Revision of the fossil crustacean *Blaculla brevipes*, and description of a new caridean shrimp (Crustacea: Decapoda: Dendrobranchiata) from the Upper Jurassic Solnhofen Lithographic Limestones of Schernfeld (Germany)

Norbert Winkler*

D-14532 Stahnsdorf, Germany

*E-mail: norbert_winkler@t-online.de

Abstract

The validity and synonymy of *Blaculla brevipes* cannot be established beyond doubt, and thus the name is considered a nomen dubium. Subsequently, a new species of caridean shrimp, *Blaculla haugi* nov. sp., is described from the Upper Jurassic Solnhofen lithographic limestones of Schernfeld near Eichstätt (Lower Tithonian, Hybonotum Zone). The new species differs from the other members in the genus *Blaculla* mainly with regard to the armature of the rostrum and shape of the chelae of the first pereiopods, as well as in the overall-habitus.

Key Words: Caridea, Solnhofen Lithographic Limestones, Tithonian.

1. Introduction

The decapod infraorder Caridea Dana, 1852 is comprised of 3438 extant species in 389 genera (De Grave & Fransen 2011). Moreover, 58 fossil species of carideans are listed in 36 genera (Schweitzer et al. 2010; extended by Schweigert 2011; Brandt & Schulz 2013; Winkler 2013, 2014). The fossil representatives come from various periods of geological time and geographical localities. Several of the groups date back to the Triassic; an important source stratum for fossils of these animals is the Bergamo area in northern Italy (Garassino & Teruzzi 1993). Other records come from the Jurassic of Eichstätt (Schweigert 2011). The Late Jurassic lithographic limestones of southern Germany represent an important source of new information on fossil representatives of carideans. Münster (1839) and Oppel (1862) described important caridean genera from this area, including *Udora* Münster, 1839, *Udorella* Oppel, 1862, *Hefriga* Münster, 1839, and *Blaculla* Münster, 1839. Additional taxa have subsequently been described from this area, i.e. *Schmelingia wulfi* Schweigert, 2002, *Buergerocaris psittacoides* Schweigert & Garassino, 2004, *Udora koschnyi* Schweigert & Garassino, 2004, *Pleopteryx kuempeli* Schweigert & Garassino, 2004, *Hefriga proboscidewulfi* Schweigert & Garassino, 2004, *Hefriga norbertwinkleri* Schweigert, 2011, *Harthofia polzi* Schweigert, 2011, *Schernfeldia schwarzi* Schweigert, 2011, *Occultocaris frattigianii* Winkler, 2013, and *Occultocaris frattigianii* Winkler, 2014 (Schweigert 2002; Schweigert & Garassino 2004; Polz 2007, 2008; Schweigert 2011; Winkler 2013, 2014). Fossil carideans from the Cretaceous, mostly described by A. Garassino of Milan, Italy, have been reported from Lebanon (Garassino 1994), Italy (Garassino 1998; Bravi & Garassino 1998a,b; Bravi et al. 1999; Garassino & Bravi 2003), Spain (Rabadà 1993;
Garassino 1997), and China (Garassino et al. 2002). In this paper a species historically assigned to the genus *Blaculla* is revised, and a new species in the same genus is described.

2. Revision of the fossil crustacean *Blaculla brevipes* 

Genus *Blaculla* Münster, 1839

Type species: *Blaculla nicoides* Münster, 1839, subsequent designation by Glaessner (1929: 66)

Solnhofen species: *Blaculla nicoides* Münster, 1839; ?*Blaculla brevipes* Münster, 1839; *Blaculla sieboldi* Oppel, 1862

?*Blaculla brevipes* (Münster, 1839)

1839 *Blaculla brevipes* Münster; p. 76, Pl. 29, fig. 2
1853 *Blaculla brevipes* Münster in Frischmann; p. 32
1862 *Blaculla brevipes* Münster in Oppel; p. 103, Pl. 30, fig. 4
1904 *Blaculla brevipes* Münster in Walther; p. 173
1922 *Blaculla brevipes* Münster in Balsas; p. 143
1925 *Blaculla brevipes* Münster in Van Straelen; p. 105
2005 *Blaculla brevipes* Münster in Garassino & Schweigert; p. 15

Stratigraphic range: Upper Jurassic (Tithonian)

Type locality: Eichstätt (according to Münster's description)

Material: Oppel (1862) reported six specimens belonging to this species, i.e. Münster's holotype, deposited in the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, and five specimens in the Redenbacher collection, today housed in the Museum für Naturkunde of the Humboldt-University at Berlin. All six specimens are included in the analysis presented in this paper:

BSPG AS VII 728 – Münster (1839: pl. 29, fig. 2)
BSPG AS VII 728 – Oppel (1862: pl. 30, fig. 4)
MNHB S 1103 – Oppel (1862: p. 103, not figured)
MNHB S 3798 – Oppel (1862: p. 103, not figured)
MNHB S 3799 – Oppel (1862: p. 103, not figured)
MNHB S 3807 – Oppel (1862: p. 103, not figured)
MNHB S 3809 – Oppel (1862: p. 103, not figured)

Discussion: Münster (1839) described this species based on a single incomplete specimen. Oppel (1862) subsequently pointed out that, in contrast to *Blaculla nicoides* (Münster 1839), the second pereiopods of *B. brevipes* are somewhat shorter and the chelae of the first pereiopods seem to be thicker. However, Van Straelen (1925) indicated that there is no recognizable difference with regard to the length of the second pereiopods. The above-mentioned studied specimens are only fragmentarily preserved and therefore it is not possible to identify the main morphological characters. The lack of diagnostic characters does not allow further comparison with the other species of the genus. As a result, I consider *Blaculla brevipes* a nomen dubium because it is impossible to confirm its validity based on the type materials nor to resolve its synonymy.

3. Description of a new caridean shrimp

3.1. Material and methods

The material used for the description includes the holotype of *B. haugi*: S1 (CL 6.8, TL 37, L Schernfeld). For comparison, the following 10 specimens of *B. nicoides* were also studied: S2 (CL 9.2, L Eichstätt, coll. Rüdel, Gröbenzell); S3 (CL 8.8, L Schernfeld, coll. Winkler, Stahnsdorf); S4 (CL 6.0, L Schernfeld, coll. Winkler, Stahnsdorf); S5 (CL 5.6, L Schernfeld, coll. Winkler, Stahnsdorf); S6 (CL 9.0, L Schernfeld, coll. Frattigiani, Laichingen); S7 (CL 9.0, L Schernfeld, coll. Frattigiani, Laichingen); S8 (CL 5.6, L Schernfeld, coll. Frattigiani, Laichingen); S9 (CL 4.7, L Eichstätt, coll. Fauser, Schwäbisch-Gmünd); S10 (CL approximately 7.5, L Eichstätt, coll. Resch, Eichstätt); S11 holotype of *B. nicoides* (CL nv, L Solnhofen, BSPG AS VII 729); additionally the holotype of *B. sieboldi* was studied: S12 (CL 9.5, L Solnhofen, BSPG AS I 973).

The holotype of *B. haugi* comes from the Upper Jurassic Solnhofen lithographic limestones (Eichstätt Formation; Lower Tithonian, Hybonotum Zone) in southern Germany, and occurs on a limestone slab that is ~4 mm thick. Specimen preparation was carried out with various needles and scrapers. Because the sclerotization of the exoskeleton of crustaceans preserved in lithographic limestone brightly fluoresces, fluorescence was used in the study of the fossil. This way even the most delicate features, which otherwise would remain barely discernible, can be observed and adequately documented photographically. For the documentation of the holotype specimen, a macro-fluorescence set up was used (Haug et al. 2011). The images were captured 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 cyan filters. A red filter was mounted onto the lens. With this, primarily the light emitted from the fossil (roughly of orange colour) was detected by the camera. Processing 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 stacked together using the Photomerge function of Adobe Photoshop CS3 to produce a high-resolution image. For the documentation of S2 and S3 a Pentax Optio 450 was used, for S2 additionally fluorescence.
that are diagnostic for the type species *Blaculla nicoides* Münster, 1839. As a result, the specific diagnosis is emended.

**Emended diagnosis (based on S2 unless otherwise indicated):** Small to medium-sized caridean; 

### Abbreviations:
- S1–S12 = specimen 1–12
- CL = carapace length, 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
- BSPG = Bayerische Staatsammlung für Paläontologie und Geologie in Munich, Germany
- MNHB = Museum für Naturkunde der Humboldt-Universität in Berlin, Germany
- JME = Jura-Museum Eichstätt, Germany
- coll. = collection
- PIRLW = ratio: length to width of PI chelae
- RTLWC = ratio: TL to width of carapax
- PILF = length of fingers of PI chelae
- nv = not or only partially visible
- mf = movable finger
- ff = fixed finger

### 3.2. Systematic palaeontology

Diagnostic characters of the Caridea: Classification of Caridea follows Mc Laughlin (1980) and De Grave et al. (2009), and is largely based on extant taxa. All members of the 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. 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 Alpheoidea predicates on the key to Recent Superfamilies of Caridea, which is based largely on the form of the two anterior pairs of pereiopods (Chace & Manning 1972, modified from Holthuis 1955; Holthuis 1993).

Order Decapoda Latreille, 1803
Infraorder Caridea Dana, 1852
Superfamily ?Alpheoidea Rafinesque, 1815
Family uncertain

Genus *Blaculla* Münster, 1839

Type species: *Blaculla nicoides* Münster, 1839, subsequent designation by Glaessner (1929: 66)

Species included in genus: *Blaculla nicoides* Münster, 1839; *Blaculla sieboldi* Oppel, 1862; *Blaculla hauugi* nov. sp., this paper.

Remarks: Because of the excellent preservation of S2 and S10 additional characters can be identifi...
Description (based on the holotype specimen; for detailed measurements, refer to Tab. 1): The holotype of *Blaculla haugi* (Pl. 1, Fig. 1) is a well preserved moult embedded in lateral view; body well-sclerotized, curved; surface of body equipped with a distinct pattern of subparallel striae (Pl. 2, Fig. 1). Rostrum directed forwardly, 0.75 times as long as carapace, slightly curved dorsally with a pointed distal extremity (Pl. 1, Fig. 2); longer than distal margin of third article of antennular peduncle (Pl. 1, Fig. 2); not reaching the end of the antennal scale; dorsal margin armed with 7 preserved teeth, complete original number obviously 10 (consecutively completed at the place of a gap, due to preservation), obliquely directed forwardly, ventral margin armed with 6 forwardly directed teeth, the first three of which notably longer than the others, rostrum formula 3+7/6 (Pl. 2, Fig. 4). Carapace 0.7 times as wide as long, sub-rectangular in outline, no carina or spines recognizable, ventral margin bent, no epigastric tooth, orbital margin slightly rounded, eyes not recognizable.

*Blaculla haugi* nov. sp.

Holotype: Specimen illustrated in Pl. 1, Fig. 1, deposited in the SMNS, number 70286 (ex coll. N. Winkler).

Etymology: The epithet is proposed in honour of Carolin and Joachim Haug, who studied numerous fossil decapod crustaceans, especially its larval states, and considerably expanded our knowledge of Late Jurassic crustacean evolution.

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: 1 specimen.

Diagnosis: Slender body; carapace and pleon with a pattern of subparallel striae; rostrum forwardly directed, dorsal and ventral margin armed; PI with claw-like chela; PI chelae broader and longer than PII chelae.

---

Table 2: Comparison between *B. haugi* (holotype specimen), *B. nicoides* and *B. sieboldi*

<table>
<thead>
<tr>
<th>Specimen</th>
<th>TL</th>
<th>PIRLW</th>
<th>PILF</th>
<th>RTLWC</th>
<th>Propodus and carpus length in mm</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>B. haugi</em> Holotype</td>
<td>37</td>
<td>2.16</td>
<td>mf &lt; ff</td>
<td>7.4</td>
<td>16/nv</td>
</tr>
<tr>
<td><em>B. nicoides</em> (S2)</td>
<td>43</td>
<td>4.60</td>
<td>mf = ff</td>
<td>4.0</td>
<td>35/nv</td>
</tr>
<tr>
<td><em>B. nicoides</em> (S3)</td>
<td>35</td>
<td>4.25</td>
<td>mf = ff</td>
<td>3.9</td>
<td>65/45</td>
</tr>
<tr>
<td><em>B. nicoides</em> (S4)</td>
<td>28</td>
<td>4.00</td>
<td>mf = ff</td>
<td>4.6</td>
<td>22/19</td>
</tr>
<tr>
<td><em>B. nicoides</em> (S5)</td>
<td>27</td>
<td>nv</td>
<td>mf = ff</td>
<td>4.2</td>
<td>23/nv</td>
</tr>
<tr>
<td><em>B. nicoides</em> (S6)</td>
<td>40</td>
<td>4.30</td>
<td>mf = ff</td>
<td>4.6</td>
<td>nv/nv</td>
</tr>
<tr>
<td><em>B. nicoides</em> (S7)</td>
<td>39</td>
<td>3.88</td>
<td>mf = ff</td>
<td>4.6</td>
<td>26/nv</td>
</tr>
<tr>
<td><em>B. nicoides</em> (S8)</td>
<td>24</td>
<td>4.00</td>
<td>mf = ff</td>
<td>4.7</td>
<td>27/nv</td>
</tr>
<tr>
<td><em>B. nicoides</em> (S9)</td>
<td>23</td>
<td>5.00</td>
<td>mf = ff</td>
<td>4.6</td>
<td>15/nv</td>
</tr>
<tr>
<td><em>B. nicoides</em> (S10)</td>
<td>32</td>
<td>nv</td>
<td>mf = ff</td>
<td>4.5</td>
<td>44/22</td>
</tr>
<tr>
<td><em>B. nicoides</em> Holotype</td>
<td>nv</td>
<td>3.92</td>
<td>mf = ff</td>
<td>nv</td>
<td>nv</td>
</tr>
<tr>
<td><em>B. sieboldi</em> Holotype</td>
<td>37</td>
<td>4.28</td>
<td>mf = ff</td>
<td>4.6</td>
<td>48/31</td>
</tr>
</tbody>
</table>
nular peduncle, flagella preserved up to 50.0 mm, 1.4 of body length, proximal portions fused.

Mandible, maxillula, maxillipeds 1, and maxillipeds 2 not preserved, third maxilliped not overreaching antennal scale in lateral view, dactylus 0.17 of propodus length, propodus and carpus approximately of same length, all articles without setae or spines (Pl. 1, Fig. 1).

PI broader and shorter than PII, PI approximately 0.2 of PII length as far as visible, PI ischium and merus not visible, PI chelate, propodus with palm stout, surface smooth, movable and fixed finger strong, fixed finger in lateral view curved downward and inward, movable finger 0.5 of fixed finger length, 0.7 of palm length (Pl. 1, Fig. 4); PII longest of all pereiopods, PII ischium and merus not visible, carpus elon-
Uropods with protopod ending in several points; uropodal endopod as long as exopod, without teeth; diaeresis not visible (Pl. 1, Fig. 1).

3.3. Comparisons

Because the annulated PII is a characteristic fea-
ture of the genus *Blaculla*, the new fossil described above is assigned to this genus with confidence. According to Holthuis (1951, 1993) we can distinguish the different genera and species of Caridea based on the number of rostral teeth, but the presence of further characters may also be significant for the identification of a new fossil species or genus (e.g., von Rintelen & Cai 2009).

Comparison of the new species described in this paper with other fossil carideans (based on the original descriptions) shows that, besides *B. haugi*, several other genera of Caridea possess at least one tooth on the ventral margin of the rostrum, including *Harthofia bergeri* Polz, 2007, *H. blumenbergi* Polz, 2007, and *H. polzi* Schweigert, 2011, *Hefriga rogerfrattigianii* Schweigert, 2011, and *H. norbert-winkleri* Schweigert, 2011, *Schemfeldia schweigerti* Winkler, 2013 from the Upper Jurassic, as well as *Palaemon antonellae* Garassino & Bravi, 2003 from the Lower Cretaceous (Polz 2007; Schweigert 2011; Schweigert & Garassino, 2004, with regard to both the infrageneric and species level within *Caridea*). Nevertheless, all these latter taxa clearly differ from *B. haugi* in the number of dorsal and ventral teeth of the rostrum. The second pereiopods of *B. haugi* are considerably elongated. This feature occasionally occurs, e.g., in specimens of the species *S. schweigerti* and *P. antonellae*; however, in all of these animals the PII carpus is not annulated.

Like *B. haugi* the Late Jurassic *Caropenaeus peterbuergeri* Schweigert & Garassino, 2005 shows an annulated PII carpus (Schweigert & Garassino 2005). Nevertheless, *C. peterbuergeri* is assigned to the infraorder Penaeidea de Haan, 1849. The rostra in members of this infraorder are distinguished primarily by the shape and dentation, additionally the PII carpus of *C. peterbuergeri* is annulated, too.

*Blaculla haugi* superficially resembles the Late Jurassic *Blaculla nicoidei* Münster, 1839, the type species of this taxon (see Münster 1839). However, several morphological details discriminate *B. haugi* from this taxon: (1) *B. haugi* differs from *B. nicoidei* in the armature of the rostrum, *B. haugi* with 10 dorsal and 6 ventral teeth, *B. nicoidei* with 13 dorsal and 4 ventral teeth (S2). *Blaculla haugi* possesses three dorsal rostral teeth posterior to the orbital margin, while *B. nicoidei* shows none (S7) (see rostrum formulae above and Pl. 2, Fig. 2; Pl. 2, Fig. 4). Moreover, the ventral teeth of the rostrum in *B. haugi* are extending to shortly before the tip of the rostrum, while those of *B. nicoidei* keep more distance to the distal end of the rostrum. Additionally, the size of the teeth is different; (2) Another important difference is the size of the chelae of PI, especially with regard to the relation between length and width of PI chela. The PIRLW in *B. haugi* (holotype, see Tab. 2) is 2.16. The median ratio of 8 examined specimen (juveniles and adults) of *B. nicoidei* is 4.24 (variations of 3.88 to 5.00). To minimise size-related intraspecific differences the median ratio of 4 examined specimen of *B. nicoidei* (TL 35 to 43 mm, for comparison TL of *B. haugi* = 37 mm) was calculated and used. It amounts to 4.26. The primary reason of this ratio-difference between *B. haugi* and *B. nicoidei* is the width and relative shortness of the chela of *B. haugi*; (3) The fixed finger of PI chela of *B. haugi* is significantly longer than the movable finger of PI chela. *Blaculla nicoidei* shows both fingers of PI chela of equal length; (4) The overall-habitus of *B. haugi* is clearly more slender than in *B. nicoidei*. The PIRLWC in *B. haugi* (holotype, see Tab. 2) is 7.4. The ratio of 9 examined specimen (juveniles and adults) of *B. nicoidei* ranges between 3.9 and 4.7 (midpoint 4.4), for adults (TL 32 to 43 mm) it ranges from 3.9 to 4.6 (midpoint 4.3). The primary reason of this ratio-difference between *B. haugi* and *B. nicoidei* is the slenderness of *B. haugi*.

*Blaculla haugi* differs from *Blaculla sieboldi* Oppel, 1862 in the shape and dentation of the rostrum. *Blaculla sieboldi* with 7 dentally located teeth (as far as visible), ventral dentation not recognizable because of the poor state of preservation. *Blaculla sieboldi* differs significantly in the shape of the chelae of the first and the second pereiopods. Both fingers of PI are of equal length, the PIRLW amounts to 4.28. The PIRLWC resembles that of the type species and is 4.6. Additionally, *B. sieboldi* lacks the distinct pattern of subparallel striae, its surface is smooth.

The length of PII (propodus and carpus) of *B. haugi* is 16 mm. The PII length of *B. nicoidei* (propodus and carpus) ranges between 22 (S10) and 65 (S3, see Pl. 2, Fig. 3) mm (valid for specimens more than 32 mm TL, for further measurements refer to Tab. 2). The PII length (propodus and carpus) of *B. sieboldi* is 48 mm. Although the PII length of *B. haugi* in comparison to *B. nicoidei* and *B. sieboldi* is significantly shorter, it is impossible to assign it as a feature on species level within *Blaculla*, because of the length-variety of PII.

*Blaculla haugi* is distinctly different from all other fossil carideans, e.g., *Pleopteryx kuempelii* Schweigert & Garassino, 2004, *Buergerocaris psittacoides* Schweigert & Garassino, 2004, with regard to both the armature and shape of the rostrum, and in the shape of the pereiopods (Schweigert & Garassino 2004).

*Blaculla haugi* exhibits several morphological details that clearly distinguish this taxon from all other described fossil caridean genera and from the other species of the genus *Blaculla*. Introduction of a new species is therefore necessary to include this specimen with its unique combination of characters. Although this new species, *B. haugi*, is based on a set of well-defined diagnostic characters, it is impossible to assign it with certainty to a family or superfamily. However, according to Chace & Manning (1972) it may be possible to assign this new taxon to the superfamily Alpheoidea Rafinesque, 1815 because the first pereiopods are stouter than the second ones. Moreover, the second pereiopods are divided into two or more joints.
3.4. Palaeoecology and taphonomy of *Blaculla haugi*

Based on the strong and broad chelae of PI, it is likely that *B. haugi* lived as a predator or scavenger (Schweigert & Garassino 2004). Moreover, the markedly elongate second pereopods might represent adaptations to a detritus-feeding lifestyle (cf. Schweigert & Garassino 2004). The relatively long antennae might have carried various specialized receptors facilitating the detection and recognition of nearby objects. The long and slender rostrum presumably functioned as an aid in stabilization (Raae & Raae 2008). The limited number of fossils discovered to date of this species suggest that *B. haugi* perhaps lived outside the lithographic limestone basins, and its record within this Lagerstätte depended on lucky circumstances (Schweigert 2007).

Acknowledgements

My sincere thanks go to G. Schweigert (Stuttgart) for his enriching comments. I also sincerely thank C. Haug and J.T. Haug (both Munich) for providing excellent images and a detailed report. I wish to thank C. Neumann (MNHB) as well as M. Nose (BSPG) and M. Kölbl-Ebert (JME) for kindly granting permission to study several specimens for comparison. I am much obliged to A. Winkler (Stahnsdorf) for useful advice and skilful preparation, as well as for providing detailed line-drawings, and to J. Winkler for assembling the two photographic plates. I am indebted to the reviewer, A. Garassino (Milan), for insightful comments and suggestions, and to M. Krings (Munich) for proofreading of the manuscript. Furthermore, my thanks are due to R. Frattigiani (Laichingen), P. Rüdel (Gröbenzell), U. Resch (Eichstätt), and D. Fauser (Schwäbisch Gmünd) for providing detailed line-drawings, and to J. Winckler for useful advice and skilful preparation, as well as for providing detailed line-drawings, and to J. Winckler for assembling the two photographic plates. I am indebted to the reviewer, A. Garassino (Milan), for insightful comments and suggestions, and to M. Krings (Munich) for proofreading of the manuscript. Furthermore, my thanks are due to R. Frattigiani (Laichingen), P. Rüdel (Gröbenzell), U. Resch (Eichstätt), and D. Fauser (Schwäbisch Gmünd) for providing specimens.

4. References


Münster G. Graf zu. 1839. Decapoda Macroura. Abbildung und Be-