N. Jb. Geol. Paläont. Abh. 260/2, 131–140
published online March 2011

Article

The decapod crustaceans of the Upper Jurassic Solnhofen Limestones: A historical review and some recent discoveries

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With 8 figures

Schweigert, G. (2011): The decapod crustaceans of the Upper Jurassic Solnhofen Limestones: A historical review and some recent discoveries. – N. Jb. Geol. Paläont. Abh., **260**: 131–140; Stuttgart.

Abstract: The Solnhofen Limestones represent one of the most important sources for crustacean diversity in the Jurassic and even for their fossil record in the Mesozoic. A brief overview of the history of science since the beginning of 18th century and the circumstances of the fossil recoveries are provided. The fossils come from various localities of slightly different ages (late Kimmeridgian – early Tithonian). Most specimens did not live at their later places of burial, but were swept in as exuviae from more or less distant neighboring environments. These reasons are responsible for the great diversity of genera and species described so far. Three species of caridean shrimps from the Solnhofen Limestones of Eichstätt and Zandt are newly introduced: *Hefriga rogerfrattigianii*, *Hefriga norbertwinkleri*, and *Harthofia polzi*.

Key words: Solnhofen Limestones, history of science, Decapoda, Crustacea, Jurassic, Caridea.

1. Introduction

Decapod crustaceans from the Solnhofen Limestones were described already in the 18th century, but not named (Baier 1708; Knorr & Walch 1755-1773; Fig. 1). Since the intensive exploitation of these limestones for lithography (from 1800 onwards), many new quarries opened in a large area spanning from Langenaltheim in the West to Painten or Kelheim in the East and Southeast. Many fossils were recovered and purchased mostly by amateurs from the quarrymen. In the first half of the 19th century Friedrich v. Schlotheim, Hermann v. Meyer, Ernst F. Germar, and especially Georg Graf zu Münster described numerous taxa, often based on very poorly preserved or sometimes even faked material (Schlotheim 1820, 1822; Germar 1827; v. Meyer 1836; Münster 1839). Albert Oppel revised all previously established species in a monograph and added several more genera and species (Oppel 1861, 1862). Woodward (1866) soon after added a very rare taxon based on a single specimen purchased by the British Museum together with other Solnhofen fossils including the first *Archaeopteryx* skeleton. For a short time, research was stimulated by the discovery of Recent crustacean faunas from the deep sea during expeditions in the 19th century (Voyager, Valdivia) which were compared with fossil material (e.g., Balss 1924). However, in the first half of the 20th century there was little progress (Peiser 1904; v. Knebel 1907), apart from systematic compilations (Van Straelen 1924-1925; Glaessner 1929). The 'Treatise' volume on decapod crustaceans (Glaessner 1969) was mostly

DOI: 10.1127/0077-7749/2011/0162
www.schweizerbart.de
0077-7749/2011/0162 $ 2.50

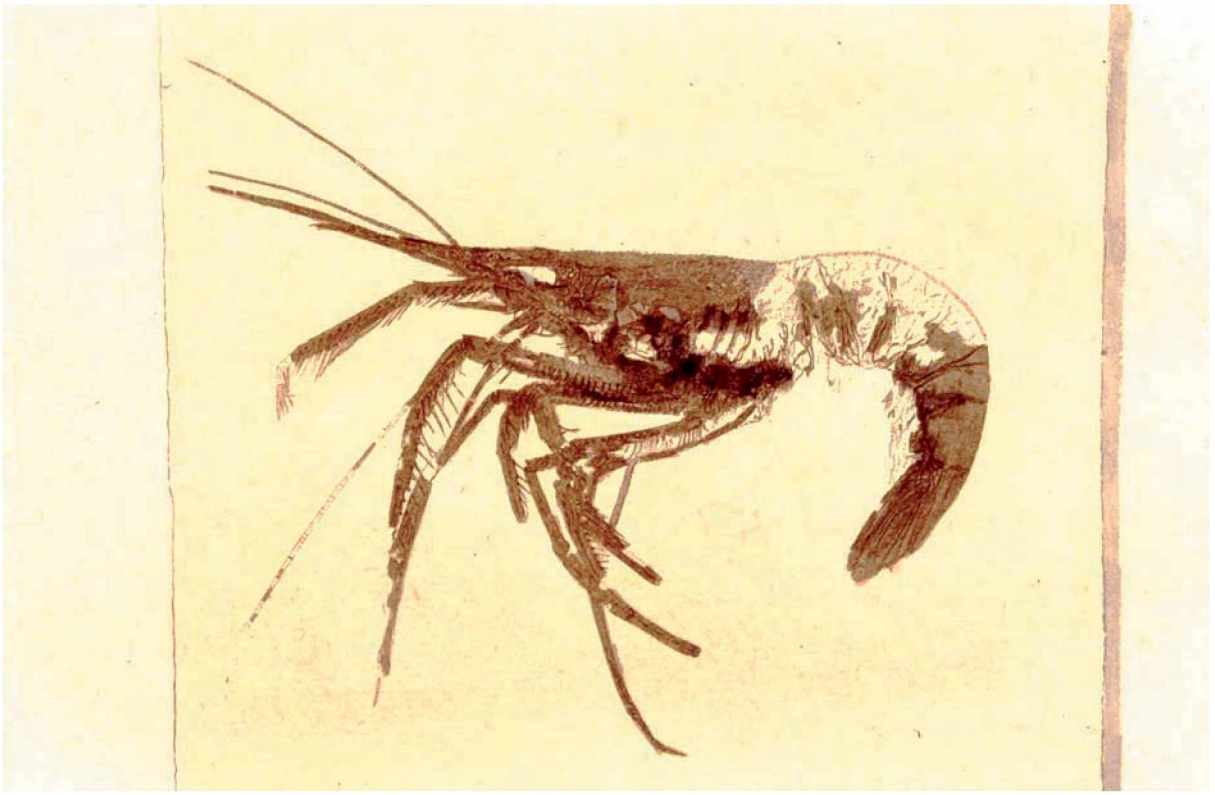

Fig. 1. One of the first published decapod crustaceans from the Upper Jurassic Solnhofen Limestones, later named as *Aeger spinipes* (Desmarest), from Knorr & Walch (1855-1873).

based on these data. In the second half of the 20th century the late Reinhard Förster dealt with decapod crustaceans from the Solnhofen Fossillagerstätten, but he focused on the re-study of already described taxa (Förster 1966, 1967, 1973, 1977). Hermann Polz was the first who recognized and studied ontogenetic stages of palinuran larvae (see Polz 1987 for a summary and references therein). Although some additional larval material has been recovered and studied (Haug et al. 2010), his work is still essential. In the 1990ies, Karl-Albert Frickhinger, a fossil trader and amateur collector, visited numerous institutional and private collections for preparing an exhaustive encyclopedia of Solnhofen fossils. The two published volumes (Frickhinger 1993, 1999) gave an enormous pulse for the interest in Solnhofen fossils in general. Also several scientific excavations of lithographic limestones and plattenkalks started independently in other areas (see Fig. 2; Brunn in Eastern Bavaria, Nusplingen in Swabia, Schamhaupten in the Eichstätt area, Wattendorf in Northern Franconia; Röper et al. 1996; Dietl & Schweigert 2001; Viohl & Zapp 2006, 2007; Fürsich et al. 2007), and much new material was recovered. Other fossils come from special quarries for amateur collectors and tourists (Blumenberg, Solnhofen, Mühlheim) and from commercial fossil excavations (Painten). A better communication between scientists, amateurs and fossil traders, triggered by an internet website dedicated exclusively to Solnhofen fossils (http://forum.solnhofen-fossilienatlas.de) brought to light excellently preserved material. Some of the new specimens have been meanwhile described (e.g., Polz 1990, 2000, 2007, 2008; Schweigert et al. 2000; Schweigert 2001b, 2002, 2003, 2010; Schweigert & Röper 2001; Schweigert & Garassino 2003, 2004, 2005a, b, 2006; Garassino & Schweigert 2004).

In 2006, Garassino & Schweigert revised the reptants, mostly based on the available type specimens and some additional material for comparisons and completion of descriptions. New taxa, however, were excluded from that study. Apart from brachyurans, which are – with very few exceptions (e.g. Fig. 3; Garassino et al. 2005a) – almost absent in this lithology, the Solnhofen-type limestones are one of

the most important data source for decapod crustacean phylogeny and diversification in the Late Jurassic. Most new taxa concern natant shrimps and prawns, but also in polychelidians and other reptants (erymids, glypheids) still undescribed species are present in various collections and wait for their description.

2. Geological settings

Because of their excellent preservation ("Konservat-Fossillagerstaette") and rarity of benthic organisms the Upper Jurassic Solnhofen-type limestones are thought to represent lagoonal environments with rather hostile conditions at the seafloor (Barthel et al. 1990). But this is a generalized view, and not all observations fit well with this oversimplified model. There exist numerous basin structures in the area which are isolated from each other, having their own local environments and evolution and are characterized by typical individual faunas and lithologies. The stratigraphic framework of these various localities of laminated limestones in the Solnhofen and Eichstätt quarry area (Fig. 4) was almost neglected in the past, but has become almost clarified recently (Schweigert 2007b). However, there are rather few contemporaneous localities in Franconia outside the laminated limestones which allow a precise biostratigraphical dating, so that it is still hardly possible to reconstruct high-resolution time-slices in that area. However, from co-occurring coral reefs and mapping data it is obvious that the deposition depth probably never exceeded 200 metres, and some localities must have been even much shallower, surrounded by small islands covered with shrubby vegetation adapted to dry habitats. For more details on the environment see e.g. Keupp et al. (2007) and literature cited therein.

3. Material and taphonomy

Many of the decapod specimens from the Solnhofen Limestones do not represent carcasses but exuviae (Schweigert 2007a). These exuviae show different stages of decay which must have occurred prior to their burial. Hence, most of these taxa have not lived in the place of their burial but in reefal habitats or other environments in the surroundings. The exuviae which result from molting were brought in by occasional currents. This is especially the case for adult reptants, because the lagoonal environments in which the laminates were deposited often had a seafloor hostile for life due to high salinity or oxygen depletion. Sometimes, however, interactions between the animals and the sea floor are obvious, like track-ways of reptants, resting traces, and traces of molting and feeding (e.g., Vallon & Röper 2006; Schweigert 2007a).

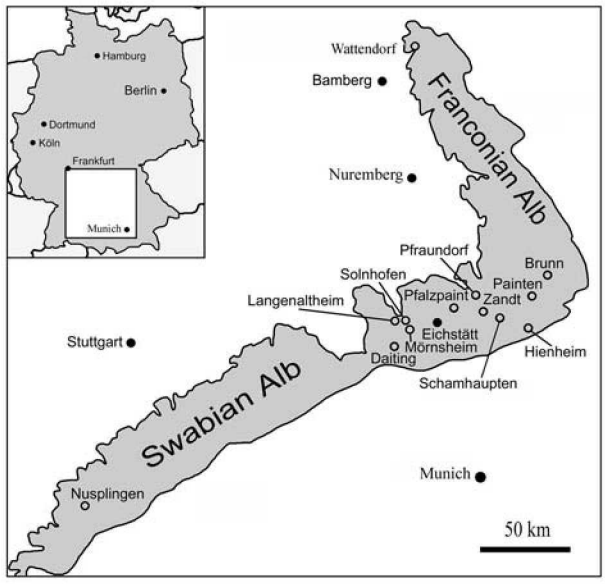

Fig. 2. Occurrences of Solnhofen-type platy limestones in southern Germany (modified from Fürsich et al. 2007).

Fig. 3. Poorly preserved brachyuran with partly preserved appendages, Lower Tithonian, Hybonotum Zone; Zandt, Solnhofen Limestones, Zandt Member (coll. R. Frattigiani). Scale equals 5 mm.

New documentation methods like ultraviolet illumination and other photographical techniques were often successfully used for the study of morphological details (see e.g., Tischlinger 2002; Haug et al. 2009), UV photography was also partly used in this study. The specimens were skillfully prepared mechanically where necessary.

Fig. 4. Typical quarry in the Eichstätt district, where the platy Upper Jurassic Solnhofen Limestones (Eichstätt Formation, lower Hybonotum Zone) are quarried for floor and roof tiles.

The specimens of new taxa described below are housed in the collection of the Staatliches Museum für Naturkunde Stuttgart, Germany (SMNS).

4. Description of new caridean species

For the higher systematic placement of the described taxa the recent compilation by Schweitzer et al. (2010) is followed.

Order Decapoda Latreille, 1802
Infraorder Caridea Dana, 1852
Superfamily Bresilioidea Calman, 1896
Family Alvinocarididae Christoffersen, 1986

Genus *Harthofia* Polz, 2008

Type species: *Harthofia bergeri* Polz, 2008

Other species included: *Harthofia blumenbergi* Polz, 2008 [imprint 2007]; *Harthofia polzi* n. sp. (herein).

Harthofia polzi n. sp.
Fig. 5

Etymology: Named in honor of Hermann Polz (Geisenheim) who studied numerous arthropods and their larvae from the Solnhofen Limestones and thus considerably contributed to our present knowledge on Late Jurassic crustacean diversity.

Holotype: Specimen illustrated in Fig. 5, SMNS no. 67746.

Further material: Two further specimens belonging to this species were discovered in the private collections of Alfred Walkowiak (Hausen) and Peter Kaczmekat (Wassertrüdigen).

Type locality and horizon: Zandt (25 km E of Eichstätt); Solnhofen Group, Zandt Member (see Zeiss 1977) Lower Tithonian, basal Hybonotum Zone (Schweigert 2007).

Occurrence: Zandt and Eichstätt (SW Germany).

Stratigraphical range: Only known from the lower part of the Hybonotum Zone (Upper Jurassic, Tithonian).

Diagnosis: See Polz (2008: 10) for the genus. In *Harthofia polzi* pereiopods I and II are isochelous.

Description: The holotype is an imperfectly preserved specimen with the first two pairs of pereiopods and poor remains of additional pereiopods IV and V, which are very slender and achelate. The carpi in pereiopods I and II are both extremely short and equally-shaped. The merus in both pereiopods has the same length as the chelae. Fixed and movable fingers slightly curved, arranged parallel to each other. Occlusal surface of fingers finely serrate but lacking prominent teeth. The length of the chelae is ca. 6 mm. Maxillipeds III not discernible. The carapace bears a characteristic claviform rostrum which is both dorsally and ventrally serrate. Laterally, there is a short

Fig. 5. *Harthofia polzi* n. sp., holotype. Solnhofen Limestones, Zandt Member, Lower Tithonian, Hybonotum Zone; Zandt (ca. 25 km E Eichstätt). SMNS 67746 (ex coll. R. Frattigiani). Scale equals 5 mm.

crest on the rostrum. In the holotype ca. 4 dorsal and 5 ventral teeth occur. Dorsal margin of carapace straight; its ventro-posterior margin widely expanded. Antennae and antennules not preserved, except of very poor remains of their bases, which are covered by large scaphocerites. Surface of carapace and abdomen finely punctuated (similarly arranged pattern but coarser than in *Hefriga* spp.). Abdomen only partly preserved in the holotype, showing pleura of the second abdominal somite overlapping to both sides. Telson, uropods and pleopods not preserved in the holotype but expected to look like in the other species of the genus. This could be proved in the specimens of *H. polzi* in private collections. There, the pattern of punctuate pits on the shell is well-preserved. In the carapace it these lines are arranged perpendicular to the long axis – like in *Hefriga* – but oblique in the adjacent abdominal somites, independent from the lateral margins of the somites.

Comparisons: *Harthofia polzi* n. sp. resembles the two other described species of this genus but differs in the outline of the propodi of the pereiopods I and II, which are more slender and almost equal in size and shape.

Superfamily and Family incertae sedis

Genus *Hefriga* Münster, 1839

Type species: *Hefriga serrata* Münster, 1839, subsequently designated by Glaessner (1929).

Other species included: *Hefriga frischmanni* Oppel, 1862; *Hefriga proboscideawulfi* Schweigert & Garasssino, 2004, *Hefriga rogerfrattigianii* n. sp. (herein), *Hefriga norbertwinkleri* n. sp.

Hefriga rogerfrattigianii n. sp.
Figs. 6-7

Etymology: After Roger Frattigiani (Laichingen) who detected numerous specimens of previously unknown decapods from the Solnhofen Limestones and kindly donated the holotype for description.

Holotype: Specimen illustrated in Fig. 6, SMNS no. 67744.

Further material: A second specimen is housed in the private collection of Roger Frattigiani (Laichingen).

Type locality and horizon: Vicinity of Eichstätt; Eichstätt Formation, Obere Schiefer Member (see Zeiss 1977); Lower Tithonian, early Hybonotum Zone (Schweigert 2007).

Occurrence: Only known from the vicinity of Eichstätt (SW Germany).

Stratigraphical range: Lower Tithonian, Hybonotum Zone.

Diagnosis: Species of *Hefriga* with a long rostrum bearing 8 dorsal and 2 ventral teeth.

Description: The holotype is a moderately preserved molt with all pereiopods and antennae preserved. Antennae short, bi-ramose. Length from tip of rostrum to tip of telson measures 50 mm. Carapace subrectangular, with long rostrum. Rostrum straight forwardly directed, with 8 densely arranged dorsal teeth. Ventrally 2 teeth were observed, discernible only at high magnification or using UV illumination (Fig. 7). Orbits well-developed, eyes not

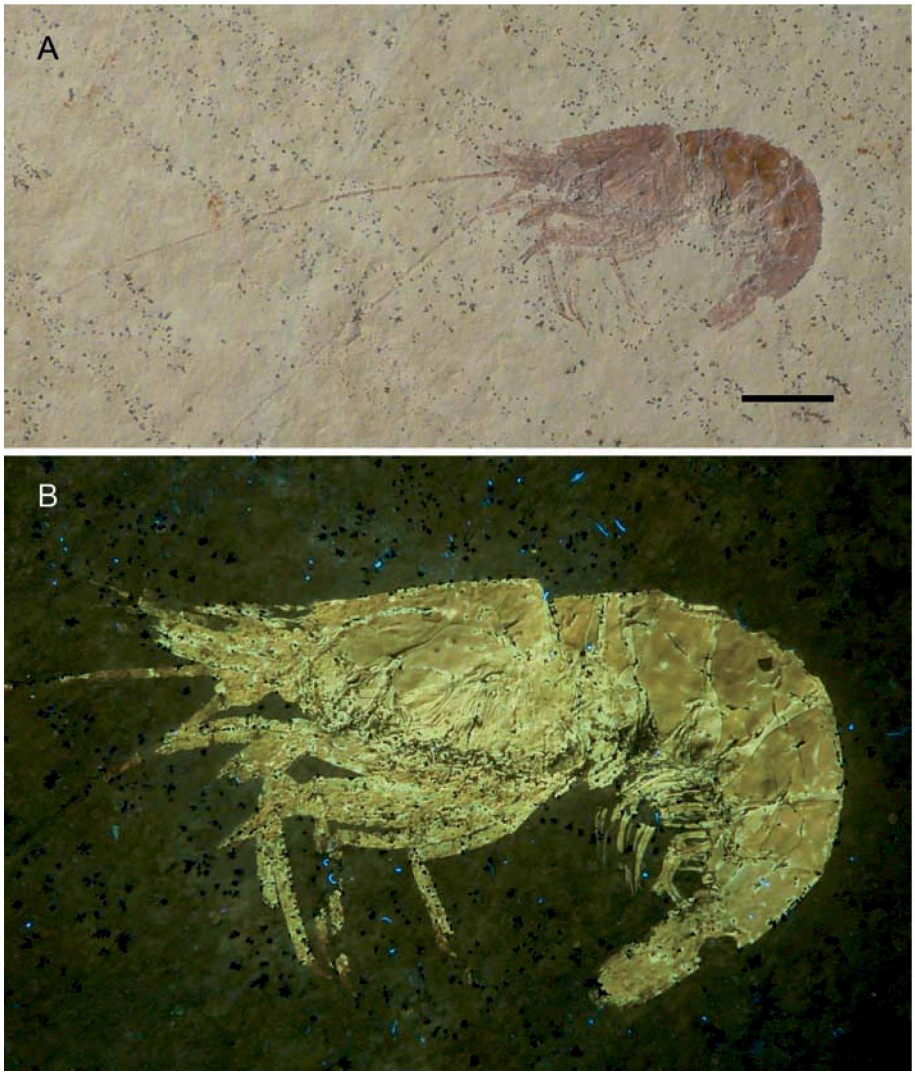

Fig. 6. *Hefriga rogerfrattigianii* n. sp., holotype. Solnhofen Limestones, Eichstätt Formation, Lower Tithonian, Hybonotum Zone; vicinity of Eichstätt. **A** – Photograph with normal illumination, scale equals 10 mm; **B** – slightly enlarged view under UV illumination, photograph by courtesy of H. Tischlinger. SMNS 67744 (ex coll. R. Frattigiani).

preserved. Surface of the shell of carapace and abdomen covered with a delicate pattern of fine pores probably related to setae in the living animal. Pereiopod I long, ending in a minute chela. Pereiopod II very short and strong, chela with thick simple fingers equal in length. Pereiopods III-V moderately strong, almost equal in length, with long terminal claws. At the basis of the terminal claws, a short spine occurs. Abdomen with long, well-developed pleopods. Telson bears several movable spines aside the symmetry line. In the additional specimen observed their number is counted as ca. 9. Uropodal exopodites with diaeresis.

Comparisons: *Hefriga rogerfrattigianii* n. sp. differs from all other species of *Hefriga* and closely related taxa in the occurrence of two ventral teeth in the rostrum.

Hefriga norbertwinkleri n. sp.
Fig. 8

Etymology: Named after Norbert Winkler (Stahnsdorf) who kindly donated the holotype for description.

Holotype: Specimen illustrated in Fig. 8, SMNS no. 67745.

Type locality and horizon: Vicinity of Eichstätt; Eichstätt Formation, Obere Schiefer Member (see Zeiss 1977); Lower Tithonian, early Hybonotum Zone (Schweigert 2007).

Occurrence: Only known from the vicinity of Eichstätt (SW Germany).

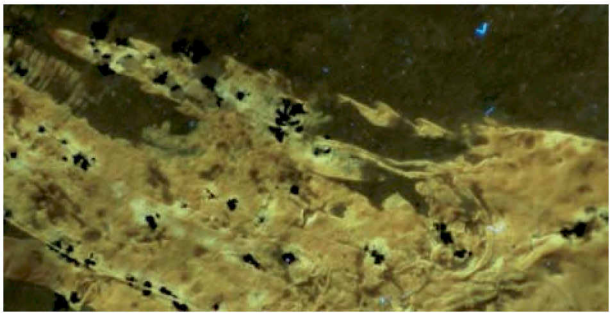

Fig. 7. *Hefriga rogerfrattigianii* n. sp., enlarged partial view of Fig. 6B showing the rostrum with dorsal and ventral teeth. Photograph by courtesy of H. TISCHLINGER.

Stratigraphical range: Lower Tithonian, Hybonotum Zone.

Diagnosis: Species of *Hefriga* showing spiny needle-like extensions of the chelae in pereiopods II and the rostrum showing 10 dorsal and 3 ventral teeth.

Description: The specimen is a moderately preserved molt lying on the surface of a bedding plane. Length from tip of rostrum to tip of telson measures 50 mm. Carapace subrectangular, with long, slightly downwards-dipping rostrum. Rostrum with 10 short, densely spaced dorsal teeth and 3 ventral teeth. Shell of carapace and abdomen covered with typical punctuate pattern arranged in lines like in other species of the genus. Orbits well-developed, eyes not preserved. Antennae about as long as the body, antennules not preserved. Terminal article of maxilliped III elongate, with a rounded tip. Pereiopod II very strong, with thick fingers ending in a needle-like prolonged tip. Pereiopods III-V achelate, weak, with terminal claws being relatively short. Abdominal somites ventrally rounded, with lateral margins of somite II expanding previous and posterior one. Pleopods bi-ramose, well-developed. Telson bearing a lateral row of at least 6 movable spines. Uropodal diaeresis present.

Comparisons: The species is morphologically very close to *Hefriga frischmanni* OPPEL, 1862, but differs from the latter in the number of dorsal teeth in the rostrum (only 9 in *H. frischmanni*) and in the additional development of three ventral teeth which are not observed in *H. frischmanni*. In respect of the general shape of the rostrum and the spiny chelae, *H. norbertwinkleri* n. sp. and *H. rogerfrattigianiii* n. sp. are closer related to each other than to the further species assigned to this genus. However, I refrain from putting the three above mentioned taxa into a separate genus, as POLZ (2009 [imprint 2008]) did when he erected *Alcmonacaris*, which is another species closely related to *Hefriga* s. str. There was no reason given why *Alcmonacaris* should not be placed in *Hefriga*. Obviously, multiple ecological niches existed in the vicinity of the lagoonal environments that were simultaneously occupied by different species of the same genus.

Acknowledgements

Numerous enthusiatic amateur collectors provided information and donated specimens for description: PETER BÜRGER (Bad Hersfeld), UWE ELLER (Dümpelfeld), ROGER FRATTIGIANI (Laichingen), Peter Kaczmekat (Wassertrüdingen) GÜNTER KOSCHNY (Bad Soden), DIETER KÜMPEL (Wuppertal), UDO RESCH (Berlin), PETER RÜDEL (Gröbenzell), HELMUT TISCHLINGER (Stammham), NORBERT WINKLER (Stahnsdorf), ALFRED WALKOWIAK (Hausen), and MATTHIAS WULF (Rödelsee). MARTINA KÖLBL-EBERT (Jura-Museum Eichstätt), MATTHIAS MÄUSER (Naturkunde-Museum Bamberg), MARTIN NOSE (Bayerische Staatssammlung für Paläontologie und Geologie, Munich), and MARTIN RÖPER (Museum Solnhofen) gave access to institutional collections under their care. HELMUT TISCHLINGER provided photographs for study by using ultraviolet illumination. The journal's referees are thanked for their valuable advice. Many thanks to all these individuals!

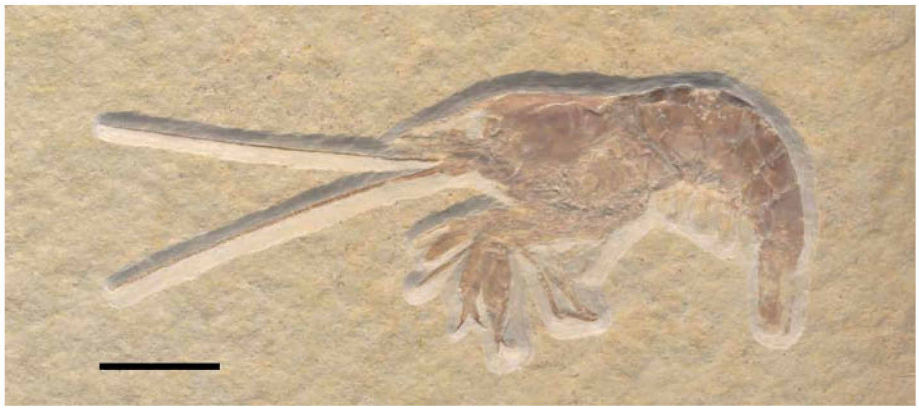

Fig. 8. *Hefriga norbertwinkleri* n. sp., holotype. Solnhofen Limestones, Eichstätt Formation, Lower Tithonian, Hybonotum Zone; vicinity of Eichstätt. SMNS 67745 (ex coll. N. WINKLER). Scale equals 10 mm.

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Manuscript received: August 16th, 2010.
Revised version accepted: November 15th, 2010.

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