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A new caridean shrimp (Crustacea: Decapoda: Dendrobranchiata) from the Upper Jurassic Solnhofen Lithographic Limestones of Schernfeld (South Germany)

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Abstract

A new genus and species of caridean shrimps, *Occultocaris frattigianii* nov. gen. et sp., is described from the Upper Jurassic Solnhofen Lithographic Limestones of Schernfeld near Eichstätt (Lower Tithonian, Hybonotum Zone). It differs from other genera of carideans primarily in the armature of the rostrum in combination with the shape of the chelae of the first and second pereiopods.

Key Words: Caridea, Solnhofen Lithographic Limestones, Tithonian.

Zusammenfassung

Eine neue Gattung und Art von Garnelen aus der Unterordnung Caridea, *Occultocaris frattigianii* nov. gen. nov. sp., wird aus den oberjurassischen Solnhofener Plattenkalken von Schernfeld bei Eichstätt beschrieben (Unter-Tithonium, Hybonotum-Zone). Sie unterscheidet sich von anderen Gattungen der Caridea in erster Linie in der Bezahnung des Rostrums in Kombination mit der Gestalt der Scheren der ersten und zweiten Pereiopoden.

Schlüsselwörter: Caridea, Solnhofener Plattenkalke, Tithonium

1. Introduction

The decapod infraorder Caridea Dana, 1852 is comprised of 3438 extant species in 389 genera (De Grave & Fransen 2011). Moreover, 52 fossil species of carideans are listed in 33 genera (Schweitzer et al. 2010). The Upper Jurassic lithographic limestones of the region of Eichstätt represent an important source of well preserved fossil assemblages. Besides vertebrates, invertebrates as well as plants are preserved in the limestones; however, apart from mass occurrences of the planktonic crinoid *Saccocoma tenella* these limestones are relatively poor in fossils. Among the invertebrates, natantian shrimps play an important role (Röper et al. 2000). Within the natantians, the carideans are very diverse. Among them, only the well-known *Hefriga serrata* Münster, 1839 appears to be quite frequent (Schweigert & Garassino 2003). In addition to this long since known fossil caridean, several other taxa from this area have recently been added, including *Schmelingia wulfi* Schweigert, 2002, *Buergerocaris psittacoides* Schweigert & Garassino, 2004, *Udora koschnyi* Schweigert & Garassino, 2004, *Pleopteryx kuempeli* Schweigert & Garassino, 2004, *Harthofia blumenbergi* Polz, 2007, *Harthofia bergeri* Polz, 2007, *Alcmonacaris winkleri* Polz, 2008, *Hefriga rogerfrattigianii* Schweigert, 2011, *Hefriga norbertwinkleri* Schweigert, 2011, *Harthofia polzi* Schweigert, 2011, and *Schernfeldia schweigerti* Winkler, 2013 (Münster 1839; Schweigert 2002; Schweigert & Garassino 2004; Polz 2007, 2008; Schweigert 2011; Winkler 2013). Most of these new genera or species are very rare or known only from single specimens. The bulk of the decapod fossils are represented by exuviae in various stages of decay (Schweigert 2011). This paper describes a new natantian genus based on several exquisitely preserved fossils.

2. Material and methods

The description is based on 12 specimens: S1 Holotype (CL 11.0, TL 52.8, L Schernfeld); S2 Paratype (CL 8.5, TL 40.5, L Wintershof); S3 (CL 10.0, L Schernfeld, coll. Winkler, Stahnsdorf); S4 (CL 6.5,

L Schernfeld, coll. Winkler, Stahnsdorf); S5 (CL 9.0, L Schernfeld, coll. Winkler, Stahnsdorf); S6 (CL not to scale, L Schernfeld, coll. Winkler, Stahnsdorf); S7 (CL 11.5, L Birkhof, coll. Frattigiani, Laichingen); S8 (CL 6.5, TL 33.0, L Eichstätt, coll. Frattigiani, Laichingen); S9 (CL 10.0, L Eichstätt, coll. Resch, Eichstätt); S10 (CL 11.5, L unknown, coll. Felthaus, Vlotho); S 11 (CL 10.5, L unknown, coll. Felthaus, Vlotho); S12 (CL 11.5, L Schernfeld, coll. Winkler, Stahnsdorf).

The total length of the specimens range between 29.9 mm (S4) and 53.0 mm (S10). The holotype comes from the Upper Jurassic Solnhofen Lithographic Limestones (Eichstätt Formation; Lower Tithonian, Hybonotum Zone) in southern Germany. The specimen occurs on a limestone slab that is 9 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 litographic limestone brightly fluoresces, fluorescence was used in the analysis of the fossil. In this way even the most delicate features, which otherwise would not or only barely be discernible, could be observed and adequately documented photographically. For the documentation of the holotype specimen, a macro-fluorescence set up was used (Haug et al. 2011). Digital images were taken with a Canon Rebel T3i camera with a MP-E 65mm macro lens. Light was provided by three evenly distributed LED torches, each equipped with a cyan filter. A red filter was mounted onto the lens. With this, mainly the light emitted from the fossil (roughly of orange colour) was detected by the camera. Processing of images followed Haug & Haug (2011); only the red channel is informative (other channels originate from scattered light), the image is then desaturated and the histogram optimised. Several images were stitched together using the Photomerge function of Adobe Photoshop CS3 to produce a high-resolution image. The paratype and S4 were documented on a Keyence BZ-9000 fluorescence microscope. A 2x objective was used, resulting in a magnification of approximately 20x. An excitation wavelength of 543 nm (green) was used. To overcome the limited depth of field a stack of images was recorded and fused into a single sharp image. Several of these images (of different image details) were stitched to yield a high-resolution image (e.g., Haug et al. 2008, 2009, 2011).

Abbreviations:

S1-S12 = specimen 1-12
CL = carapace length (approximately), measured in mm from the level of the posterior margin of the orbit to the midpoint of the posterodorsal margin of the carapace
TL = total body length, measured in mm from the tip of the rostrum to the end of the telson
L = locality
PI-PV = pereiopods I-V
SMNS = Staatliches Museum für Naturkunde Stuttgart, Germany
coll. = collection

3. Systematic palaeontology

Diagnostic characters of the Caridea: The classification of Caridea follows McLaughlin (1980) and is largely based on extant taxa. All members of Caridea exhibit the following complement of external features: (1) the second pleonal pleura overlap the pleura of both the first and third pleomeres; (2) the first two pairs of pereiopods chelate (except in Procarididae); (3) pereiopods III, IV and V achelate; (4) the rostrum is extremely variable in both length and armature; (5) antennular peduncle with three articles; (6) a telson bearing several small movable spines. Mouthpart morphology is usually difficult to assess in fossil shrimps and prawns from the Solnhofen Limestones due to the mostly lateral embedding of fossils.

The classification to the superfamily Bresilioidea predicates on the key to Recent Superfamilies of Caridea, which is based largely on the form of the anterior pairs of pereiopods (Chace & Manning 1972; modified from Holthuis 1955). However, Martin & Davis (2001) regard the superfamily Bresiloidea as an admittedly artificial taxon.

Order Decapoda Latreille, 1803
Infraorder Caridea Dana, 1852
Superfamily ?Bresilioidea, Calman, 1896
Family uncertain

Genus *Occultocaris* nov. gen.

Type species: *Occultocaris frattigianii* nov. sp.

Etymology: The genus name is a combination of the Latin *occultus* (= hidden) and the Greek *caris* (= shrimp), and refers to the first and second pereiopods that are hardly discernible in most specimens.

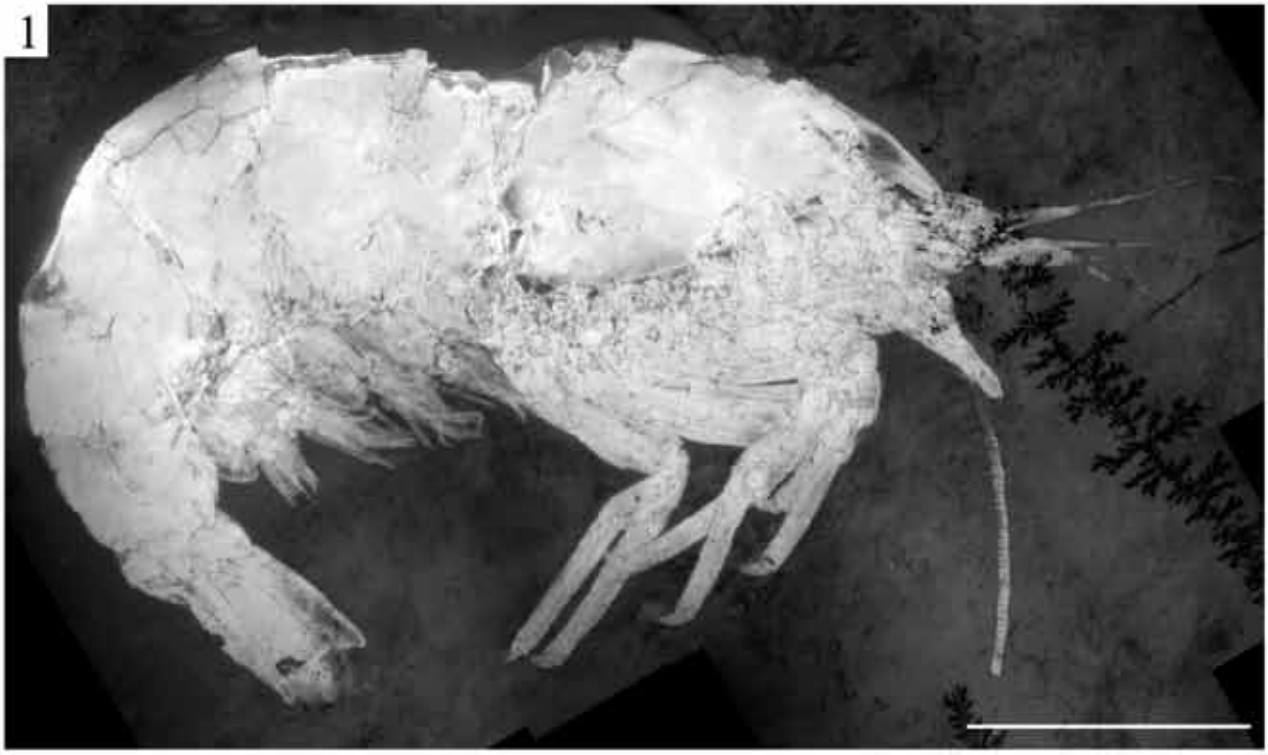
Diagnosis: See diagnosis of the type species.

Included species: Monospecific.

Occultocaris frattigianii nov. sp.
Pls 1, 2

Holotype: Specimen illustrated in Pl. 1, Fig. 1, de-

Plate 1: *Occultocaris frattigianii* nov. gen. nov. sp. Quarry district of Eichstätt (Schernfeld); Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. Holotype, SMNS 70224/1 and S3. **(1)** Overview of holotype specimen under fluorescence; scale bar = 10 mm. **(2)** Overview of holotype specimen; scale bar = 10 mm. **(3)** Rostrum and antennal scale of holotype specimen under fluorescence; scale bar = 3 mm. **(4)** Pleomere and telson of holotype specimen under fluorescence; scale bar = 10 mm. **(5)** Overview of specimen 3; scale bar = 10 mm.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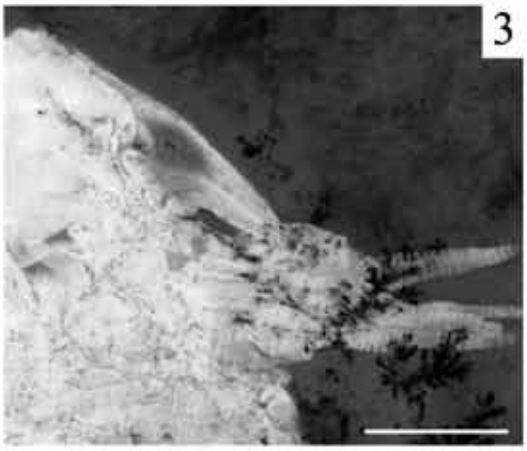
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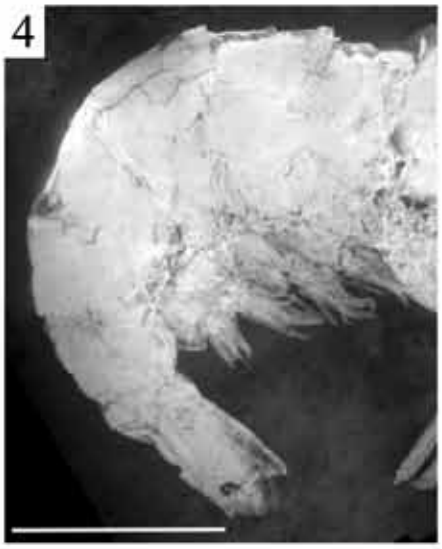
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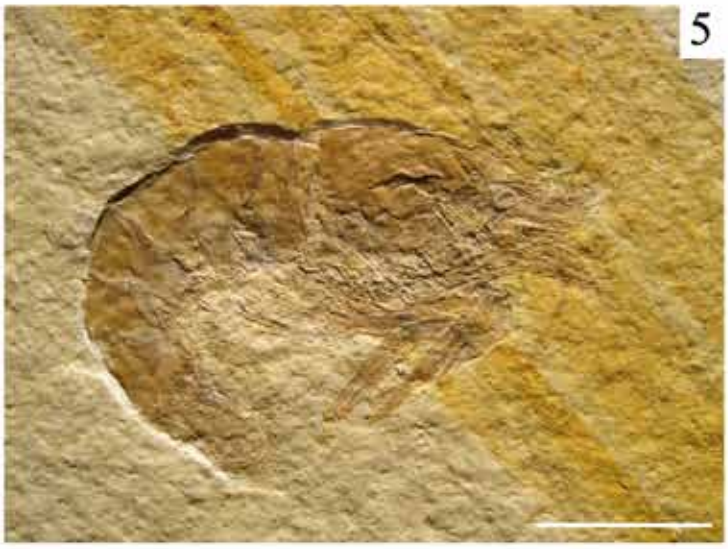
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posited in the SMNS, accession number 70224/1 (ex coll. N. Winkler).

Paratype: Specimen illustrated in Pl. 2, Fig. 1, deposited in the SMNS, accession number 70224/2 (ex coll. R. Frattigiani).

Etymology: The epithet is proposed for Mr. Roger Frattigiani, who kindly donated the paratype of the type species and first recognised the peculiarity of the specimen.

Gender: Feminine.

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

Type horizon and age: Solnhofen Group, Upper Eichstätt Formation (after Zeiss 1977), Lower Tithonian, Hybonotum Zone.

Studied material: 12 specimens.

Diagnosis: Slender caridean with inconspicuously punctate carapace and pleon; rostrum forwardly directed, dorsal and ventral margins unarmed; PI-PII chelate; PI slightly shorter than PII; PI chelae broader than PII chelae.

Description (based on the holotype specimen unless otherwise indicated): The holotype of *Occultocaris frattigianii* (Pl. 1, Fig. 1) is an excellently preserved moult embedded in lateral view; body well-sclerotised, curved; surface of body inconspicuously equipped with shallow punctations (Pl. 1, Fig. 2). For measurements, refer to Table 1.

Rostrum of holotype specimen directed forwardly, slightly curved ventrally with a pointed distal extremity (Pl. 1, Fig. 3), reaching distal margin of first article of antennular peduncle in S2; (Pl. 2, Fig. 1), not reaching the end of the antennal scale; dorsal and ventral margins unarmed, with lateral rostral carina extending to the tip of the rostrum; rostrum of juveniles unarmed and slightly curved ventrally, too (S8).

Carapace 0.8 times wider than long, subrectangular in outline, grooves not recognizable, ventral margin bent; with antennal spine directed forwardly in lateral view (S4) (Pl. 2, Fig. 4); no epigastric tooth; orbital margin evenly rounded, somewhat narrow (S7).

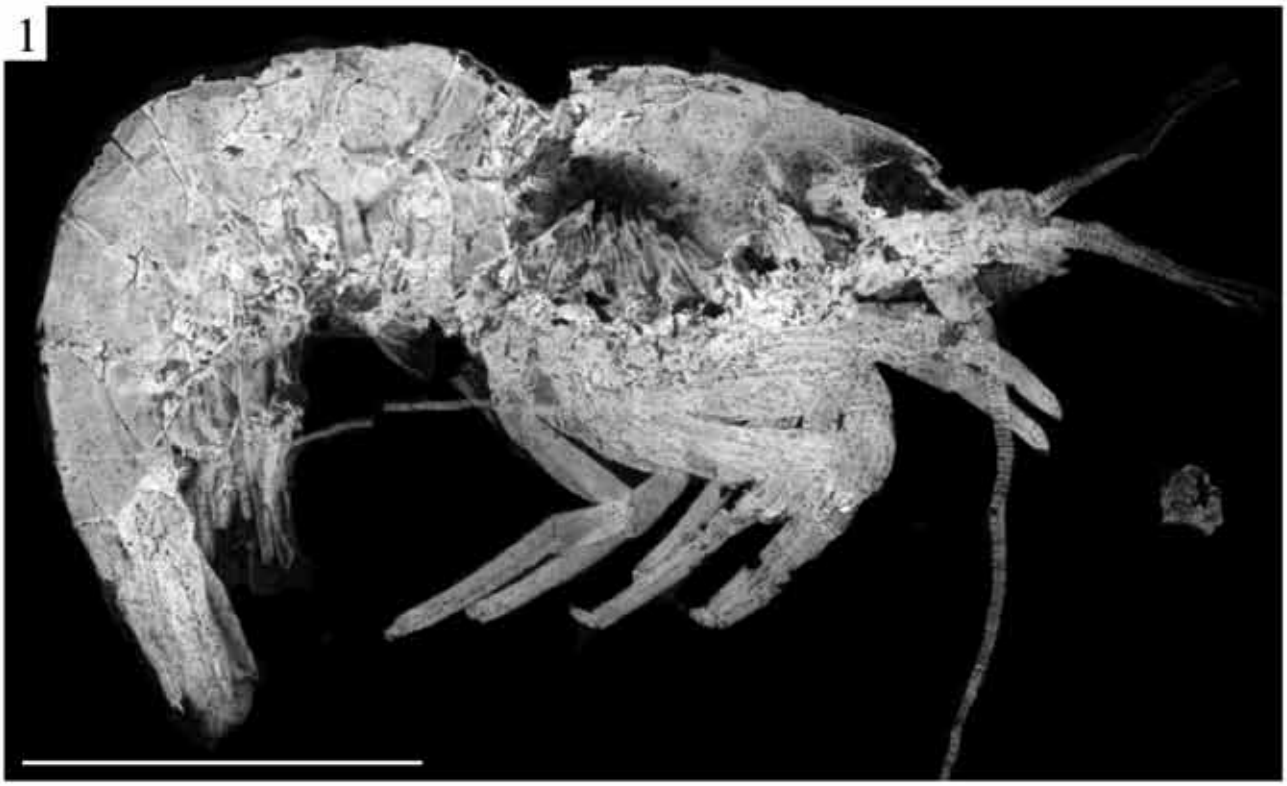
Pleon rounded dorsally, in lateral view pleomeres subrectangular in outline, third pleomere slightly longer than the others, sixth pleomere with posterior lobes partially embracing base of telson; pleura of all pleomeres broadly rounded, overlapping protopods of pleopods; pleura of the second pleomere partly overlapping those of pleomeres I and III, ventral margin of pleura smooth (Pl. 1, Fig. 4).

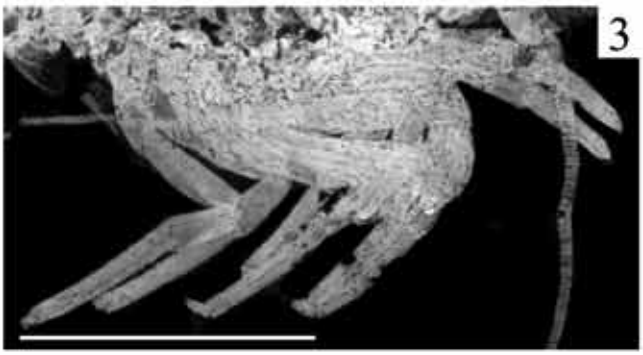
Telson not reaching posterior margin of uropodal endopod, distinctly narrowed posteriorly, somewhat

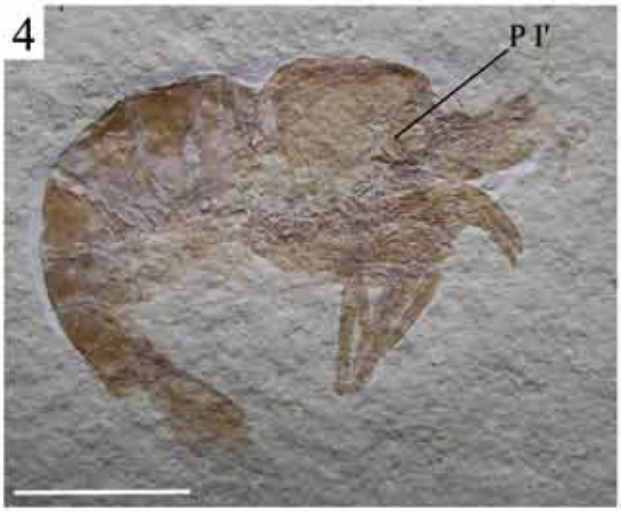
Table 1: Measurements of the holotype specimen of *Occultocaris frattigianii* nov. gen. et sp.; l = left, r = right

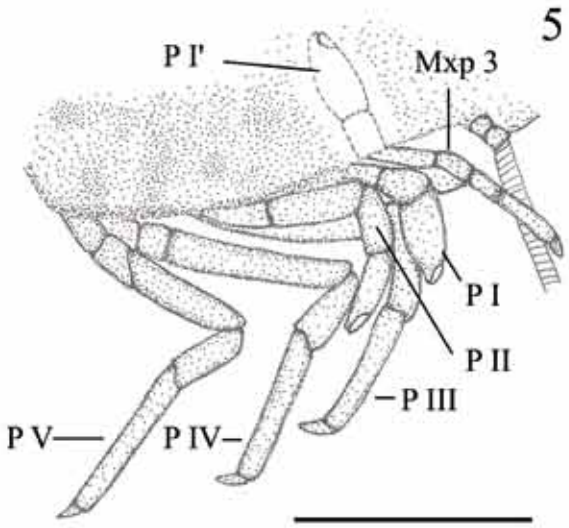
***Occultocaris frattigianii* (holotype)**	Measurements (in mm)
Carapace width	8.7
Rostrum length	5.8
Antennular peduncle, total length	1.9
Antennal peduncle, total length	2.5
Antennal scale	3.0
Mxp3, total length	7.9
P I propodus (incl. fixed finger)	3.3
P II propodus (incl. fixed finger)	3.0
P II carpus	1.7
P II merus	3.0
P II ischium	1.0
P III dactylus (r)	1.0
P III propodus (r)	4.6
P III carpus (r), approximately	2.0
P III merus (r), approximately	4.8
P III ischium (r)	1.7
P IV dactylus (l) and (r)	1.0
P IV propodus (r)	5.4
P IV carpus (r)	2.3
P IV merus (r)	6.9
P IV ischium (r)	1.1
P V dactylus (l) and (r)	1.0
P V propodus (l) and (r)	5.5
P V carpus (l) and (r)	2.8
P V merus (l)	3.9
P V ischium (l)	1.0
P III - V, width approximately	0.9
Pleomere 1	3.4
Pleomere 2	5.8
Pleomere 3	7.1
Pleomere 4	5.0
Pleomere 5	4.6
Pleomere 6	4.6
Uropods	8.1
Telson	7.4

Plate 2: *Occultocaris frattigianii* nov. gen. nov. sp. Quarry district of Eichstätt (Schernfeld); Solnhofen Lithographic Limestones (Upper Eichstätt Formation), Lower Tithonian, Hybonotum Zone. Paratype, SMNS 70224/2 and S4. **(1)** Overview of paratype specimen under fluorescence; scale bar = 11 mm. **(2)** Overview of paratype specimen; scale bar = 11 mm. **(3)** Pereiopods I-V of paratype specimen under fluorescence; scale bar = 9 mm. **(4)** Overview of specimen 4; P = pereiopod; scale bar = 6 mm. **(5)** Line-drawing of pereiopods I-V and third maxilliped, reconstruction after holotype specimen and paratype specimen; P = pereiopod; Mxp3 = third maxilliped; scale bar = ~8 mm.






P I'


P I'
Mxp 3
P I
P II
P III
P IV
P V

longer than the sixth pleomere, length 1.9 times anterior width, armed with at least one spine (Pl. 1, Fig. 4). Eyestalk remarkably short (S3) (Pl. 1, Fig. 5).

Antennular peduncle not reaching distal margin of antennal scale (S2, S4); surface smooth, basal article longest, ultimate and penultimate articles approximately of same length, all with equal width (S5, S9); superior lateral flagellum preserved up to 7.8 mm, superior mesial flagellum somewhat shorter than lateral flagellum, preserved up to 5.6 mm; proximal portions of antennular flagella considerably increasing in width.

Antenna with ischiocerite, merocerite, and carpocerite (third, fourth, and fifth articles of anntennal peduncle) approximately of same length, surface smooth; antennal scale lanceolate, with a pointed distal extremity, somewhat longer than distal end of ultimate article of antennular peduncle (S2); flagella, as far as visible, preserved up to 21.0 mm (S2 23.0 mm, completely preserved), 0.6 of body length (S2).

Mandible, maxillula, maxilliped 1, and maxilliped 2 not preserved; third maxilliped overreaching antennal scale in lateral view, dactylus 0.35 of propodus length (S2, S4), propodus distinctly longer than carpus (S2, S4), carpus and merus approximately of same length, ischium somewhat longer (S4), all articles without setae or spines (Pl. 2, Fig. 2; Pl. 2, Fig. 4).

PI broader and slightly shorter than PII; PI approximately 0.9 of PII length (S2); PI ischium, merus and carpus not visible, PI chelate; propodus with palm stout, movable and fixed finger short and strong, of approximately the same length, 0.24 of palm length (S2) (Pl. 2, Fig. 3); PII merus longest, PII chelate, propodus with palm slender than palm of PI, shape of fingers resemble those of PI, PII fingers 0.25 of palm length (Pl. 1, Fig. 1); all specimens at least with one chela of PI and/or PII turned up (e.g., S4, S5, S6, S7, S9, S12) due to taphonomic circumstances (Pl. 2, Fig. 4); PIII-PV achelate and generally similar in length and structure, dactyli short, all articles unarmed with exception of PIV merus, PIV slightly longest of all pereiopods due to elongation of merus (Pl. 2, Fig. 5), PIV merus with a few short spines, hardly discernible because of preservation.

Pleopods well preserved, biramous; protopods approximately as long as exopods, appendix interna or appendix masculina not visible (Pl. 1, Fig. 4).

Uropods with distinct protopod ending in a sharp point; uropodal endopod as long as exopod, lacking teeth; uropodal exopodites with diaeresis (Pl. 1, Fig. 4).

4. Comparisons

The number of rostral teeth is of great importance in the discrimination of the different genera and species of Caridea (Holthuis 1951), but additional characters may also be significant for the identification of new fossils (e.g., von Rintelen & Cai 2009).

A comparison of the new form described in this paper with other fossil caridean genera (based on the original descriptions) shows that: (1) Besides *O. frattigianii* the following genera of fossil carideans posses a completely unarmed rostrum: *Udora koschnyi* Schweigert & Garassino, 2004 (Schweigert & Garassino 2004), and *Schmelingia wulfi* Schweigert, 2002 (Schweigert 2002) from the Upper Jurassic, as well as *Bannikovia maikopensis* Garassino & Teruzzi, 1996 (Garassino & Teruzzi 1996) from the Lower Miocene, and *Yongjicaris zhejiangensis* Garassino et al., 2002 (Garassino et al. 2002) from the Lower Cretaceous, as well as *Morscrangon acutus* Garassino & Jakobsen, 2005 (Garassino & Jacobsen 2005) from the Lower Eocene. However, all these taxa clearly differ from *O. frattigianii* in the shape of the pereiopods. The shape and the armature of the rostrum of *O. frattigianii* is of great consistency since juveniles show the same rostrum-features as the adults; (2) The first pereiopods of *O. frattigianii* are equipped with broad chelae and the first pereiopod is slightly shorter than the second. A similar combination of features does not occur in any other fossil caridean; (3) *O. frattigianii* superficially resembles the Late Jurassic *Hefriga serrata* Münster, 1839 (Münster 1839), the type species of the genus *Hefriga*. However, there are several morphological details that discriminate *O. frattigianii* from *Hefriga*. Firstly, *O. frattigianii* differs from *H. serrata* in the armature of the rostrum (*H. serrata* with about 10 dorsal teeth). Secondly, the surface of the carapace and pleon of *H. serrata* show a delicate pattern of subparallel striae, whereas the surface of *O. frattigianii* shows inconspicuous shallow punctations. Thirdly, the shape of the chelae of PI and PII is distinctly different from those of *H. serrata*; (4) *O. frattigianii* differs from all other fossil carideans [i.e. *Pleopteryx kuempeli* Schweigert & Garassino, 2004, *Buergerocaris psittacoides* Schweigert & Garassino, 2004 (Schweigert & Garassino 2004), *Alcmonacaris winkleri* Polz, 2008 (Polz 2008), *Schernfeldia schweigerti* Winkler, 2013 (Winkler 2013), and the representatives of *Harthofia* Polz, 2007 (Polz 2007; Schweigert 2011)] in the armature and the shape of the rostrum, as well as in the shape of the pereiopods.

Occultocaris frattigianii exhibits several morphological details that clearly distinguish this taxon from all earlier described fossil caridean genera, and we propose therefore a new genus and species to include the specimens with their unique combination of characters. Although the new genus *Occultocaris* has well-defined special characters, it is impossible to assign it to a family or superfamily with certainty. According to Chace & Manning (1972), however, it may be possible to assign this new taxon to the superfamily Bresilioidea Calman, 1896 because of the fact that the first pereiopods are stouter and slightly shorter than the second pereiopods.

5. Palaeoecology and taphonomy of *Occultocaris frattigianii*

The strong and broad chelae strongly suggest that *O. frattigianii* was a predator or scavenger (Schweigert & Garassino 2004). The rather long antennae probably was equipped with a variety of different receptors in order to detect and recognise nearby objects (Raabe & Raabe 2008). The co-occurrence of various ontogenetic stages of a single palaeobiospecies (here: *O. frattigianii*) may be a result of autochthonous lifestyle, or at least to a habitat in close proximity to the burial place (Schweigert 2007). Six of twelve specimens included in this study come from Schernfeld, four others from nearby localities. Very recently an additional specimen was discovered from Schernfeld (coll. Hoffmann, Spalt). The relative frequency of this taxon in a small area in the northern vicinity of Eichstätt corroborates the hypothesis that the place of burial was not far away from the original habitat of this shrimp (Schweigert 2007). Moreover, *O. frattigianii* probably was not rare in the palaeoecosystem, but has not been recognised previously because it occurs together with other superficially similar taxa, and the first and second pereiopods, which are the most important distinguishing character, are not normally discernible.

The taphonomic circumstances that caused the typical preservational state of the *O. frattigianii* specimens are comparable to those of many eryonids. Whereas at least one chela of *O. frattigianii*'s PI and/or PII is turned up, the pereiopods I of many eryonids are pointing backward. This was caused by the heavy chelae, which usually hang down from the drifting exuvia, became cought in the seafloor first (Schweigert 2007).

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