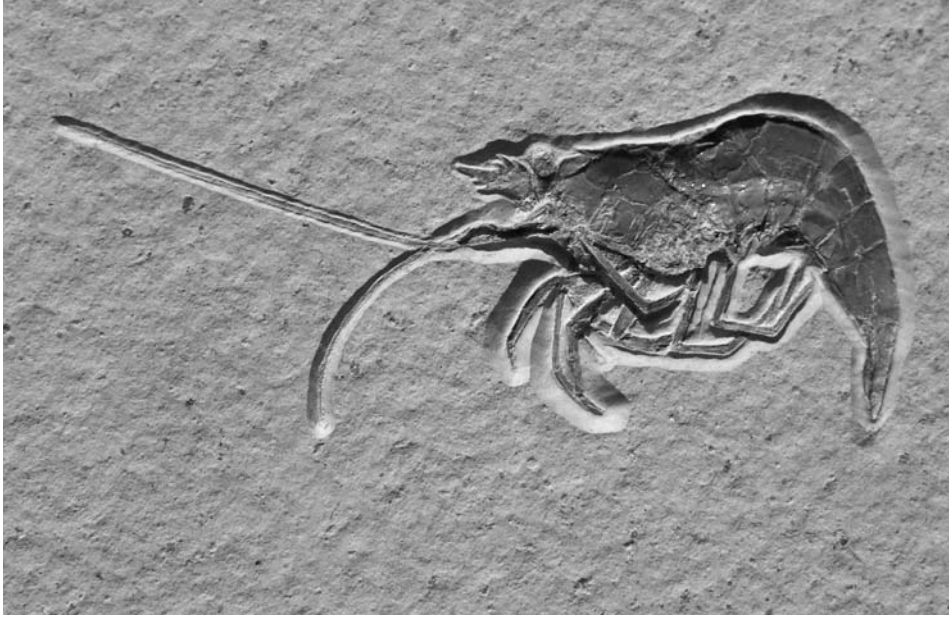


Fig. 1. *Albertoppelia kuempeli* n. gen. n. sp., holotype. Quarry district of Eichstätt; Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. – Top: Photograph under normal illumination; bottom: Photograph using ultraviolet illumination. SMNS 64945 (ex coll. D. KÜMPEL, Wuppertal). – Width of figures: 11.0 cm.

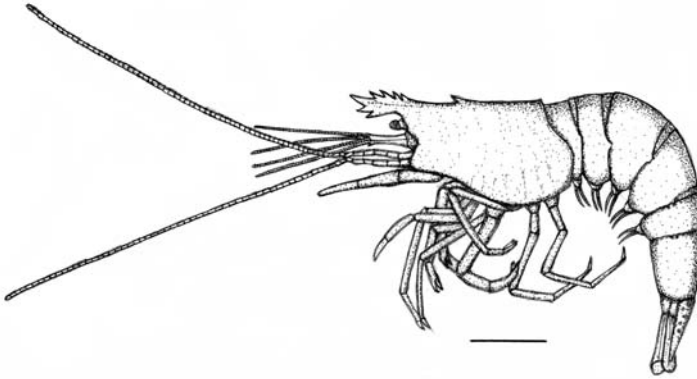


Fig. 2. Reconstruction of *Albertoppelia kuempeli* n. gen. n. sp. – Scale equals approximately 1 cm.

posterior third, and bears a curved postero-ventral margin. The remarkably high, dome-shaped rostrum bears 4 dorsal teeth, of which the 3 anterior ones are visible in the holotype, whereas the most posterior one known from other specimens is hidden by the stalked eye. The ventral part of the rostrum exhibits 2 frontal teeth, whereas 3 additional teeth are located more laterally and may be easily overlooked. An epigastric tooth is present behind the rostrum

The antennae of the holotype have a preserved length of 58 mm. The antennules are not preserved in the holotype. In another specimen they are poorly preserved, being short and biflagellate. The scaphocerites are hardly discernible, but ventrally curved. The 3rd maxillipeds are long and slender. Pereiopods I–III are chelate, with weak, short pincers. Pereiopods I are the strongest, while III are the longest. Pereiopods IV–V are both achelate and almost equal in length. They bear a thin, pointed, terminal dactylus.

In the abdomen, somites III and VI are much longer than the others. The pointed telson is covered by small, round pits. All pleopods are biramose, but poorly preserved in the studied specimens. The long, slender uropodal exopodites bear a diaeresis (see SCHWEIGERT & GARASSINO 2003b, pl. 1, fig. d), which is not visible in the holotype because of a folded burial position of the uropods.

Discussion. – The shape of the rostrum with 2 ventral teeth is unique among penaeids from the Upper Jurassic. Concerning pereiopods I being shortest but strongest, there is some resemblance to *Bylgia* MÜNSTER, 1839, but the latter differs in very elongate pereiopods III. In *Drobna* MÜNSTER, 1839 the surface of the carapace and abdomen is punctate, and the rostrum lacks ventral teeth.

The arrangement of the abdominal somites and pleura as well as the presence of 3 anterior pairs of chelate pereiopods indicates its assignment to penaeids.

Genus *Pseudodusa* n. gen.

Type species: *Pseudodusa frattigianii* n. sp.

Derivation of name: After a superficial similarity with *Dusa* MÜNSTER, 1839.

Diagnosis: See diagnosis of the type species.

Pseudodusa frattigianii n. sp.

Figs. 3–5

Holotype: Specimen figured as Fig. 3, housed in the collection of the SMNS, no. 65011 (ex coll. R. FRATTIGIANI).

Paratype: Specimen figured as Fig. 4, housed in the collection of the SMNS, no. 65012 (ex coll. K. HENNE).

Derivation of name: After ROGER FRATTIGIANI, Laichingen, who kindly donated the holotype.

Type locality: Eichstätt, S Franconia, Bavaria, S Germany.

Type horizon: Solnhofen Group, Upper Eichstätt Formation (see ZEISS 1977, fig. 8; Lower Tithonian, Hybonotum Zone).

Studied Material: 5 specimens (holotype; paratype; 2 additional specimens in private collections of G. KOSCHNY, Bad Soden, and 1 specimen in private collection of R. FRATTIGIANI, Laichingen).

Occurrence: Lower Tithonian (Hybonotum Zone) of Eichstätt.

Diagnosis. – Small penaeid with smooth carapace; rostrum anteriorly directed, coarsely serrate, with ventral tooth; pereopods I–III chelate, pereopods III extremely prolonged, carpopodites lacking swollen endings.

Description. – The holotype of *Pseudodusa frattigianii* n. gen. n. sp. is an excellently preserved moult lying on the surface of a bedding plane. Its length is about 73 mm. In the paratype the rostrum is preserved, easily visible by using ultraviolet illumination. On the dorsal side of the rostrum, 6 teeth are developed. There is one ventral tooth developed which is positioned opposite to the most anterior dorsal tooth. The carapace and abdomen are smooth. The carapace is subrectangular, with a broad triangular antennal spine. The antennae have a preserved length of 80 mm, thus reaching about the total length of the carapace and abdomen of the animal. The antennules are not preserved. Stalked eyes are developed. The scaphocerites are mostly covered by the antennal spine. The 3rd maxillipeds are broad and well-developed.

Pereopods I–III are chelate. Pereopods III are elongate, bearing slender propodites with long, straight fingers lacking teeth. The chelae of pereopods II resemble those of pereopods III, being slightly shorter. The chelae of pereopods I are strongest of all pereopods. In pereopods III, the carpus is almost twice as long as the manus. Pereopods IV–V are achelate and almost equal in size.

The abdominal somites bear well-developed pleura. The ventral margins of the pleura are smooth. The pleopods are biramous. The telson is long and pointed, but not sculptured. The uropodal exopodites are not completely preserved in any specimen, but a diaeresis is inferred to be present from the curved margin of their preserved proximal endings.

Discussion. – *Pseudodusa frattigianii* n. gen. n. sp. differs from *Dusa denticulata* MÜNSTER in having a more robust, straight rostrum bearing a single ventral tooth, and especially in lacking swollen proximal and distal endings of the carpopodites of the pereopods III. Moreover, the ventral margins of the abdominal pleura are lacking a serration.

In some respects, *Pseudodusa frattigianii* n. gen. n. sp. resembles very small specimens of “*Bylgia*” of the *B. haeberleini*-group (*B. haeberleini* MÜNSTER, *B. hexadon* MÜNSTER), but differs from the latter in lacking an epigastric tooth of the carapace and showing much taller propodites of pereopods III, which are extremely long in *Pseudodusa*. Moreover, in the *B. haeberleini*-group, the rostrum is curved ventrally.

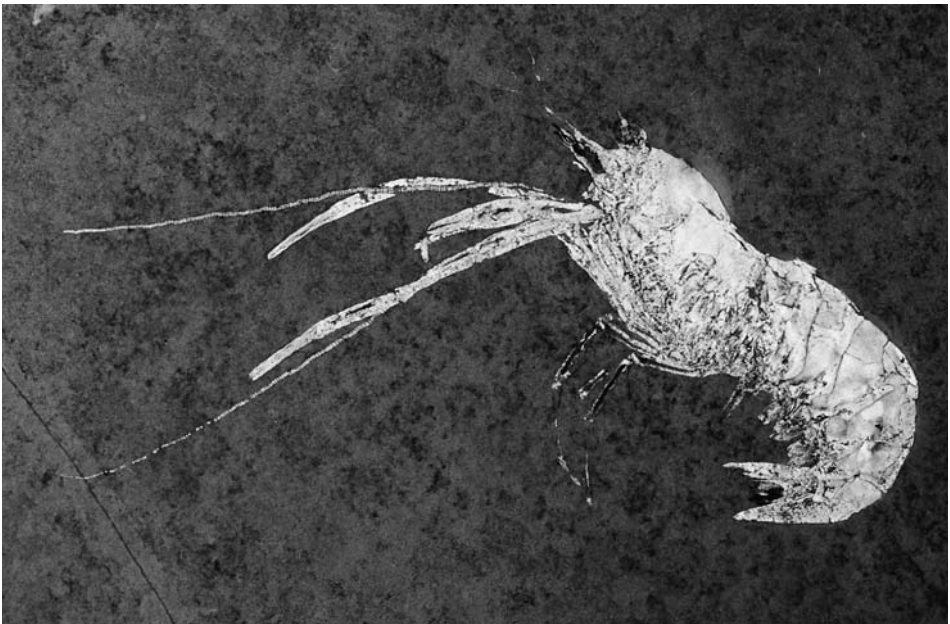


Fig. 3. *Pseudodusa frattigianii* n. gen. n. sp., holotype. Quarry district of Eichstätt; Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. – Top: Photograph under normal illumination; bottom: Photograph using ultraviolet illumination. SMNS 65011 (ex coll. R. FRATTIGIANI, Laichingen). – Width of figures: 15.0 cm.

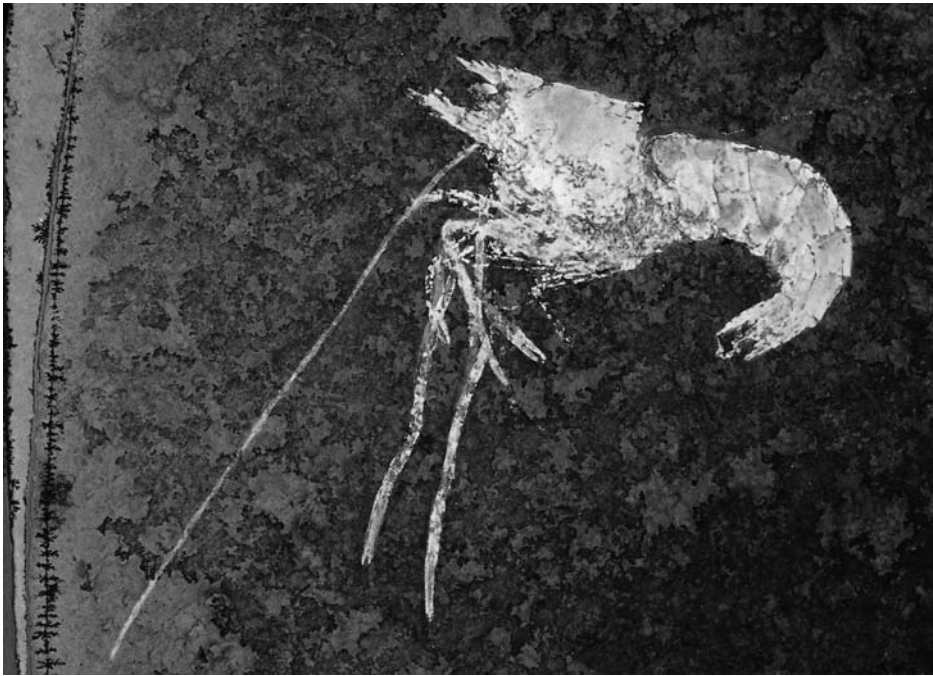


Fig. 4. *Pseudodusa frattigianii* n. gen. n. sp., paratype. Quarry district of Eichstätt; Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. – Top: Photograph under normal illumination; bottom: Photograph using ultraviolet illumination. SMNS 65012 (ex coll. K. HENNE, Stuttgart). – Width of figures: 7.8 cm.

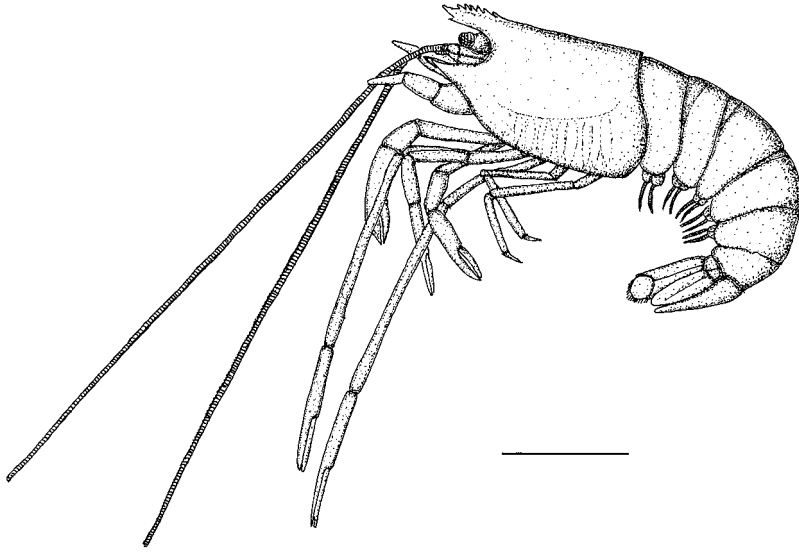


Fig. 5. Reconstruction of *Pseudodusa frattigianii* n. gen. n. sp. – Scale equals approximately 1 cm.

Possibly, *Pseudodusa* is closely related to this still unnamed genus hitherto included in *Bylgia* (SCHWEIGERT & GARASSINO, in prep.).

Pseudodusa frattigianii n. gen. n. sp. differs from *Antrimpos* MÜNSTER, 1839 in the following features: antennae are much shorter, pereiopods I are much stronger than pereiopods II–III, epigastric tooth is absent, and last abdominal somite is not prolonged. In some respects, *Pseudodusa* also resembles members of the Euzuzygida, being also characterized by elongate pereiopods III, but the 1st pleopods are biramose in *Pseudodusa*, not uniramous as in euzuzygids (cf. SCHRAM 1986: 279). The arrangement of the abdominal somites and pleura as well as the presence of 3 anterior pairs of chelate pereiopods, however, indicates its assignment to penaeids.

Genus *Bylgia* MÜNSTER, 1839

Type species: *Bylgia spinosa* MÜNSTER, 1839, subsequently designated by OPPEL (1862: 100).

Bylgia ruedeli n. sp.

Figs. 6, 8a

Holotype: Specimen figured as Fig. 6, housed in the collection of the SMNS, no. 65013 (ex coll. P. RÜDEL).

Derivation of name: After PETER RÜDEL, Gröbenzell, the former owner of the holotype.

Type locality: Öchselberg quarry near Breitenhill, S Franconia, Bavaria, S Germany (see BAUSCH 1963).

Type horizon: Solnhofen Group, Painten Formation, Öchselberg Member (see ZEISS 1977, fig. 8; Kimmeridgian/Tithonian boundary beds).

Studied Material: Holotype.

Occurrence: Kimmeridgian/Tithonian boundary beds of Öchselberg.

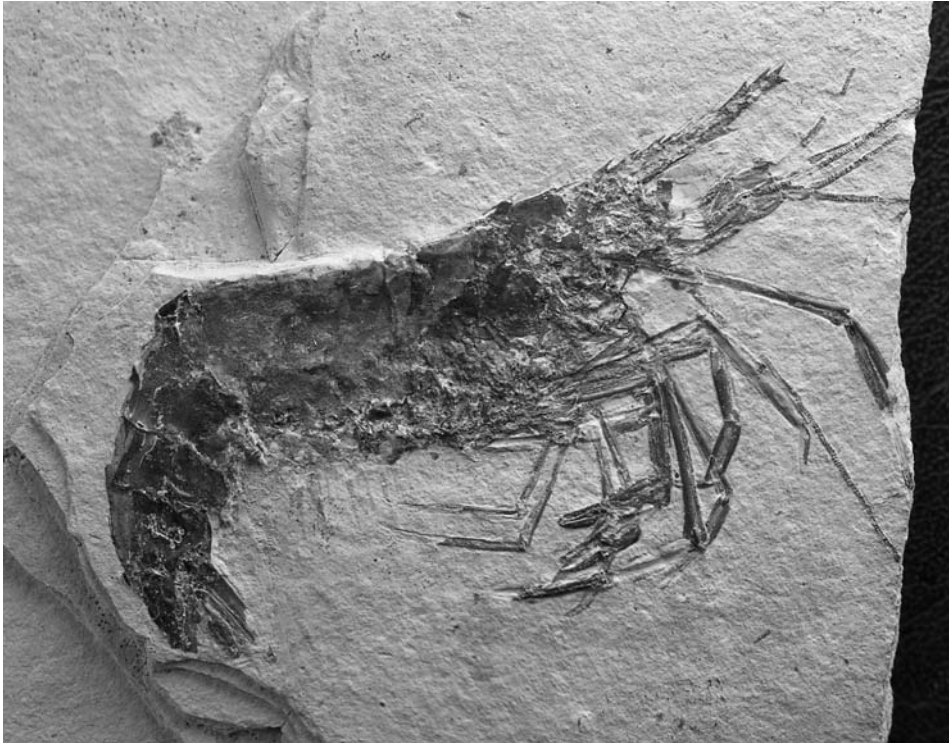


Fig. 6. *Bylgia ruedeli* n. sp.; Öchselberg quarry near Breitenhill, S Franconia, Bavaria; Solnhofen Lithographic Limestones (Painten Formation, Öchselberg Member), Kimmeridgian/Tithonian boundary beds. SMNS 65013 (ex coll. P. RÜDEL, Gröbenzell). – Width of figure: 16.0 cm.

Diagnosis. – *Bylgia* species bearing 8 dorsal teeth on a very long rostrum, and an epigastric tooth.

Description. – The holotype is a moderately preserved moult; the dorsal part of the abdomen which was part of the not available counter-plate, is missing and partly restored by a brown-coloured painting. Its total length is about 106 mm. The carapace is relatively short. Its ventral and anterior margins are not clearly discernible due to poor preservation. Both carapace and abdomen have smooth surfaces. A very long rostrum is upwardly curved anteriorly with a trispinose tip. On its dorsal side, 8 forwardly directed teeth are present. Posteriorly, the epigastric tooth is present behind the rostrum. There are 2 ventral teeth, one of which located approximately opposite to the fourth one on the dorsal side of the rostrum, the other one is located just below the tip.

The antennae are moderately long, but incompletely preserved. The antennules, which are biflagellate, look like those of *B. spinosa* MÜNSTER (see OPPEL 1862, pl. 29, fig. 1). Stalked eyes are developed. The scaphocerites are poorly preserved; they are supposed to have looked like those of *B. spinosa*. The 3rd maxillipeds are relatively long and slender. Pereiopods I–III are chelate, increase in size from the 1st to the 3rd pair, the latter remarkably enlarged and bearing slender propodites with gracile smooth fingers. The broadest, strongest propodites are developed in short

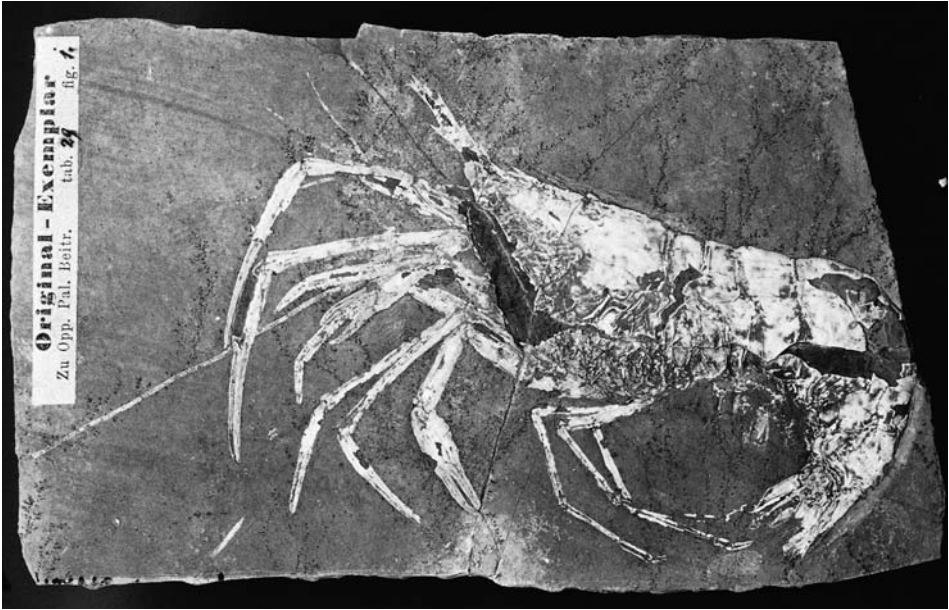


Fig. 7. *Bylgia spinosa* MÜNSTER, holotype. Quarry district of Eichstätt; Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. – Photograph using ultraviolet illumination. BSPM AS VII 713 (coll. G. GRAF ZU MÜNSTER). – Width of figure: 12.5 cm.

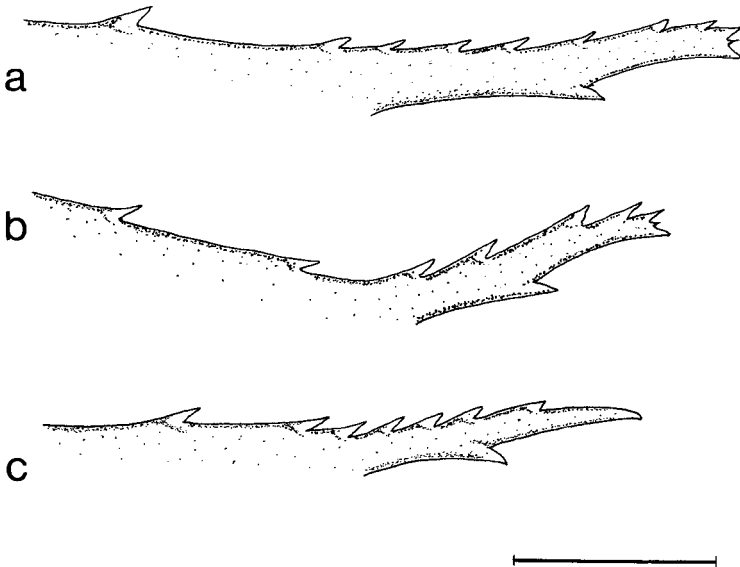


Fig. 8. Comparison of rostra in a. *Bylgia ruedeli* n.sp., b. *Bylgia spinosa* MÜNSTER, and c. “*Bylgia*” *hexadon* MÜNSTER. – Scale equals 5 mm.

pereiopods I. The pereiopods IV–V are achelate and almost equal to one another in length.

The abdominal somites are equal in length. The biramose pleopods are well developed; in the holotype they are preserved in the abdominal somites I–III. The telson is pointed. The uropodal exopodites are not completely preserved, but interpreted to bear a curved diaeresis, as in the closely related type species, *B. spinosa* MÜNSTER (Fig. 7). This feature, however, was overlooked in the reconstruction of the holotype given by OPPEL (1862, pl. 29, fig. 1) which was reproduced by GLAESSNER (1969, fig. 253.4).

Discussion. – In contrast to the type species *Bylgia spinosa* MÜNSTER, *B. ruedeli* n. sp. differs – at equal sizes of compared specimens – in having a much longer rostrum with 8 instead of only 6 dorsal teeth (see Fig. 8). The fingers of the pereiopods II and III are much shorter than in *B. spinosa*. The other two Jurassic species hitherto assigned to *Bylgia*, “*B.*” *hexadon* MÜNSTER and “*B.*” *haeberleinii* MÜNSTER, differ in several significant characters from the type species and *B. ruedeli* n. sp., for example in having a different type of rostrum (see Fig. 8c). They will be separated from *Bylgia* s. str. and joint in a new genus during the revision of decapod crustaceans from the Solnhofen Lithographic Limestones (GARASSINO & SCHWEIGERT, in prep.). Following GLAESSNER (1969), *Bylgia* is assigned to penaeids.

Genus *Koelga* MÜNSTER, 1839

Type species: *Koelga curvirostris* MÜNSTER, designated herein.

Remarks. – OPPEL (1862) previously stated that most taxa originally included in the genus *Koelga* must be attributed to other species or are based on very poorly preserved material, hence representing nomina dubia. The only remaining valid species is *Koelga curvirostris* MÜNSTER, which OPPEL tentatively included in *Drobna* MÜNSTER, 1839. To stabilise the generic name *Koelga* we here designate *K. curvirostris* subsequently as the type species, its holotype figured photographically for the first time as Fig. 9.

Emended diagnosis. – Small to medium sized penaeids; carapace with slightly curved dentate rostrum, with upwardly pointing tip and ventral tooth; antennae very long; surface of carapace and abdomen punctate; anterior 3 pairs of pereiopods chelate, others achelate; pereiopods III strongest; abdominal somite III slightly longer than preceding one; uropods slender, diaeresis present.

Included species: *Koelga curvirostris* MÜNSTER, *Koelga muensteri* n. sp.

Koelga muensteri n. sp.

Fig. 10

? 1999 unbenannter Schwimmkrebs. – FRICKHINGER, p. 42, fig. 65.

Holotype: Specimen figured as Fig. 10, housed in the collection of the SMNS, no. 65356 (ex coll. R. FRATTIGIANI).

Derivation of name: In honour of GEORG GRAF ZU MÜNSTER (1776–1844), enthusiastic collector and one of the first workers who scientifically described decapod crustaceans from the Solnhofen Lithographic Limestones (MÜNSTER 1839; today his crustacean collection is housed in the BSPM).

Type locality: Eichstätt, S Franconia, Bavaria, S Germany.

Type horizon: Solnhofen Group, Upper Eichstätt Formation (see ZEISS 1977, fig. 8; Lower Tithonian, Hybonotum Zone).



Fig. 9. *Koelga curvirostris* MÜNSTER, holotype (= MÜNSTER 1839, pl. 22, fig. 3). Quarry district of Eichstätt; Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. – Top: Photograph under normal illumination; bottom: Photograph using ultraviolet illumination. BSPM AS VII 727 (coll. G. GRAF ZU MÜNSTER). – Width of figures: 8.8 cm.

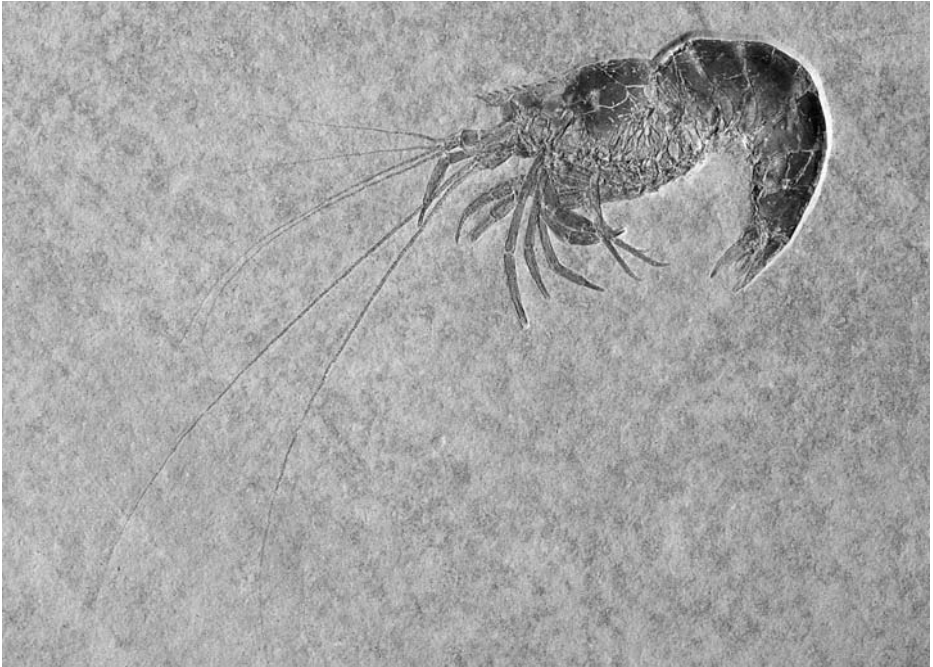


Fig. 10. *Koelga muensteri* n. sp., holotype. Quarry district of Eichstätt; Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. – Top: Photograph under normal illumination; bottom: Photograph using ultraviolet illumination. SMNS 65356 (ex coll. R. FRATTIGIANI, Laichingen). – Width of figures: 16.4 cm.

Studied material: 3 specimens (holotype; 2 further cf.-specimens in private collections of P. BÜRGER, Bad Hersfeld, and D. KÜMPEL, Wuppertal).

Occurrence: Lower Tithonian (Hybonotum Zone) of Eichstätt.

Diagnosis. – Large species of *Koelga*, rostrum bearing 7 dorsal teeth; surface of carapace and abdomen roughly punctate.

Description. – The carapace and abdomen as well as the pereopods are covered with small, rather widely scattered pits. The total length of the adult holotype is 106 mm. The carapace is subtriangular, with a curved postero-ventral margin. The antennal spine is not visible. The rostrum is weakly curved, its tip is pointed upward, with 7 teeth, and the epigastric tooth follows at a short distance posterior to the rostrum. The latter is broken off in the holotype. The ventral tooth is located opposite and slightly in front of the most anterior dorsal tooth.

The antennae are a little longer than the body; their length is about 115 mm. The biflagellate antennules are less than half as long as the antennae. Both flagellae differ in their lengths, the longer one is about 60 mm, the shorter one about 43 mm. The eyes are well-developed, with a short basal stalk. The shape of the scaphocerites is unknown. The 3rd maxillipeds are long and slender; like the other appendices, they show a sparsely punctate surface. Pereiopods I–III are chelate, isochelous, they decrease in length from the 1st to the 3rd. Pereiopods IV are achelate. Pereiopods V are presumed to be achelate but are not preserved in the holotype. Pereiopods III are strongest, with broad propodites, in which the hand is as long as both fingers. The margin of the propodus of pereopod IV exhibits small spines.

The abdominal somites are remarkably high with well-developed pleura. Each pleuron of the somites overlaps the preceding one. The ventral margins of the pleura are smooth. Abdominal somite VI is somewhat longer than somite V. The pleopods are not preserved in the holotype, but interpreted to be bi-ramose as in *K. curvirostris* MÜNSTER.

Two other (cf.-)specimens, in which the rostrum is not clearly visible because of a torsion of the carapace, exhibit a well-preserved telson with slender uropods; their exopodites bear a curved diaeresis. The telson is pointed. In contrast to most other Upper Jurassic penaeids they are ornamented with scattered pustules and a median ridge. These features, however, are not well visible in the holotype, due to the poor preservation status of the telson and its lateral embedding.

Discussion. – *Koelga muensteri* n. sp. differs from the type species in its much higher rostrum with 7 dorsal teeth (without counting the epigastric tooth) and its much larger adult size. The punctuation of the carapace and abdomen is much less dense than in *Drobna*, which seems to be a very closely related penaeid.

Infraorder Caridea DANA, 1852

Superfamily Procaridoidea CHACE & MANNING, 1972

Family uncertain

Genus *Udora* MÜNSTER, 1839

Type species: *Udora brevispina* MÜNSTER, 1839, subsequently designated by OPPEL (1862: 112).

Udora koschnyi n. sp.

Figs. 11–13

Holotype: Specimen figured as Fig. 11, housed in the collection of the SMNS, no. 65015 (ex coll. G. KOSCHNY).

Derivation of name: In honour of GÜNTER KOSCHNY, Bad Soden, who kindly donated the holotype of this new species.

Type locality: Eichstätt, S Franconia, Bavaria, S Germany.

Type horizon: Solnhofen Group, Upper Eichstätt Formation (see ZEISS 1977, fig. 8; Lower Tithonian, Hybonotum Zone).

Studied material: 2 specimens (holotype; 1 additional adult specimen (Fig. 12) in private collection of P. RÜDEL, Gröbenzell).

Occurrence: Lower Tithonian (Hybonotum Zone) of Eichstätt.

Diagnosis. – *Udora* with remarkably enlarged pereopods I–III.

Description. – The holotype of *Udora koschnyi* n. sp. is a moderately preserved moult of a juvenile specimen. Its length is 34 mm. The other studied specimen (Fig. 12) is 66 mm long. More details of its anatomy are discernible by using ultraviolet illumination. The surface of the carapace and abdomen is very finely punctate, only visible in a few better-preserved parts. The dorsal margin of the carapace is straight, lacking an epigastric tooth. Anteriorly, it ends in a short rostrum, which seems to be smooth. The posterior margin of the carapace is strongly indented.

The antennae and antennules are poorly preserved in both studied specimens. The length of the biflagellate antennules is about equal to the length of the dorsal carapace, whereas the antennae are as long as the entire body. The eyes are poorly preserved, showing a very short basal stalk. The scaphocerites are long and pointed, showing a lateral crest. The 3rd maxillipeds have marginal spines. Pereiopods I–III are remarkably enlarged, their carpopodites and meropodites are remarkably elongate. The posterior 2 pairs of pereiopods are much shorter. All pereiopods are achelate. The mentioning of chelate pereiopods I in *Udora* by GLAESSNER (1969) is erroneous. Lateral spines are not detectable in the pereiopods.

In the abdomen, the pleura of the abdominal somite II is widest of all pleura. The pleopods are biramose and equally developed in all somites. The telson and uropods are poorly preserved. Interestingly, the telson ends in a fork, similar to that in Recent *Palaemon*. The presence of a curved diaeresis in *U. brevispina* MÜNSTER, was overlooked in the otherwise accurate description and reconstructions provided by OPPEL (1862, pl. 37, figs. 1–2). This diaeresis is also present in *Udora koschnyi* n. sp.

Discussion. – *Udora koschnyi* n. sp. mainly differs from *U. brevispina* MÜNSTER in its much longer and spineless pereiopods I–III, which is not a character of juveniles as previously thought (as in juvenile *Aeger*, cf. FÖRSTER 1967), because it is also present in the well-preserved adult specimen (Fig. 12). In contrast, the antennae and antennules are much longer in *U. brevispina*. *Udora varispina* MÜNSTER is a subjective synonym of *U. brevispina* MÜNSTER, because the type specimens do not differ significantly from one another (GARASSINO & SCHWEIGERT, in prep.). However, it cannot be excluded that *U. brevispina* MÜNSTER and *U. koschnyi* n. sp. represent different sexes. Since none of the two studied specimens of *U. koschnyi* n. sp. has sexual differentiations such as petasmae or appendices masculinae preserved, both taxa must be kept taxonomically separate. In *U. brevispina*, the carapace bears the postorbital and hepatic spines, which are only visible in a few well-preserved specimens (Fig. 14). Most probably, these spines are also present but are not preserved in *U. koschnyi* n. sp.

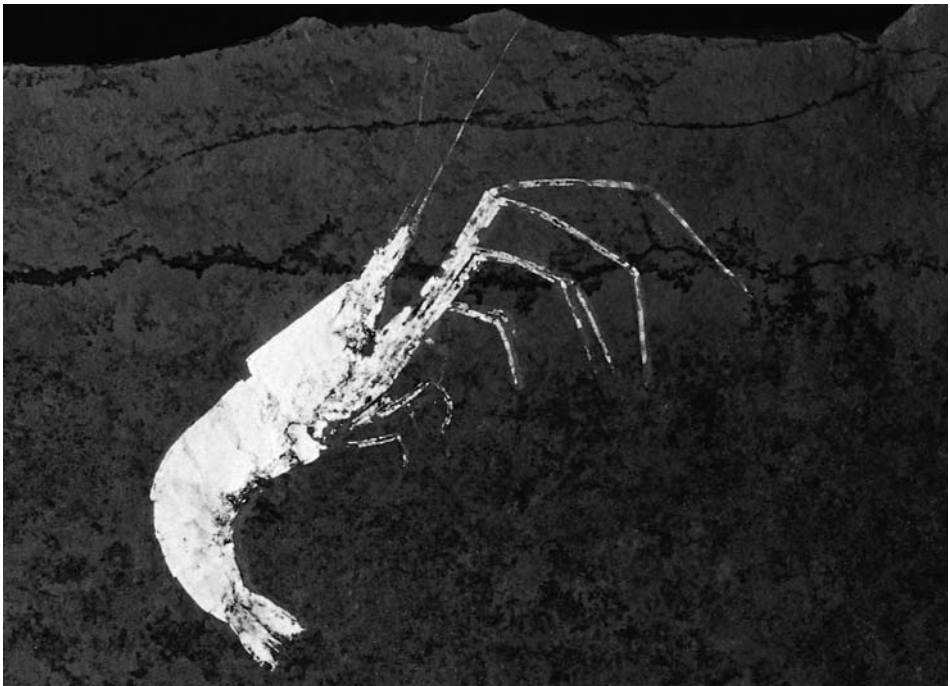


Fig. 11. *Udora koschnyi* n. sp., juvenile specimen, holotype. Quarry district of Eichstätt; Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. – Top: Photograph under normal illumination; bottom: Photograph using ultraviolet illumination. SMNS 65015 (ex coll. G. KOSCHNY, Bad Soden). – Width of figures: 7.9 cm.



Fig. 12. *Udora koschnyi* n. sp., adult specimen. Quarry district of Eichstätt; Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. – Photograph using ultraviolet illumination. Private collection of P. RÜDEL, Gröbenzell. – Width of figure: 10.5 cm.

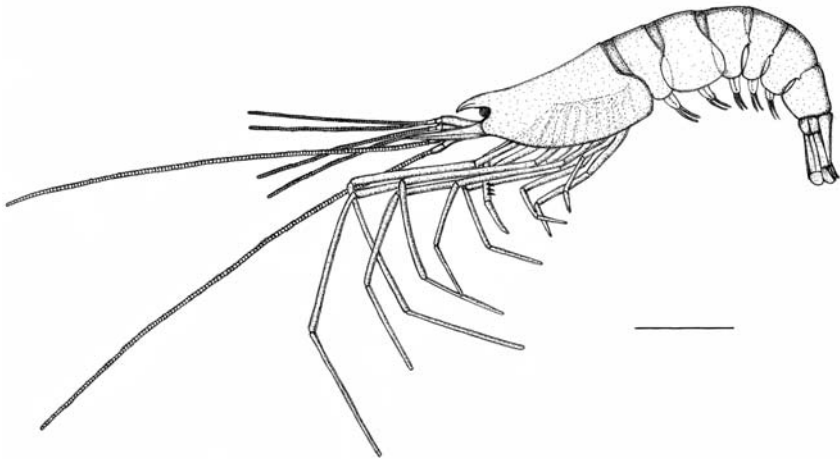


Fig. 13. Reconstruction of *Udora koschnyi* n. sp. – Scale equals approximately 1 cm.

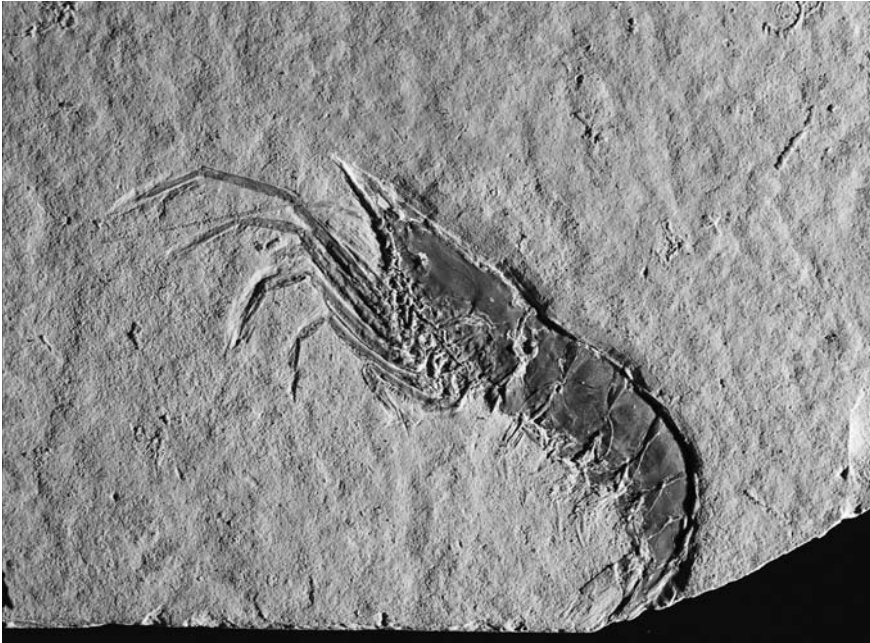


Fig. 14. *Udora brevispina* MÜNSTER. Quarry district of Eichstätt; Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. BSPM 1964 XXIII 593. – Width of figure: 8.9 cm.

The absence of chelate pereiopods appears to be a primitive character within carideans placing this genus in Procaridoidea CHACE & MANNING, 1972. Within Jurassic genera, this feature is also known from the next described one, *Pleopteryx*, which differs otherwise strongly by enigmatic pleopodal differentiations.

Superfamily and family uncertain

Genus *Pleopteryx* n. gen.

Type species: *Pleopteryx kuempeli* n. sp.

Derivation of name: From Greek *pteryx* = feather, after the feather-like appendices of the pleopods.

Diagnosis: See diagnosis of the type species.

Pleopteryx kuempeli n. sp.

Figs. 15–18

v 2003b Eukyphid (n. gen., n. sp.). – SCHWEIGERT & GARASSINO, p. 178, fig. 3 c.

Holotype: Specimen figured as Fig. 15, housed in the collection of the SMNS, no. 64943 (ex coll. D. KÜMPEL).

Paratypes: Specimens figured as Figs. 16–17, SMNS 64942, 64944.

Derivation of name: In honour of DIETER KÜMPEL, Wuppertal, who kindly donated important specimens of the new species for this study.

Type locality: Eichstätt, S Franconia, Bavaria, S Germany.

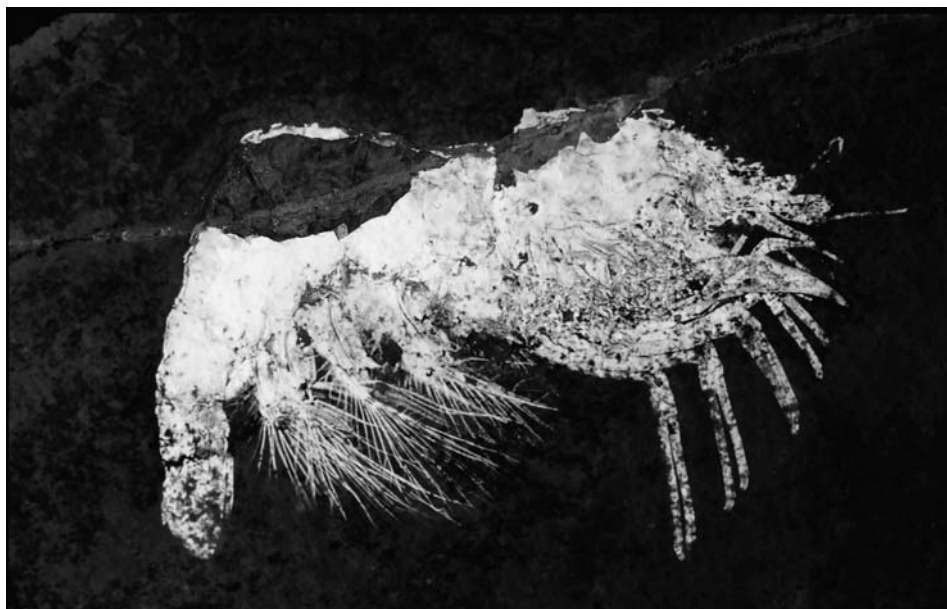


Fig. 15. *Pleopteryx kuempeli* n. gen. n. sp., holotype. Quarry district of Eichstätt; Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. – Top: Photograph under normal illumination; bottom: Photograph using ultraviolet illumination. SMNS 64943 (ex coll. D. KÜMPEL, Wuppertal). – Width of figures: 7.0 cm.

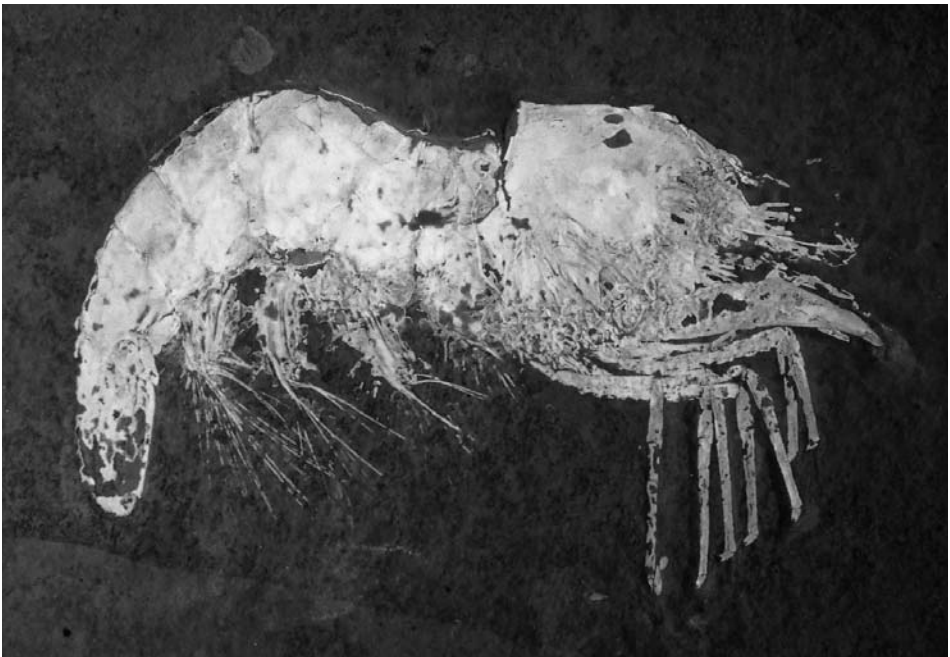
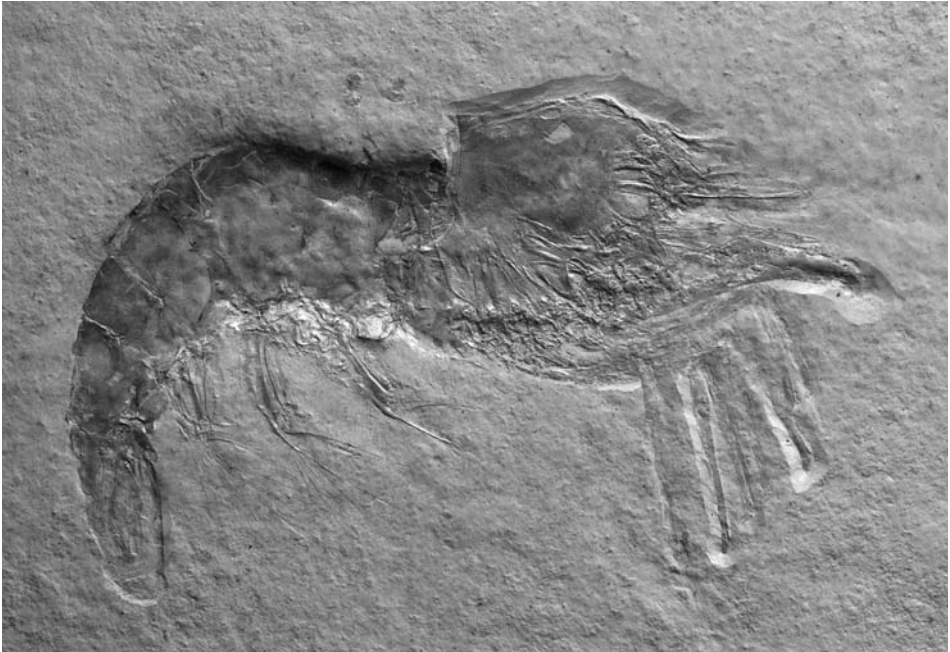


Fig. 16. *Pleopteryx kuempeli* n. gen. n. sp., paratype 1. Quarry district of Eichstätt; Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. – Top: Photograph under normal illumination; bottom: Photograph using ultraviolet illumination. SMNS 64942 (ex coll. W. LUDWIG, Berlin). – Width of figures: 6.0 cm.



Fig. 17. *Pleopteryx kuempeli* n. gen. n. sp., paratype 2. Quarry district of Eichstätt; Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. – Top: Photograph under normal illumination; bottom: Photograph using ultraviolet illumination. SMNS 64944 (ex coll. D. KÜMPEL, Wuppertal). – Width of figures: 9.0 cm.

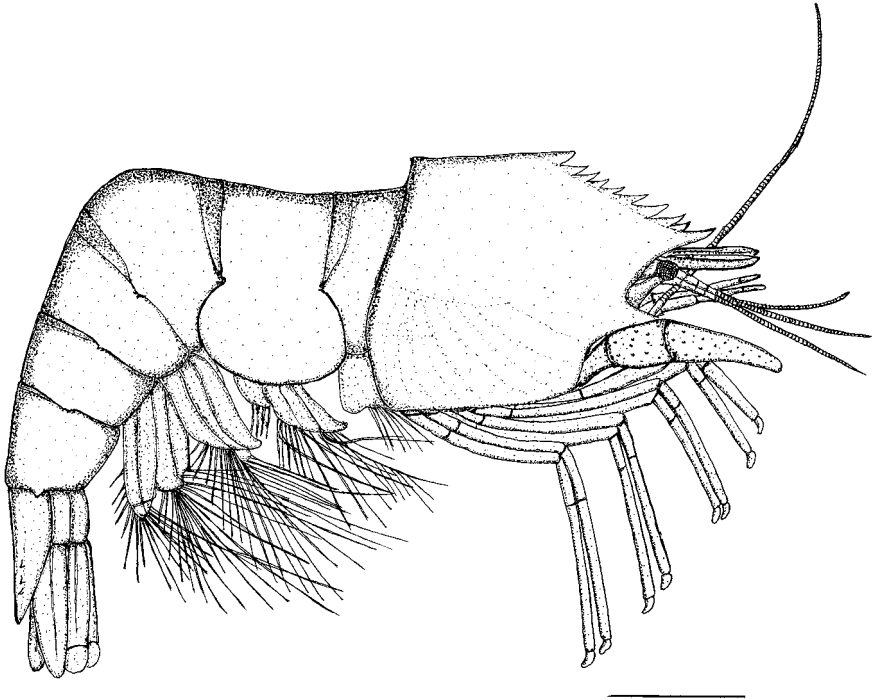


Fig. 18. Reconstruction of *Pleopteryx kuempeli* n. gen. n. sp. The strong structure in the ocular incision represents the scaphocerites. Obviously the position of the cephalic appendices appears a little displaced due to decay before burial. – Scale equals approximately 1 cm.

Type horizon: Solnhofen Group, Upper Eichstätt Formation (see ZEISS 1977, fig. 8; Lower Tithonian, Hybonotum Zone).

Studied material: 4 specimens (holotype; 2 paratypes; 1 additional specimen in private collection of G. KOSCHNY, Bad Soden).

Occurrence: Lower Tithonian (Hybonotum Zone) of Eichstätt.

Diagnosis. – Carapace smooth; rostrum serrate; pereopods I achelate, very strong, prominent; size of other pereopods continuously increasing from 2nd to 5th pair, all achelate; pleopods with large, feather-like appendices covering biramose flagella.

Description. – The holotype is a strongly sclerotized moult embedded on the lower surface of a thin limestone plate. Its length is about 70 mm. The surface of the carapace and abdomen is smooth. The carapace is relatively short and high, with a declining fronto-dorsal margin and a marked antennal spine. The strongly serrated rostrum, grading to the dorsal carapace without interruption, is only preserved in the holotype, in the other studied specimens it is hidden due to an oblique embedding. The eyes are stalked.

The antennae are short and very delicate, their length is only about half of the length of the entire body. Their bases are covered with small pustules. The poorly preserved antennules, most probably threeflagellate, are exclusively discernible in the paratype 2 (Fig. 17). The scaphocerites exhibit a lateral crest. The 3rd maxillipeds are long and slender. The achelate pereopods I are very prominent and strongly

sclerotized. Their surface bear small pustules scattered in an irregular pattern. Their length is about equal to the carapace length.

The abdominal somites exhibit well-developed pleura; somite II is the widest. Their ventral border is smooth. The pleopods are biramose and only visible in one specimen (Fig. 17), which was otherwise poorly prepared. In good preservation state they are covered by large, enigmatic feather-like appendices (possibly representing endites) laterally attached to the pleopods. Thus, the appendices do not represent a differentiation of the pleopods only developed in females but occur in both sexes. The short telson exhibits a pointed tip and an almost smooth surface, apart from a few lateral spikes in the posterior part. In the exopodites of the uropods the diaeresis is developed, but it is not easily discernible in any of the studied specimens.

Discussion. – According to available data (cf. HOLTTHUIS 1955), giant, feather-like appendices of the pleopods are a unique character within fossil and Recent carideans. If these lateral appendices of the pleopods or the strong pereopods I are well preserved, it is impossible to misidentify this taxon. Achelate pereopods I–III are very rare in fossil carideans, besides *Pleopteryx* they are also present in *Udora* MÜNSTER, 1839.

Genus *Buergerocaris* n. gen.

Type species: *Buergerocaris psittacoides* n. sp.

Derivation of name: From Greek *caris* = shrimp, and PETER BÜRGER, Bad Hersfeld, who donated the holotype of the type species and many other important new taxa from the Solnhofen Lithographic Limestones.

Diagnosis: See diagnosis of the type species.

Buergerocaris psittacoides n. sp.

Figs. 19–22

v 1994 Unbenannter Panzerkrebs. – FRICKHINGER, p. 127, fig. 228.

v 2001 Penaeidae nov. gen. nov. sp. – DIETL & SCHWEIGERT, p. 71.

Holotype: Specimen figured as Fig. 19, housed in the collection of SMNS, no. 65010 (ex coll. P. BÜRGER).

Derivation of name: From Latin *psittacus* = parrot; after the shape of the fingers of the 2nd pereopod resembling a parrot's beak.

Type locality: Eichstätt, S Franconia, Bavaria, S Germany.

Type horizon: Solnhofen Group, Upper Eichstätt Formation (see ZEISS 1977, fig. 8; Lower Tithonian, Hybonotum Zone).

Studied Material: 5 specimens (holotype; 1 specimen from the vicinity of Eichstätt in private collection of R. FRATTIGIANI, Laichingen; 1 specimen of same provenance in private collection of P. BÜRGER, Bad Hersfeld (Fig. 20); 1 pair of chelae from the Solnhofen Lithographic Limestones of Apfeltal near Mörsheim in the private collection of M. WULF, Rödelsee; 1 strongly bitten moult with chelae from the Nusplingen Lithographic Limestone, Fig. 21, SMNS 64413).

Occurrence: Lower Tithonian (Hybonotum Zone) of Eichstätt and Mörsheim, Upper Kimmeridgian of Nusplingen (Beckeri Zone, Ulmense Subzone).

Diagnosis. – Small caridean with smooth carapace and abdomen; rostrum serrate dorsally; pereopods I–III chelate, pereopods I strongest, bearing propodites with short, strong, isochelous fingers.

Description. – The holotype is a moderately preserved moult. Its length is about 68 mm. The surface of the carapace and abdomen is smooth. The carapace is



Fig. 19. *Buergerocaris psittacoides* n. gen. n. sp., holotype. Quarry district of Eichstätt; Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. – Top: Photograph under normal illumination, distal part of antenna is an artefact; bottom: Photograph using ultraviolet illumination. SMNS 65010 (ex coll. P. BÜRGER, Bad Hersfeld). – Width of figures: 8.9 cm.

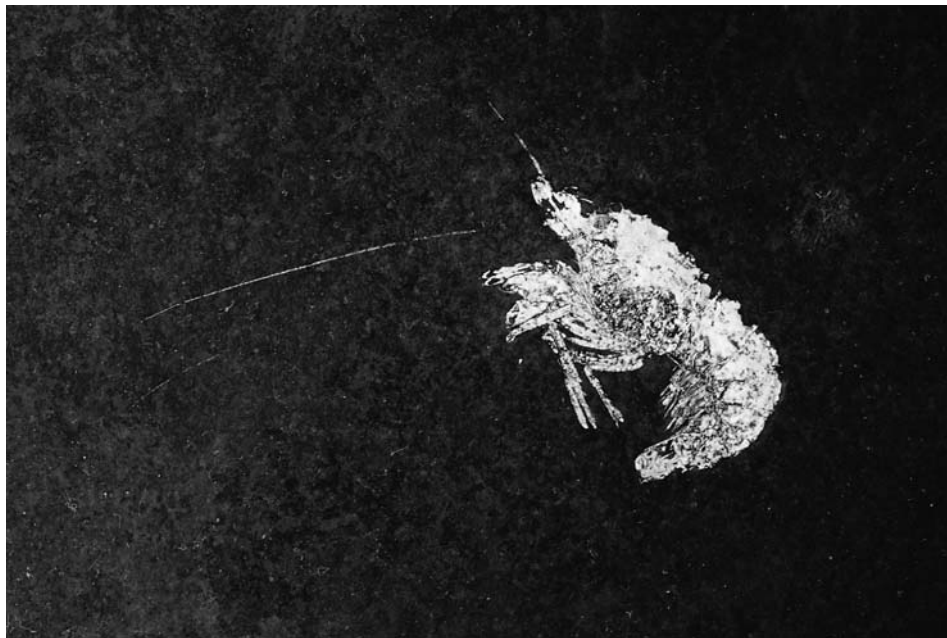


Fig. 20. *Buergerocaris psittacoides* n. gen. n. sp., same location and age as Fig. 19. (Coll. P. BÜRGER, Bad Hersfeld). – Photograph using ultraviolet illumination. – Width of figure: 10.0 cm.



Fig. 21. *Buergerocaris psittacoides* n. gen. n. sp., bitten moult consisting of several damaged pereopods. Nusplingen, Swabia; Nusplingen Lithographic Limestone, bed L (see section in DIETL et al. 1998), 10–15 cm from top; Upper Kimmeridgian, Beckeri Zone, Ulmense Subzone. Photograph using ultraviolet illumination. SMNS 64413a (excavation campaign 2000). – Width of figure: 4.5 cm.

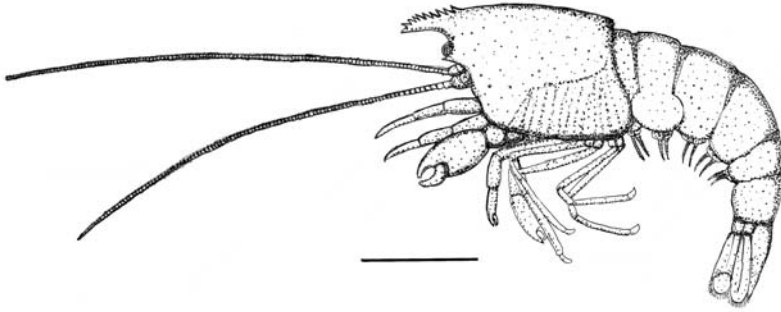


Fig. 22. Reconstruction of *Buergerocaris psittacoides* n. gen. n. sp.; exact length of antennae unknown. – Scale equals approximately 1 cm.

subrectangular in outline, with a short antennal spine. In one of the studied specimens (in private collection of R. FRATTIGIANI), the poorly preserved rostrum bears 9 dorsal teeth.

The antennae which are visible by using ultraviolet illumination are 25 mm in length. They end abruptly at a fracture within the plate. Thus, their original length was larger, reaching approximately the length of the body (see Fig. 20). The antennules are not preserved in the holotype and missing or only very incompletely preserved in the other studied specimens. Also the scaphocerites are not discernible. The eyes are well-developed. The 3rd maxillipeds are long and slender. The anterior 3 pairs of pereiopods are very similar in shape, but differ in size. Pereiopods I are the strongest. Both pereiopods I and II exhibit broad, isochelous propodites, and the chelae resemble the beak of a parrot. Both fingers are short, strong and equal in size. Pereiopods III also bear isochelous chelae. Both pereiopods IV and V are achelate, and almost equal in size.

In the abdomen, the pleura of somite II are wider than those of somites I and III. Due to its rather poor preparation, this character could be easily overlooked in the holotype, but is clearly visible in the specimen figured by FRICKHINGER (1994, fig. 228). The 6th abdominal somite is the longest. The pleopods are biramose. The telson is smooth and pointed. In the exopodites of the uropods the diaeresis is developed. The tail fan is poorly preserved in the holotype, but is easily discernible in another specimen from the BÜRGER collection (Fig. 20).

Discussion. – The shape of the fingers of pereiopods I and II is so typical, that a misidentification of *Buergerocaris* with other shrimps seems impossible. The presence of 3 pairs of chelate pereiopods is unusual in carideans, in most of which only 2 chelate pairs are developed. In this feature, *Buergerocaris* appears advanced and resembles primitive astacids like *Uncina* or *Malmuncina* (see SCHWEIGERT et al. 2003, SCHWEIGERT & GARASSINO 2003a), whereas the strongly curved abdomen, the well-developed pleopods and the remarkably short carapace lacking furrows better fits with carideans.

Genus *Hefriga* MÜNSTER, 1839

Type species: *Hefriga serrata* MÜNSTER, 1839, subsequently designated by OPPEL (1862).

Remarks. – The spelling *Hefriga* “*sorrata*” in MÜNSTER (1839) which was adopted by FÖRSTER (1967: 170) is a lapsus calami: In the figure caption it is correctly written “*serrata*” and a second taxon simultaneously introduced by MÜNSTER was named *H. subserrata*, clearly referring to the previously described *H. serrata*, and the serrate rostrum developed in this species. Hence the spelling “*serrata*” is correct and must be used (ICZN 1999, Art. 32.5.1).

Hefriga proboscideawulfi n. sp.

Fig. 23

Holotype: Specimen figured as Fig. 23, housed in the collection of JME, no. SOS 4879 (ex coll. M. WULF).

Derivation of name: From Latin *proboscis* = proboscis, referring to the ventrally directed shape of the rostrum, and in honour of MATTHIAS WULF, Rödelsee, who kindly donated the holotype.

Type locality: Zandt, S Franconia, Bavaria, S Germany.

Type horizon: Solnhofen Group, Painten Formation, Zandt Member (see ZEISS 1977, fig. 8; Lower Tithonian, Hybonotum Zone).

Studied material: Holotype.

Occurrence: Lower Tithonian (Hybonotum Zone) of Zandt.

Diagnosis. – Species of *Hefriga* with finely dentate, ventrally curved rostrum.

Description. – The holotype is a well preserved moult lying on a soft chalky bedding surface. Its length is about 42 mm. The surface of the carapace and abdomen is covered by a delicate pattern of subparallel striae, which is typical of *Hefriga* (cf. FÖRSTER 1967). The carapace is relatively short and high, with a rounded ventral margin and a well-developed antennal spine. The rostrum is ventrally curved and bears about 12 small, forwardly-directed, dorsal teeth.

A short fragment of one of the antennae is preserved. The basis of the antennules and some remains of the short antennules are visible. The scaphocerites are relatively broad, bearing a lateral crest. The shortly stalked eyes are large, but incompletely preserved. The 3rd maxillipeds are strong.

Pereiopods I–II are expected to be chelate, similar to those of *Hefriga serrata* MÜNSTER (FÖRSTER 1967). However, the chelae are not preserved in the holotype since they were not fully regenerated after an amputation or autotomy. The posterior 3 pairs of pereiopods are achelate, almost equal in size, and have dactyls with a rounded tip. The propodites bear very tiny spines on their posteriorly directing sides.

The pleura of abdominal somite II broadly extend onto both the previous and the following somites. In the pleopods of somites II–VI, only long bases are preserved, and the flagellae are missing. In somite I a petasma is developed, therefore the holotype is male. The telson ends in short appendices at the pointed tip, and it bears several short lateral processes at each side. The uropodal exopodites exhibit a curved di-aeresis.

Ultraviolet illumination of the specimen does not provide further details, because the fluorescence is too weak, as in many decapods from the lithographic limestones of Zandt.

Discussion. – The remarkably long, ventrally curved shape of the rostrum is unique in *Hefriga* and unknown from other shrimps of the Upper Jurassic. In *Hefriga serrata* MÜNSTER and *H. frischmanni* OPPEL the rostrum is straight.

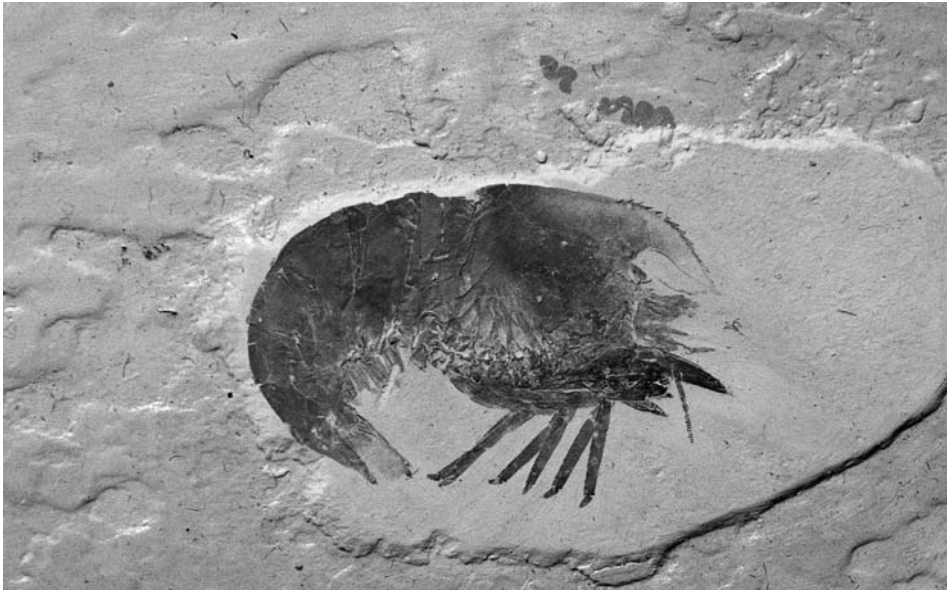


Fig. 23. *Hefriga proboscideawulfi* n. sp., holotype. Zandt, S Franconia, Bavaria; Solnhofen Lithographic Limestones (Painten Formation, Zandt Member), Lower Tithonian, Hybonotum Zone. – Top: complete specimen; bottom: Detail of the frontal area with the rostrum. JME SOS 4879 (ex coll. M. WULF, Rödelsee). – Width of top figure: 5.0 cm.

3. Diversity of penaeids and carideans in the Solnhofen Lithographic Limestones

Within penaeids, *Antrimpos speciosus* MÜNSTER and *Aeger spinipes* (DESMAREST) represent the most common natant decapods of the Upper Jurassic lithographic limestones of S Franconia although they are rare or even totally missing in some of the fossil-bearing sites. Several smaller penaeids or juveniles of uncertain affinity sometimes occur in masses or clusters, suggesting that they may have lived in groups. However, some genera are always extremely rare, like the herein newly described *Albertoppelia*, *Buergerocaris*, *Pseudodusa*, but also *Bylgia* and *Koelga*, pointing to a much larger decapod diversity in the Late Jurassic palaeoenvironments.

Apart from the moderately frequent, but often incompletely preserved *Hefriga serrata* MÜNSTER, caridean decapods are also very rare. On the other hand, these lithographic limestones hitherto represent the only source of carideans from the Late Jurassic at all. Most new taxa are only recorded by a single or very few specimens. This might be explained by several different reasons:

- (a) Some quarries which were open in the 18th or 19th century and proliferated interesting material are now abandoned and mostly covered with rubbish, or totally exploited, so that no further material from these sites is available.
- (b) Specimens of some taxa are poorly preserved and are therefore not sold by the workers in the quarries, or are ignored by fossil collectors.
- (c) The original habitat was far away from the place of burial so that there was little chance for delicate exuviae to become fossilised.
- (d) Individuals of the new taxa lived in habitats normally separated from the lagoonal areas by ecological barriers. Today, the most diverse decapod faunas come from coral reefs (NEUMANN et al. 1997), in which shrimps and prawns are never preserved in situ due to their weak mineralisation of the carapace. In these shallow-marine settings, only the occurrence of some internally structured microcoprolites (e.g. *Favreina*, *Palaxius*; SCHWEIGERT et al. 1997) might point to the existence of decapods.
- (e) Specimens of new taxa were not recognized as differing from already known taxa which have a similar morphology.
- (f) Decapod crustaceans are mainly purchased by enthusiastic private collectors, and only few of them by institutional collections; thus, they are usually not available for study.
- (g) Some of the rare decapod crustacean species were adapted to very specialised environmental conditions and lived solely, not in groups.

A combination of all these factors is responsible for the incomplete state of documentation which is still a fact regarding the present fossil record of decapod crustaceans, even in lithographic limestone lithology.

4. Palaeoecology of the newly described taxa

Since in most cases the place of burial of the crustacean moults of the lithographic limestones is not identical with the original habitat of the living animals, palaeoecological assumptions are mainly based on a functional analysis of the preserved remains.

All decapod crustaceans studied herein, except *Koelga muensteri* n. sp. and *Buergerocaris psittacoides* n. gen. n. sp., exhibit relatively short antennae and well-developed complex eyes adapted to well-lighted conditions suggesting that their favourite habitats were shallow water environments – Recent decapods living in deep, dark environments have long antennae and reduced eyes, ore are blind. In anatomical details like the development of the chelae, there are significant differences due to different life styles and/or different prey. This is also triggered by their provenance from the Eichstätt or Zandt area, where the diversity of benthic organisms is remarkably higher than in the more pelagic setting of the lithographic limestones of Solnhofen and Langenthalheim, most probably due to favourable coral reef or well-oxygenated hardground environments in the near-shore surroundings. Other forms could have lived in algal or non-rigid sponge meadows at moderately shallow water depths.

Pincer-like chelae are common in several decapod species. In the well-known *Dusa* and in *Pseudodusa* n. gen., the chelate pereopods III are extremely prolonged. Similar chelae, however, are also developed in several species of *Antrimpos*, *Bylgia*, and in *Hefriga frischmanni* OPPEL. Most likely, this feature represents an adaptation to a detritus feeding lifestyle (SCHÄFER 1954). This kind of food source is often hidden in small cavities and fissures in a complexly structured shallow habitat. In contrast, short, strong chelae, like those in *Buergerocaris*, clearly suggest a strongly armoured prey. Thus, the latter appears to have lived as a predator or as a scavenger.

The enormously enlarged appendices of the pleopods in *Pleopteryx* appear to have had a very special function. One might be the adaptation of the pleopods for hatching a large amount of eggs, but the delicate feathery structure of these appendices more likely points to a subsidiary function for respiration, in addition to that of the gills. If so, *Pleopteryx* would have been adapted to low-oxygenated conditions, but not in lagoonal environments. Otherwise *Pleopteryx* would have been much more common in the laminates. Possibly, *Pleopteryx* lived in small pools developed in coastal areas near small islands, where oxygenation decreased during isolation in a hot and dry climate, as suggested by the coeval low-diversity macroflora adapted to longer-lasting low precipitation rates. Today, these settings are favourably inhabited by crabs, the diversification of which took place after Jurassic times, mainly in the Late Cretaceous and in the Tertiary.

5. References

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