Ann. Naturhist. Mus. Wien, Serie A	121	257–289	Wien, 15 Jan. 2019

Paguroid anomurans from the Tithonian Ernstbrunn Limestone, Austria – the most diverse extinct paguroid assemblage on record

René H. B. Fraaije[1], Cristina Robins[2], Barry W. M. van Bakel[1,3], John W. M. Jagt[4] & Friedrich Bachmayer†

(with 5 figures)

Manuscript submitted on September 9th, 2017,
the revised manuscript on March 14th, 2018.

Abstract

Following several studies of anomuran (galatheoid) and brachyuran decapod crustaceans during recent years, we here present the first account of hermit crab carapaces and/or shields (Paguroidea) that are contained in the extensive Ernstbrunn Limestone collections at the Naturhistorisches Museum Wien (Vienna, Austria). These comparatively small-sized specimens are assignable to the families Annuntidiogenidae, Diogenidae, Gastrodoridae, Paguridae, Parapylochelidae, Pilgrimchelidae, Pylochelidae and Schobertellidae.With at least 18 species, in eight families, the Tithonian (Late Jurassic) paguroid fauna from Ernstbrunn is by far the most diverse extinct assemblage recorded to date. For the first time, Jurassic representatives of the family Paguridae are described on the basis of carapaces. Most of the material available was collected or obtained and recognised as paguroid in nature by one of us (FB) in the 1940s to 1960s. Unfortunately, the opportunity to describe these formally never presented itself to FB, despite the fact that typescripts on numerous new species were ready to be published. The majority of specimens, photographs and typescripts, recently rediscovered, form the basis of the present study. Species recorded here, in alphabetical order, are: *Ammopylocheles mclaughlinae*, *Annuntidiogenes elongatus* nov. spec., *An. hoelderi* nov. spec., *Bachmayerus gasparici* nov. spec., *B. matushyznyi* nov. spec., *Cretatrizocheles doerflesensis* nov. spec., *Eopaguropsis grandis* nov. spec., *E. schindewolfi* nov. spec., *Gastrodorus* spp., *Masticacheles minimus*, *Mesoparapylocheles strouhali* nov. spec.,

[1] Oertijdmuseum, Bosscheweg 80, 5283 WB Boxtel, the Netherlands; e-mail: info@oertijdmuseum.nl

[2] University of California at Berkeley, Museum of Paleontology, 1101 Valley Life Sciences Building, Berkeley, CA 94720-4780; e-mail: cristina.robins@gmail.com

[3] Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, the Netherlands; e-mail: barryvanbakel@gmail.com

[4] Natuurhistorisch Museum Maastricht, de Bosquetplein 6–7, 6211 KJ Maastricht, theNetherlands; e-mail: john.jagt@maastricht.nl

ZooBank LSID: urn:lsid:zoobank.org:pub:844C2807-E1A5-4D39-8D75-1CB8C1B36456

M. zapfei nov. spec., *Munitheites kuepperi* nov. spec., *Pilgrimcheles vonmeyeri*, *Pretrizocheles cocullo* nov. gen., nov. spec., *Protopagurus janoscheki* nov. gen., nov. spec., *Tithopaguristes porosus* nov. gen., nov. spec. and *Ululapagurus oroszyi* nov. spec. A novel key to marine paguroid families, based on carapace morphology, is added.

Keywords: Hermit crabs, new taxa, Upper Jurassic, central Europe, reefs.

Introduction

The famous locality of Ernstbrunn, situated about 50 km north of Vienna in northeast Austria, comprised six quarries around the small village of Dörfles and six outcrops along the road to Klement (Bachmayer 1947). Only Steinbruch I and Werk II (quarry I and quarry "Werk II", the latter being the main site of limestone extraction in the Ernstbrunn region today; also termed Ernstbrunn 2) north of Dörfles, Klafterbrunn Steinbruch I and Steinbruch Klement I were noted by Bachmayer (1947) to have yielded remains of decapod crustaceans. Later collections delivered crustaceans from additional sites, including quarry Dörfles V, on the west side of the Steinberg hill (see Schneider *et al*. 2013: tab. 1 for locality co-ordinates). Today, only a few outcrops remain accessible, so possibilities of additional collecting are severely limited.

Over 6,000 decapod crustacean remains are registered and housed at the Naturhistorisches Museum Wien (abbreviation: NHMW; see Schneider *et al.* 2013, Andreas Kroh, pers. comm., December 2017). Some specimens studied herein were encountered in lots that had not been formally registered, deriving from material collected, but never studied in detail, by Bachmayer. All material was collected over a period of forty years, starting in 1940, mainly by Friedrich Bachmayer and his father in law Karl Oroszy. The majority of decapod crustacean collections at NHMW originates from quarries Ernstbrunn II, Dörfles I and V (Bachmayer 1947; Andreas Kroh, pers. comm., January 2014). Unfortunately, for many specimens the exact sampling locality has not been recorded. Judging from Bachmayer's unpublished manuscripts, however, most of the material originally collected by Karl Oroszy (that is material numbered in black ink and today registered under repository numbers starting with 1990/0041/...) derives from "Werk II" (Andreas Kroh, pers. comm., July 2018).

The first decapod crustacean species from the Ernstbrunn Limestone was listed by Moericke (1889). Subsequently, Glaessner (1931) and Bachmayer (1947, 1955) provided more detailed species lists, while Bachmayer (1948) recorded a single species of brachyuran and several taxa of isopod-infested anomurans from this unit. Bachmayer (1958, 1959) was the first to describe and illustrate the early paguroid *Gastrodorus neuhausensis* von Meyer, 1864. Almost three decades later, Wehner (1988) mentioned several taxa from Ernstbrunn in her dissertation on "prosopid" brachyurans.

Bachmayer had plans to publish a monograph of all decapod crustacean taxa from Ernstbrunn (see Bachmayer 1959; unpublished letters in NHMW archives), but his death in 1989 put an end to this project. FB's legacy comprises several typescripts, with

photographs, in which numerous new galatheoid, paguroid and brachyuran taxa are designated, named and described in detail, almost ready for publication. Most of the taxon names given in these typescripts, honouring many of FB's colleagues in the 1950s and 1960s, are retained in the present contribution.

To illustrate FB's knowledge of paguroid carapaces, which in his time were unknown from the fossil record, we here add a citation from one of his typescripts (dated *c.* 1960):

"Vor einiger Zeit gelang es mir, in dem oberjurassischen Korallenriffkalk von Ernstbrunn, Cephalothoraxreste zu finden, die man sicher den Paguriden zurechnen darf. Es liegen bereits mehr als 60 Exemplare vor, die sich auf etwa ein Dutzend Arten verteilen. Es muss auffallen, dass in allen diesen Fällen der Cephalothorax genau so wie bei den heute lebenden Paguridenformen, nur ein kurzes Stück über die Cervicalfurche hinaus verkalkt ist, während der ganze Hinterteil fehlt; offenbar war dieser weichhäutig und nicht erhaltungsfähig. Das geschilderte Belegmaterial gestattet den Schluss, dass die Organisation der Paguride vom Oberjura bis in die Gegenwart die gleiche geblieben ist. Die Paguriden sind also eine recht konservative Tiergruppe. Die ganze Lebensweise war offenbar die gleiche. Somit geben uns die neuesten Funde einen weiteren kleinen Einblick in die Bionomie dieser eigenartiger Crustaceengruppe." (translated: *"Some time ago, I managed to find cephalothorax remains in the Upper Jurassic Korallenriffkalk of Ernstbrunn, undoubtedly attributable to paguroids. Already in excess of 60 specimens are available, representing about a dozen species. Notable is that in all of these cases, as in extant paguroids, the cephalothorax is calcified only a short distance below the cervical groove, while the entire posterior portion is missing; obviously this was soft and did not preserve well. The material referred to permits the conclusion that paguroid organisation from the Upper Jurassic to the present day has remained the same. Thus, paguroids are a conservative animal group. The whole mode of life apparently was the same. As such, the newest finds present a further insight into the bionomics of this peculiar group of crustaceans."*

Exactly why FB's studies of extinct paguroids were never completed is unknown, but the fact that he was the head of the Geologisch-Paläontologische Abteilung and subsequently, in 1972, became the first director of the Naturhistorisches Museums Wien (Kollmann & Zapfe 1979) likely had something to do with it. More recent additions (in pencil) to the older typescripts reveal that, at times, he returned to this work as his knowledge of fossil paguroids increased. In 1990, the Bachmayer Collection was purchased from his daughter, Christine Prenner, a librarian at the NHMW at the time.

Brachyurans from Ernstbrunn have recently been described by Feldmann & Schweitzer (2009) and Schweitzer & Feldmann (2008, 2009a–b, 2010b–d), while Schweitzer & Feldmann (2010a) and Robins *et al*. (2012, 2013, 2016) recorded porcellanid and galatheoid anomurans, respectively. Of note is that Robins *et al.* (2013) already confirmed the presence of several paguroid taxa in the Ernstbrunn collections. Unfortunately, at the time the papers above were written, the original typescripts were unavailable, thus, none of the type designations by one of us (FB) was adopted, nor were any of the photographs and remarks in FB's typescripts used.

Nearly all paguroid shields and carapaces described in the present study were collected at Dörfles Werk II, Steinbruch Dörfles I, Steinbruch Klafterbrunn 1, and Steinbruch Klement 1, by FB and his father in law, the amateur palaeontologist Karl Oroszy, who was a stamp dealer in Vienna. Bachmayer (1947) was the first to mention paguroid remains from Ernstbrunn, under the names of *Palaeopagurus squamosus* and *P. granulosus*, but he failed to supply further details, which is why these have to be considered *nomina nuda*. A visit (January 2014) by two of us (RHBF, BWMvB) to the Naturhistorisches Museum Wien and the subsequent loan of about 150 specimens, together with numerous black and white photographs and typescripts from FB form the basis of the present monographic treatment of paguroid carapaces from Ernstbrunn. Associated paguroid tergites and chelae will be the subject of a forthcoming paper.

Paguroid faunal composition in the Tithonian of Ernstbrunn is quite similar to that of the Kimmeridgian at Nusplingen, southern Germany (Fraaije 2014). The main differences between the two localities are the greater average carapace size and higher diversity in the Ernstbrunn Limestone.

Stratigraphy

Due to Alpine tectonics, the Ernstbrunn Limestone, together with the Klentnice Beds and the Klement Formation, now appear as klippen, *i. e.*, thrust sheets, within deformed autochthonous Molasse sediments (Bachmayer 1964; Schneider *et al*. 2013). On the basis of extensive ammonite collections made by FB, Zeiss (2001) proposed a middle middle to early late Tithonian age (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone) for the Ernstbrunn Limestone. Most ammonites (14 genera, 37 species) were collected from the Ernstbrunn Werk II quarry, but in view of the admixture of highly variable facies between and within the different klippen and outcrops, it is most likely that there are differences in age (Schneider *et al*. 2013). A study of benthic foraminifera and dasycladalean algae by Moshammer & Schlagintweit (1999) revealed a middle/late Tithonian to middle Berriasian age for the Ernstbrunn Limestone.

Fossils are well known from this unit. An overview of the commonest groups, *i. e.*, algae, foraminifera, hydrozoans, corals, bivalves, gastropods, cephalopods, brachiopods, decapod crustaceans, echinoderms and fishes, was presented by Bachmayer (1954, 1964) and Grill (1968). The most detailed account of Ernstbrunn Limestone fossils to date is that by Schneider *et al*. (2013), who recorded the major faunal groups, inclusive of several of the most speciose (*e. g.*, Scleractinia, Bivalvia, Gastropoda, Brachiopoda and Echinoidea). However, most of these have never been studied in detail.

According to Grill (1968), the fossiliferous whitish limestones, without terrestrial influx, known as the Ernstbrunn Limestone proper, reflect deposition on a differentiated carbonate platform. Limestones excavated at the large Dörfles Kalkwerk II quarry (Kalkgewerkschaft Ernstbrunn) consist predominantly of patch reefs, whereas the small quarries on the western half of the Steinberg, document a more lagoonal development (Hofmann 1990).

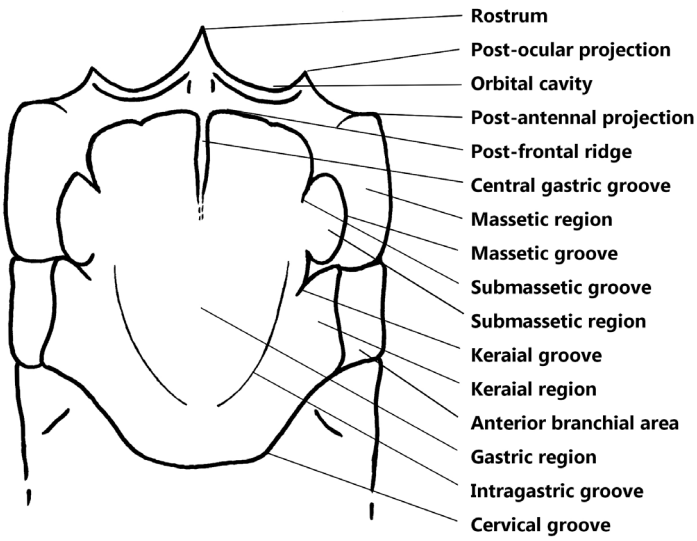

Fig. 1. Morphological terminology of paguroid carapaces used in the present study.

Carapace morphology and evolution of Mesozoic paguroids

Our insight into the diversity and evolutionary history of Mesozoic paguroids has increased considerably during the last decade. FRAAIJE *et al.* (2008) and VAN BAKEL *et al.* (2008) were the first to describe paguroid carapaces of the families Diogenidae, Gastrodoridae and Pylochelidae, of late Early Cretaceous and Late Jurassic age, respectively. Later, FRAAIJE *et al.* (2012a–c, 2013a, b, 2014, 2017a, b) and FRAAIJE (2014) added a large number of Late Mesozoic hermit crabs, all from reef settings. SCHWEIGERT *et al*. (2013) erected a new family, Schobertellidae, to accommodate taxa from Lower Jurassic shallow-shelf strata. Recently, GAŠPARIČ *et al.* (2016) and FRAAIJE *et al.* (2017b) erected new paguroid families.

For more detailed data on early paguroid evolution and possible phylogenetic pathways we refer to FRAAIJE (2014). New carapace morphological terms were introduced by FRAAIJE *et al*. (2012b, c, 2014). A summary of paguroid carapace morphologies is illustrated here in Figure 1.

Inclusive of specimens described in the present study, in excess of 50 carapace-based Mesozoic paguroid taxa are known at present, accommodated in eight families of which the Gastrodoridae, Pilgrimchelidae and Schobertellidae comprise exclusively Mesozoic representatives.

In his landmark study on *Pagurus bernhardus* (LINNAEUS, 1758), PILGRIM (1973: p. 366) noted that, *"In common with most Paguridea, the carapace shows much more variation in texture than is found in other Decapoda, leading to the differentiation of reasonably well-defined regions. This is particularly marked in the typical shelter-inhabiting hermit*

crabs…". With PILGRIM's remark in mind it is unfortunate, for palaeontologists, that there is not a single taxonomic study on extant paguroids that pays attention to carapace morphology. Taxonomic keys for paguroids at the family level, such as the ones published by MCLAUGHLIN (2003), are based primarily on differences in morphology of appendages such as antennules, pleopods, maxillipeds or pereopods. With only fossil carapaces and/or shields, without attached appendages, at hand we herewith propose a key to marine paguroid families based on carapace morphologies.

Key to marine paguroid families based on carapace morphologies

1. Shield subcylindrical 2
   Shield non-subcylindrical 7
2. Cervical, postcervical and branchiocardiac grooves all present 3
   Cervical groove not reaching lateral sides ..... Pylochelidae
   Cervical groove reaching lateral sides 4
3. Gastric region smooth, usually arrowhead-shaped ..... Parapylochelidae
   Gastric region ornamented, not arrowhead-shaped ..... Gastrodoridae
4. Massetic and keraial regions well delineated ..... Pilgrimchelidae
   Massetic and keraial regions not delineated or poorly so 5
5. Shield about as long as wide ..... Schobertellidae
   Shield considerably longer than wide 6
6. Right cheliped with "pseudo-fixed finger" ..... Xylopaguridae
   Right cheliped operculate ..... Pylojacquesidae
7. Intragastric grooves parallel to cervical groove ..... Annuntidiogenidae
   Intragastric grooves forming Y-linea ..... Calcinidae
   Intragastric grooves absent 8
8. Cervical groove subcircular ..... Parapaguridae
   Cervical groove centrally usually V-shaped, massetic usually extending to post-antennal projection, chelipeds subequal in size or left cheliped distinctly larger, often pronounced frontal ridge, medially divided by central gastric groove ..... Diogenidae
   Cervical groove usually centrally U-shaped, massetic usually not extending to post-antennal projection, chelipeds of distinctly different size, right always larger ..... Paguridae

Especially within the speciose families Diogenidae and Paguridae, taxonomy is in need of further refinement.

Systematic palaeontology

We adopt the classification of extinct paguroids on the basis of carapaces as proposed by Fraaije (2014).

Abbreviations: NHMW – Naturhistorisches Museum Wien (Natural History Museum Vienna), Vienna, Austria.

Order Decapoda Latreille, 1802

Infraorder Anomura H. Milne Edwards, 1832

Superfamily Paguroidea Latreille, 1802

Family Annuntidiogenidae Fraaije, 2014

Type genus: *Annuntidiogenes* Fraaije, van Bakel, Jagt & Artal, 2008, by original designation.

Diagnosis: Shield longer than wide, divided into distinct regions by grooves; central gastric groove; convex postrostral ridge usually present; elongated massetic region; medial part of posterior intragastric grooves (also known as Y-linea) parallel to posteriormost groove.

Genus *Annuntidiogene*s Fraaije, van Bakel, Jagt & Artal, 2008

Type species: *Annuntidiogenes ruizdegaonai* Fraaije, van Bakel, Jagt & Artal, 2008, by original designation.

Included species: *Annuntidiogenes elongatus* nov. spec., *An. hoelderi* nov. spec., *An. jurassicus* Fraaije, 2014, *An. massetispinosus* Fraaije, van Bakel & Jagt, 2017, *An. sunuciorum* Fraaije, van Bakel, Jagt & Artal, 2008, *An. ruizdegaonai*, and *An. worfi* Fraaije, van Bakel, Jagt, Klompmaker & Artal, 2008.

***Annuntidiogenes hoelderi* nov. spec.**
(Figure 2A, B)

Diagnosis: Shield ovate, divided into distinct regions by grooves; scabrous ornament on anterior and posterior gastric regions; long central gastric groove; long rostrum extending beyond postocular spines; convex postrostral ridge; elongated massetic region; posterior intragastric grooves parallel to posteriormost groove.

Etymology: Named after Prof. Dr Helmut Hölder (18 January 1915–26 August 2014), formerly at Münster Universität, Münster (Germany).

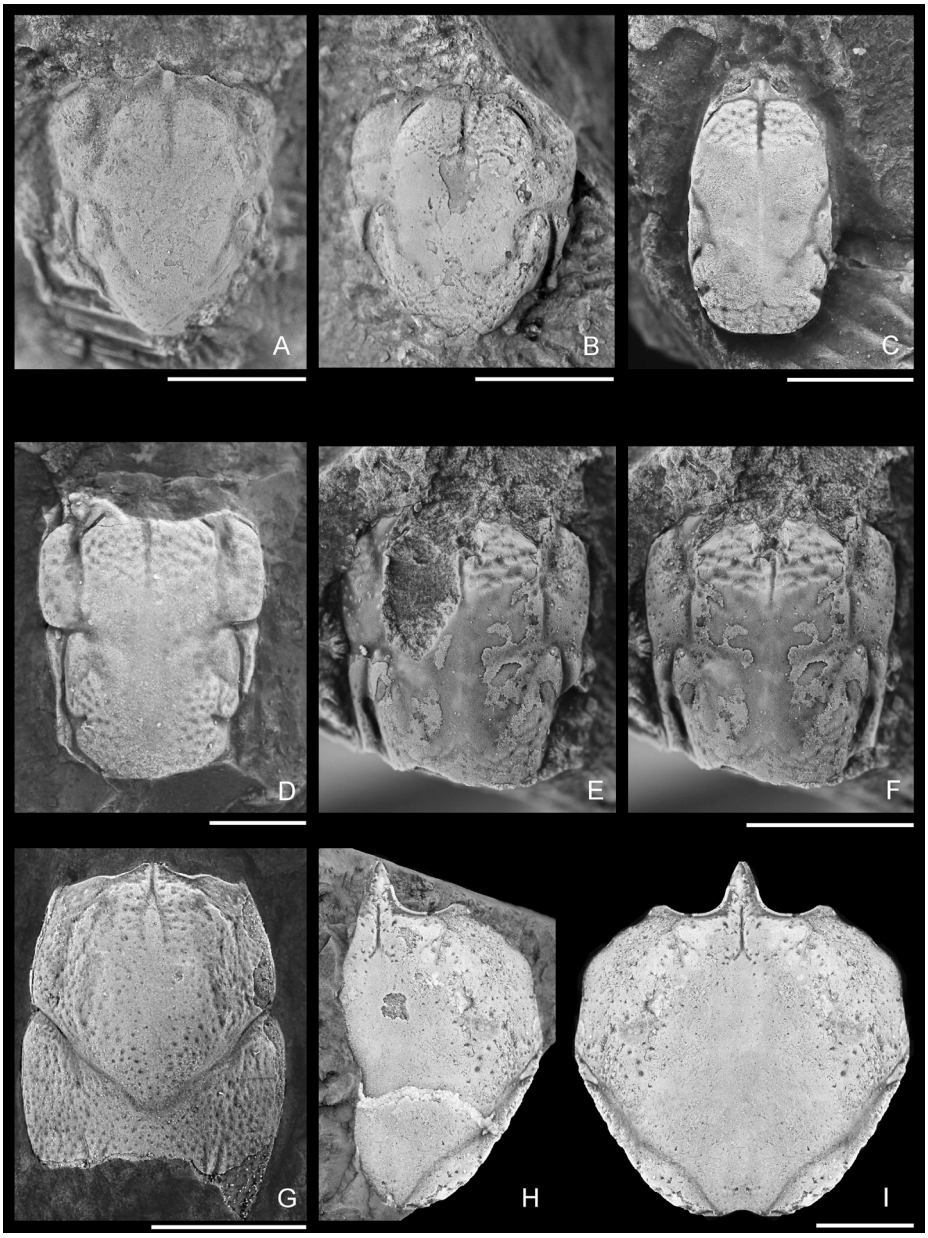

Fig. 2. **A**: *Annuntidiogenes hoelderi* nov. spec., holotype (NHMW 1990/0041/3958). **B**: *Annuntidiogenes hoelderi* nov. spec., paratype (NHMW 1990/0041/3697). **C**: *Annuntidiogenes elongatus* nov. spec., holotype (NHMW 1990/0041/4911). **D**: *Bachmayerus matushyznyi* nov. spec., holotype (NHMW 1990/0041/2785). **E**: *Bachmayerus gasparici* nov. spec., holotype (NHMW 2017/0093/0001). **F**: Composite of *Bachmayerus gasparici* nov. spec., holotype (NHMW 2017/0093/0001). **G**: *Eopaguropsis schindewolfi* nov. spec., holotype (NHMW 1990/0041/3369). **H**: *Eopaguropsis grandis* nov. spec., holotype (NHMW 1990/0041/3364). **I**: Composite of *Eopaguropsis grandis* nov. spec., holotype (NHMW 1990/0041/3364). Scale bars for A–D, and F equal 2 mm, those for G and I 5 mm.

Type material: Holotype (NHMW 1990/0041/3958, leg. K. OROSZY), a near-complete shield (maximum carapace length, as preserved, 4.0 mm; maximum shield width 3.2 mm); paratype (NHMW 1990/0041/3697), a near-complete shield (length, without rostrum, 4.0 mm; maximum shield width 3.2 mm). In addition, about half a dozen other, less complete specimens, none of which have been designated types.

Type locality: "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Type stratum: Ernstbrunn Limestone, dated by ZEISS (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Description: Shield ovate, divided into distinct regions by grooves. Triangular spinose rostrum; broad concave orbital margin ending in blunt triangular postocular projections; long central gastric groove anteriorly proceeding into convex, subcircular postorbital ridges posteriorly effacing into posteriormost groove. Elongated massetic region, greatest width anteriorly, posteriorly bounded by thin lateral branchial area. Long posterior intragastric keraial grooves, not connected medially. Posteriormost groove broadly V-shaped.

Remarks: Intragastric grooves (also known as Y-linea in extant paguroids) parallel to the cervical groove are a unique characteristic of representatives of the family Annuntidiogenidae. *Annuntidiogenes hoelderi* nov. spec. is the sixth species in this genus to be described. It can be distinguished from the late Early Cretaceous (late Albian) *A. ruizdegaonai* and *A. worfi*, the latest Cretaceous (late Maastrichtian) *A. massetispinosus* and *A. sunuciorum*, as well as the only other Late Jurassic Species, *A. jurassicus*, in having a much sharper V-shaped cervical groove and less convex subcircular postorbital ridges.

Annuntidiogenes elongatus nov. spec.

(Figure 2C)

Diagnosis: Elongated annuntidiogenid with stout, ridged rostrum; long, central gastric groove crenulated anteriorly, extending into mid-gastric ridge posteriorly; coarsely pitted antero- and posterolateral gastric regions.

Etymology: In reference to the narrow and long shield.

Type material: Holotype (NHMW 1990/0041/4911), a near-complete shield (maximum shield length, as preserved, 4.0 mm; maximum shield width 2.4 mm).

Type locality: The types were purchased in 1990 from FB's daughter, Christine PRENNER, but provenance details, except for the general indication of the Ernstbrunn area, were not available. Probably, this material originated from "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Type stratum: Ernstbrunn Limestone, dated by ZEISS (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Description: Moderately sized, cylindrical annuntidiogenid with crenulated anterior gastric region, centrally divided by long, irregularly pitted, gastric groove, extending into mid-gastric ridge posteriorly. Gastric region surrounded by deep cervical groove with three constrictions forming a threefold convex lateral side. Intragastric groove parallel to cervical groove deepest at anterolateral side fading posterocentrally towards a faint posterocentral groove, forming the Y-linea. Posterolateral part of gastric region very coarsely pitted, anterolateral part of gastric region covered with oblique, convex rows of coarse pits. Massetic regions not preserved. Parts posterior of shield not preserved.

Remarks: *Annuntidiogenes elongatus* nov. spec. is the seventh representative of the genus recorded to date. It can be distinguished from the late Early Cretaceous (late Albian) *A. ruizdegaonai* and the latest Cretaceous (late Maastrichtian) *A. massetispinosus* and *A. sunuciorum*, as well as the other Late Jurassic *Annuntidiogenes hoelderi* nov. spec. (see above) and *A. jurassicus*, in having a much coarser crenulated anterior gastric region, a smooth central gastric region and strongly convex subcircular postorbital ridges. It is most closely related to *A. worfi*, from which it can be differentiated by a U-shaped cervical groove and a ridged rostrum.

Family Diogenidae Ortmann, 1892

Genus *Bachmayerus* Fraaije, van Bakel, Jagt & Skupien, 2013

Type species: *Bachmayerus cavus* Fraaije, van Bakel, Jagt & Skupien, 2013, by original designation.

Included species: *Bachmayerus cavus*, *B. matushyznyi* nov. spec., and *B. gasparici* nov. spec.

***Bachmayerus matushyznyi* nov. spec.**

(Figure 2D)

Diagnosis: Diogenid with long, central gastric groove; large, elongated massetic and kerial regions; long keraial region extending parallel to shield midline; long and narrow anterior branchial area; U-shaped cervical groove, coarsely pitted shield.

Etymology: Named after Dr Matúš Hyžný, palaeocarcinologist and friend, currently at the Comenius University (Bratislava, Slovakia), and of great help in the preparation of the present study.

Type material: Holotype (NHMW 1990/0041/2785), a near-complete shield (maximum shield length, as preserved, 6.0 mm; maximum shield width 4.5 mm).

Type locality: The types were purchased in 1990 from FB's daughter, Christine Prenner, but provenance details, except for the general indication of the Ernstbrunn area, were not available. Probably, this material originated from "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Type stratum: Ernstbrunn Limestone, dated by ZEISS (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Description: Diogenid with crenulated and coarsely pitted anterior gastric region centrally divided by long, irregular pitted, gastric groove; large, elongated and well-delineated massetic and kerial regions; massetic region not extending beyond postorbital ridge; keraial region indented by angled, shallow groove; long and narrow anterior branchial area; U-shaped cervical groove, coarsely pitted shield. Parts posterior of cervical groove not preserved.

Remarks: *Bachmayerus matushyznyi* nov. spec. differs from *Bachmayerus cavus* and *B. gasparici* nov. spec. in having considerably more setal pores, in particular on the mid-gastric region and an angled groove in the keraial region.

***Bachmayerus gasparici* nov. spec.**

(Figure 2E, F)

Diagnosis: Diogenid with ridged, triangular rostrum; long, central gastric groove; large, elongated massetic region; long keraial region under an angle of *c*. 30 degrees to shield midline; coarsely pitted shield mainly at anterior and posterior gastric and lateral regions.

Etymology: Named after Rok GAŠPARIČ, Slovenian palaeocarcinologist and friend.

Type material: Holotype (NHMW 2017/0093/0001), a near-complete shield (maximum shield length, as preserved, 4.5 mm; maximum shield width 3.0 mm). Paratype NHMW 1990/0041/0193, a partial shield, maximum shield width 4.5 mm.

Type locality: "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Type stratum: Ernstbrunn Limestone, dated by ZEISS (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Description: A diogenid with ridged, triangular rostrum; crenulated anterior gastric region centrally divided by long, irregularly pitted, central gastric groove; large, elongated massetic region; long keraial region extending under an angle of *c*. 30 degrees to shield midline; coarsely pitted shield mainly at anterior and posterior gastric and lateral regions. Posterior parts of shield not preserved.

Remarks: *Bachmayerus gasparici* nov. spec. differs from congeners in having a keraial region in an angular position directed towards the massetic region.

Genus *Eopaguropsis* VAN BAKEL, FRAAIJE, JAGT & ARTAL, 2008

Type species: *Eopaguropsis loercheri* VAN BAKEL, FRAAIJE, JAGT & ARTAL, 2008, by original designation.

Included species: *Eopaguropsis blausteinensis* Fraaije, Schweigert & van Bakel, 2017, *E. grandis* nov. spec., *E. loercheri*, *E. nidiaquilae* Fraaije, Krzemiński, van Bakel, Krzemińska & Jagt, 2012, and *E. schindewolfi* nov. spec.

Eopaguropsis schindewolfi nov. spec.

(Figure 2G)

Diagnosis: Carapace rectangular; shield slightly longer than wide, broadest at anterior part of posterior carapace; distinct triangular rostrum; broad, rimmed orbital cavities; deep, V-shaped, sinuous cervical groove; central gastric process.

Etymology: In honour of Prof. Dr Otto H. Schindewolf (7 June 1896–10 June 1971), formerly at Tübingen Universität, Tübingen (Germany).

Type material: Holotype (NHMW 1990/0041/3369, leg. K. Oroszy), a near-complete carapace (shield length, without rostrum, 8.2 mm; maximum carapace length, as preserved, 10.9 mm, maximum shield width 8.2 mm); paratype (NHMW 1990/0041/5073), a partial carapace (maximum length 5.0 mm); paratype (NHMW 2017/0093/0002), a partial carapace (maximum length 6 mm); paratype (NHMW 2017/0093/0003), a near-complete external mould of a very small carapace (maximum length and width 3.0 and 2.0 mm, respectively).

Type locality: "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Type stratum: Ernstbrunn Limestone, dated by Zeiss (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Description: Carapace rectangular, markedly longer than wide, strongly convex in transverse section, convex in longitudinal section. Shield as long as wide. Broad triangular rostrum. Slightly concave, rimmed orbital cavity ending in blunt outer orbital spine, followed by slightly concave antennal cavity, without a rim, ending with a triangular post-antennal spine. Prominent central gastric process ending in incision at base of rostrum. Large mesogastric process. Elongated massetic and gastric regions. Prominent V-shaped, very deep, sinuous cervical groove, widest and deepest anterolaterally; recurved kink halfway to lateral border. Anterior part of dorsal carapace less calcified. Except for narrow mid-gastric field, complete carapace more or less homogeneously covered with setal pores.

Remarks: *Eopaguropsis schindewolfi* nov. spec. differs from both *E. loercheri* and *E. nidiaquilae* in having a shield which is narrower than the posterior part of the carapace, in a less clearly delineated and ornamented massetic region and a denser and more homogeneous setal pore ornament on the shield. *Eopaguropsis grandis* nov. spec. (see below) and *E. blausteinensis* can be differentiated on the basis of a significantly smaller mesogastric process.

***Eopaguropsis grandis* nov. spec.**
(Figure 2H, I)

Diagnosis: Shield as long as wide, broadest at anterior part; distinct triangular rostrum; broad, rimmed orbital cavities; deep, V-shaped, sinuous cervical groove; diminutive central gastric process.

Etymology: Alluding to its relative size.

Type material: Holotype (NHMW 1990/0041/3364, leg. K. OROSZY), right half of shield (length, without rostrum, 17 mm; maximum shield width, as reconstructed, 18 mm)

Type locality: "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Type stratum: Ernstbrunn Limestone, dated by ZEISS (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Description: Carapace rectangular, markedly longer than wide, strongly convex in transverse section, convex in longitudinal section. Shield as long as wide. Broad triangular rostrum. Slightly concave, rimmed orbital cavity ending in blunt outer orbital spine, followed by slightly concave antennal cavity, without a rim, ending with a triangular post-antennal spine. Prominent central gastric process ending in an incision at base of rostrum. Elongated massetic and gastric regions. Prominent V-shaped, very deep, sinuous cervical groove, widest and deepest anterolaterally; recurved kink halfway to lateral border. Anterior part of dorsal carapace less calcified. Except for narrow mid-gastric strip, complete carapace more or less homogeneously covered with setal pores.

Remarks: *Eopaguropsis grandis* nov. spec. differs from all congeners in having the smallest gastric process and the lowest number of pores on the posterior part of the shield.

Genus *Tithopaguristes* nov. gen.

Type species: *Tithopaguristes porosus* nov. spec.

Gender: Masculine.

Etymology: In reference to the stratigraphic age (Tithonian) of this form.

Diagnosis: Diogenid shield, longer than wide; rimmed and ridged rostrum, all regions of shield covered with pores; prominent central gastric ridge and gastric process; deep cervical groove fading towards massetic groove incising lateral sides; massetic region longer than wide and extending to same level as postrostral ridge; well-delineated keraial regions.

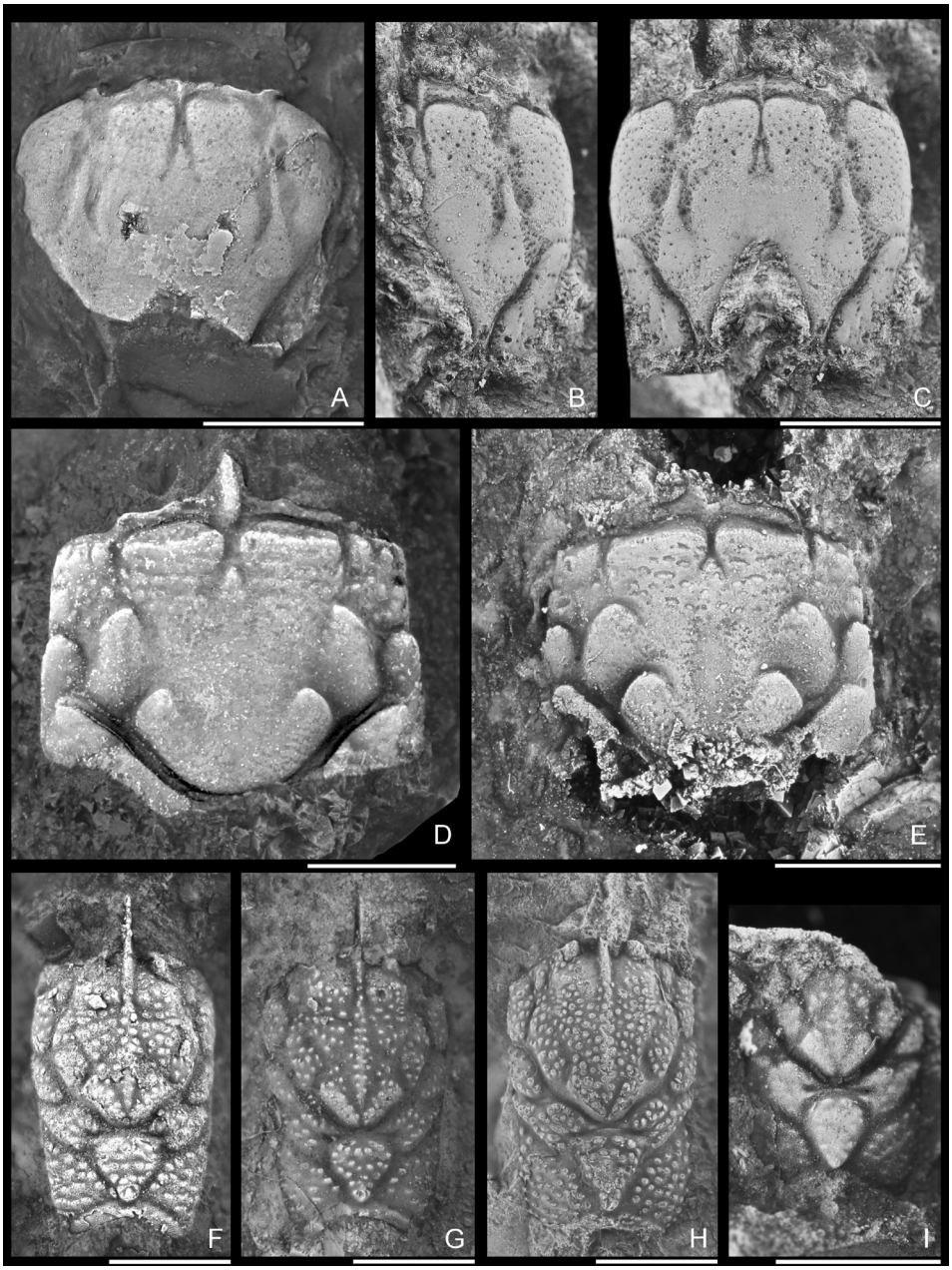

Fig. 3. **A**: *Tithopaguristes porosus* nov. gen., nov. spec., holotype (NHMW 1990/0041/3178). **B**: *Tithopaguristes porosus* nov. gen., nov. spec., paratype (NHMW 1990/0041/1421). **C**: Composite of *Tithopaguristes porosus* nov. gen., nov. spec., paratype (NHMW 1990/0041/1421). **D**: *Ululapagurus oroszyi* nov. spec., holotype (NHMW 1990/0041/3480). **E**: *Ululapagurus oroszyi* nov. spec., paratype (NHMW 1990/0041/5162). **F–I**: *Gastrodorus* spp. (from left to right: NHMW 1990/0041/4282, NHMW 1990/0041/0132, NHMW 1990/0041/1493, NHMW 1990/0041/4660). Scale bars for A and C equal 5 mm, those for D and E 2 mm, and those for F–I 1 mm.

***Tithopaguristes porosus* nov. gen., nov. spec.**
(Figure 3A-C)

Diagnosis: Large shield, wider than long, well areolated, covered with large pores, except on medial gastric region; broad-based, probably triangular, rostrum with ridge extending to central gastric groove; large globose massetic, three times as long as broad, extending to same level as postrostral ridge; elongated anterior branchial area; postrostral ridge indented by central gastric groove with gastric process; well-delineated keraial regions tapering anteriorly, cervical groove incising anterolateral side through posterior massetic groove. Smallest pores on gastric region.

Etymology: In reference to the numerous setal pits on the shield.

Type material: Holotype (NHMW 1990/0041/3178, leg. K. OROSZY), a near-complete shield (maximum estimated length, exclusive of rostrum, 9.0 mm; maximum width 10 mm). Paratype (NHMW 1990/0041/1421, leg. K. OROSZY), a near-half complete shield (maximum estimated length, exclusive of rostrum, 7.0 mm; maximum reconstructed width 8.0 mm),

Type locality: "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Type stratum: Ernstbrunn Limestone, dated by ZEISS (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Description: Large shield, wider than long, well areolated, covered with large pores; broad-based, rimmed, probably triangular, rostrum with ridge extending to central gastric groove; large globose massetic, three times as long as broad, extending to same level as postrostral ridge; elongated anterior branchial area; short, pronounced postrostral ridge indented by central gastric groove with gastric process; well-delineated keraial regions, cervical groove incising anterolateral side through posterior massetic groove. Massetic and keraial grooves covered with large pores.

Remarks: *Tithopaguristes* nov. gen. is assigned to the Diogenidae on the basis of the non-cylindrical shape of the shield and the massetic region that extends to the postfrontal ridge. Similar to other Jurassic diogenid genera such as *Bachmayerus*, *Eopaguropsis* and *Ululapagurus* (see below), the shield in *Tithopaguristes* nov. gen. is also covered with large setal pores.

Genus *Ululapagurus* FRAAIJE, 2014

Type species: *Ululapagurus vanbakeli* FRAAIJE, 2014, by original designation.

Included species: *Ululapagurus oroszyi* nov. spec. and *U. vanbakeli.*

***Ululapagurus oroszyi* nov. spec.**
(Figure 3D, E)

Diagnosis: Shield well areolated; relatively short massetic; small rounded anterior branchial area; undulose subrostral ridge; short mesogastric process; sharp triangular, ridged rostrum; gastric ornament anteriorly crenulated; well-delineated keraial regions, cervical groove incising anterolateral side.

Etymology: Named after the late Viennese amateur palaeontologist and tireless collector, Karl Oroszy (1923–27 August 1987), who recovered numerous decapod crustaceans from Ernstbrunn, inclusive of most of the type material presented here.

Type material: Holotype (NHMW 1990/0041/3480), an incomplete carapace (maximum shield length, exclusive of rostrum, 4.0 mm; maximum shield width 5.2 mm); paratypes are an incomplete shield (NHMW 1990/0041/0194; maximum width 8.3 mm) and a near-complete shield (NHMW 1990/0041/5162) (maximum length, exclusive of rostrum, 3.5 mm; maximum width 4.1 mm).

Type locality: "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Type stratum: Ernstbrunn Limestone, dated by Zeiss (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Description: Shield wider than long (exclusive of rostrum), convex in transverse section, slightly convex in longitudinal section; sharp and extremely long, triangular, ridged and finely tuberculate rostrum; pronounced frontal ridge, medially divided by central gastric groove, posteriorly extending into distinct triangular gastric process. Owl-shaped gastric region bordered posteriorly by deep cervical groove and less deep lateral keraial and massetic grooves anteriorly; globose, divided massetic region covered with coarse tubercles; small, rounded and coarsely tuberculate anterior branchial area. Anteriormost part of posterior branchial area also coarsely tuberculate. Elongated, inflated submassetic region with longitudinal axis directed inwards, almost parallel to lateral side of rostrum. Elongated, inflated keraial with longitudinal axis almost perpendicular to submassetic region. Submassetic, keraial and posteriormost central part of gastric almost smooth. Anterior part of gastric region ornamented by few rows of tubercles parallel to frontal ridge.

Remarks: The characteristic owl-shaped gastric region distinguishes this genus from other diogenids. *Ululapagurus oroszyi* nov. spec. is easily distinguished from the only other representative of the genus, the type species *U. vanbakeli*, by its wider-than-long shield, more inflated keraial, submassetic and anterior branchial regions and ornamentation of anterior gastric region.

Family Gastrodoridae van Bakel, Fraaije, Jagt & Artal, 2008

Genus *Gastrodorus* von Meyer, 1864

Type species: *Gastrodorus neuhausensis* von Meyer, 1864, by monotypy.

***Gastrodorus* spp.**
(Figure 3F–I)

Included species: *Gastrodorus bzowiensis* Krzemińska, Krzemiński, Fraaije, van Bakel& Jagt, 2015, *G. cretahispanicus* Klompmaker, Artal, Fraaije & Jagt, 2011, *G. kotoucensis* Fraaije, van Bakel, Jagt & Skupien, 2013, and *G. neuhausensis* von Meyer, 1864.

Type locality: Provenance details are not available for these specimens, but they most probably originated from the "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Type stratum: Ernstbrunn Limestone, dated by Zeiss (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Material: Near-complete carapaces: NHMW 1990/0041/0132 (maximum length 3.0 mm; maximum width 1.5 mm), NHMW 1990/0041/1493, NHMW 1990/0041/4282 (maximum length 3.0 mm; maximum width 1.5 mm), NHMW 1990/0041/4660 (maximum length 2.5 mm; maximum width 1.5 mm).

Discussion: The presence of distinctly delineated massetic and anterior branchial areas, a pronounced keraial region, cervical and branchiocardiac grooves and (remnants of) a postcervical groove in *Gastrodorus* shows gastrodorids to be basal members of the Paguroidea (Fraaije 2014). The carapace morphology of *Gastrodorus* is characterised by wide intraspecific variation, which makes taxonomic subdivisions difficult. To date, four forms have been formally named, *i.e.*, *Gastrodorus neuhausensis*, *G. kotoucensis*, *G. bzowiensis* (all of Late Jurassic age) and *G. cretahispanicus* from the upper Albian. The main points of variation in carapace morphology of species of *Gastrodorus* involve the shape and ornament of the cardiac region, the shape and size of the keraial, massetic, mesobranchial and urogastric regions, overall tubercle size and the length of the median gastric ridge and postrostral ridges (Fraaije 2014). Differences are very gradual within "assemblages" and also ontogenetic changes have been observed (Krzemińska *et al*. 2013). Bachmayer (1958) already interpreted morphological differences in *Gastrodorus* as an expression of sexual dimorphism, on the basis of material from the Tithonian of Ernstbrunn. The variation noted in specimens of *Gastrodorus* in the present assemblage concerns an admixture of morphological traits seen in all three Late Jurassic species that are known to date. More material and statistical studies (see Krzemińska *et al*. 2013, 2015) are needed in order to assess the Ernstbrunn gastrodorids in more detail; for the time being, they are left in open nomenclature.

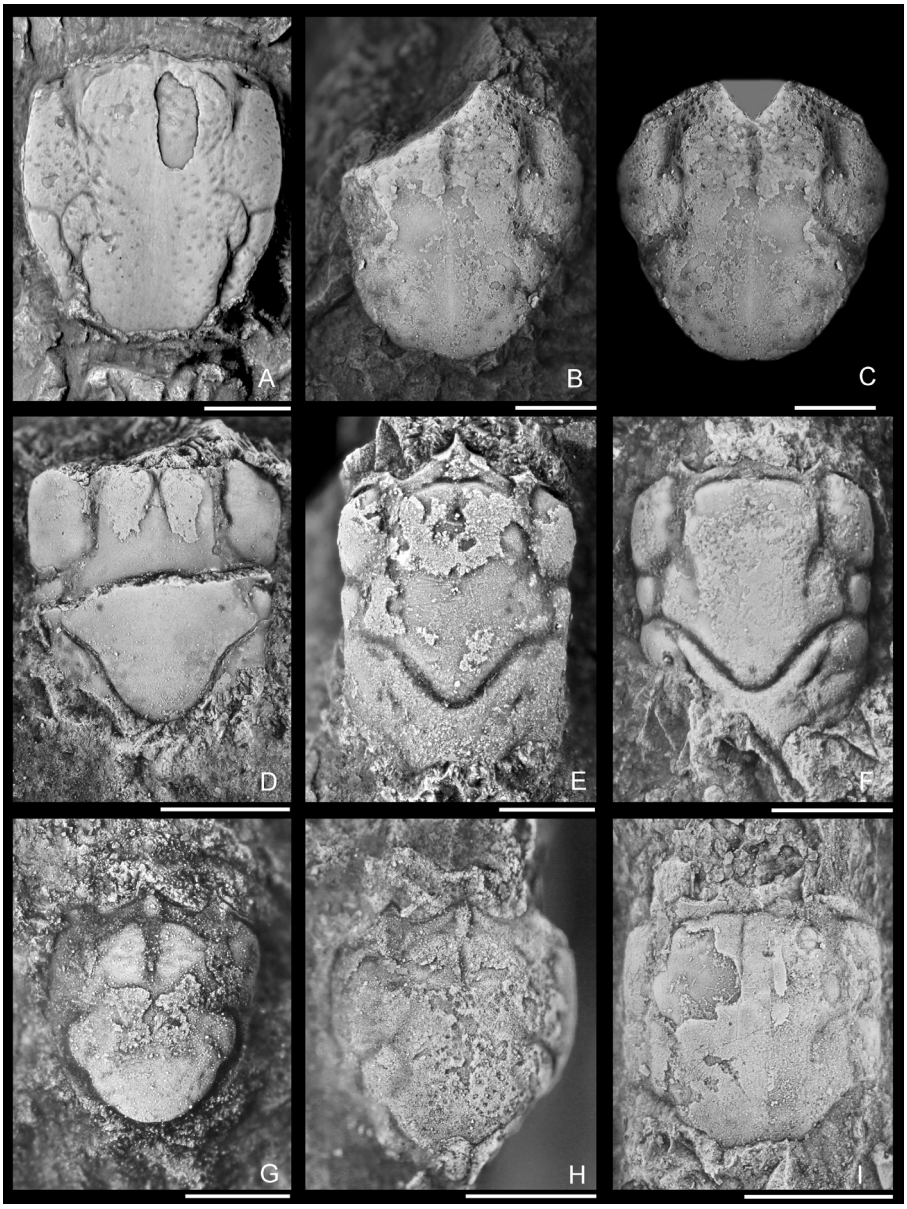

Fig. 4. **A**: *Protopagurus janoscheki* nov. gen., nov. spec., holotype (NHMW 1990/0041/3481). **B**: Juvenile *Protopagurus janoscheki* nov. gen., nov. spec., paratype (NHMW 1990/0041/4322). **C**: Composite of juvenile *Protopagurus janoscheki* nov. gen., nov. spec., paratype (NHMW 1990/0041/4322). **D**: *Mesoparapylocheles strouhali* nov. spec., holotype (NHMW 1990/0041/3320). **E**: *Mesoparapylocheles zapfei* nov. spec., holotype (NHMW 1990/0041/5069). **F**: *Mesoparapylocheles zapfei* nov. spec., paratype (NHMW 1990/0041/0517). **G**: *Masticacheles minimus* FRAAIJE, 2014 (NHMW 1990/0041/1447). **H**: *Masticacheles minimus* FRAAIJE, 2014 (NHMW 1990/0041/5057). **I**: *Pilgrimcheles vonmeyeri* FRAAIJE, 2014 (NHMW 1990/0041/3882). Scale bar for A equals 5 mm, those for B, C, E, and F 1 mm, those for D and I 2 mm, and those for G and H 0.5 mm.

Family Paguridae LATREILLE, 1802

Genus *Protopagurus* nov. gen.

Type species: *Protopagurus janoscheki* nov. spec.

Gender: Masculine.

Etymology: In reference to the stratigraphic age of this form.

Diagnosis: Well-areolated shield, longer than wide, covered with pores; cervical groove centrally U-shaped, incising anterolateral side through posterior massetic groove; large massetic region not extending to post-antennal projection, shallow central gastric groove; well-delineated, reniform keraial regions.

Remarks: *Protopagurus* nov. gen. is the oldest known representative of the Paguridae.

***Protopagurus janoscheki* nov. gen., nov. spec.**
(Figure 4A–C)

Diagnosis: Large shield, longer than wide, well areolated, covered with large pores; large globose massetic, twice as long as broad; small elongated anterior branchial area; short, shallow central gastric groove; well-delineated, reniform keraial regions, cervical groove incising anterolateral side through posterior massetic groove.

Etymology: In honour of Dr Robert JANOSCHEK (deceased 1986), respected colleague of one of us (FB).

Type material: Holotype (NHMW 1990/0041/3481, leg. K. OROSZY), a near-complete shield (maximum length, exclusive of rostrum, 17.0 mm; maximum width 15.0 mm). Paratypes: NHMW 1990/0041/4322 (leg. K. OROSZY), an incomplete shield of a juvenile individual (maximum length, exclusive of rostrum, 4.0 mm; maximum width 3.0 mm) and NHMW 1990/0041/1812a (leg. K. OROSZY), an incomplete shield (no measurements possible).

Type locality: "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Type stratum: Ernstbrunn Limestone, dated by ZEISS (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Description: Large shield, longer than wide, well areolated, covered with large pores; large globose massetic, twice as long as broad; small elongated anterior branchial area; short, shallow central gastric groove extending in a faint ridge to posterior margin; well-delineated, reniform keraial regions, cervical groove incising anterolateral side through posterior massetic groove. Rostrum and posterior part of carapace not preserved.

Remarks: Morphologically, the shield of *Protopagurus* nov. gen. is close to that of genera such as *Diacanthurus* MCLAUGHLIN & FOREST, 1997 and *Lophopagurus* MCLAUGHLIN, 1981. Characteristic of this group of paguroids is that the large and elongated massetic does not extend to the frontal margin.

Family Parapylochelidae Fraaije, Klompmaker & Artal, 2012

Genus *Mesoparapylocheles* Fraaije, Klompmaker & Artal, 2012

Type species: *Mesoparapylocheles michaeljacksoni* Fraaije, Klompmaker & Artal, 2012, by original diagnosis.

Included species: *Mesoparapylocheles jaegeri* Fraaije, 2014, *M. michaeljacksoni*, *M. schweigerti* Fraaije, 2014, *M. strouhali* nov. spec., and *M. zapfei* nov. spec.

***Mesoparapylocheles strouhali* nov. spec.**
(Figure 4D)

Diagnosis: Relatively large shield, well calcified, almost as broad as long; short and deep central gastric groove extending posteriorly into a distinct gastric process; large, smooth and globose massetic regions and considerably smaller, globose anterior branchial area. Gastric region arrowhead-shaped, pointing posteriorly. Renifrom keraial region with large pit centrally. Posterior part of carapace less well calcified and poorly preserved.

Etymology: In honour of Prof. Dr Hans Strouhal (2 October 1897–25 January 1969), former director of the Naturhistorisches Museum Wien. Apparently Dr Strouhal was in function when FB prepared his typescripts on the Ernstbrunn paguroids, which dates these as pre-1962, *i. e.*, the year in which Dr Strouhal retired (Beier 1969).

Type material: Holotype (NHMW 1990/0041/3320, leg. K. Oroszy), a near-complete shield (maximum shield length, as preserved, 4.0 mm; maximum shield width 3.8 mm).

Type locality: "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Type stratum: Ernstbrunn Limestone, dated by Zeiss (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Description: Well-calcified, relatively large shield, width equalling length, rostrum not preserved; cervical groove most prominent centrally, initially convex posteriorly, proceeding slightly concave and oblique anteriorly; dorsal surface of shield smooth. Short and deep anterior central gastric groove, extending posteriorly into small triangular gastric process. Large, undivided and globose massetic region and considerably smaller, globose anterior branchial area. Renifrom keraial region with large pit centrally. Posterior margin of shield straight in centre and following concave lateral curvature. Posterior carapace less well calcified, smooth with some pits, where preserved.

Remarks: The presence of a triangular gastric process differentiates *Mesoparapylocheles strouhali* nov. spec. from all congeners.

Mesoparapylocheles zapfei nov. spec.
(Figure 4E, F)

Diagnosis: Shield well-calcified, well-areolated, with distinct regions, including large, smooth and globose massetic region and considerably smaller, globose anterior branchial area. Prominent broad-based, triangular rostrum. Distinct triangular postocular spines. Distinct subrounded postrostral ridge without central indention. Gastric region arrowhead-shaped, pointing posteriorly. Renifrom keraial region. Deep and long post-cervical groove extending parallel to cervical groove. Distinct cardiac region. Posterior part of carapace less well calcified and never completely preserved.

Type material: Holotype (NHMW 1990/0041/5069, leg. K. OROSZY), a near-complete carapace (maximum shield length, rostrum excluded, 2.8 mm; maximum width 2.5 mm). Paratypes are NHMW 1990/0041/0517, …/0602, …/0604, …/0935, …/1930, …/2079, …/2344, …/3317, …/4045, with maximum lengths (rostrum excluded) and widths of 2.3, 1.6, 2.0, 2.9, 2.5, 2.2, 1.1, 2.6 and 1.9 mm and 2.3, 2.0, 2.4, 3.0, 2.5, 2.5, 1.2, 2.9 and 2.3 mm, respectively.

Etymology: Named after Prof. Dr Dr Helmuth ZAPFE (16 September 1913–5 July 1996), former director of the Geologisch-Paläontologische Abteilung des Naturhistorischen MuseumWien.

Type locality: "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Type stratum: Ernstbrunn Limestone, dated by ZEISS (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Description: Diminutive, well-calcified, smooth and well-areolated shield, convex transversely, slightly convex longitudinally. Broad-based triangular rostrum. Orbital cavity ellipsoidal, bounded by triangular, slightly upturned, post-ocular spine. Ocular-frontal area exceeding half of maximum width. Pronounced subcylindrical post-rostral ridge fading towards keraial region. Posteriorly pointed, arrowhead-shaped gastric region, bounded posteriorly by deep V-shaped cervical groove. Very prominent and globose anterior massetic region. Anterior branchial area globose, size about one-quarter of massetic region. Typically reniform keraial regions anteriorly at widest part of cervical groove. Elongated mesobranchial region exhibiting deep and long postcervical groove parallel to and medially between cervical and branchio-cardiac grooves. Subrounded pentagonal cardiac posteriorly bounded by branchiocardiac groove. Posterior part of carapace less well calcified, therefore no completely preserved carapaces found.

Remarks: Accounting for over 28 per cent of the assemblage, *Mesoparapylocheles* is the commonest element amongst the Ernstbrunn paguroid fauna. *Mesoparapylocheles zapfei* nov. spec. differs from congeners in lacking an indented postrostral ridge and in having relatively long and pronounced postcervical grooves parallel to the cervical groove. One of us (FB) was the first to recognise this diminutive form as a taxonomically

very interesting one and provisionally assigned it to the paguroids, preliminarily referring to it as "*Semipagurus*". In describing a late Albian species from reefal limestones in Navarra, northern Spain, Fraaije *et al*. (2012a) noted that *Mesoparapylocheles* was closely related to the extant genus *Parapylocheles*. This genus is now known from across Europe, occurring in shallow-water reefal limestones of Oxfordian, Kimmeridgian, Tithonian and Albian age.

Family Pilgrimchelidae Fraaije, 2014

Genus *Masticacheles* Fraaije, Krzemiński, van Bakel, Krzemińska & Jagt, 2014

Type species: *Masticacheles longirostris* Fraaije, Krzemiński, van Bakel, Krzemińska & Jagt, 2014, by original diagnosis.

***Masticacheles minimus* Fraaije, 2014**
(Figure 4G, H)

Diagnosis: Reference is made to Fraaije (2014) for a detailed description of this taxon.

Material: A near-complete shield (NHMW 1990/0041/1447, leg. K. Oroszy), maximum shield length, rostrum excluded, 1.5 mm; maximum width 1.0 mm; a near complete shield (NHMW 1990/0041/5057, leg. K. Oroszy), maximum shield length, rostrum excluded, 1.5 mm; maximum width 1.0 mm.

Locality: "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Stratigraphy: Ernstbrunn Limestone, dated by Zeiss (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Remarks: At first sight, small-sized annuntidiogenid shields appear similar to shields of pilgrimchelids, but they can be easily differentiated in that only in the former is the Y-linea present. *Masticacheles minimus* was the second representative of the genus to be described, differing from the type species, *M. longirostris*, in the possession of a more rounded, less delineated keraial region and a more pronounced postorbital rim (Fraaije 2014).

Genus *Pilgrimcheles* Fraaije, Krzemiński, van Bakel, Krzemińska & Jagt, 2014

Type species: *Pilgrimcheles karolinae* Fraaije, Krzemiński, van Bakel, Krzemińska & Jagt, 2014, by original designation.

Pilgrimcheles vonmeyeri FRAAIJE, 2014
(Figure 4I)

Diagnosis: Reference is made to FRAAIJE (2014) for a detailed description of this taxon.

Material: A near-complete shield (NHMW 1990/0041/3882, leg. K. OROSZY), (maximum shield length, rostrum excluded, 3.5 mm; maximum width 3.0 mm).

Locality: The types were purchased in 1990 from FB's daughter, Christine PRENNER, but provenance details, except for the general indication of the Ernstbrunn area, were not available. The material probably originated from "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Stratigraphy: Ernstbrunn Limestone, dated by ZEISS (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Family Pylochelidae BATE, 1888

Subfamily Trizochelinae FOREST, 1987

Genus *Ammopylocheles* VAN BAKEL, FRAAIJE, JAGT & ARTAL, 2008

Type species: *Ammopylocheles mclaughlinae* VAN BAKEL, FRAAIJE, JAGT & ARTAL, 2008, by original designation.

Ammopylocheles mclaughlinae VAN BAKEL, FRAAIJE, JAGT & ARTAL, 2008
(Figure 5A, B)

Diagnosis: Reference is made to VAN BAKEL *et al.* (2008) for a detailed description of this taxon.

Material: Six fragmentary carapaces (NHMW 1990/0041/0957, …/3315, …/3811, …/4638, …/4897 a, and …/5058, leg. K. OROSZY), with shield lengths of 3.8, 7.1, 2.8, 4.4, 7.0 and 4.0, and maximum shield widths of 3.0, 6.0, 2.8, 4.0, 6.0 and 3.6 mm, respectively.

Locality: "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Stratigraphy: Ernstbrunn Limestone, dated by ZEISS (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Remarks: *Ammopylocheles mclaughlinae* is by far the commonest element at Nusplingen (FRAAIJE 2014) and Geisingen (VAN BAKEL *et al*. 2008) in southern

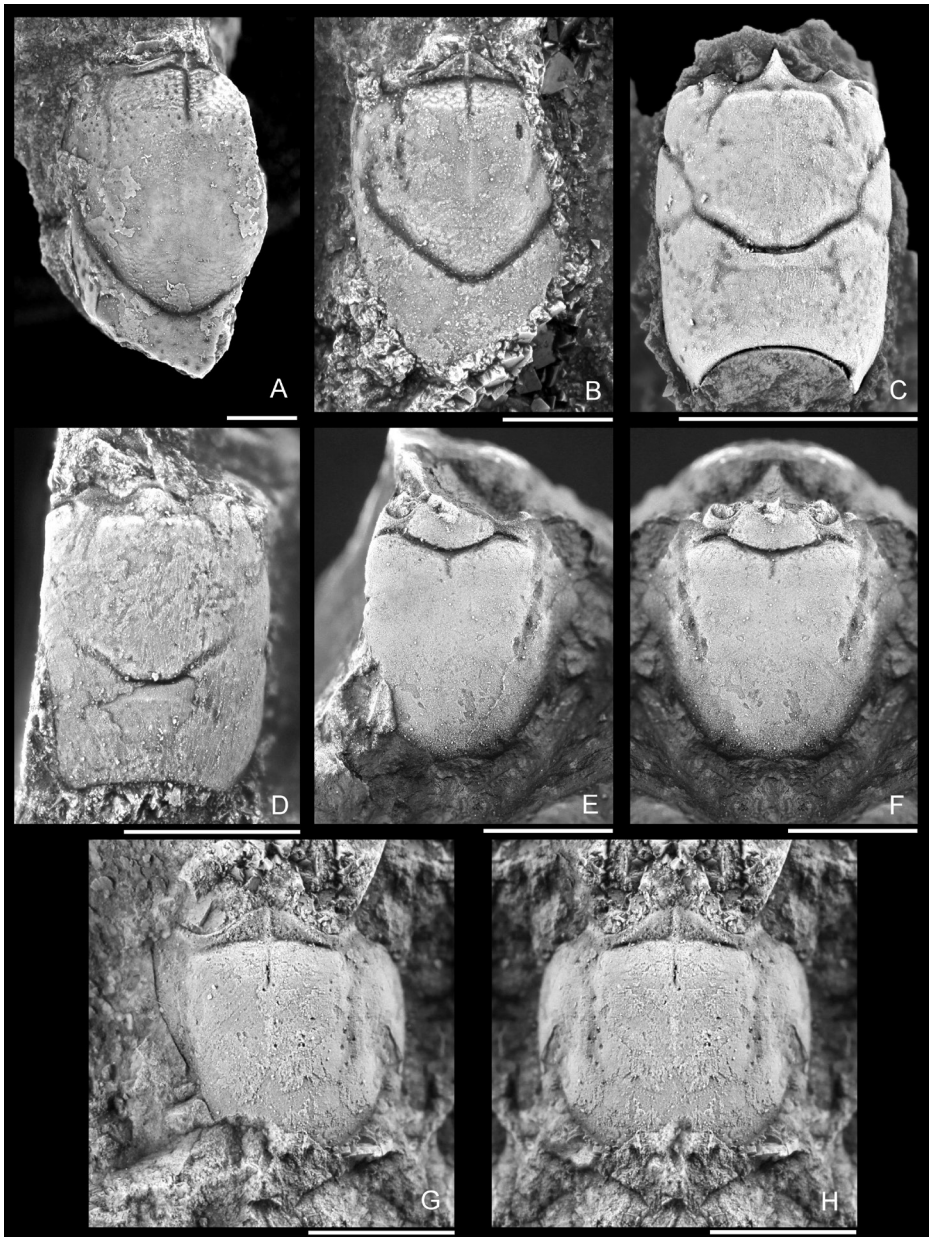

Fig. 5. **A**: *Ammopylocheles mclaughlinae* van Bakel, Fraaije, Jagt & Artal, 2008 (NHMW 1990/0041/3315). **B**: *Ammopylocheles mclaughlinae* van Bakel, Fraaije, Jagt & Artal, 2008 (NHMW 1990/0041/3811). **C**: *Munitheites kuepperi* nov. spec., holotype (NHMW 1990/0041/3306 a). **D**: *Munitheites kuepperi* nov. spec., paratype (NHMW 1990/0041/1959). **E**: *Cretatrizocheles doerflesensis* nov. spec., paratype (NHMW 2017/0093/0004). **F**: Composite of *Cretatrizocheles doerflesensis* nov. spec., paratype (NHMW 2017/0093/0004). **G**: *Pretrizocheles cocullo* nov. gen., nov. spec., holotype (NHMW 2017/0093/0005). **H**: Composite of *Pretrizocheles cocullo* nov. gen., nov. spec., holotype (NHMW 2017/0093/0005). Scale bars equal 2 mm.

Germany, but it is rather uncommon to rare at Ernstbrunn. The same holds true for *Gastrodorus*. Slight morphological differences in the post-frontal ridge, from near-straight to convex and occasionally undulose, in specimens of *A. mclaughlinae* are interpreted as intraspecific variation and possibly reflect sexual dimorphism (FRAAIJE 2014). Interestingly, smaller (*i. e.*, more juvenile) individuals of this species have no pores, or only a few pores, on the posterior carapace portion, while larger (*i. e.*, older) specimens have numerous large setal pores. This might reflect a change in habitat or mode of life during ontogeny.

Genus *Cretatrizocheles* FRAAIJE, KLOMPMAKER & ARTAL, 2012

Type species: *Cretatrizocheles olazagutiensis* FRAAIJE, KLOMPMAKER & ARTAL, 2012, by original designation.

Included species: *Cretatrizocheles doerflesensis* nov. spec. and *C. olazagutiensis.*

***Cretatrizocheles doerflesensis* nov. spec.**

(Figure 5E, F)

Diagnosis: Shield smooth, longer than wide; prominent triangular rostrum, considerably longer than postocular and post-antennal projections. Short central gastric groove at posteriormost part of deep, concave and undulose post-rostral ridge. Distinct lateral gastric grooves. Cervical groove medially straight, then curving anteriorly towards massetic region. Posterior carapace, appendages, abdomen and cuticle not preserved.

Etymology: Named after the small village of Dörfles, where the types were collected.

Type material: Holotype (NHMW 1990/0041/0174), an incomplete carapace (maximum shield length, as preserved, 4.0 mm; maximum shield width 3.3 mm). Paratype (NHMW 2017/0093/0004), an incomplete carapace (shield length, without rostrum, 4.0 mm; maximum shield width 3.2 mm).

Type locality: The types were purchased in 1990 from FB's daughter, Christine PRENNER, but provenance details, except for the general indication of the Ernstbrunn area, were not available. The material probably originated from "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Type stratum: Ernstbrunn Limestone, dated by ZEISS (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Description: Shield smooth, strongly calcified, about as long as wide; prominent triangular rostrum, considerably longer than postocular and post-antennal projections. Short central gastric groove at posteriormost part of deep, concave and undulose post-rostral ridge. Distinct lateral gastric grooves originating posterior to massetic

region and effacing into undulose post-rostral ridge. Cervical groove medially straight, then curving anteriorly towards massetic region. Posterior carapace, appendages, abdomen and cuticle not preserved.

Remarks: Up to now, the genus *Cretatrizocheles* was known exclusively from upper Albian reefal limestones of Navarra, northern Spain. *Cretatrizocheles doerflesensis* nov. spec. differs from the type species, *C. olazagutiensis*, in having a more pronounced and concave postrostral ridge that becomes more angular laterally.

Genus *Pretrizocheles* nov. gen.

Type species: *Pretrizocheles cocullo* nov. spec.

Gender: Masculine.

Etymology: In reference to the close morphological similarity to the extant genus *Trizocheles* FOREST, 1987.

Diagnosis: A pylochelid shield with broadly triangular, centrally ridged rostrum, extending beyond postocular spines; subcircular orbital cavities; absence of post-antennal projections; long, nearly straight postrostral ridge perpendicular to long central gastric groove.

Remarks: Extant trizochelines display all shield characters of *Pretrizocheles* nov. gen., with the exception of a cervical groove that extends into the massetic groove and of a continuous ridge from tip of rostrum to postrostral ridge. Some species of the extant pylochelid genus *Cheiroplatea* BATE, 1888 also have pronounced subcircular "orbits", but lack the rim and a strongly protruding rostrum and have short, curved postrostral ridges.

***Pretrizocheles cocullo* nov. gen., nov. spec.**

(Figure 5G, H)

Diagnosis: A pylochelid shield, slightly wider than long; with broadly triangular, centrally ridged rostrum, extending beyond postocular spines; rimmed, subcircular orbital cavities; absence of post-antennal projections; long, postrostral ridges perpendicular to long central gastric groove. Hemicircular cervical groove extending into massetic groove. Long submassetic groove parallel to longitudinal axis and covered with few large pores.

Etymology: In reference to the cap-like (Latin *cocullo*) appearance of the shield.

Type material: Holotype (NHMW 2017/0093/0005), a near-complete shield (maximum length, exclusive of rostrum, 4.0 mm; maximum width 3.5 mm).

Type locality: The type was purchased in 1990 from FB's daughter, Christine PRENNER, but provenance details, except for the general indication of the Ernstbrunn area,

were not available. The material probably originated from "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Type stratum: Ernstbrunn Limestone, dated by ZEISS (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Description: A pylochelid shield, slightly wider than long; with broadly triangular, centrally ridged rostrum, extending beyond postocular spines; rimmed, subcircular orbital cavities; absence of post-antennal projections; long, nearly straight postrostral ridges perpendicular to long central gastric groove. Hemicircular cervical groove extending into massetic groove. Long submassetic groove parallel to longitudinal axis and covered with few large pores.

Family Schobertellidae SCHWEIGERT, FRAAIJE, HAVLIK & NÜTZEL, 2013

Genus *Munitheites* LŐRENTHEY, *in* LŐRENTHEY & BEURLEN, 1929

Type species: *Munitheites palfyi* LŐRENTHEY, *in* LŐRENTHEY & BEURLEN, 1929, by original designation.

Included species: *Munitheites kuepperi* nov. spec. and *M. palfyi*.

***Munitheites kuepperi* nov. spec.**
(Figure 5C, D)

Diagnosis: Carapace cylindrical, narrowing slightly posteriorly and anteriorly, strongly convex transversely. Pronounced, broad-based, triangular rostrum. Postocular spines present. Extent of regional definition varying widely; massetic and anterior branchial area of equal size; short post-cervical groove at lateral part of prominent urogastric area which is about half of total width; ornament usually not well preserved, but when present consisting of a cover of coarse pores forming reticulate pattern, in particular on posterior part. Faint central ridge on anterior part of carapace.

Etymology: Named after Dr Klaus KÜPPER, a young and promising palaeontologist and co-author of one of us (FB) (BACHMAYER & KÜPPER 1952), who died in 1957 at the age of 27.

Type material: Holotype (NHMW 1990/0041/3306 a, leg. K. OROSZY), complete carapace (maximum length, exclusive of rostrum, 2.2 mm; maximum width 1.8 mm). Paratypes are NHMW 2007z0149/0109, 1990/0041/0496, …/1498, …/1766, …/1959, and …/3235 (leg. K. OROSZY), with maximum lengths and widths of 2.5, 3.0, 1.3, 1.9, 2.5 and 3.0 mm, and 2.1, 2.5, 0.8, 1.4, 2.0 and 2.2 mm, respectively.

Type locality: "Dörfles Kalkwerk II" (Kalkgewerkschaft Ernstbrunn), Steinberg, *c.* 2 km north of Ernstbrunn, northeast Austria.

Type stratum: Ernstbrunn Limestone, dated by Zeiss (2001) as middle middle to early late Tithonian (*Richterella richteri* Zone to *Micracanthoceras microcanthum* Zone, *Simplisphinctes* Subzone).

Description: Cylindrical carapace narrowing slightly posteriorly, strongly convex transversely, slightly to moderately convex longitudinally, especially posteriorly. Stout, broad-based, triangular rostrum. Indefinite triangular postantennal spine present on lateral edge of frontal margin, more pronounced triangular postocular spine equidistant between postantennal spine and rostrum. Broad, flat postfrontal band, interrupted by rostral projection. Cervical groove moderately defined posteriorly, more weakly defined anteriorly. Large massetic and anterior branchial areas of about equal size. Gastric region large; slightly vaulted anteriorly. Cardiac region slightly raised from remainder of posterior portion, extending to posterior margin. Short post-cervical groove at lateral end of prominent urogastric area. Ornament not well preserved on most specimens. Where present, it consists of equal-sized and evenly spaced setal pits, forming a reticulate pattern, especially on posterior part; few tubercles present on anterior of carapace, especially within gastric region. Posterior margin very weakly rimmed. Ventral surface and appendages not preserved.

Discussion: To date, *Munitheites palfyi* has been recorded solely from Tithonian limestones near the town of Alsórákos in the "Komitat Nagykülküllő"(Nagy-Külküllő), a small area within what is now Transylvania, Romania. Patrulius (1959) referred to a new Tithonian species of *Munitheites* from Sinaia (Romania), but, although he rephrased the diagnoses of both *Munitheites* and *Munitheites palfyi*, he failed to name or present a detailed description of that new form.

The genus *Munitheites* has long been considered a galatheoid (Robins *et al*. 2013). However, general carapace shape, the small rostrum, the groove structure and posterior preservational style favour alliance with members of the superfamily Paguroidea. It was reassigned to the Pylochelidae by Robins *et al*. (2013). However, *Munitheites* has a cervical groove that reaches and incises the lateral sides of the carapace and we therefore transfer it here to the closely related Schobertellidae (see Fraaije 2014: p. 143, fig. 15). The presence of post-cervical grooves and a (partially) delineated cardiac is seen exclusively in the most primitive paguroids (Fraaije 2014); it groups the Gastrodoridae, Parapylochelidae and Schobertellidae as most closely related basal paguroid families.

The extent of regional definition in *Munitheites kuepperi* nov. spec. varies amongst specimens, most of which lack portions of the posterior margins. Lőrenthey (*in* Lőrenthey & Beurlen 1929) mentioned the relatively poor condition of the specimen available to him as justification for considering *Munitheites* as a subgenus. In comparison to the preservation of co-occurring galatheoids and prosopids, it is likely that the carapace of *Munitheites*, as with most paguroids, was either weaker or thinner, not preserving as well as other decapod crustacean groups.

Munitheites kuepperi nov. spec. differs from *M. palfyi* in the relative lack of definition of the epigastric region, the position of the anterior spines, the place of incision at the lateral

sides of the cervical groove and the posterior narrowing of the carapace. Differences mentioned are based on the illustration in Lőrenthey & Beurlen (1929) as well as on the original description. A re-examination of the type specimen will undoubtedly yield more concrete details, but despite various attempts to trace it in the collections of the Geological Institute in Budapest, we have so far been unsuccessful in doing so. Although faint post-antennal spines are present, *Munitheites* is best referred to the Schobertellidae, following the key presented by Fraaije (2014: p. 143, fig. 15) and herein (see above). *Munitheites* is second in rank to *Mesoparapylocheles* in constituting the commoner elements at Ernstbrunn, accounting for about 25 per cent of the total fauna.

Ackowledgements

Andreas Kroh, Thomas Nichterl, and Matúš Hyžný assisted us, in every possible way, to make the extensive Bachmayer Collection available for study. Matúš Hyžný also helped in trying to locate the holotype of *Munitheites* in the collections of the Geological Institute at Budapest. Thea Fraaije-van Boom is thanked for her patience during the many writing sessions at Kenyeri, Hungary. Adiël Klompmaker assisted with locating additional paguroid material within the Ernstbrunn Collections at NHMW.

References

Bachmayer, F. (1947): Die Crustaceen aus dem Ernstbrunner Kalk der Jura-Klippenzone zwischen Donau und Thaya. – Jahrbuch der Geologischen Bundesanstalt Wien, **90**: 35–47.

Bachmayer, F. (1948): Pathogene Wucherungen bei jurassischen Dekapoden. – Sitzungsberichte der Österreichischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse, Abteilung I, **157**: 263–266.

Bachmayer, F. (1954): Ein Korallenriff in Niederösterreich. – Universum, **1954**/15: 461–468.

Bachmayer, F. (1955): Die Crustaceenfauna der tithonischen Riffkalke von Ernstbrunn und Stramberg. – Paläontologische Zeitschrift, **29**: 5–6.

Bachmayer, F. (1958): Ein bemerkenswerter fossiler Krebsrest aus dem Jurakalk von Ernstbrunn (Niederösterreich). – Veröffentlichungen aus dem Naturhistorischen Museum Wien, neue Folge, **1**: 16.

Bachmayer, F. (1959): Neue Crustaceen aus dem Jura von Stramberg (ČSR). – Sitzungsberichte der Österreichischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse, Abteilung I, **168**: 937–944.

Bachmayer, F. (1964): Ein Korallenriff in Niederösterreich. – In: Bachmayer, F., Cornelius-Furlani, M., Kamptner, E., Kirnbauer, F., Kollmann, H.A. & Zapfe, H. (eds): Schätze im Boden. Bilder aus Österreichs geologischer Vergangenheit. – Veröffentlichungen aus dem Naturhistorischen Museum, neue Folge, **5**: 115–124.

Bachmayer, F. & Küpper, K. (1952): Eine bemerkenswerte Krabbe aus dem Badener Tegel (Torton) von Soos im Wiener Becken. – Verhandlungen der Geologischen Bundesanstalt Wien, **1952**: 200–205.

Bate, C.S. (1888): Report on the Crustacea Macrura collected by the H.M.S. Challenger during the years 1873–1876. – In: Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–76. Zoology, **24**: 1–942.

Beier, M. (1969): Hans Strouhal. – Annalen des Naturhistorischen Museums in Wien, **73**: 35–36.

Feldmann, R.M. & Schweitzer, C.E. (2009): Revision of Jurassic Homoloidea de Haan, 1839, from the Ernstbrunn and Štramberk limestones, Austria and the Czech Republic. – Annalen des Naturhistorischen Museums in Wien, Serie A, **111**: 183–206.

Forest, J. (1987): Les Pylochelidae ou «Pagures symétriques» (Crustacea Coenobitoidea). – In: Crosnier, A. (ed.): Résultats des Campagnes MUSORSTOM, Volume 3. – Mémoires du Muséum national d'Histoire naturelle, Série A, **137**: 1–254.

Fraaije, R.H.B. (2014): Diverse Late Jurassic anomuran assemblages from the Swabian Alb and evolutionary history of paguroids based on carapace morphology. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **273**: 121–145.

Fraaije, R.H.B., van Bakel, B.W.M., Jagt, J.W.M. & Artal, P. (2008): New decapod crustaceans (Anomura, Brachyura) from mid-Cretaceous reefal deposits at Monte Orobe (Navarra, northern Spain), and comments on related type-Maastrichtian material. – In: Steurbaut, E., Jagt, J.W.M. & Jagt-Yazykova, E.A. (eds): Annie V. Dhondt Memorial Volume. – Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, **78**: 193–208.

Fraaije, R.H.B., van Bakel, B.W.M., Jagt, J.W.M., Klompmaker, A.A. & Artal, P. (2009): A new hermit crab (Crustacea, Anomura, Paguroidea) from the mid-Cretaceous of Navarra, northern Spain. – Boletín de la Sociedad Geológica Mexicana, **61**: 13–16.

Fraaije, R.H.B., Klompmaker, A.A. & Artal, P. (2012a): New species, genera and a family of hermit crabs (Crustacea, Anomura, Paguroidea) from a mid-Cretaceous reef of Navarra, northern Spain. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **263**: 85–92.

Fraaije, R.H.B., Krzemiński, W., van Bakel, B.W.M., Krzemińska, E. & Jagt, J.W.M. (2012b): The earliest record of pylochelid hermit crabs from the Late Jurassic of southern Poland, with notes on paguroid carapace terminology. – Acta Palaeontologica Polonica, **57**: 647–654.

Fraaije, R.H.B., Krzemiński, W., van Bakel, B.W.M., Krzemińska, E. & Jagt, J.W.M. (2012c): The earliest record of a diogenid hermit crab from the Late Jurassic of the southern Polish Uplands, with notes on paguroid carapace terminology. – Acta Palaeontologica Polonica, **57**: 655–660.

Fraaije, R.H.B., van Bakel, B.W.M., Jagt, J.W.M. & Skupien, P. (2013a): First record of paguroid anomurans (Crustacea) from the Tithonian-lower Berriasian of Štramberk, Moravia (Czech Republic). – Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, **269**: 251–259.

Fraaije, R.H.B., van Bakel, B.W.M., Jagt, J.W.M., Artal, P., Krzemiński, W. & Krzemińska, E. (2013b): New data on paguroid evolution. – In: Krobicki, M. (ed.): 5th Symposium on Mesozoic and Cenozoic decapod crustaceans (5 SMCDC), 25–27 June 2013, Kraków (Poland). – p. 25, Warszawa (Polish Geological Institute, National Research Institute).

Fraaije, R.H.B., Krzemiński, W., van Bakel, B.W.M., Krzemińska, E. & Jagt, J.W.M. (2014): New Late Jurassic symmetrical hermit crabs from the southern Polish Uplands and early paguroid diversification. – Acta Palaeontologica Polonica, **59**: 681–688.

Fraaije, R.H.B., Schweigert, G. & van Bakel, B.W.M. (2017a): New Late Jurassic (Kimmeridgian) paguroids from the Swabian Alb, southern Germany. – Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, **285**: 117–121.

Fraaije, R.H.B., van Bakel, B.W.M. & Jagt, J.W.M. (2017b): A new paguroid from the type Maastrichtian (Upper Cretaceous, the Netherlands) and erection of a new family. – Bulletin de la Société géologique de France, **187**: 155–158.

Gašparič, r., Fraaije, R.H.B., Robin, N. & De Angeli, A. (2016): The first record of paguroids from the Eocene of Istria (Croatia) and further phylogenetic refinement of the Paguroidea (Crustacea, Anomura). – Bulletin of Geosciences, **91**: 467–480.

Glaessner, M. (1931): Geologische Studien in der äusseren Klippenzone. – Jahrbuch der Geologischen Bundesanstalt Wien, **81**: 84–97.

Grill, R. (1968): Erläuterungen zur Geologischen Karte des nordöstlichen Weinviertels und zu Blatt Gänserndorf. – 155 pp., Wien (Geologische Bundesanstalt).

Hofmann, T. (1990): Der Ernstbrunner Kalk im Raum Dörfles (Niederösterreich): Mikrofazies und Kalkalgen. – Unpublished master's thesis, Universität Wien, 164 pp.

Klompmaker, A.A., Artal, P., Fraaije, R.H.B. & Jagt, J.W.M. (2011): Revision of the family Gastrodoridae (Crustacea, Decapoda), with description of the first species from the Cretaceous. – Journal of Paleontology, **85**: 226–233.

Kollmann, H.A. & Zapfe, H. (1979): Wirkl. Hofrat Prof. Dr. Friedrich Bachmayer. – Annalen des Naturhistorischen Museums in Wien, **82**: 1–9.

Krzemińska, E., Krzemiński, W., Fraaije, R.H.B., van Bakel, B.W.M. & Jagt, J.W.M. (2013): How did this hermit crab grow? An allometric study of two species of *Gastrodorus* (Decapoda, Gastrodoridae). – In: Krobicki, M. (ed.): 5th Symposium on Mesozoic and Cenozoic decapod crustaceans (5 SMCDC). 25–27 June 2013, Kraków (Poland). – p. 60, Warszawa (Polish Geological Institute & National Research Institute).

Krzemińska, E., Krzemiński, W., Fraaije, R.H.B., van Bakel, B.W.M. & Jagt, J.W.M. (2015): Allometric ontogenetic changes in two Late Jurassic gastrodorid hermit crabs (Crustacea, Decapoda, Anomura) from central Europe. – Journal of Systematic Palaeontology, **14**: 1–10.

Latreille, P.A. (1802–1803): Histoire naturelle, générale et particulière, des Crustacés et des Insectes, Tome 3. – 467 pp., Paris (Dufart).

Linnaeus, C. (1758): Systema Naturae, per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata **1** (6). – iii + 824 pp., Holmiae (Laurentius Salvius).

Lőrenthey, E. & Beurlen, K. (1929): Die fossilen Dekapoden der Länder der Ungarischen Krone. – Geologica Hungarica, **3**: 1–420.

McLaughlin, P.A. (1981): Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species: Part I. Ten new genera of the Paguridae and a redescription of *Tomopagurus* A. Milne Edwards and Bouvier. – Bulletin of Marine Science, **31**: 1–30.

McLaughlin, P.A. (2003): Illustrated keys to families and genera of the superfamily Paguroidea (Crustacea: Decapoda: Anomura), with diagnoses of genera of Paguridae. – Memoirs of Museum Victoria, **60**/1: 111–144.

McLaughlin, P.A. & Forest, J. (1997): Crustacea Decapoda: *Diacanthurus* gen. nov., a new genus of hermit crabs (Paguridae) with both Recent and fossil representation, and the descriptions of two new species. – In: Crosnier, A. (ed.): Résultats des Campagnes MUSORSTOM, Vol. 18. – Mémoires du Muséum national d'Histoire naturelle, **176**: 236–259.

Meyer, H. von (1864): Briefliche Mittheilungen. Notiz über neue Prosoponiden und über *Gastrodorus*. – Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, **1864**: 206–211.

Milne Edwards, H. (1832): Extrait d'une Lettre sur les caractères des Crustacés Anomures, adressée à M. Audouin. – Annales des Sciences naturelles, Zoologie et Biologie animale, **26**: 255–256.

Moericke, W. (1889): Die Crustaceen der Stramberger Schichten. – Palaeontologische Mittheilungen aus dem Museum des koeniglich Bayerischen Staates, **3**: 43–72.

Moshammer, B. & Schlagintweit, F. (1999): The Ernstbrunn Limestone (Lower Austria): new data on biostratigraphy and applied geology. – Abhandlungen der Geologischen Bundesanstalt Wien, **56**: 553–565.

Ortmann, A.E. (1892): Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen, IV. Theil. Die Abtheilungen Galatheidea und Paguridea. – Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere, **6**: 241–325.

Patrulius, D. (1959): Contributions à la systématique des décapodes néojurassiques. – Revue de Géologie et de Géographie, **3**: 249–257.

Pilgrim, R.L.C. (1973): Axial skeleton and musculature in the thorax of the hermit crab, *Pagurus bernhardus* [Anomura: Paguridae]. – Journal of the Marine Biological Association of the United Kingdom, **53**: 363–396.

Robins, C.M., Feldmann, R.M. & Schweitzer, C.E. (2012): The oldest Munididae (Decapoda: Anomura: Galatheoidea) from Ernstbrunn, Austria (Tithonian). – Annalen des Naturhistorischen Museums in Wien, Serie A, **114**: 289–300.

Robins, C.M., Feldmann, R.M. & Schweitzer, C.E. (2013): Nine new genera and 24 new species of the Munidopsidae (Decapoda: Anomura: Galatheoidea) from the Jurassic Ernstbrunn Limestone of Austria, and notes on fossil munidopsid classification. – Annalen des Naturhistorischen Museums in Wien, Serie A, **115**: 167–251.

Robins, C.M., Feldmann, R.M., Schweitzer, C.E. & Bonde, A. (2016): New families Paragalatheidae and Catillogalatheidae (Decapoda: Anomura: Galatheoidea) from the Mesozoic, restriction of the genus *Paragalathea*, and establishment of 6 new genera and 20 new species. – Annalen des Naturhistorischen Museums in Wien, Serie A, **118**: 65–131.

Schneider, S., Harzhauser, M., Kroh, A., Lukeneder, A. & Zuschin, M. (2013): Ernstbrunn Limestone and Klentnice beds (Kimmeridgian-Berriasian; Waschberg-Ždánice Unit; NE Austria and SE Czech Republic): state of the art and bibliography. – Bulletin of Geosciences, **88**: 105–130.

Schweigert, G., Fraaije, R.H.B., Havlik, P. & Nützel, A. (2013): New Early Jurassic hermit crabs from Germany and France. – Journal of Crustacean Biology, **33**: 802–817.

Schweitzer, C.E. & Feldmann, R.M. (2008): Revision of the genus *Laeviprosopon* Glaessner, 1933 (Decapoda: Brachyura: Homolodromioidea: Prosopidae) including two new species. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **250**: 273–285.

Schweitzer, C.E. & Feldmann, R.M. (2009a): Revision of the Prosopinae *sensu* Glaessner, 1969 (Crustacea: Decapoda: Brachyura) including four new families, four new genera, and five new species. – Annalen des Naturhistorischen Museums in Wien, Serie A, **110**: 55–121.

Schweitzer, C.E. & Feldmann, R.M. (2009b): New species of Longodromitidae Schweitzer & Feldmann, 2009, from the Ernstbrunn Formation, Late Jurassic (Tithonian), Austria. – Annalen des Naturhistorischen Museums in Wien, Serie A, **111**: 207–224.

Schweitzer, C.E. & Feldmann, R.M. (2010a): Earliest known Porcellanidae (Decapoda: Anomura: Galatheoidea) (Jurassic: Tithonian). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **258**: 243–248.

SCHWEITZER, C.E. & FELDMANN, R.M. (2010b): The genus *Coelopus* ÉTALLON, 1861 (Brachyura: Glaessneropsoidea: Longodromitidae) with new species. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **258**: 51–60.

SCHWEITZER, C.E. & FELDMANN, R.M. (2010c): Revision of *Cycloprosopon* and additional notes on *Eodromites* (Brachyura: Homolodromioidea: Goniodromitidae). – Annalen des Naturhistorischen Museums in Wien, Serie A, **112**: 169–194.

SCHWEITZER, C.E. & FELDMANN, R.M (2010d): A new family of Mesozoic Brachyura (Glaessneropsoidea) and reevaluation of *Distefania* CHECCHIA-RISPOLI, 1917 (Homolodromioidea: Goniodromitidae). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **256**: 363–380.

VAN BAKEL, B.W.M., FRAAIJE, R.H.B., JAGT, J.W.M. & ARTAL, P. (2008): An unexpected diversity of Late Jurassic hermit crabs (Crustacea, Decapoda, Anomura) in Central Europe. – Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, **250**: 137–156.

WEHNER, G. (1988): Über die Prosopiden (Crustacea, Decapoda). – Inaugural dissertation, Universität München, 154 pp.

ZEISS, A. (2001): Die Ammonitenfauna der Tithonklippen von Ernstbrunn, Niederösterreich. – Neue Denkschriften des Naturhistorischen Museums in Wien, **6**: 1–116.