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Revision of Jurassic Homoloidea De Haan, 1839, from the Ernstbrunn and Štramberk limestones, Austria and the Czech Republic

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(With 5 figures)

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Abstract

Evaluation of brachyuran decapod crustaceans exhibiting *lineae homolicae* from the Tithonian (Upper Jurassic) Ernstbrunn and Štramberk limestones in Austria and the Czech Republic has resulted in a major realignment of taxa within the Jurassic Homoloidea. A new family, Tithonohomolidae, is erected to accommodate *Tithonohomola armata* Blaschke, 1911, and *T. tuberculata* nov. spec. as well as a nov. gen., *Tenuihomola*, which comprises *Tenuihomola longa* Moericke, 1897, and *T. ortwini* nov. spec. A new genus and species, *Doerflesia ornata*, along with two species within the genus *Gastrodorus* are assigned to the Homolidae. Homolids appear to have evolved in warm, shallow, reefal environments in western and central Europe during the Late Jurassic.

Key words: Brachyura, Homoloidea, Jurassic, Austria, Czech Republic

Introduction

The Homoloidea de Haan, 1839, embraces three families of primitive crabs characterized by possession of ecdysial sutures referred to as *lineae homolicae*. Within the superfamily, only the Homolidae de Haan, 1839, has a fairly robust fossil record spanning the Jurassic to Holocene. One of the other families, the Poupiniidae Guinot, 1991, is represented by a single fossil species from the Maastrichtian (Upper Cretaceous) of Antarctica (Feldmann et al. 1993), and the Latreilliidae Stimpson, 1858, is known only from the Holocene. Among the Homolidae, extant forms have recently been studied (Guinot & Richer de Forges 1995) and fossil taxa have been discussed, with the emphasis on Cretaceous and Paleogene species from western North America (Schweitzer et al. 2004). These studies have defined the limits of the family and, with few exceptions, fossils assigned to the Homolidae conform to the current concept of the family. One group of the homolids has not been subjected to a modern re-examination, the Jurassic species.

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Fig. 1. Map showing the location of Ernstbrunn, Austria, and Štramberk, Czech Republic, where specimens for the present study were collected.

The Homolidae arose in the Late Jurassic with the oldest records in western and central Europe. Four species in two genera, *Gastrodorus* VON MEYER, 1864, and *Tithonohomola* GLAESSNER, 1933, have been identified from the Jurassic (GLAESSNER 1969). Work in progress on the Tithonian (Upper Jurassic) rocks near Štramberk, Czech Republic, and at the Ernstbrunn quarries, near Ernstbrunn, Austria (fig. 1), has yielded an exceptionally diverse decapod fauna, including several previously unknown taxa referable to the Homolidae. Examination of type material of the described species coupled with a study of the new specimens has led to the conclusion that Jurassic Homolidae are more diverse than previously thought and are in need of revision.

The purpose of the present work is to examine the Jurassic homolids, describe new species from the Štramberk and Ernstbrunn limestones, and re-assess the generic arrangement of taxa consistent with the modern definition of the family.

The primary basis for this work is the collection of more than 7,000 specimens of arthropods, including decapods, brought together under the direction of FRIEDRICH BACHMAYER during the 1950s (BACHMAYER 1959). The specimens from Ernstbrunn were collected by BACHMAYER and colleagues, some were numbered, but only the isopods were described and published (BACHMAYER 1949, 1955); a few decapods were recorded from Štramberk (BACHMAYER 1959). He apparently intended to monograph the decapods from Ernstbrunn (BACHMAYER 1959) but the work was never undertaken. His specimens are housed at the Naturhistorisches Museum Wien and have now been made available to the authors and their students for study. The present revision of the Jurassic Homolidae is one part of that research effort.

Institutional abbreviations

BSP	Bayerische Staatsammlung für Paläontologie und historische Geologie München (Munich), Germany
NHMW	Naturhistorisches Museum Wien (Vienna), Austria
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany

Systematic Palaeontology

Infraorder Brachyura LINNAEUS, 1758

Section Dromiacea DE HAAN, 1833

Superfamily Homoloidea DE HAAN, 1839

Family Homolidae DE HAAN, 1839

Included Jurassic genera: *Doerflesia* nov. gen.; *Gastrodorus* VON MEYER, 1864.

Discussion: Extant representatives of the Homoloidae have recently been reviewed by GUINOT & RICHER DE FORGES (1995), and the post-Jurassic fossil representatives of Homolidae have been summarized by SCHWEITZER et al. (2004). GUINOT & RICHER DE FORGES (1995: 291) provided diagnostic characteristics of the family including several features of the dorsal carapace that are useful in assigning fossils to the family, such as an ovoid to quadrangular carapace, rarely narrowing anteriorly; presence of *lineae homolicae* and cervical and branchiocardiac grooves; a pair of pseudorostral spines; and orbits that are either absent or poorly developed. Occasionally, an orbital region is present. Re-assessment of one of the Jurassic genera that had previously been assigned to the family, *Tithonohomola* GLAESSNER, 1933, has led to the conclusion that the genus as perceived by that author contains species better placed in two genera to be assigned to a separate homoloid family. Those decisions are discussed below.

Retention of *Gastrodorus* within the Homolidae is subject to question. The two species assigned to the genus clearly exhibit *lineae homolicae* and, thus, are referable to the Homoloidea, but they lack apparent pseudorostral spines.

Definition of the new genus *Doerflesia* is less controversial. The genus bears all the characteristics of the family and, furthermore, is very similar in general configuration to extant genera. This addition to the group of Jurassic homolids is particularly significant because it is the earliest occurrence, to date, of a taxon that appears to be ancestral to extant forms.

Genus *Doerflesia* nov. gen.

Type species: *Doerflesia ornata* nov. spec.

Included species: *Doerflesia ornata*.

Diagnosis: Quadrate inter-lineal carapace element with weakly convex *lineae homolicae*, two prominent antero-dorsally directed pseudorostral spines; apparently lacking supraorbital spines; complex, tuberculate hepatic regions; mesogastric region markedly bilobed posteriorly; metagastric and urogastric regions joined axially by a large boss and separated by shallow grooves laterally; cardiac region broadly separated from posterior border by elongate intestinal region.

E t y m o l o g y : The generic name refers to the village of Dörfles, Austria, near the site where the holotype was collected. The gender is feminine

D i s c u s s i o n : Recognition of *Doerflesia* as a new genus is based upon the overall outline of the inter-lineal portion of the carapace, development of two very large pseudorostral spines that are directed upward and forward, configuration of the metagastric and urogastric regions, and development of an elongate intestinal region separating the cardiac region from the posterior border. This combination of characters distinguishes the genus from all other fossil forms, to our knowledge. Certainly, *Doerflesia* can be distinguished from *Gastrodorus* which has an outline that tapers posteriorly, lacks the pseudorostral spines but possesses a long, slender axial rostral spine, and shows no fusion of the metagastric and urogastric regions. Genera within the Tithonohomolidae nov. fam., *Tithonohomola* GLAESSNER, 1933, and *Tenuihomola* nov. gen., have sulcate, downturned rostra, lack pseudorostral spines, and exhibit complex orbital structures of spines and eaves. Additionally, the cardiac region in species within the Tithonohomolidae extends nearly to the posterior border. Thus, the genus is unique.

The new genus is quite different from the Cretaceous genera discussed by SCHWEITZER et al. (2004). The extremely large pseudorostral spines, narrow orbital region, development of the large tubercle uniting the metagastric and urogastric regions and overall granulation are key morphological features of *Doerflesia* that are not found in any of the Cretaceous taxa. In overall appearance, *Doerflesia* is most similar to *Latheticocarcinus* BISHOP, 1988; however, the latter is characterized by a broader inter-lineal part of the carapace, a prominently bifid rostrum, tiny pseudorostral spines, and distinctly separated metagastric and urogastric regions.

***Doerflesia ornata* nov. spec.**

(fig. 2)

T y p e s : The holotype, Naturhistorisches Museum Wien (NHMW) 2007z0149/0015, and paratype, NHMW 1912/0006/0696.

L o c u s T y p i c u s : The holotype was collected in the Ernstbrunn quarries, near Dörfles, Austria. The paratype was collected near Štramberk, Czech Republic.

S t r a t u m T y p i c u m : The holotype was preserved in Tithonian (Upper Jurassic) rocks of the Ernstbrunn Limestone. The paratype was preserved in Tithonian (Upper Jurassic) rocks of the Štramberk Limestone.

E t y m o l o g y : The trivial name is from the Latin, *ornatus*, the past participle of *ornare* = to adorn, in reference to the ornamentation on the inter-lineal part of the carapace, particularly the hepatic region.

D i a g n o s i s : As for genus.

D e s c r i p t i o n : Inter-lineal part of carapace length = 14.7 mm, width = 8.8 mm; rectangular, with widest part at level of epibranchial region; moderately vaulted transversely, less so longitudinally. Regions well-defined by smooth grooves. Rostrum axially sulcate, termination not known; with pair of large pseudorostral spines directed antero-

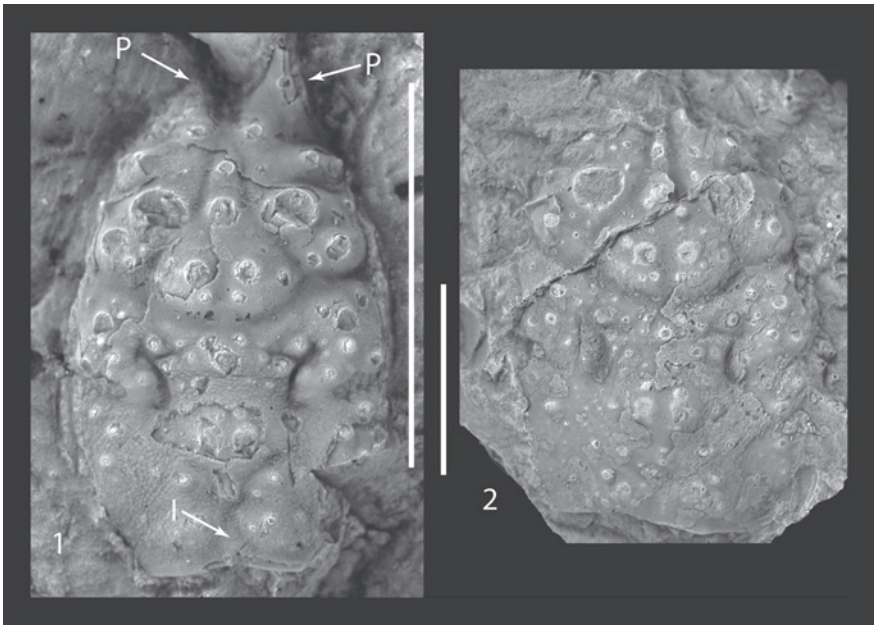

Fig. 2. *Doerflesia ornata* nov. gen. and nov. spec. 1, dorsal view of plaster cast of holotype, NHMW 2007z0149/0015, from the Ernstbrunn Limestone, Tithonian, from near Dörfles, Austria; 2, dorsal view of plaster cast of paratype, NHMW 1912/0006/0696, from the Stramberk Limestone, Tithonian, from near Štramberk, Czech Republic. I = intestinal region; P = pseudorostral spines. Scale bars equals 10 mm.

dorsally. Orbits not known. Anterolateral and posterolateral margins (*lineae homolicae*) smoothly convex. Posterior margin wide, concave, with narrow, well defined rim.

Epigastric region defined by tubercles positioned just posterior to pseudorostral spines. Mesogastric region defined by smooth grooves laterally and well-defined cervical groove posteriorly, flask shaped; anterior projection short, extends to level of anteriormost protogastric spines and bears one axial tubercle; posterior part of mesogastric region with three large tubercles arrayed in forward-directed triangle and four smaller ones along posterior margin; posterior part of mesogastric region with subtle axial depression. Cervical groove concave-forward axially, curves to become convex forward posterior to protogastric region. Metagastric region and urogastric region joined axially, transversely ovoid, bearing single, pustulose axial tubercle; the two regions each bearing small tubercles and separated laterally by groove. Cardiac region pentagonal, wider than long, margins concave; two transversely placed nodes situated near midline. Intestinal region long, narrow, depressed.

Protogastric and hepatic regions fused, granular, with two swollen areas; anteriormost smaller, bearing one tubercle; posteriormost larger, bearing four tubercles of which the one situated axially at midlength of mesogastric region is largest and the one situated postero-laterally to it is only slightly smaller. Epibranchial region swollen, circular, tuberculate, one large tubercle centrally located. Mesobranchial region small, circular,

with single tubercle; defined posteriorly and axially by distinct branchiocardiac groove which forms concave-forward arc. Metabranchial region weakly tumid, bearing pair of small tubercles and pair of large tubercles axially and cluster of three small tubercles at anterolateral corner.

Remainder of carapace, sternum, abdomen, and appendages not preserved.

Discussion: Recognition of this new species represents the earliest occurrence of a representative of the Homolidae that bears a strong resemblance to extant forms. This is significant because it confirms the antiquity of the family as currently defined.

Presence of *Doerflesia ornata* in a Jurassic carbonate reef habitat suggests that the genus originated in warm, shallow, marine conditions. Extant representatives are known to inhabit a wide variety of environments ranging from a few metres to bathyal depths and including rocky, sandy, shelly, and muddy substrates (SAKAI 1976). WILLIAMS (1984: 262) also noted their occurrence in reefal habitats. Thus, although the range of habitats occupied by members of the family has certainly expanded, some continue to live in sites similar to the apparent habitat of origin of the group.

The paratype, NHMW 1912/0006/0696, was originally referred to *Oxythyreus armatus* by BLASCHKE (1911). That species has now been designated the type species of *Tithonohomola* GLAESSNER, 1933. The specimen herein considered a paratype of *E. ornata* bears little resemblance to the holotype of *O. armatus* (BLASCHKE 1911: p. 1, fig. 2), but it closely resembles the holotype of *Doerflesia ornata*.

Genus *Gastrodorus* VON MEYER, 1864

1864 *Gastrodorus* VON MEYER: 208.
1925 *Eopagurus* BEURLEN: 494.

Type species: *Prosopon* (*Gastrodorus*) *neuhausense* VON MEYER, 1864: 208.

Included species: *Gastrodorus neuhausense* VON MEYER, 1864; *Gastrodorus granulatus* FÖRSTER, 1985.

Diagnosis: Carapace elongate, quadrate, longer than wide, greatest width in subhepatic region; bearing long, smooth rostrum; orbits not strongly developed; regions well defined by deep, smooth grooves; cervical groove strongest; branchiocardiac groove well-developed, extending to distinct posterior rim; branchial area well differentiated into epibranchial, mesobranchial, and metabranchial areas; cardiac region triangular, extending nearly to posterior rim.

Discussion: Placement of *Gastrodorus* in suprageneric categories has been difficult and has resulted in three very different views. BEURLEN (1925) erected a new hermit crab genus, *Eopagurus*, to accommodate the type species of *Gastrodorus*. GLAESSNER (1929b) considered *Eopagurus* to be a junior synonym of *Gastrodorus* and placed the latter within the brachyuran family Homolidae. This view was supported through subsequent work by BACHMAYER (1959) who studied crustaceans from Štramberk, Czech Republic. Subsequently, FÖRSTER (1985) named another species of *Gastrodorus*, *G. granulatus*, and placed it and the type species within the squat lobster family Galathei-

dae. Such disparate views on the placement of the genus have arisen because it bears an unusual combination of characters.

The only remains known of *Gastrodorus* are those of the carapace. The cuticle is well-calcified throughout the length of the carapace. The carapace is longer than wide; has a strongly vaulted transverse cross section; has relatively low flanks; bears a long, slender, smooth rostrum; exhibits two, well-defined, transverse grooves; and has a complex array of distinct regions. This is a confusing combination of characters. The overall shape of the carapace and the presence of a well-developed rostrum are reminiscent of macrurans. The relatively strong development of the carapace anterior to the cervical groove resembles some pagurids, but the presence of a long rostrum, well-defined regions, and a well-calcified carapace posterior to the cervical groove is quite unlike pagurids. Presence of a long, needle-like rostrum, the overall carapace shape, and a well-developed cervical groove suggest placement with the galatheids; however, the presence of a strong branchiocardiac groove, details of the posterior carapace and the overall development of regions argue against placement there. Finally, the development of the carapace regions, possession of two strong transverse grooves and the relatively short lateral sides support placement with dromiacean crabs, specifically the Homolidae. Based upon the preserved material, the problems with this placement include the elongate, lobster-like form and the presence of a very long rostrum. Thus, based upon the criteria typically employed in debate about the placement of *Gastrodorus*, no clear assignment is forthcoming.

In an attempt to resolve this quandary, morphological features of the carapace were scored in the manner used by SCHRAM & DIXON (2004). That study, based upon an earlier analysis by DIXON et al. (2003), attempted to integrate fossil decapods into a phylogenetic analysis of the group. Those characters which could be observed on specimens of *Gastrodorus*, numbered 39 – 44 (SCHRAM & DIXON 2004: 18), were scored according to the scheme defined by DIXON et al. (2003: 948-949). The characters included nature of the rostrum, calcification of the cuticle, shape of the carapace, transverse groove development, shape of the posterior margin of the carapace, and development of an axial suture. The combination of characters exhibited by *Gastrodorus* was unique, as compared against the combination of characters scored for all the taxa in the phylogenetic studies of SCHRAM & DIXON (2004: Appendix 1). Because none of the characters defining nodes on the trees was identified in the SCHRAM & DIXON (2004) paper, it was not possible to interpret the comparison. Had characters defining the nodes of the trees been identified, it would have been possible to attempt to place *Gastrodorus* on the tree based upon shared characters. Although the placement would not have been conclusive, it would have been suggestive of its familial affinities. Additionally, some of the scored characters identified by SCHRAM & DIXON were seemingly quite ambiguous. For example, in the definition of character states by DIXON et al. (2003), short rostra were grouped along with lack of rostrum, and there was no stated basis for distinguishing short from long rostra by them. Shape of the postero-dorsal margin was equally difficult to interpret based upon their definition. The brachyurans in the phylogenetic study (SCHRAM & DIXON 2004) were not scored in terms of this character. Examination of a variety of crabs suggests that some could be scored in nearly all the character states enumerated for this character.

Comparison of the morphology of *Gastrodorus* with representatives within each of the taxa previously suggested to embrace the genus indicates that placement within the Homolidae is most likely, until additional evidence indicates otherwise. One character that seems to have been overlooked in morphological analyses of decapods is the presence of a well-defined cardiac region. This region is either not expressed or only very subtly expressed on the carapace of decapods, other than brachyurans. Within the Brachyura, the cardiac region is clearly expressed on all but a few taxa. For example, some of the Raninidae have very smooth carapaces on which development of regions is difficult or impossible to recognize; however, some of these taxa do have weakly expressed branchiocardiac grooves defining the cardiac region. Similarly, some of the Carpiliidae have smooth carapaces revealing little indication of regions. These are features that in all likelihood were secondarily derived from forms with well-developed regions. Possession of two well-developed transverse grooves is not unique to the Brachyura, but it is certainly a hallmark of the Dromiacea. Distinct branchiocardiac grooves are not typical of either the Paguridae or the Galatheidae. Additionally, the development of regions on *Gastrodorus* is quite like that of several dromiaceans groups, including the Homolidae. The lack of development of the lateral sides is suggestive of the latter family rather than the other families within the section Dromiacea.

The ventral border of the lateral sides terminates along a nearly straight line that is difficult to expose in preparation, but it appears to be a nearly straight border extending from the posterior margin to a position below the subhepatic region at the anterior margin. This edge may represent one of three types of boundaries. It could represent the true edge of the carapace and, because that part of the carapace is not strongly calcified, it is not readily exposed. Alternatively, the edge may represent a *linea homolica*, or similar ecdysial suture. Finally, it is possible that the line marks the edge of calcification of the carapace and the more ventral, uncalcified parts of the carapace are not preserved. This latter condition is illustrated by living *Homolodromia* spp. and the Jurassic *Pithonoton marginatum* von Meyer, 1842 (Schweitzer & Feldmann 2008 [imprint 2007], pl. 1), among others. Our conclusion that the margin represents a *linea homolica* is based upon its position and shape of the margin. The boundary between well-calcified and uncalcified cuticle in the Homolodromioidea defines the ventral part of the branchial regions but does not extend onto the regions anterior to the cervical groove as it does in *Gastrodorus* (Schweitzer & Feldmann 2008 [imprint 2007]: pl. 1, fig. A). It tends to be an arcuate margin that curves posterodorsally and then posteriorly rather than being straight and parallel the upper surface of the carapace. *Lineae homolicae* generally are straighter and do extend to the anterior margin of the carapace.

The one feature exhibited by *Gastrodorus* that is unlike most crabs is the presence of a long, thin rostrum. However, examination of representatives of the Homolidae illustrated by Guinot & Richer de Forges (1995) reveals that several species, notably within the genera *Homolax* Alcock, 1899, and *Paromolopsis* Wood-Mason *in* Wood-Mason & Alcock, 1891, do have elongate rostra. To be sure, these are not as long, relative to the carapace length, as the rostrum of *Gastrodorus*; however, this is judged to represent a question of degree rather than the presence of a character that would categorically exclude the genus from the brachyurans.

Gastrodorus neuhausense VON MEYER, 1864
(fig. 3)

1864 *Prosopon* (*Gastrodorus*) *Neuhausense* VON MEYER: 208.
1902 *Gastrodorus Neuhausense* H. V. MEYER– HAIZMANN: 526; pl. 14, fig. 6A and B.
1908 *Gastodorus Neuhausense* H. V. MEYER – ENGEL: 426; *not* pl. 5, fig. 18.
1913 *Gastr. Neuhausense* – E. FISCHER: 52.
1925 *Eopagurus neuhausensis* – BEURLEN: 494; figs 1, 2.
1929a *Gastrodorus neuhausensis* V. MEY. – GLAESSNER, [Dekapodenstudien]: 147
1929b *G. neuhausensis* V. MEYER – GLAESSNER, [Fossilium Catalogus]: 180.
1933 *G. neuhausensis* V. MEY. – GLAESSNER: 182.
1969 *G. neuhausensis* (VON MEYER) – GLAESSNER: R490.
1985 *Gastrodorus neuhausensis* V. MEYER – FÖRSTER: 56.

Material examined: NHMW 1990z0041/0100, NHMW 1990z0041/0103, NHMW 1990z0041/1822, NHMW 1990z0041/1930, NHMW 1990z0041/3876, NHMW 1990z0041/3955b, NHMW 1990z0041/4244, NHMW 1990z0041/4421, NHMW 1990z0041/4903, SMNS 10866, and SMNS 67364.

Occurrence: The newly assigned material was collected under the direction of FRIEDRICH BACHMAYER from Upper Jurassic (Tithonian) rocks at the Ernstbrunn quarries near Dörfles, Austria. The specimens from the Staatliches Museum für Naturkunde, Stuttgart, were collected from the Upper Jurassic "*Pseudomutabilis*-Schichten" from Monkberg, a hill near the village of Salmendingen in the west of the Swabian Alb, Germany (G. SCHWEIGERT, personal comm., 2/2008).

Diagnosis: Carapace small, elongate quadrate, narrowing somewhat posteriorly; rostrum blade-like, laterally compressed, axially keeled; cardiac region triangular; surface strongly granular.

Description: Carapace small, narrowing slightly posteriorly, longitudinally planar, transversely strongly arched; greatest width measured at level of subhepatic regions, about 60 % length, excluding rostrum. Carapace regions elevated, coarsely granular, defined by deep, smooth grooves.

Front narrow, about 11 % maximum width with long, slender, smooth rostrum, about 23 % carapace length excluding rostrum. Rostrum blade-like, laterally compressed, axially keeled, dorso-ventral height twice width. Fronto-orbital width about 64 % maximum width. Orbits forward-directed, with well-developed, short, supra-orbital spine defining position at which upper orbital margin curves ventro-laterally. Outer orbital corner tightly rounded. Anterolateral margin weakly convex. Posterolateral margin straight; margins converge slightly posteriorly; amount of convergence variable. Posterior margin strongly concave forward, strongly rimmed. Lateral sides short, defined ventrally by a nearly straight line extending from posterior margin to position ventral to subhepatic region at which point the margin curves dorsally to outer orbital corner.

Mesogastric region quadrangular posteriorly and drawn into narrow, lanceolate anterior process merging anteriorly into smooth rostral crest. Posterior-most part of mesogastric region with two prominent, ovoid, gastric muscle swellings; entire surface of region with moderately sized granules. Epigastric regions transversely ovoid, not well defined, granular. Protogastric regions as wide as epigastric region anteriorly, narrowing posteriorly; bounded laterally by distinct, sinuous groove separating protogastric region

Fig. 3. *Gastrodorus neuhausense* von Meyer, 1864. All specimens from the Ernstbrunn Limestone, Tithonian, from near Dörfles, Austria except (6). 1, dorsal view of NHMW 1990z0041/4421; 2, dorsal view of NHMW 1990z0041/3876; 3, dorsal view of NHMW 1990z0041/1822; 4, right lateral view of NHMW 1990z0041/3876, showing development of rostrum and subhepatic region; 5, oblique frontal view of NHMW 1990z0041/1822, showing development of orbital region; 6, dorsal view of a specimen illustrated by Haizmann (1902: pl. 14, fig. 6a) and collected from the "*Pseudomutabilis*-Schichten" from Monkberg, a hill near Salmendinger, western Swabian Alb, Germany. The illustration lacks a scale and was copied from a photograph found in the Bayerische Staatsammlung für Paläontologie und historische Geologie, München, Germany, by Günter Schweigert. 7, dorsal view of NHMW 1990z0041/0103; 8, dorsal view of NHMW 1990z0041/4244. Scale bars equal 1 mm.

from inflated, bilobed, granular hepatic region and ovoid, inflated subhepatic region. A smooth ovoid depressed area bearing a central boss lies between epigastric and subhepatic regions.

Cervical groove prominent, forming parabolic arc from midline to posterior end of subhepatic region where it curves laterally onto lateral flanks.

Cardiac region an equilateral triangle, extending to posterior rim, with straight or weakly convex lateral margins; separated from metabranchial region by deep branchiocardiac groove; surface with transversely ovoid granules.

Branchial region with well-defined epibranchial, mesobranchial, and metabranchial regions. Ovoid, granular epibranchial region and weakly bilobed mesobranchial region which is broadest axially and narrows as it curves posterior to epibranchial bear transversely ovoid granules. Metabranchial region large, well-defined, bears transversely ovoid, forward-directed terraced lines; bounded axially and anteriorly by smoothly arched, well-defined branchiocardiac groove which extends to posterior rim.

Abdomen, sternum, and appendages not known.

D i s c u s s i o n : Only two species have so far been assigned to *Gastrodorus*, and they can readily be distinguished from one another. The type species, *G. neuhausense* is substantially longer than wide, is quadrate in outline with the widest point near the anterior of the carapace, has a triangular cardiac region, and is heavily ornamented with nodes. The carapace of *G. granulatus* is interpreted to be slightly longer than wide, ovoid with the widest point near the midlength, with a more pentagonal cardiac region than that of *G. neuhausense*, and is finely granular overall (FÖRSTER 1985).

The type and sole specimen of *Gastrodorus granulatus* is from the Middle Jurassic (upper Bajocian) from near Basel, Switzerland. The type series of *G. neuhausense* was collected from near a small village, Amstetten, near Geisingen, which lies south-southwest from Tübingen, Germany (VON MEYER 1864). That material was deposited in Munich and was still there in the early twentieth century, because HAIZMANN (1902) studied the 12 available specimens for comparison with the material he had collected at Monkberg (SCHWEIGERT, pers. comm., 21/2/2008). The material of VON MEYER is now lost, presumably destroyed in World War II. However, because HAIZMANN studied the original type series and assured himself that his specimens were conspecific with those of VON MEYER, BACHMAYER (1959) designated one of the specimens illustrated by HAIZMANN as the neotype. In his synonymy of the species, BACHMAYER (1959: 941) incorrectly referred to the specimen as having been illustrated by HAIZMANN (1902: pl. 16, fig. 6a and b) In designating the neotype, he referred to the same work but cited pl. 16, fig. 2b. The correct citation for the illustration, based upon examination of HAIZMANN (1902) is pl. 14, fig. 6b. That specimen is deposited in the Sammlung des Institutes für Geologie und Paläontologie der Universität Tübingen, Germany. Additional material, including the specimen illustrated herein (fig. 3.6), from the same site, is deposited in the Staatliches Museum für Naturkunde, Stuttgart. The Monkburg specimens were collected from the Upper Jurassic "*Pseudomutabilis*-Schichten" (G. SCHWEIGERT, pers. comm. 21/1/2008). To our knowledge, the only other site from which *G. neuhausense* has been reported is near Štramberk, Czech Republic from the Stramberger Schichten of Tithonian (Late Jurassic) age (BACHMAYER 1959). Thus, this report of the species from the quarries at

Ernstbrunn, represents the first notice of the species in Austria. Indeed, the Ernstbrunn locality is further remarkable because eight excellently preserved specimens of the species have been collected from these quarries.

Family Tithonohomolidae nov. fam.

Type genus: *Tithonohomola* GLAESSNER, 1933.

Included genera: *Tithonohomola* GLAESSNER, 1933; *Tenuihomola* nov. gen.

Diagnosis: Inter-lineal portion of cephalothorax longer than wide; extra-lineal regions of cephalothorax not known. Rostrum broad and tapering or downturned and blunt. Orbits directed anterolaterally, with two prominent orbital eaves. Regions well-defined, tumid, often tuberculate or nodose.

Discussion: Inclusion of *Tithonohomola* and *Tenuihomola* within the Homoloidea is justified on the basis of the presence of well-developed *lineae homolicae*. The genera cannot be assigned to the Homolidae, however, because the rostrum is broad, downturned, blunt, and lacks pseudorostral spines. The orbits, which are lacking or simple in the Homolidae, are complex in both *Tithonohomola* and *Tenuihomola.* The structure of their orbits, with orbital eaves separated from one another by a deep re-entrant, is unlike any structure seen in true Homolidae. Thus, the definition of a new family is warranted.

Genus *Tithonohomola* GLAESSNER, 1933

1933 *Tithonohomola* GLAESSNER: 182.
1969 ?*Tithonohomola* GLAESSNER – GLAESSNER: R491.
1992 ?*Titanohomola* GLAESSNER, 1933, n. n. – BISHOP: 62.
1992 ?*Titanohomola* GLAESSNER, 1933, n. n. – BISHOP & BRANNEN: 321.

Type species: *Oxythyreus armatus* BLASCHKE, 1911: 150, by original designation

Included species: *Tithonohomola armata* (BLASCHKE, 1911); *T. tuberculata* nov. spec.

Diagnosis (translated from German, GLAESSNER, 1933: 182, additions in square brackets): "Cephalothorax long and narrow, only the part within the *lineae homolicae* known. The rostrum is a broad plate, narrow in front. Regions distinctly fully developed, vaulted upward [swollen], set with strong conical tubercles. Two especially distinct protogastric tubercles, two lateral intestinal [tubercles] present posterior from the end of the cardiac region."

Emended diagnosis: Inter-lineal portion of cephalothorax about 60 % as wide as long, triangular, widens to maximum width in branchial region. Extra-lineal regions of cephalothorax not known. Rostrum broad at base, tapering to point, axially sulcate. Orbits with two prominent orbital eaves which may be nodose. Orbital eaves curved anterolaterally, narrowly separated. Axial regions well defined by grooves, bearing relatively coarse nodes. Cardiac region nearly circular, bearing two nodes arrayed

transversely and extending nearly to posterior margin. Lateral regions less well differentiated.

D i s c u s s i o n : At the time of naming of the genus *Tithonohomola*, GLAESSNER (1933) assigned two species, *T. armata* (BLASCHKE) and *T. longa* (MOERICKE, 1897) to it. In a footnote (GLAESSNER 1933: 179), he indicated that the first-listed species in newly-named genera was the type species; thus, *Tithonohomola armata* is the type species of the genus. Interestingly, GLAESSNER (1969: fig. 302,2) illustrated *T. longa* rather that the type species. This introduced the possibility of misinterpreting the concept of the genus.

Comparison of the type specimens of these two species with the generic diagnosis indicates that they are not conspecific and that the original generic descriptors are a composite of the characteristics of the two species. The overall shape, long and narrow, characterizes *T. longa* (W/L = 0.5) but does not describe the overall shape of *T. armata* (W/L = 0.63) particularly well. The rostrum of *T. armata* is broad at the base and tapers to a point; however, that of *T. longa* appears to be either bifid or downturned with two prominent basal nodes. It is noteworthy that the illustration of the type specimen (BLASCHKE 1911: pl. 1, fig. 5) shows the front as being rounded and apparently broken, whereas the type specimen exhibits a fully exposed rostrum. The regions are prominently swollen on *T. longa*, but are only moderately elevated and indistinctly differentiated on *T. armata*. Tubercles are prominent on *T. armata*, but they are much less well developed on *T. longa.* The tubercles described as being posterior to the cardiac region are prominent round bosses on the flanks of the intestinal region on *T. longa*. The type specimen of *T. armata* lacks these tubercles but has two well-developed tubercles on the cardiac region. This mix of characters necessitates an emended diagnosis, based solely on members of *Tithonohomola sensu stricto*.

WEHNER (1988, p. 122) referred *Nodoprosopon echinora* COLLINS, 1985, to *Tithonohomola*, a position that was supported by COLLINS, 1997. However, examination of the type specimen of the species confirmed that *lineae homolicae* are lacking and that the lateral sides of the carapace are present. Thus, SCHWEITZER et al. (2007) retained placement in *Nodoprosopon.*

***Tithonohomola armata* (BLASCHKE, 1911)**
(fig. 4.1)

1911 *Oxythyreus armatus* BLASCHKE, 1911: 150.
1924 *Oxythyreus armatus* BLASCHKE – VAN STRAELEN: 369. [imprint 1925]
1933 *Tithonohomola armata* (BLASCHKE, 1911) – GLAESSNER: 182.
1969 ?*Tithonohomola armata* (BLASCHKE) – GLAESSNER: R491.
1988 *Tithonohomola armata* (BLASCHKE, 1911) – WEHNER: 121; pl. 8, fig. 5.
1997 *Tithonohomola armata* (BLASCHKE, 19119 – COLLINS: 53.
2007 *Tithonohomola armata* (BLASCHKE, 1911) – SCHWEITZER et al.: 110.

M a t e r i a l e x a m i n e d : Holotype, Naturhistorisches Musuem Wien (NHMW) 1908/0009/0294.

O c c u r r e n c e : The sole specimen referred to this species was collected from Upper Jurassic limestones of the Štramberk Formation, near Štramberk, Czech Republic.

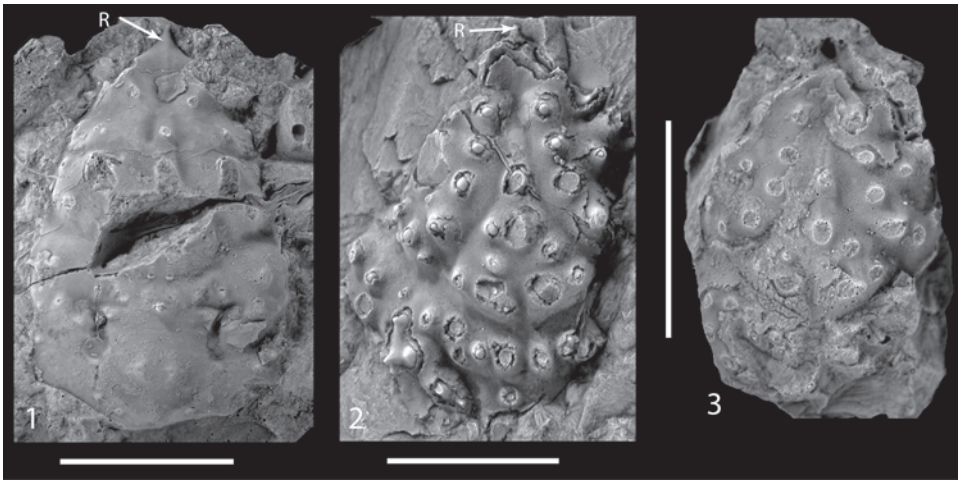

Fig. 4. *Tithonohomola* spp. 1, *Tithonohomola armata* (BLASCHKE, 1911), dorsal view of plaster cast of holotype, NHMW 1908/0009/0294, from the Upper Jurassic Štramberk Limestone, near Štramberk, Czech Republic. 2-5, *Tithonohomola tuberculata* nov. spec. 2, dorsal view of holotype, NHMW 1990z004104001, from the Ernstbrunn Limestone, Tithonian, from near Dörfles, Austria. 3, dorsal view of plaster cast of paratype, NHMW Beck 1903, from the Upper Jurassic Štramberk Limestone, near Štramberk, Czech Republic. Scale bars equal 10 mm.

D i a g n o s i s : Inter-lineal part of carapace triangular; rostrum broad at base and tapering to sharp tip, with weak axial keel; surface generally smooth, with few tubercles.

D e s c r i p t i o n : Inter-lineal part of carapace moderately large for family, length = 24.3 mm, width = 16.3 mm; triangular with widest part near posterior corner; moderately vaulted transversely and longitudinally. Axial regions well defined by grooves; lateral regions less well defined.

Rostrum broad at base, tapering to sharp tip, axially sulcate with very weak median keel; sides of rostrum smooth, very slightly concave. Upper orbital margin with supraorbital projection at base of rostrum; remainder of orbital area broken, only base of one orbital eave preserved. Anterolateral and posterolateral margins (*lineae homolicae*) diverge posteriorly, weakly convex. Posterior margin wide, sinuous; lateral parts weakly concave and axial part convex.

Epigastric region defined by tubercles positioned just posterior to supraorbital projection. Mesogastric region flask-shaped; anterior projection extends to level of epigastric tubercles and bears two axial tubercles; posterior part of mesogastric region broken but with subtle depression at midpoint of posterior margin. Metagastric region transversely ovoid, bearing two large axial tubercles; separated from mesogastric region by smoothly concave-forward, deeply impressed cervical groove. Cardiac region wider than long, margins rounded; two transversely placed nodes situated near midline. Intestinal region not discernable.

Protogastric and hepatic regions confluent, poorly defined by subtle swellings and prominent tubercles; two or three tubercles on swollen area near position of orbital eave,

one large tubercle at position between midlength of mesogastric region and *linea*, and one smaller tubercle between large tubercle and cervical groove. Epibranchial region circular, with single tubercle, weakly swollen, not well differentiated from mesobranchial region. Mesobranchial region transversely ovoid, defined posteriorly and axially by distinct branchiocardiac groove which forms concave-forward arc. Metabranchial region weakly tumid, bearing two small tubercles.

Remainder of carapace, sternum, abdomen, and appendages not preserved.

D i s c u s s i o n : The species is distinguishable from the only other species referred to the genus, *Tithonohomola tuberculata* nov. spec., by having a weak axial keel on the rostrum and a relatively smooth inter-lineal carapace bearing relatively few tubercles. In all other regards, the two species are quite similar.

To our knowledge, the species had not been illustrated subsequent to the figure by BLASCHKE (1911: pl. 1, fig. 2) until the work of WEHNER (1988: pl. 8, fig. 5). As noted above, the original illustration did not fully represent the morphology of the species; the rostrum was assumed to be missing. However, WEHNER's illustration correctly portrays the specimen. This has subsequently been confirmed by examination of the holotype, as illustrated herein.

Tithonohomola tuberculata **nov. spec.**
(figs 4.2, 4.3)

M a t e r i a l e x a m i n e d : Holotype, Naturhistorisches Museum Wien (NHMW) 1990z0041/4001, and paratype NHMW Beck 1903.

L o c u s T y p i c u s : Štramberk, Czech Republic

S t r a t u m T y p i c u m : Upper Jurassic Štramberk Limestone

E t y m o l o g y : The trivial name refers to the strongly tuberculate nature of the carapace, which readily distinguishes this species from the type species.

D i a g n o s i s : Interlineal part of carapace triangular, rostrum broad at base, tapering to sharp tip, axis sulcate, smooth; interlineal part of carapace coarsely tuberculate throughout.

D e s c r i p t i o n : Inter-lineal part of carapace moderately large for family, length of most complete specimen = 22.5 mm, width = ca. 16 mm; triangular with widest part near posterior corner; moderately vaulted transversely and longitudinally. Axial regions well defined by grooves; lateral regions less well defined.

Rostrum broad at base, tapering to sharp tip, axially sulcate; sides of rostrum smooth, very slightly convex, upturned. Upper orbital margin complex, with supraorbital projection at base of rostrum and two anteriorly curving orbital eaves defined by narrow, deep reentrants. Posterior-most orbital eave bifid. Anterolateral and posterolateral margins (*lineae homolicae*) diverge posteriorly, convex. Posterior margin wide, sinuous; lateral parts weakly concave and axial part convex.

Epigastric region defined by strong tubercles positioned just posterior to supraorbital projection. Mesogastric region flask-shaped; anterior projection extends nearly to level

of epigastric tubercles, becomes indistinct anteriorly, and bears one axial tubercle; posterior part of mesogastric region with prominent depression at midpoint of posterior margin that extends to midpoint of posterior part of region and with three large tubercles arrayed in forward-directed triangle and four or more smaller tubercles. Metagastric region transversely ovoid, bearing numerous small tubercles; separated from mesogastric region by smoothly concave-forward, deeply impressed cervical groove and indistinctly differentiated from cardiac region. Cardiac region wider than long, margins rounded; bearing two transversely placed tubercles situated near midline and numerous smaller tubercles. Cardiac region tapers posteriorly into indistinct intestinal region.

Protogastric and hepatic regions confluent, poorly defined by subtle swellings and prominent tubercles; about six tubercles parallel to cervical groove and groove separating mesogastric and hepatic regions, and one tubercle at base of posteriormost orbital eave. Epibranchial and mesobranchial regions finely tuberculate, swollen, not well differentiated, defined posteriorly and axially by distinct branchiocardiac groove which forms concave-forward arc. Metabranchial region weakly tumid, bearing numerous small tubercles.

Remainder of carapace, sternum, abdomen, and appendages not preserved.

D i s c u s s i o n : The lack of an axial keel on the rostrum and the coarsely and densely tuberculate surface of the inter-lineal carapace readily distinguishes this species from the type species. Unlike the type species, *Tithonohomola tuberculata* is known from both the Štramberk and Ernstbrunn localities.

Another specimen, NHMW 2007z0149/0018, has been tentatively assigned to the species. The specimen, from the Ernstbrunn Limestone at Dörfles, Austria, consists of the posterior half of the inter-lineal part of the carapace and, although the conformation of the visible parts of the mesogastric, metagastric, and epibranchial regions are consistent with the placement, the cardiac and metabranchial regions differ in that the cardiac region is less well defined than in typical members of the species and the ornamentation on both regions is more uniform and finely tuberculate. The specimen is much smaller than the others referred to the species so that the morphological differences may reflect its being a juvenile. Until better material is discovered, we consider this placement to be questionable.

Tenuihomola **nov. gen.**

T y p e s p e c i e s : *Prosopon longum* MOERICKE, 1897: 59.

I n c l u d e d s p e c i e s : *Tenuihomola longa* (MOERICKE, 1897); *T. ortwini* nov. spec.

E t y m o l o g y : The name is derived from the Latin word *tenuis* = thin and *Homola*, the generic name of the type genus of the Homolidae and Homoloidea. The gender is feminine.

D i a g n o s i s : Inter-lineal portion of cephalothorax approximately 50 % as wide as long, rectangular, slightly wider in branchial region. Extra-lineal portion of cephalothorax unknown. Rostrum broad, termination bilobed, blunt, downturned, axially sulcate.

Orbits with two prominent orbital eaves about as long as wide, broadly separated by deep reentrants. Axial and lateral regions well defined by grooves. Cardiac region ovoid, lacking nodes. Metabranchial region with two broad, elongate ridges.

D i s c u s s i o n : As discussed above, the overall shape of the inter-lineal part of the carapace of *Tenuihomola* spp. is long and parallel sided, whereas that of *Tithonohomola* spp. is triangular; the rostrum on species in the former genus is triangular and pointed, and that of *Tenuihomola* spp. is blunt and bilobed; the orbital architecture of *Tenuihomola* includes two orbital eaves that are broadly separated, whereas those of *Tithonohomola* are closely spaced; and the distinct development of regions on *Tenuihomola* precludes placement in *Tithonohomola* which has weakly differentiated regions. Thus, definition of a new genus within the Tithonohomolidae is warranted.

Tenuihomola longa **(MOERICKE, 1897)**
(figs 5.1-5.3)

1897 *Prosopon longum* MOERICKE: 59; pl. 6, fig. 11.
1911 *Prosopon longum* MÖRICKE – BLASCHKE: 151.
1924 *Avihomola longa*, MOERICKE sp., 1889 – VAN STRAELEN: 348 [misprinted as 248 in text]; fig. 157. [imprint 1925]
1929b (*P.*) *longum* MOERICKE, 1889 – GLAESSNER: 344.
1933 *Tithonohomola longa* (MOER.) – GLAESSNER: 182.
1969 ?*Tithonohomola longa* (MOERICKE) – GLAESSNER: R491; fig. 302,2.
1972 *T. longa* (MÖRICKE 1889) – WRIGHT & COLLINS: 42
1988 *T. longa* (MOERICKE, 1889) – WEHNER: 121
1997 *Tithonohomola longa* (MÖRICKE, 1889) – COLLINS: 53.

M a t e r i a l e x a m i n e d : Holotype, Bayerische Staatsammlung für Paläontologie und historische Geologie München, Germany (BSP) AS III 321, plus NHMW 1990z0041/0770, and NHMW 1990z0041/3354.

O c c u r r e n c e : The holotype was collected from the Tithonian (Upper Jurassic) Štramberk Limestone, near Štramberk, Czech Republic. The referred specimens were collected from the Tithonian rocks at the Ernstbrunn quarries, near Dörfles, Austria.

D i a g n o s i s : Inter-lineal part of carapace long and slender, rectangular; rostrum broad at base, axially sulcate, strongly downturned; orbital eaves smooth, separated by broad reentrants; overall surface lacking coarse ornamentation.

D e s c r i p t i o n : Inter-lineal part of carapace small for family, length of holotype and most complete specimen = 12.2 mm, width = 6.3 mm; rectangular, widening slightly to posterior corner; moderately vaulted transversely and nearly flat longitudinally. Regions well defined by grooves.

Rostrum broad at base, tapering distally, strongly downturned, axially sulcate; sides of rostrum smooth, straight, upturned. Upper orbital margin complex, with supraorbital projection at base of rostrum and two broad, smooth orbital eaves defined by broad, deep reentrants. Anterolateral and posterolateral margins (*lineae homolicae*) diverge slightly posteriorly, straight. Posterior corner rounded, posterior margin concave.

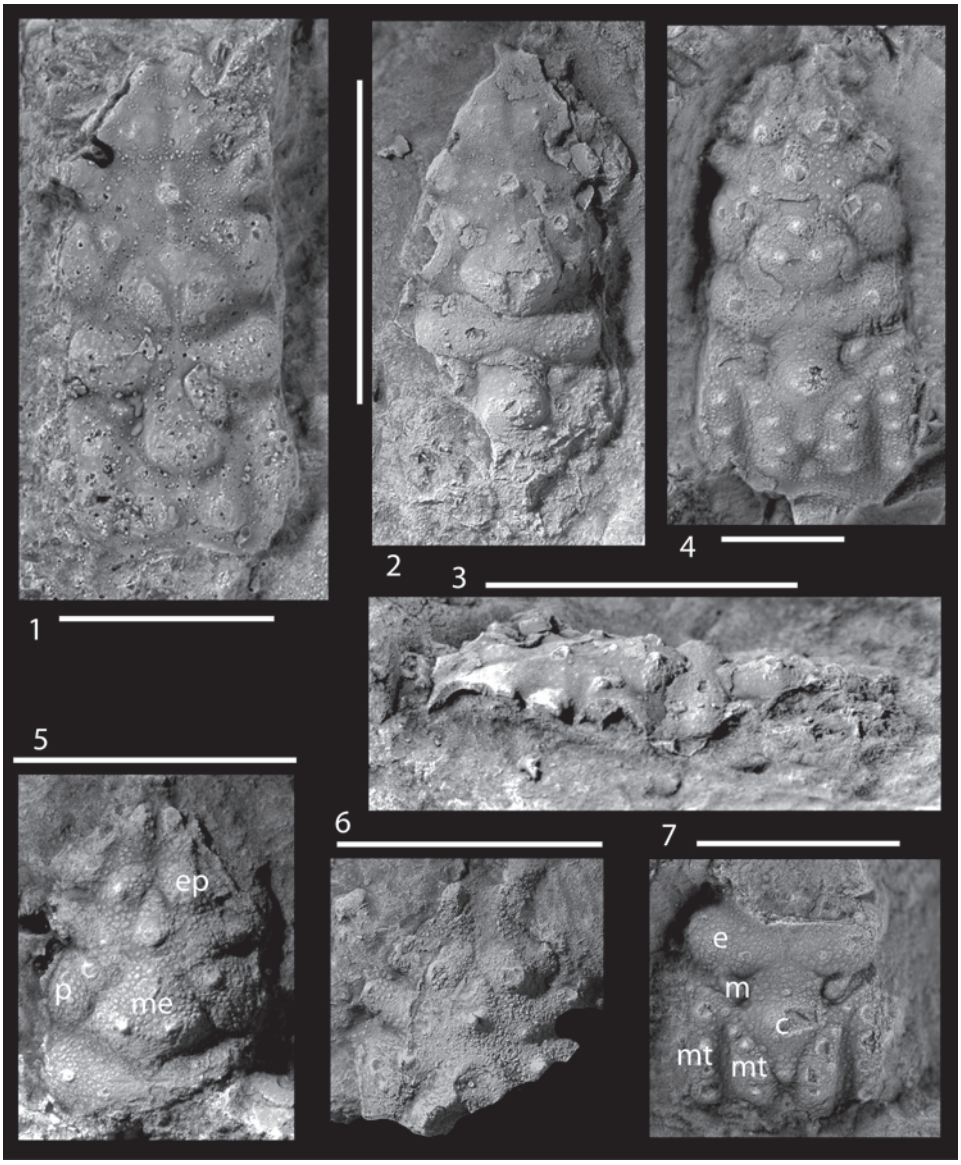

Fig. 5. *Tenuihomola* spp. 1-3, *Tenuihomola longa* (Moericke, 1897). 1, dorsal view of plaster cast of holotype, BSP AS III 321, from the Upper Jurassic Štramberk Limestone, near Štramberk, Czech Republic. 2, 3, Dorsal and lateral views of NHMW 1990z0041/0770, from the Ernstbrunn Limestone (Tithonian) from near Dörfles, Austria. 4-7, *Tenuihomola ortwini* nov. spec. from the Ernstbrunn Limestone (Tithonian) from near Dörfles, Austria. 4, dorsal view of holotype, NHMW 2007z0149/0017. 5, dorsal view of anterior part of carapace, paratype NHMW 1990z0041/0316, showing placement of anterior regions. ep = epigastric region; me = mesogastric region; p = protogastric region. 6, dorsal view of rostral area and left orbital region, paratype NHMW 1990z0041/2915. 7, dorsal view of posterior part of carapace, paratype NHMW 2007z0149/0016, showing placement of posterior regions. c = cardiac region; e = epibranchial region; m = mesobranchial region; mt = metabranchial region. Scale bars equal 5 mm.

Protogastric regions defined by subtle swellings positioned between supraorbital projections. Anterior projection of mesogastric region weakly defined, bearing single tubercle. Posterior part of mesogastric region pentagonal with subtle depression at midpoint of posterior margin that extends to midpoint of posterior part of region and with three large tubercles arrayed in forward-directed triangle. Metagastric region depressed, not well defined; separated from mesogastric region by broad, shallowly V-shaped, deeply impressed cervical groove and indistinctly differentiated from cardiac region. Cardiac region longer than wide, quadrate, margins rounded; bearing large, swollen boss at posterior end. Cardiac region tapers posteriorly into indistinct, depressed intestinal region.

Epigastric regions tumid, bearing single strong tubercle on axial side. Epibranchial region large, swollen, transversely ovoid. Mesobranchial regions are small swellings near cardiac region, defined posteriorly and axially by distinct branchiocardiac groove which forms concave forward arc. Metabranchial region large, with large, longitudinal swelling laterally and smaller, nearly circular swellings flanking intestinal region. Surface of carapace very finely granular on elevated regions, smooth in grooves.

Remainder of carapace, sternum, abdomen, and appendages not preserved.

D i s c u s s i o n : Although this species was selected as the reference illustration of the genus *Tithonohomola* by GLAESSNER (1969: fig. 302,2), it bears little resemblance to the type species of that genus and, therefore, it has been designated the type species of a new genus, *Tenuihomola*.

The species can be readily distinguished from the only other species within the genus, *Tenuihomola ortwini* nov. spec. by the lack of distinctive finely tuberculate ornamentation and the presence of nearly circular nodes on the metabranchial region flanking the intestinal region on the type species. *Tenuihomola ortwini* bears tubercles on all of its regions and has longitudinally ovoid elevations on the metabranchial region flanking the intestinal region. Therefore, the two species cannot be confused.

***Tenuihomola ortwini* nov. spec.**
(figs 5.4-5.7)

M a t e r i a l e x a m i n e d : The holotype, Naturhistorisches Museum Wien, Austria (NHMW) 2007z0149/0017, and paratypes, NHMW 1990z0014/0316, NHMW 1990z0014/2915, NHMW 2007z0149/0016, and NHMW 2007z0149/0019.

L o c u s T y p i c u s : The holotype and paratypes were collected in the Ernstbrunn quarries, near Dörfles, Austria.

S t r a t u m T y p i c u m : The types were collected from the Tithonian (Upper Jurassic) Ernstbrunn Limestone.

E t y m o l o g y : The trivial name honours Dr. Ortwin SCHULTZ, Naturhistorisches Museum Wien, who facilitated the authors' work at the museum and for his tireless efforts to locate specimens in the BACHMAYER Collection.

D i a g n o s i s : Inter-lineal part of carapace long and slender, rectangular; rostrum broad at base, axially sulcate, strongly downturned; orbital eaves with small, terminal nodes, separated by broad reentrants; regions bear moderately coarse tubercles.

D e s c r i p t i o n : Inter-lineal part of carapace small for family, length of holotype and most complete specimen = 16.4 mm, width = 8.6 mm; rectangular, widening slightly to posterior corner; moderately vaulted transversely and nearly flat longitudinally. Regions well defined by grooves.

Rostrum narrow, tapering distally, strongly downturned, axially sulcate; sides of rostrum smooth, straight. Upper orbital margin complex, with antero-laterally directed supraorbital spine at base of rostrum and two broad orbital eaves bearing small terminal nodes and bounded by broad, deep reentrants. Anterolateral and posterolateral margins (*lineae homolicae*) diverge slightly posteriorly, straight. Posterior corner rounded. Posterior margin concave.

Epigastric region defined by distinct swellings and central tubercle, positioned between supraorbital projections. Anterior projection of mesogastric region defined by groove, extending to level of epigastric tubercles and bearing single tubercle. Posterior part of mesogastric region ovoid, with three large tubercles arrayed in forward-directed triangle. Metagastric region depressed, not well defined; separated from mesogastric region by narrow, V-shaped, deeply impressed cervical groove and indistinctly differentiated from cardiac region. Cardiac region longer than wide, quadrate, margins rounded; bearing large, swollen boss at posterior end. Cardiac region tapers posteriorly into depressed intestinal region bearing two axial nodes.

Protogastric regions with circular swelling posteriorly and nearly flat region anteriorly, bearing strong tubercle on axial side and two smaller tubercles. Epibranchial region large swollen, transversely ovoid, bearing central tubercle. Mesobranchial regions are small swellings near cardiac region, defined posteriorly and axially by distinct branchiocardiac groove which forms concave forward arc. Metabranchial region large, with large, longitudinal swelling with four longitudinal tubercles laterally and smaller, longitudinal swelling with four or five tubercles flanking intestinal region. Surface of carapace coarsely granular throughout.

Remainder of carapace, sternum, abdomen, and appendages not preserved.

D i s c u s s i o n : As discussed above, this species is readily distinguished from the type species, largely on the basis of its ornamentation. *Tenuihomola ortwini* has particularly distinctive ornamentation on the metabranchial regions. The elongate elevated areas along the margins of the region and flanking the intestinal region each bear numerous coarse tubercles; those on the margin of the metabranchial region are arrayed in a longitudinal row, and those on the axial elevation are set in a curvilinear pattern. This pattern permits identifying the species even if only the posterior regions are preserved.

Taxonomic summary and conclusions

Study of the homolid decapods from the Štramberk and Ernstbrunn limestones, along with re-examination of type material of previously named species, has resulted in the recognition of a new family, the Tithonohomolidae. As a result, the genus *Tithonohomola* has been moved to the new family as the type genus. In addition to the type species, *Tithonohomola armata*, a second species, *T. tuberculata* has been named. The species previously referred to as *Tithonohomola longa* now forms the type species of

a new genus, *Tenuihomola*, embracing *Tenuihomola longa* and the new species, *Tenuihomola ortwini*. Within the Homolidae, as recognized herein, a new genus and species, *Doerflesia ornata*, represents a form that is quite similar to extant homolids, suggesting that it may represent the rootstock of modern taxa. *Gastrodorus* continues to be considered a member of the Homolidae, based primarily on its possession of *lineae homolicae*. Although it has been assigned to other groups, configuration of its pattern of regions, particularly the well-developed cardiac region, supports placement within the Brachyura. The early appearance, geologically, of the homolids in shallow, warm water, reefal habitats of the Štramberk and Ernstbrunn rocks is consistent with the contention that the family evolved there; a summary of their modern habitat preferences confirms that family representatives continue to occupy reef environments as well as other, deeper-water settings.

Acknowledgements

Ortwin SCHULTZ and Andreas KROH, Naturhistorishes Museum Wien, located material from both the Ernstbrunn quarries and from Štramberk. The Ernstbrunn material was collected under the supervision of Friedrich BACHMAYER. SCHULTZ & KROH also provided casts of specimens and arranged for the loan of a large number of specimens that form the basis for this work. Thomas HOFMANN and KROH led us on informative field trips to the Ernstbrunn quarries. Specimens of *Gastrodorus neuhausense* from the type area were made available by G. SCHWEIGERT, Staatliches Museum für Naturkunde, Stuttgart, Germany. He also provided essential information regarding the type area, the fate of the type material, and an illustration of a specimen of *Gastrodorus* studies by HAIZMANN. Work in Vienna and laboratory study at Kent State University was supported by NSF EF 0531670 to FELDMANN and SCHWEITZER.

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