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Article

Diverse Late Jurassic anomuran assemblages from the Swabian Alb and evolutionary history of paguroids based on carapace morphology

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With 15 figures and 1 table

Abstract: From late Kimmeridgian (Late Jurassic) shallow-marine limestones on the Westerberg, close to Nusplingen (Swabian Alb, southern Germany), highly diverse assemblages of anomurans are recorded. The superfamily Galatheoidea is represented by abundant and relatively large carapaces of *Gastrosacus wetzleri*, the Paguroidea by comparatively small-sized carapaces, shields and sixth abdominal tergites that are assignable to the families Annuntidiogenidae n. fam., Diogenidae, Gastrodoridae, Parapylochelidae, Pilgrimchelidae n. fam. and Pylochelidae. Such diverse Mesozoic paguroid assemblages have never been recorded previously; they provide evidence of the relative abundance and diversity of paguroids in Late Jurassic shallow-marine settings. Species recorded are: *Ammopylocheles mclaughlinae*, *Ammopylocheles petersi* n. sp., *Annuntidiogenes jurassicus* n. sp., *Gastrodorus* spp., *Housacheles ovalis* n. sp., *Jurapylocheles iwonae*, *Masticacheles minimus* n. sp., *Mesoparapylocheles schweigerti* n. sp., *Mesoparapylocheles jaegeri* n. sp., *Parapylochelitergites deductius* n. sp., *Parapylochelitergites prepustulosus* n. sp., *Pilgrimcheles kersteni* n. sp., *Pilgrimcheles vonmeyeri* n. sp., *Pylochelitergites westerbergensis*, *Scututergites anteroindentatus* n. gen., n. sp., *Stagmacaris subcircularis* n. sp. and *Ululapagurus vanbakeli* n. gen., n. sp. The phylogenetic state-of-the-art, as based on carapace morphologies of Mesozoic carapace-based paguroid species known to date is outlined. The average size of Late Jurassic paguroid carapaces is considerably lesser than that of co-occurring brachyurans and galatheoids. Their small size and incomplete preservation of carapaces, with mostly only (part of) the shield retained, explains why fossil paguroids are very often overlooked in the field.

Key words: Anomura, Galatheoidea, Paguroidea, new taxa, Late Jurassic, phylogeny.

1. Introduction

The first Jurassic paguroid chelae were described by Étallon (1858), who interpreted these as chelae of lobsters, with three species assigned to *Gammarolithes*, namely *G. corallinus*, *G. virgulinus* and *G. portlandicus*. Three years later, Étallon (1861), without further explanation, transferred these three, and some other species, to *Orhomalus* and, for the first time, referred them to the Paguroidea. Slightly earlier, the first sixth abdominal paguroid tergite had been illustrated and referred to as a 'problematicum' by Quenstedt (1857). This was later named *Stagma ovale* by Quenstedt (1883) and placed in a new genus, *Stagmacaris*, by Schweigert (2006). Fraaije et al. (2012d) interpreted this taxon and other fossil examples as sixth operculate abdominal tergites of paguroid origin. The first fossil paguroid carapace was illustrated by H. von Meyer (1860, pl. 23, fig. 37), who mistook this for an abdominal part of a prosoponid crab. Wehner (1988, pl. 8, figs. 7-8) was the first to recognise the correct affiliation of this particular specimen and a few others, and assigned them to *Palaeopagurus* sp. Finally, Van Bakel et al. (2008) outlined the taxonomy of Late

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Jurassic paguroid carapaces and shields and erected a number of new genera and species.

Few major decapod crustacean groups have had such an unstable taxonomic history as the Anomura; the classification of the Paguroidea is by far the most complex of all (McLaughlin et al. 2010). Ahyong & O'Meally (2004) found strong support for the monophyly of the Anomura and, particularly unexpected at that time, was their grouping of the symmetrical hermit crab family Pylochelidae with the Galatheoidea. Tsang et al. (2008) also noted the Pylochelidae to be aligned with the Galatheoidea. The fossil history of the Anomura has only just begun to unfold (Robins 2008; Lemaitre & McLauglin 2009; Robins et al. 2013). Unfortunately, localities that yield diverse extinct anomurans are limited, and preservation is not always ideal (Robins 2008). Ahyong et al. (2010) revised the higher-level classification of the Galatheoidea to comprise four families: Galatheidae, Munididae, Munidopsidae and Porcellanidae. They concluded that the extinct galatheoid families were distinct both morphologically and ecologically.

The taxonomic placement of the genus *Gastrodorus* von Meyer, 1864 has been discussed on numerous occasions, ranging from the Galatheoidea, Homolidae, Paguroidea and Prosopidae. For a detailed historical account reference is made to Van Bakel et al. (2008) and Klompmaker et al. (2011). *Gastrodorus* has been recorded from strata of Oxfordian, Kimmeridgian, Tithonian and Albian-Cenomanian age, throughout Germany, Austria, the Czech Republic, Poland and Spain (Förster 1985; Wehner 1988; Van Bakel et al. 2008; Klompmaker et al. 2011). On the basis of morphological data of numerous recent studies of Mesozoic paguroids (Fraaije et al. 2012a-e), Fraaije et al. (2013a) have recently transferred *Gastrodorus* to the Paguroidea as a basal group. New material of paguroid chelae and even of a near-complete specimen from southern Germany described by Schweigert et al. (2013) extend the fossil record of paguroids now back to at least the late Hettangian (*c*. 205 Ma).

Loss of calcified pleonal segments, reduction or adaptation of posterior pereiopods, decalcification of the posterior carapace and asymmetry (McLaughlin 2003) subsequently evolved, from at least the Early Jurassic onwards, within the Paguroidea. From an evolutionary point of view, it would seem logical that early paguroids were more heavily calcified than extant congeners since loss of calcification came with their engaged mode of life. Following the paper by Van Bakel et al. (2008) many more hermit crab carapaces and shields have been recorded from Mesozoic strata in the Czech Republic, Poland, Spain and the Netherlands (Fraaije et al. 2008, 2012a-c, e, 2013b). Generally, the family Pylochelidae Bate, 1888 has been considered to represent the most basal paguroid group by neontologists, a notion that has support from cladistic analyses (e.g. Mclaughlin et al. 2007). However, now that more extinct taxa have become available this view has changed considerably, as demonstrated below (e.g. figs. 14-15). When collecting within Mesozoic reefal deposits is done on a millimetre (rather than centimetre) scale, our insights into the history of anomurans, and of paguroids in particular, are bound to improve substantially.

Institutional abbreviation: MAB – Oertijdmuseum De Groene Poort, Boxtel, the Netherlands.

2. Geological setting

During a field trip to the Late Jurassic of the Swabian Alb organised by the Oertijdmuseum Boxtel in 2009, an outcrop that yielded late Kimmeridgian decapod crustaceans was discovered. Close to the famous fossil Lagerstätte of the Nusplingen lithographic limestones (e.g., Dietl & Schweigert 2004), a small quarry near the summit of the Westerberg, *c*. 1,500 m northwest of the village of Nusplingen, supplied abundant and diverse anomuran and brachyuran faunas. The material studied here was collected during collecting trips in successive years (2010-2013) from well-bedded, bioclastic 'normal' facies just next to a small sponge-microbial bioherm (Fig. 1). These well-bedded limestones intercalate with marly intervals and are particularly rich in microbial crusts and sponge remains, as well as ammonites of diameters of up to 300 mm, brachiopods and echinoids. Dr. Günter Schweigert (Staatliches Museum für Naturkunde, Stuttgart) identified some of the ammonites as *Aulacostephanus pseudomutabilis* (De Loriol, 1874), a taxon which is indicative of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age. In a preliminary study, Fraaije et al. (2012d) described a new type of paguroid sixth abdominal operculate tergite from this locality.

3. Systematic palaeontology

Below, the carapace morphological terms introduced by Fraaije et al. (2012a-c, 2014) and the tergite morphological terms introduced by Fraaije et al. (2013b) are used.

Fig. 1. Collecting at the Westerberg quarry from well-bedded, bioclastic 'normal' facies (left), just next to a small sponge-algal bioherm (to the right).

Order Decapoda Latreille, 1802
Infraorder Anomura H. Milne Edwards, 1832
Superfamily Galatheoidea Samouelle, 1819
Family Munidopsidae Ortmann, 1892
Genus *Gastrosacus* von Meyer, 1851

Gastrosacus wetzleri von Meyer, 1851
Fig. 3A-C

Material: (MAB k.3230, k.3231, k.3232), all near complete carapaces, max. length including rostrum 6.5 mm. The right lower side of the specimen on Fig. 3A shows a nice example of *Kanthyloma crusta* Klompmaker, Artal, Van Bakel, Fraaije & Jagt, 2014.

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Remarks: An emended diagnosis and description will be supplied in a forthcoming study on the redescription of this species. *Gastrosacus* ranges from the Upper Jurassic (Oxfordian) to the Upper Cretaceous (Maastrichtian), with records across Europe (Robins 2008; Robins et al. 2013). The use of (parts of) internal organs, such as ossicles of the foregut (Reimann et al. 2011), or fragile appendages such as maxillipeds (Ahyong et al. 2010) for reconstructing phylogenetic relationships within anomuran (or any other decapod crustacean group, for that matter) is fraught with difficulties when extinct material is compared. The morphology of specimens of *Gastrosacus wetzleri* in the present study denote that the differentiation between the genera *Cracensigillatu*s (Robins et al., 2013) and *Gastrosacus* is better interpreted as intraspecific variation. The numerous specimens of *Gastrodorus* from the Nusplingen faunas also show an almost identical considerable morphological variation, as demonstrated below.

Mesozoic representatives of the family Munidopsidae are found in shallow-water, typically reefal, environments (Robins et al. 2013). Most extant munidopsids occur on the outer shelf or slope, down to abyssal depths (Ahyong et al. 2011).

Superfamily Paguroidea Latreille, 1802
Family Annuntidiogenidae fam. nov.

Type genus: *Annuntidiogenes* Fraaije, Van Bakel, Jagt & Artal, 2008.

Other genera included: *Aniculus* Dana, 1852*, Bathynarius* Forest, 1988*, Calcinus* Dana, 1851*, Ciliopagurus* Forest, 1995, *Dardanus* Paul'son, 1875, *Paguristes* Dana, 1852, and *Pseudopaguristes* McLaughlin, 2002.

Diagnosis: Shield longer than wide, divided into distinct regions by grooves, central gastric furrow; convex postrostral ridge usually present; elongated massetic region; medial part of posterior intragastric grooves parallel to posteriormost groove.

Remarks: In the literature the descriptive terms of paguroid carapace morphology are very scanty. In most modern biological textbooks (e.g. McLaughlin 1980), and scientific studies (e.g. Forest et al. 2000) there are no diagnostic features mentioned between rostrum and cervical furrow or linea transversalis. In many fossil and extant paguroids however diverse important diagnostic features are present on the carapace. A basal group within the Diogenidae show highly characteristic intragastric grooves parallel to, what was formerly interpreted as, the cervical groove. *Annuntidiogenes* seems to be the predecessor of this group further consisting of *Aniculus, Bathynarius, Calcinus, Ciliopagurus, Dardanus,* and *Paguristes* (Fig. 4). This groove is sparsely reported as the Y-linea in the case the intragastric grooves are connected medially (Morgan & Forest 1991). With more and more fossil specimens at hand it is tempting to regard these intragastric grooves and/or the Y-linea as remnants of the cervical groove and what has until now been considered the cervical groove in fact is the branchiocardiac groove.

Genus *Annuntidiogenes* Fraaije, Van Bakel, Jagt & Artal, 2008

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

Annuntidiogenes jurassicus n. sp.
Fig. 2G

Etymology: Named after its Jurassic age.

Material: Holotype MAB k.3349, a shield with a maximum length and width of 3 mm and 2 mm, respectively.

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

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

Description: Shield ovate, divided into distinct regions by grooves. Triangular spinose rostrum, broad concave orbital margin ending in blunt triangular post-ocular projections; long central gastric furrow anteriorly proceeding in convex, subcircular postorbital ridges posteriorly fading into posteriormost groove. Elongated massetic region, largest width anteriorly, posteriorly bounded by thin lateral branchial area. Long posterior intragastric grooves, unconnected medially. Posteriormost groove broadly V-shaped.

Remarks: *Annuntidiogenes jurassicus* n. sp. is the fourth and oldest member of the genus. *A. ruizdegaonai* Fraaije, Van Bakel, Jagt & Artal, 2008, *A. worfi* Fraaije, Van Bakel, Jagt, Klompmaker & Artal, 2008 and *A. sunuciorum* Fraaije, Van Bakel, Jagt & Artal, 2008 are all reported from the Cretaceous and differ in having a shorter massetic region and a smaller posterior part of the shield. The characteristic intragastric grooves and/or the Y-linea show two different pathways as shown in Fig. 4. One lineage runs from *Annuntidiogenes* to *Bathynarius* and the other from *Annuntidiogenes* to *Pseudopaguristes* and *Aeropaguristes*.

Family Diogenidae Ortmann, 1892
Genus *Ululapagurus* nov.

Type species: *Ululapagurus vanbakeli* n. sp.

Etymology: Combination of the Latin word for owl 'ulula' in reference to the owl-shaped gastric, and *Pagurus*.

Diagnosis: Shield well areolated; relatively short massetic; small indefinite anterior branchial area; wavy subrostral ridge; mesogastric process present; sharp triangular, ridged rostrum; gastric ornament anteriorly crenulated, posteriorly covered with pores, cervical groove reaching anterolateral side.

Ululapagurus vanbakeli n. gen. n. sp.
Fig. 2A-F

Etymology: Named after Barry Van Bakel, colleague and friend, who not only specialises in collecting and studying fossil decapod crustaceans, but also knows how to prepare and photograph them.

Types: Holotype MAB k.3240, a shield with maximum length and width of 3.0 mm and 3.0 mm, respectively; paratypes MAB k.3347, MAB k.3352, MAB k.3354, and MAB k.3380 with maximum lengths and widths of 2.0, 3.0, 2.5, 2.0 mm and 2.0, 3.0, 2.5, 2.0 mm, respectively.

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Diagnosis: As for genus (monotypic).

Description: Shield approximately as long as wide, convex in transverse section, slightly convex in longitudinal section; sharp triangular, ridged and finely tuberculate rostrum; pronounced wavy frontal ridge, medially divided by central gastric groove posteriorly extending into distinct gastric process which fades into faint mid gastric rim, most pronounced at anterior half of shield. Convex central frontal ridge extending concave laterally ending in forwardly directing spine; owl-shaped gastric region bordered by deep cervical groove posteriorly and less deep lateral gastric groove anteriorly; short, angular massetic region with dis-

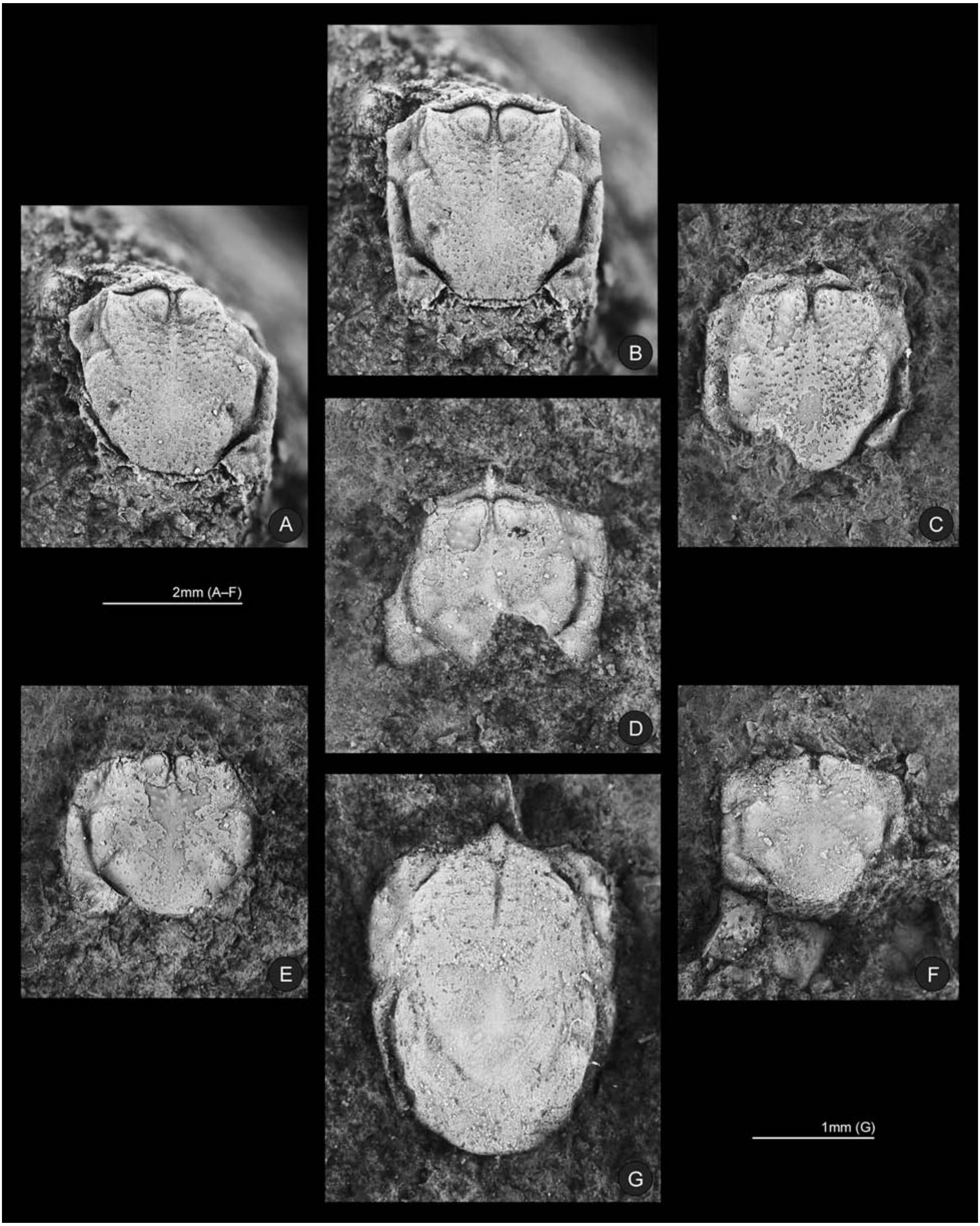

Fig. 2. **A** – *Ululapagurus vanbakeli* n. sp., holotype (MAB k.3240), **B** – mirror image composite of holotype (MAB k.3240), **C-F** – *Ululapagurus vanbakeli* n. sp., paratypes (MAB k. 3352, 3347, 3380 and 3354 respectively), **G** – *Annuntidiogenes jurassicus* n. sp., holotype (MAB k.3349).

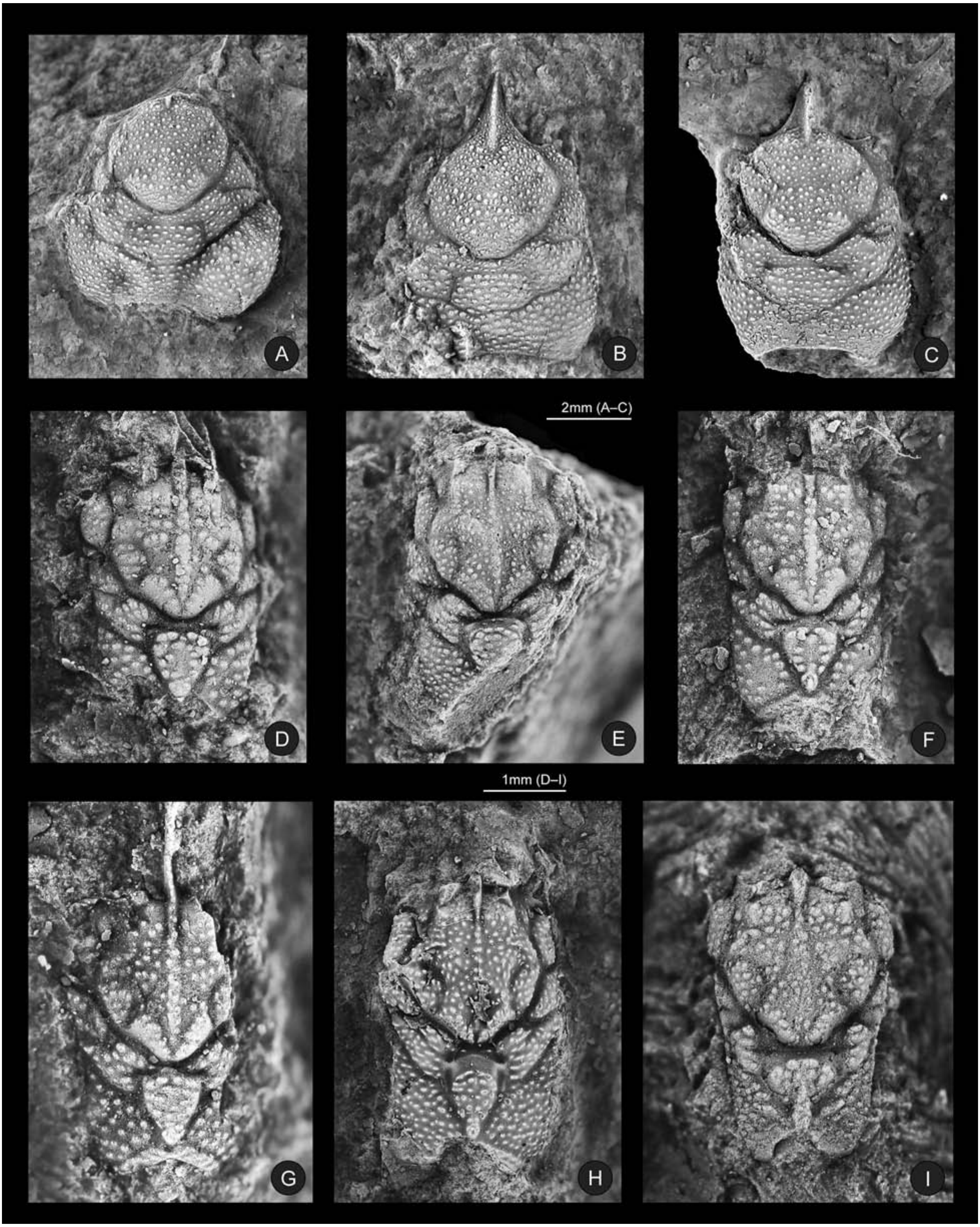

Fig. 3. A-C – *Gastrosacus wetzleri* von Meyer, 1851 (MAB k.3230, k.3232 and k.3231), **D-I** – *Gastrodorus* spp. showing considerable variation in carapace ornament and shape and morphology of the cardiac region. MAB k.3227, 3228, 3223, 3221, 3224 and 3222 respectively.

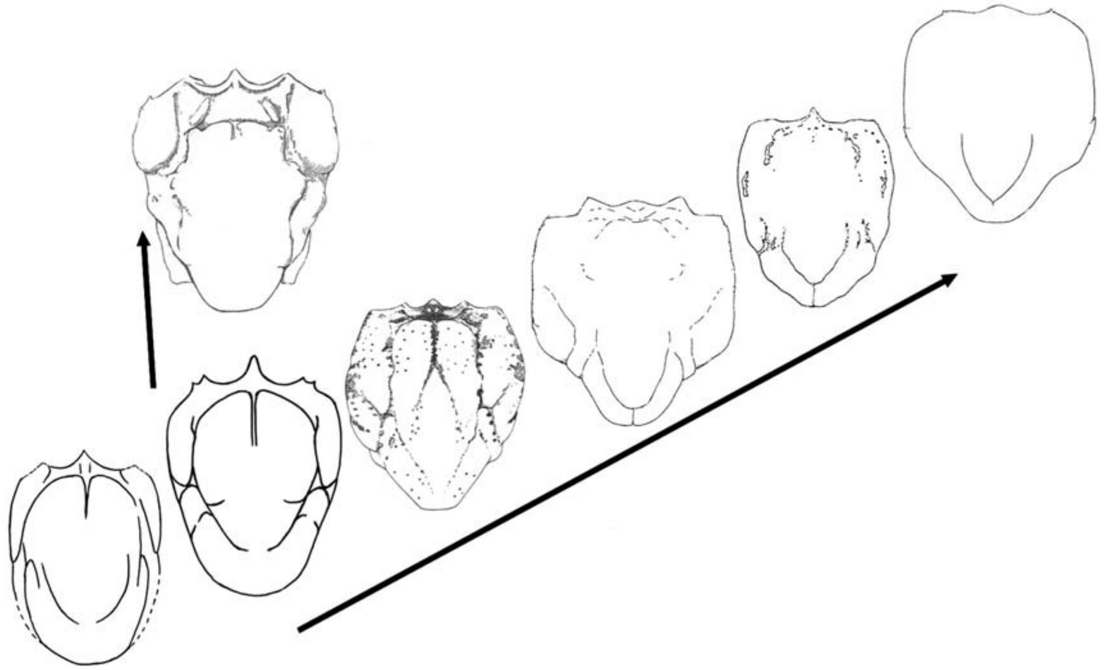

Fig. 4. From left to right shield morphology of *Annuntidiogenes* (2x), *Aniculus, Dardanus, Calcinus, Bathynarius* and top left *Pseudopaguristes*.

tinct depression centrally; small indefinite anterior branchial area. Cervical groove reaching the lateral side anteriorly at about one-third of shield length. Gastric region ornamented anteriorly by subrounded rows of crenulations, posteriorly finely covered with pores. Except for small parts of the mesobranchial areas no other parts of posterior carapace are preserved.

Remarks: A cervical groove reaching the lateral side, a lobed lateral gastric groove and a shield with setal pores are features diagnostic of other earlier diogenids, *Bachmayerus* and *Eopaguropsis* (see Fraaije et al. 2012c, 2013a). The characteristic owl-shaped gastric region distinguishes the new genus from other extinct diogenid genera.

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

Genus *Gastrodorus* von Meyer, 1864

Gastrodorus spp.

Fig. 3D-I

Material: About 50 more or less complete carapaces (max. length 5.2 mm, max. width 3.5 mm).

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Discussion: There are several similarities in carapace morphology between *Gastrosacus* and *Gastrodorus* (e.g., Förster 1985; Klompmaker et al. 2011). The most striking are the presence of an elongated, spinose rostrum with a median ridge which extends onto the anterior carapace, an ovate to subcircular cervical groove which does not reach the lateral sides (i.e., the circumgastric groove of Robins 2008), a clear branchiocardiac groove paralleling the cervical groove which reaches the lateral sides, a well-defined triangular cardiac region and the uniform, forwardly directed, spinose ornament of the entire carapace. All these characters are indicative of a close phylogenetic relationship (Fig. 5).

Following the paper by Klompmaker et al. (2011), numerous carapaces of early symmetrical paguroids have been recorded (Fraaije et al. 2012a, b, e, 2013a). The morphology of these pylochelids and parapylochelids have had a marked impact of the data used by Klompmaker et al. (2011: 229, table 1) in order to distinguish gastrodorids from paguroids and galatheoids (Fraaije et al. 2013a). With current data at hand, *Gastrodorus* can be distinguished from *Mesoparapylocheles* only by its more or less uniform spinose-tuber-

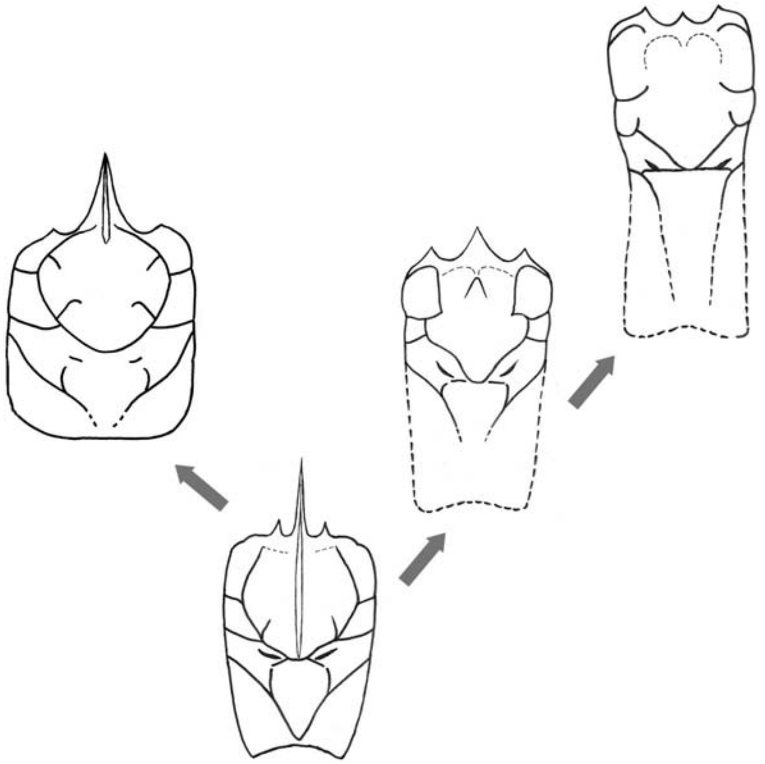

Fig. 5. Possible phylogenetic relationships between the extinct genera *Gastrodorus, Gastrosacus*, and *Mesoparapylocheles* and the extant *Parapylocheles*.

culate ornament, a longer, spiny rostrum and the location of the lateral projection. The occurrence of distinctly delineated massetic and anterior branchial areas, a pronounced keraial region, the presence of cervical and branchiocardiac grooves and (remnants of) a postcervical groove in *Gastrodorus* reveals the Gastrodoridae as a basal member of the Paguroidea (Figs. 5, 6), most closely related to the Parapylochelidae. The loss of the uniform, forwardly directed, spinose ornament, from the Gastrodoridae to the smooth Parapylochelidae, most probably is a reflection of the transition from a free-living, benthic life style to the well-known hermit crab occupation of a (moveable) shelter (e.g., Jagt et al. 2006) or cover by e.g. cnidarians.

The carapace morphology of *Gastrodorus* reveals wide intraspecific variation making taxonomic subdivisions difficult. Until recently, merely two species were named formally; the Late Jurassic *Gastrodorus neuhausensis* von Meyer, 1864 and the late Albian *Gastrodorus cretahispanicus* Klompmaker, Artal, Fraaije & Jagt 2011. Recently, a new species has been added, *Gastrodorus kotoucensis* Fraaije, Van Bakel, Jagt & Skupien, 2013, from the Tithonian of Štramberk, Czech Republic, while Krzemińska et al. (2013) noted a fourth, still unnamed, species from the Oxfordian of southern Poland. The main points of variation in the carapace morphology of *Gastrodorus* concern the shape and ornament of the cardiac region, the shape and size of the keraial, massetic, mesobranchial and urogastric regions, the size of overall tuberculation and the length of the median gastric ridge and postrostral ridges. Differences are very gradual within ‘populations’ and also ontogenetic changes have been observed (Krzemińska et al. 2013). Bachmayer (1958) already ascribed morphological differences in *Gastrodorus* as an expression of sexual dimorphism, on the basis of material from the Tithonian Ernstbrunn fauna of Austria. The variation noted in specimens of *Gastrodorus* in the present Westerberg assemblage concerns an admixture of morphological traits seen in *G. neuhausensis* (MAB k.3221) and *kotoucensis* (MAB k.3222), and maybe also new, undescribed forms. More material and statistical studies (cf. Krzemińska et al. 2013) are needed in order to make sense of these gastrodorid assemblages from the Westerberg.

Family Pilgrimchelidae nov.

Type genus: *Pilgrimcheles* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2014.

Other genera included: *Diogenicheles* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2014, *Eotylaspis* Van Bakel, Fraaije, Jagt & Artal, 2008, *Masticacheles* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2014.

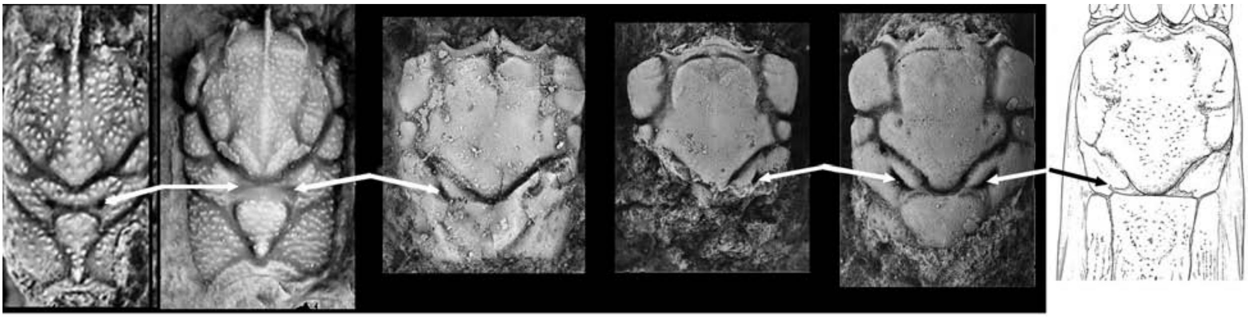

Fig. 6. Location of the postcervical groove, a feature present in the most primitive paguroids, in (from left to right): *Gastrodorus cretahispanicus* Klompmaker, Artal, Fraaije & Jagt, 2011, *G. neuhausensis* Von Meyer, 1864, *Mesoparapylocheles jaegeri* n. sp., *M. schweigerti* n. sp., *M. michaeljacksoni* Fraaije, Klompmaker & Artal, 2012. For comparative purposes the extant *Parapylocheles scorpio* Alcock, 1894 is added (extreme right).

Diagnosis: Shield well calcified, length slightly exceeding or equaling width, well areolated, with distinct regions, including large massetic and keraial regions and a small anterior branchial area. Rostrum and post-ocular spines distinct, triangular. Anterior portion of gastric region delimited by slightly convex post-rostral ridge, with central gastric groove. Typically reniform keraial region anteriorly at widest part of cervical groove, laterally bordered by a anterior branchial area. Absence of delineated cardiac region and distinct branchiocardiac and postcervical grooves presumed, but none of these preserved because of decalcification of posterior part of carapace.

Remarks: The morphology of the shield amongst representatives of the Pilgrimchelidae fam. nov. (Figs. 7-8), show closest similarities to members of the Parapylochelidae (Figs. 9-10). For that reason, these two families are here assumed to have the closest phylogenetic ties. So far, members of the new family appear to be confined to strata of Oxfordian and Kimmeridgian (Late Jurassic) age.

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

Masticacheles minimus n. sp.

Fig. 7E

Etymology: Named after its extremely small size.

Material: Holotype MAB k.3351C, an almost complete shield with a maximum length and width of 2.0 mm and 1.5 mm, respectively.

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Diagnosis: Shield well calcified, length exceeding width, well areolated, with many distinct regions, including a bipartite massetic region. Rimmed, broad-based, triangular rostrum and similar, yet smaller, post-ocular projections. Post-antennal projections less distinct. Anterior portion of gastric region delimited by post-rostral ridge. Typically reniform keraial regions laterally bodered by small angular anterior branchial area. Posterior part of carapace not preserved.

Description: Well-calcified and clearly areolated shield, length exceeding width, convex transversely, slightly convex longitudinally. Rimmed, broad-based, triangular rostrum and post-ocular projections. Post-antennal projections less distinct, not rimmed. Ocular-frontal area equalling about 60 per cent of total maximum width. Gastric region bounded posteriorly by deep cervical groove; anterior part delimited by centrally indented post-rostral ridge. Prominent, globose and elongated massetic region divided into two more or less equal portions. Relatively small, angular anterior branchial area. Posterior part of cervical groove pronounced and very deep, anteriorly curving around reniform keraial region and laterally incising lateral margin below anterior branchial area. No posterior parts of carapace preserved.

Remarks: *Masticacheles minimus* n. sp. is only the second member of the genus, differing from the type species, *M. longirostris* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2014, in having a more rounded, less delineated keraial region and a more pronounced postorbital rim.

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

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

Table 1. List of all currently known Mesozoic carapace-based paguroid taxa.

Diogenidae
Annuntidiogenes jurassicus n. sp.
Annuntidiogenes ruizdegaonai Fraaije, Van Bakel, Jagt & Artal, 2008
Annuntidiogenes sunuciorum Fraaije, Van Bakel, Jagt & Artal, 2008
Annuntidiogenes worfi Fraaije, Van Bakel, Jagt, Klompmaker & Artal, 2009
Bachmayerus cavus Fraaije, Van Bakel, Jagt, & Skupien, 2013
Eopaguropsis loercheri Van Bakel, Fraaije, Jagt & Artal, 2008.
Eopaguropsis nidiaquilae Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2012b
Striadiogenes frigerioi Garassino, De Angeli & Pasini, 2009
Ululapagurus vanbakeli n. gen. n. sp.
Gastrodoridae
Eogastrodorus granulatus (Förster, 1985)
Gastrodorus n. sp. (*sensu* Krzemińska, Krzemiński, Fraaije, Van Bakel, B.W.M. & Jagt, 2013)
Gastrodorus neuhausensis von Meyer, 1864
Gastrodorus cretahispanicus Klompmaker, Artal, Fraaije & Jagt, 2011
Gastrodorus kotoucensis Fraaije, Van Bakel, Jagt & Skupien, 2013
Parapyochelidae
Housacheles timidus Fraaije, Van Bakel, Jagt & Skupien, 2013
Housacheles ovalis n. sp.
Mesoparapylocheles michaeljacksoni Fraaije, Klompmaker & Artal, 2012
Mesoparapylocheles jaegeri n. sp.
Mesoparapylocheles schweigerti n. sp.
Pilgrimchelidae fam. nov.
Diogenicheles *theodorae* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2014
Eotylaspis wehnerae Van Bakel, Fraaije, Jagt & Artal, 2008
Masticacheles longirostris Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2014
Masticacheles minimus n. sp.
Pilgrimcheles karolinae Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2014
Pilgrimcheles kersteni n. sp.
Pilgrimcheles vonmeyeri n. sp.
Pylochelidae
Ammopylocheles mclaughlinae Van Bakel, Fraaije, Jagt & Artal, 2008
Ammopylocheles petersi n. sp.
Ammopylocheles robertboreki Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2012b
Cretatrizocheles olazagutiensis Fraaije, Klompmaker & Artal, 2012
Jurapylocheles malutka Van Bakel, Fraaije, Jagt & Artal, 2008.
Jurapylocheles iwonae Fraaije, Krzeminski, Van Bakel, Krzeminska & Jagt, 2012b
Schobertellidae
Schobertella simonsenetlangi Schweigert, Fraaije, Havlik & Nützel, 2013
Orhomalus deformis (Oppel, 1862)

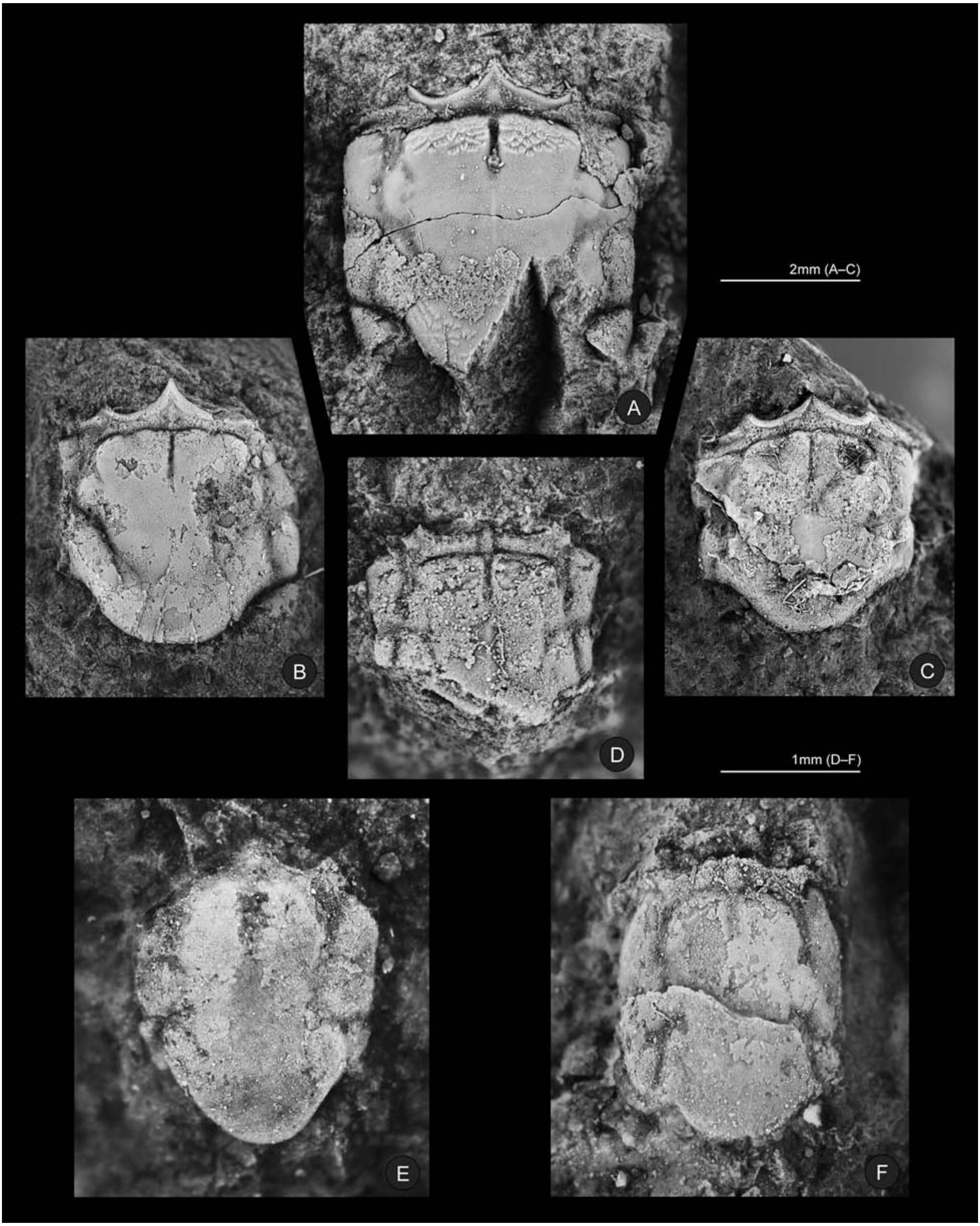

Fig. 7. A-C – *Pilgrimcheles vonmeyeri* n. sp., paratype MABk.3335, holotype MAB k.3255 and paratype MAB k.3334, **D** – *Pilgrimcheles kersteni* n. sp., holotype MAB k.3253, **E** – *Masticacheles minimus* n. sp., holotype MAB k.3351C, **F** – *Housacheles ovalis* n. sp., holotype MAB k.3248.

Pilgrimcheles vonmeyeri n. sp.
Fig. 7A-C

Etymology: Named in honour of Christian Erich Hermann von Meyer (1801-1869), a well-known German palaeontologist.

Material: Holotype MAB k.3235, a near-complete shield with a maximum length and width of 4.0 mm and 4.0 mm, respectively; paratypes MAB k.3334 and MAB k.3335 with a maximum length and width of 4.5, 5.0 mm and 4.5, 5.0 mm, respectively.

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Diagnosis: Shield well calcified, length slightly exceeding width, well areolated, with many distinct regions, including a massetic region. Rimmed, broad-based, triangular rostrum and smaller triangular, post-ocular projections. Post-antennal projections less distinct and not rimmed. Anterior portion of gastric region delimited by post-rostral ridge with central gastric groove. Large globose massetic region bordered posterocentrally by smaller, yet distinct globose submassetic region. Typically reniform keraial regions. No posterior parts of the carapace preserved.

Description: Well-calcified and clearly areolated shield, length slightly exceeding width, convex transversely, slightly convex longitudinally. Rimmed, broad-based, triangular rostrum and post-ocular projections. Post-antennal projections less distinct and not rimmed. Ocular-frontal area equaling about 55 per cent of total maximum width. Posteriorly pointed, bluntly arrowhead-shaped gastric region, bounded posteriorly by deep cervical groove; anterior part delimited by slightly undulose, post-rostral ridge and when cuticule is absent, covered by transverse crenulations. Post-rostral ridge centrally indented by relatively long gastric groove fading posteriorly into faint central rim. Prominent, globose and elongated massetic region about 160 % length of elongated anterior branchial area. Posterior part of cervical groove pronounced and very deep, anteriorly curving around reniform keraial region and laterally incising lateral margin below anterior branchial area. Anterior of keraial region a distinct oval submassetic region, bordering massetic region. Except for some very small parts posterior of anterior branchial area, no other posterior parts of carapace preserved.

Pilgrimcheles kersteni n. sp.
Fig. 7D

Etymology: Named in honour of Geon Kersten, a Dutch amateur palaeontologist and friend, who helped during several field trips and donated some of the material studied herein.

Material: Holotype (MAB k.3253), a near-complete shield (total length 1.5 mm, max. width 1.5 mm).

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Diagnosis: Shield well calcified, of near-equal length and width, well areolated, with distinct regions, including angular massetic region. Small triangular rostrum and about similarly sized post-ocular spines. Post-antennal projections less distinct. Anterior portion of gastric region delimited by post-rostral ridge with central gastric groove. Long central gastric groove fading into median gastric rim posteriorly. Typically reniform keraial regions.

Description: Well-calcified and clearly areolated shield, of about equal length and width, convex transversely, slightly convex longitudinally. Small short triangular rostrum and about equally sized post-ocular spines. Post-antennal projections less distinct. Ocular-frontal area equalling about 57 per cent of total maximum width. Gastric region, bounded posteriorly by cervical groove; anterior part delimited by post-rostral ridge. Post-rostral ridge centrally indented by relatively long gastric groove fading posteriorly into central rim, anteriorly a broad frontal ridge extending to rostrum. Prominent, angular and elongated massetic region about 140 per cent of length of narrow anterior branchial area. Cervical groove anteriorly curving around reniform keraial region and laterally incising lateral margin below anterior branchial area. Anterior of keraial region and bordering anterior massetic region distinct oval submassetic region. No posterior parts of carapace preserved.

Remarks: *Pilgrimcheles vonmeyeri* n. sp. and *P. kersteni* n. sp. can be distinguished from the type species of the genus, *P. karolinae*, in having a longer central gastric groove, smaller massetic region, longer anterior branchial area and a central gastric rim. *Pilgrimcheles vonmeyeri* n. sp. is easily differentiated from the coeval *P. kersteni* n. sp. in having a less angular massetic region, a more convex postrostral ridge, a more distinctly rimmed frontal margin and a distinct oval submassetic region.

Family Parapylochelidae Fraaije, Klompmaker & Artal, 2012
Genus *Housacheles* Fraaije, Van Bakel, Jagt & Skupien, 2013

Type species: *Housacheles timidus* Fraaije, Van Bakel, Jagt & Skupien, 2013, by original designation.

Housacheles ovalis n. sp.
Fig. 7F

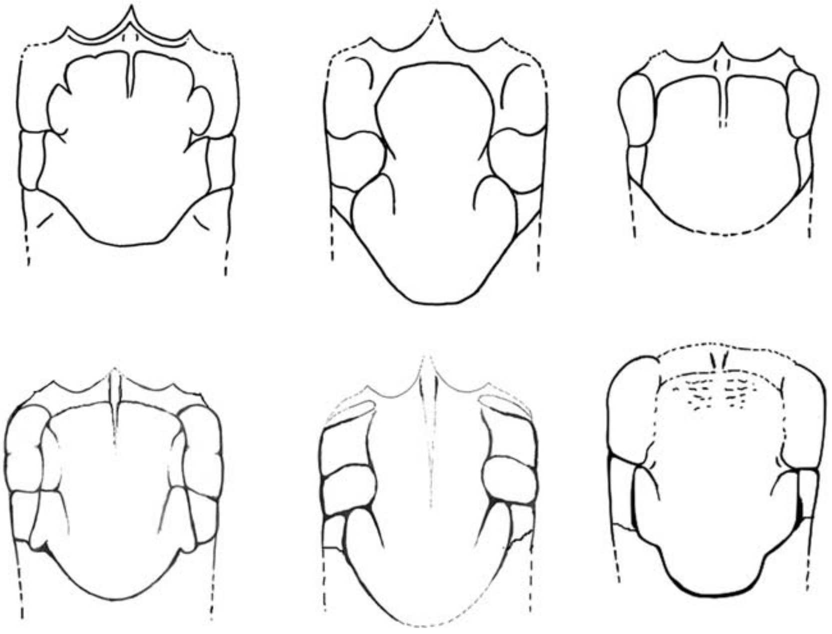

Fig. 8. All known members of the Pilgrimchelidae. Top from left to right *Pilgrimcheles vonmeyeri* n. sp., *Masticacheles minimus* n. sp., *P. kersteni* n. sp., bottom from left to right *P. karolinae*, *M. longirostris* and *Diogenicheles theodorae*.

Etymology: Named after its oval shape.

Material: Holotype MAB k.3248, a near-complete shield with a maximum length and width of 2.0 mm and 1.5 mm, respectively.

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Diagnosis: Shield well calcified, length exceeding width, well areolated, with distinct regions. Broad post-frontal area with broad post-rostral rim. Strongly elongated massetic and small-sized, subtriangular anterior branchial region. Convex, post-rostral ridges protruding anteriorly as massetic groove. Anterior portion of gastric region delimited by post-rostral ridge with long central gastric groove. Long, typically reniform keraial regions anteriorly at widest part of U-shaped cervical groove.

Description: Shield well calcified, length exceeding width, well areolated with distinct regions, including a broad post-frontal area with broad post-rostral rim. Broad-based, triangular rostrum and post-ocular projections forming distinct concave orbital margin. Convex, post-rostral ridges protruding anteriorly as the massetic groove, delineating a very elongated massetic region. Anterior portion of gastric region delimited by post-rostral ridge with long central gastric groove. Long, typically reniform keraial regions anteriorly at widest part of u-shaped cervical groove, laterally bordered by small-sized, subtriangular anterior branchial region. Cervical groove pronounced and very deep, especially around keraial region. No posterior parts of carapace preserved.

Remarks: *Housacheles ovalis* n. sp. is the second species of the genus; it can be distinguished from the type species, *H. timidus*, by a more pronounced post-rostral rim, broader post-frontal area, longer post-rostral ridges and a central gastric groove. The genera *Housacheles*, *Mesoparapylocheles* (see below) and *Parapylocheles* Alcock, 1894 are members of the Parapylochelidae. They have the convex post-rostral ridges, separated by a short central gastric ridge; elongated massetic region with a much smaller anterior branchial area; a broad post-frontal ridge; the presence of reniform keraial regions, a triangular rostrum and post-ocular projections in common. In case where a posterior carapace is preserved, post-cervical and branchial grooves and a delineated cardiac region can be seen.

Genus *Mesoparapylocheles* Fraaije, Klompmaker & Artal, 2012

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

Mesoparapylocheles schweigerti n. sp.
Fig. 9A-D, F, G

Etymology: Named after Dr. Günter Schweigert (Staatliches Museum für Naturkunde, Stuttgart), in recognition of his numerous contributions to Late Jurassic decapod crustaceans.

Material: Holotype MAB k.3257, a near complete shield (total length 2.5, max. width 2.5 mm). Paratypes MAB k. 3342, k.3343, k.3377, k.3378, k.3379, shields with parts of posterior carapace, total lengths 3.0, 2.0, 2.5, 3.0, 2.5, max. width 3.0, 2.0, 2.5, 3.0, 2.5 mm, respectively.

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Diagnosis: Shield well calcified, well areolated, with distinct regions, including a large, smooth and globose massetic region and a considerably smaller, globose anterior branchial area. Prominent broad-based, triangular rostrum. Distinct triangular post-ocular spines. Distinct subrounded postrostral ridges centrally indented by faint central gastric groove. Gastric region shaped like an arrow-head pointing posteriorly. Renifrom keraial region. Deep and short postcervical groove running parallel to cervical groove. Distinct cardiac region.

Description: Well-calcified, smooth, well-areolated shield, convex transversely, slightly convex longitudinally. Broad-based rostrum. Ocular cavity ellipsoidal, bounded by triangular, slightly upturned, post-ocular spine. Ocular-frontal area exceeding half of total maximum width, covered with row of pustules. Pronounced subcylindical post-rostral ridge fading towards keraial region, medially interrupted by shallow, broad central gastric groove, posteriorly ending in faint mesogastric process. Posteriorly pointed, arrowhead-shaped gastric region with a very faint median line, bounded posteriorly by deep V-shaped cervical groove. Very prominent and globose anterior massetic region forming widest part of shield. 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 exhibits a deep and short postcervical groove parallel and medially between cervical and branchio-cardiac groove. Subrounded pentagonal cardiac region posteriorly bounded by branchiocardiac groove.

Mesoparapylocheles jaegeri n. sp.
Fig. 9E

Etymology: Named after Dr. Manfred Jäger (retired; formerly curator at the Fossilienmuseum Werkforum Dotternhausen) for his assistance in field work during many years.

Material: Holotype (MAB k.3341), a near-complete carapace (total length 4.0, max. width 3.0 mm).

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Diagnosis: Shield well calcified, well areolated, with distinct regions, including a large, smooth and globose massetic region and a considerably smaller, globose anterior branchial area. Prominent broad-based, triangular rostrum. Distinct triangular, post-ocular spines. Postfrontal ridges centrally indented by prominent central gastric groove. Gastric region shaped like an arrowhead, pointed posteriorly. Renifrom keraial region. Deep and short postcervical groove, parallel to cervical groove. Distinct cardiac region delineated by branchiocardiac groove. Preserved parts of posterior carapace coarsely pitted.

Description: Smooth, well-calcified and well-areolated shield, subcylindrical transversely, slightly convex longitudinally. Prominent, broad-based triangular rostrum. Orbital cavity ellipsoidal, bounded by triangular, slightly upturned, post-ocular spine and faint post-antennal projections. Broad, smooth ocular-frontal area exceeding half of total maximum width. Pronounced, slightly convex post-rostral ridge extending into massetic groove. Posterior pointed arrowhead-shaped gastric region, bounded posteriorly by deep V-shaped cervical groove. Distinct deep central gastric groove. Very prominent and globose massetic region forming widest part of shield. Anterior branchial area globose, size about one-quarter of massetic region. Typically reniform keraial region anteriorly at widest part of cervical groove. Elongated mesobranchial region exhibiting short, deep, comma-shaped postcervical groove. Subrounded pentagonal cardiac region laterally bordered by branchiocardiac groove. Preserved parts of posterior carapace coarsely pitted.

Discussion: Parapylochelids are distinguished from other paguroid families in having, in addition to a cervical groove, branchiocardiac and postcervical grooves. Diagnostic is also the combination of large, globose massetic and considerably smaller, globose anterior branchial areas, an arrowhead-shaped gastric region and a well-delineated cardiac region.

To date, the family Parapylochelidae encompasses the genera *Housacheles*, *Mesoparapylocheles* and *Parapylocheles*; the latter being extant. *Housacheles* and *Mesoparapylocheles* differ from *Parapylocheles* in having a much more broadly based, more extensively protruding rostrum and better-delineated massetic and keraial regions. *Housacheles* is easily differentiated in having very narrow and long massetic regions.

Despite the considerable difference in time between the late Kimmeridgian *Mesoparapylocheles schweigerti* n. sp. and *M. jaegeri* n. sp. and the late Albian *M. michaeljacksoni*, the similarities amongst these species are striking. However, the new species can easily be distinguished from the mid-Cretaceous congener by the angular, reniform keraial regions. *Mesoparapylocheles schweigerti* n. sp. can be differentiated from *M. jaegeri* n. sp. in having subrounded post-frontal ridges centrally indented by a very short, central gastric groove and more globose massetic regions.

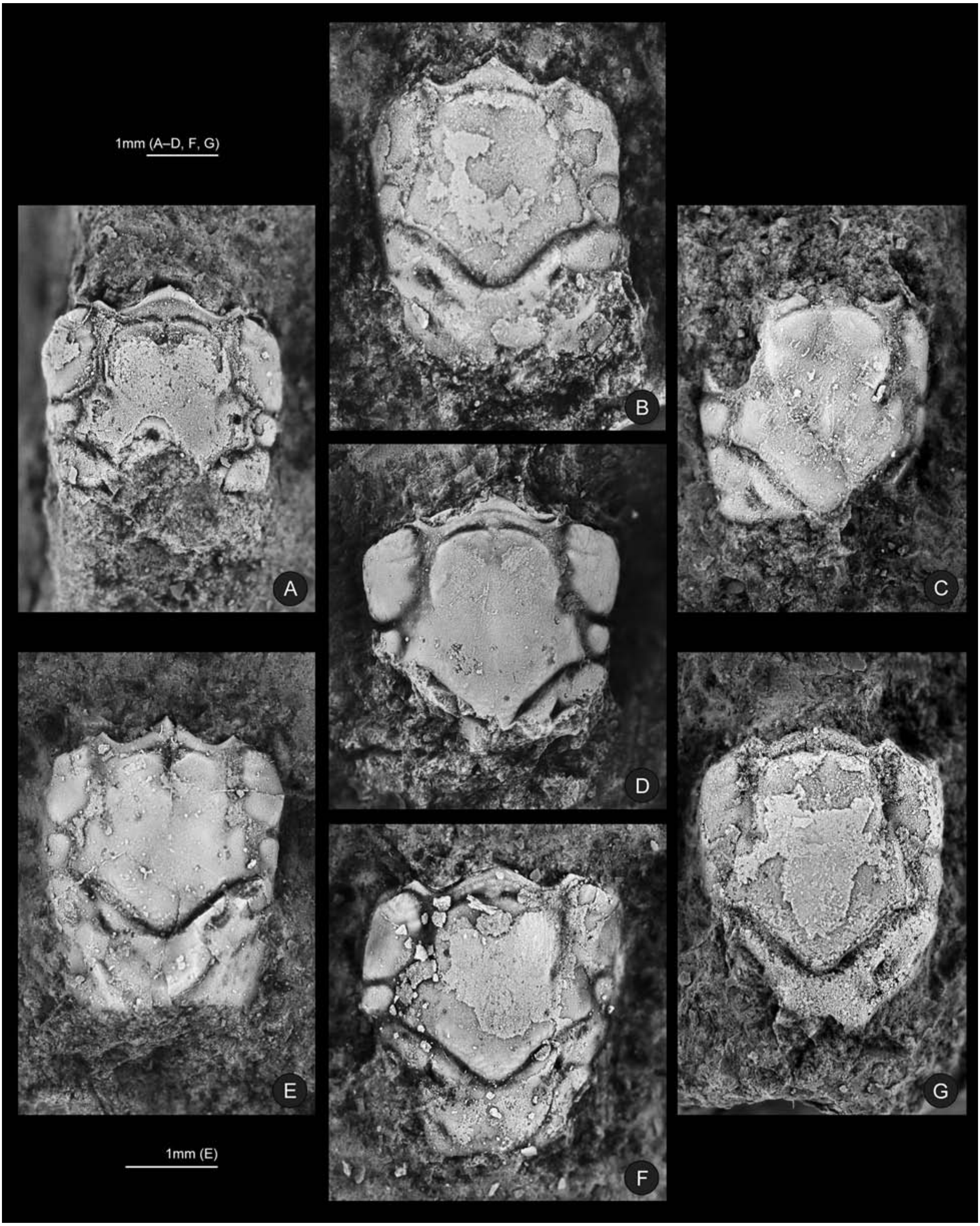

Fig. 9. A-D, F, G – *Mesoparapylocheles schweigerti* n. sp., paratype MAB k.3378, 3379, 3343, holotype MAB k.3257 and paratypes MAB k.3377 and 3342, **E** – *Mesoparapylocheles jaegeri* n. sp., holotype MAB k. 3341.

Genus *Parapylochelitergites* Fraaije, Artal, Van Bakel, Jagt & Klompmaker, 2013

Type species: *Parapylochelitergites pustulosus* Fraaije, Artal, Van Bakel, Jagt & Klompmaker, 2013, by original designation.

Parapylochelitergites deductius n. sp.

Fig. 13A, B, G

Etymology: Named after the Latin verb *deducere* meaning to deduce, in reference to the possible relationship of this tergite with carapaces of the family Parapylochelidae.

Material: Holotype MAB k.3236, a near-complete large tergite, maximum length and width 1.5 mm and 1.5 mm; paratypes MAB k.3360, 3382, near complete tergites, max. length and width 2.0, 1.5 mm and 2.0, 1.5 mm, respectively.

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Diagnosis: Subhexagonal, convex tergite; width slightly exceeding length. Prominent longitudinal median groove. Two central crescent-shaped transverse grooves curving posteriorly into median furrow. Distinct lateral bulges, bordered anteriorly by lateral groove and posteriorly by deep, long posterior notch. Surface of anterior half faintly rugose.

Description: Hexagonal tergite, convex in longitudinal and transverse sections; widest about mid-length; with a longitudinal median groove, most pronounced in posterior half where it grades into a deep posterior median furrow; two distinct central crescent-shaped transverse grooves curving posteriorly info median furrow; relatively long, undulose posterolateral notches almost parallel to lateral sides; right lateral bulge considerably smaller than right one; anterior rim smooth and slightly convex; posterior rim smooth and straight. Posterior half of tergite faintly rugose.

Remarks: The narrow, comparatively longer lateral bulges and the distinct central crescent-shaped transverse grooves distinguish this form clearly from *Parapylochelitergites pustulosus* and *P. prepustulosus* n. sp. Interestingly, in all three specimens the right lateral bulge is considerably narrower than the left one indicating an early assymetrical trend within *P. deductius* n. sp.

Parapylochelitergites prepustulosus n. sp.

Fig. 13E

Etymology: A plausible predecessor of the Albian *Parapylochelitergites pustulosus*.

Material: Holotype MAB k.3364, a near-complete tergite, maximum length and width 2.0 mm and 2.0 mm.

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Diagnosis: Subhexagonal, convex tergite; width slightly exceeding length. Prominent longitudinal median groove. Distinct lateral bulges, bordered anteriorly by lateral groove and posteriorly by deep, posterior notch. Surface of anterior half faintly rugose.

Description: Tergite subhexagonal, convex transversely and longitudinally, width slightly exceeding length. Convex anterior rim extending towards anterior part of lateral groove parallel to lateral bulges. Longitudinal median groove extending from anterior rim almost to posterior rim, being deepest in posteriormost portion, diverging close to posteriormost part. Reniform lateral bulges delimited anteriorly by distinct lateral grooves and deeply indented posterior notch. Central part of posterior rim faintly concave to straight, extending laterally towards convex, smooth margin connecting with lateral bulges. Tergite covered with fine pustules on anterior half of tergite.

Remarks: The absence of central crescent-shaped transverse grooves distinguishes this form clearly from *P. deductius* n. sp. It differs from *P. pustulosus* in having narrower posterior notches and the lateral bulges extend more anteriorly in *P. prepustulosus* n. sp.

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.

Ammopylocheles mclaughlinae Van Bakel, Fraaije, Jagt & Artal, 2008

Fig. 11A-D, F

Material: Five shields with parts of posterior carapace (MAB k. 3381, 3338, 3337, 3365a, 3339 total length 2.5, 3.0, 4.0, 4.0, 5.0, max. width 2.5, 2.0, 3.0, 3.0, 3.5 mm, respectively.

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Diagnosis: Van Bakel et al. (2008) provided detailed descriptions of several specimens of *A. mclaughlinae* which need not be repeated here.

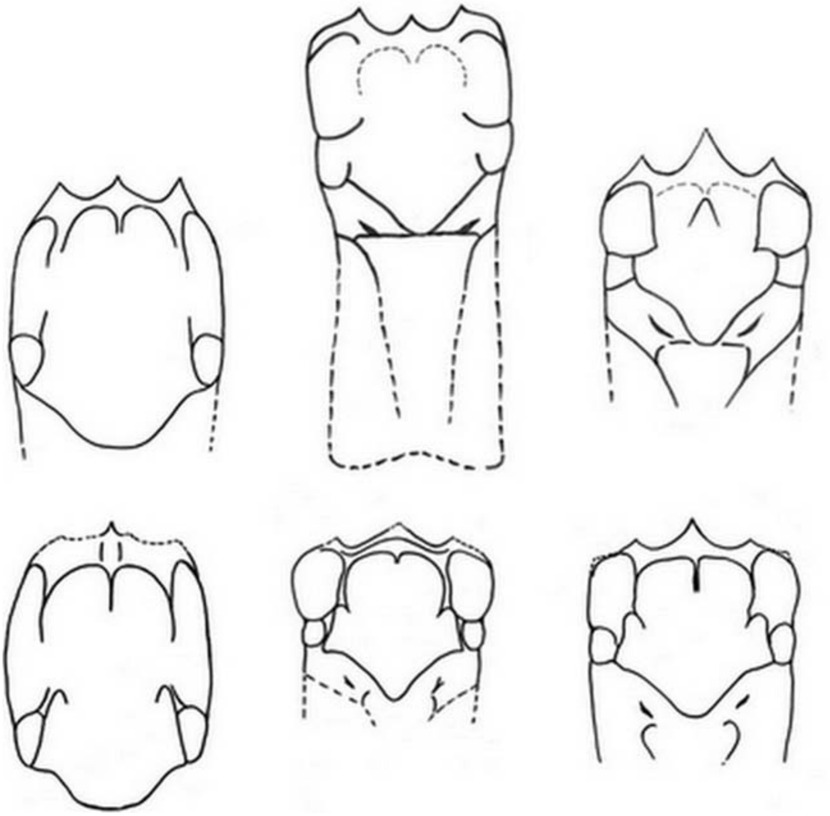

Fig. 10. All known members of the Parapylochelidae. Top from left to right *Housacheles timidus* Fraaije, Van Bakel, Jagt & Skupien, 2013 *Parapylocheles scorpio* (Alcock, 1894) and *Mesoparapylocheles. michaeljacksoni* Fraaije, Klompmaker & Artal, 2012, bottom from left to right *Housacheles ovalis* n. sp., *M. schweigerti* n. sp. and *M. jaegeri* n. sp.

Remarks: *Ammopylochele mclaughlinae* is by far the commonest faunal element at Nusplingen (the present study) and at Geisingen (Van Bakel et al. 2008). Differences in the morphology of the post-frontal ridge, from near-straight to convex and occasionally undulose, in specimens of *Ammopylocheles mclaughlinae* from Nusplingen are regarded as intraspecific variation and, possibly, sexual dimorphism.

Ammopylocheles petersi n. sp.
Fig. 11E

Etymology: Named after Werner Peters, a Dutch amateur palaeontologist and friend, who helped during several field trips and donated some of the material studied herein.

Material: A single near-complete shield with part of posterior carapace (MAB k.3256, total length 4.0, max. width 4.0 mm.

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Diagnosis: Carapace longer than broad, shield wider than long, broadest at centre of massetic regions and clearly tapering posteriorly; broad rostrum; distinct sinuous cervical furrow, central gastric groove and postfrontal ridge.

Description: Carapace longer than broad, strongly convex in transverse section, convex in longitudinal section, markedly tapering posteriorly. Shield wider than long (W/L ratio 1.14); cervical groove prominent. Where cuticule is absent, ornament of dorsal surface of gastric region consisting of small, imbricated granules on anterior and posterior sides. Long lateral gastric grooves, tending to converge axially. Small transverse post-rostral region with broad-based, triangular rostrum; transverse, convex, post-rostral ridge medially subdivided by a short, deep, central gastric groove

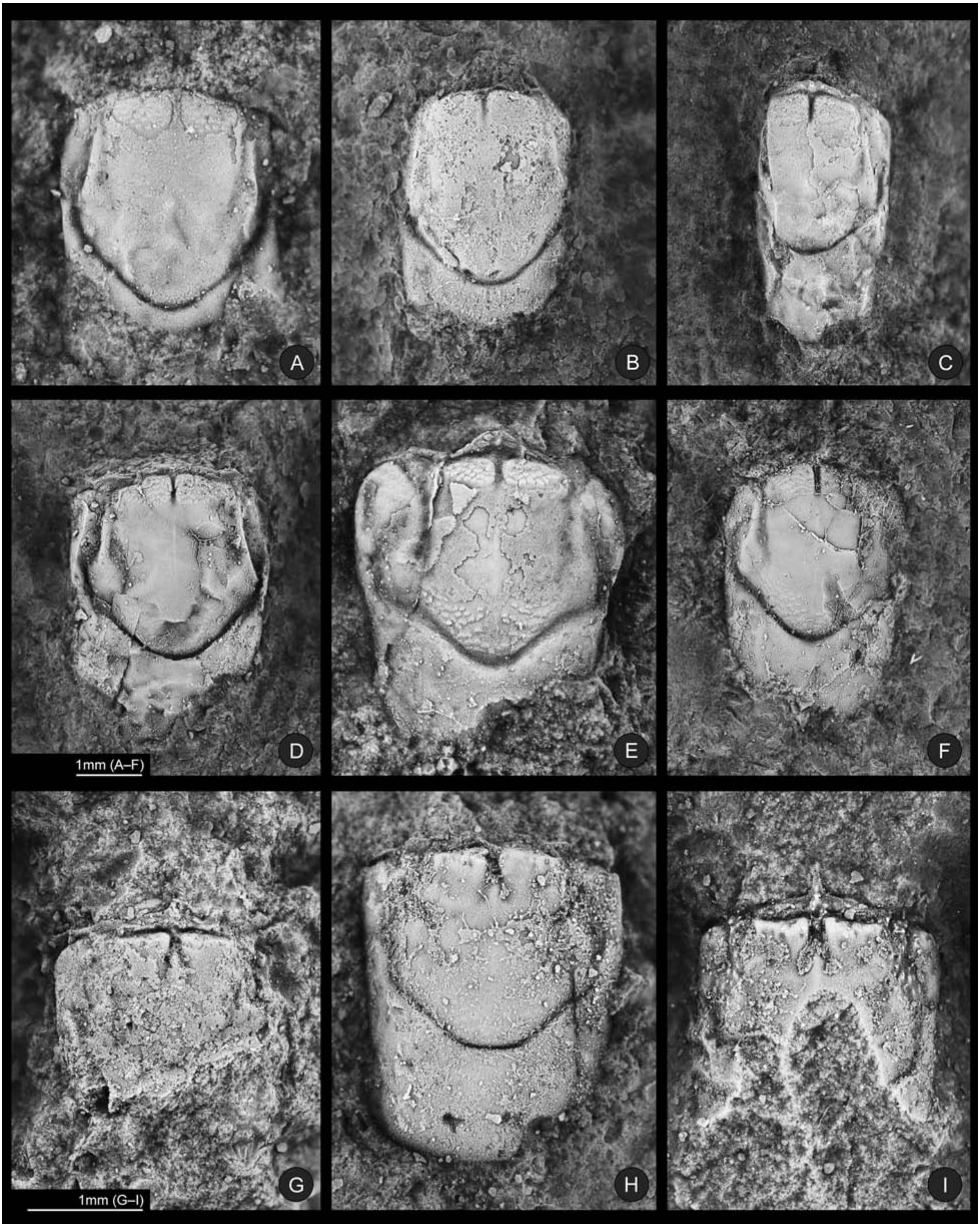

Fig. 11. A-D, F – *Ammopylocheles mclaughlinae* Van Bakel, Fraaije, Jagt & Artal, 2008, MAB k. 3381, 3338, 3337, 3365a, 3339, **E** – *Ammopylocheles petersi* n. sp., holotype MAB k. 3256, **G-I** – *Jurapylocheles iwonae* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2012b, MAB k. 3252, 3353, 3250.

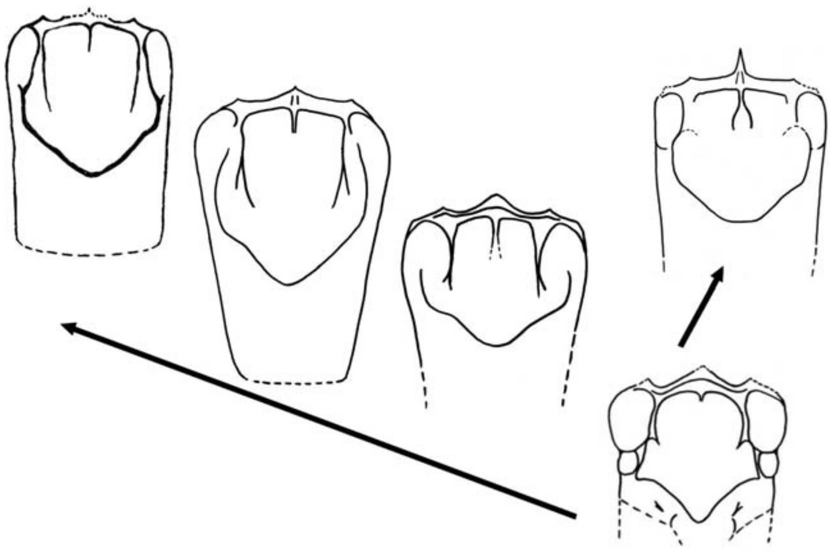

Fig. 12. Possible phylogenetic relationship between the Parapylochelidae (*Mesoparapylocheles schweigerti* n. sp. (bottom right) and the Pylochelidae (*Ammopylocheles* (left) and *Jurapylocheles* (top right)).

protruding into faint median gastric rim; postantennal projections obtuse. Lateral margins sloping, with highly globose, massetic region. Posterior carapace less well calcified, smooth, strongly tapering posteriorly.

Remarks: The new species, of late Kimmeridgian age, differs from its middle Oxfordian congener *Ammopylocheles robertboreki*, in having a larger, wider rostrum, a shorter central gastric groove, a median gastric rim, and a wider shield. *Ammopylocheles petersi* n. sp. differs from *A. mclauglinae* in having a wider and more pronounced rostrum, a posteriorly tapering carapace and a more globose massetic region. The faint median gastric ridge, visible when cuticule is absent, is a primitive character that is also seen in other Mesozoic paguroid genera such as *Annuntidiogenes*, *Diogenicheles*, *Gastrodorus*, *Mesoparapyloches*, *Pilgrimcheles,* and *Ululapagurus* n. gen.

Subfamily Mixtopagurinae FOREST, 1987
Genus *Jurapylocheles* VAN BAKEL, FRAAIJE, JAGT & ARTAL, 2008

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

Jurapylocheles iwonae FRAAIJE, KRZEMIŃSKI, VAN BAKEL, KRZEMIŃSKA & JAGT, 2012b Fig. 11G-I

Material: A near-complete carapace (MAB k.3353) maximum length 2.5 mm, maximum width 1.5 mm; MAB k.3250 and 3252 represent incomplete shields with a maximum width of 1.5 and 2.0 mm, respectively).

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Diagnosis: FRAAIJE et al. (2012b) provided a detailed description of the type material from the Oxfordian of southern Poland which need not be repeated here.

Remarks: *Jurapylocheles* has the spiniest rostrum of all Jurassic paguroids known to date. *Jurapylocheles iwonae* was first recorded from the middle to late Oxfordian of the southern Polish Uplands, northwest of Kraków. The other species of the genus, *J. malutka*, is known from the early late Kimmeridgian of Geisingen, southern Germany. *Jurapylocheles iwonae* differs from its congener in having postfrontal spines on the lateralmost edge of the post-frontal ridge.

Genus *Pylochelitergites* FRAAIJE, KRZEMIŃSKI, VAN BAKEL, KRZEMIŃSKA & JAGT, 2012d

Type species: *Pylochelitergites westerbergensis* FRAAIJE, KRZEMIŃSKI, VAN BAKEL, KRZEMIŃSKA & JAGT, 2012d.

Pylochelitergites westerbergensis Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2012d
Fig. 13F

Material: Several tergites of this species have been published in FRAAIJE et al. (2012d). Tergite MAB k.3382 with a total length of 2.0 and a max. width of 2.0 mm is added to this species.

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Diagnosis: Fraaije et al. (2012d) provided descriptions of several specimens of *P. westerbergensis* from the type locality, to which paper reference is made.

Remarks: The more or less equal abundance of pylochelid carapaces and sixth abdominal operculate tergites within the sponge-microbial reef limestones at Nusplingen and Geisingen suggests strongly that *P. westerbergensis* constitutes the abdominal sixth tergite of the trizocheline *Ammopylocheles mclaughlinae* Van Bakel, Fraaije, Jagt & Artal, 2008, but only a completely preserved animal can resolve this issue.

Genus *Scututergites* nov.

Type species: *Scututergites anteroindentatus* n. g. n. sp.

Etymology: Named after the Latin word *scutum* meaning shield, referring to the shield-like appearance.

Diagnosis: Subhexagonal, convex tergite, wider than long. Longitudinal median groove deepest at indentation of anterior margin and close to posterior margin.Distinct lateral posterior notches. Broadly pointed posterior margin.

Scututergites anteroindentatus n. g. n. sp.
Fig. 13D

Etymology: Referring to the central indentation in the anterior margin.

Holotype: MAB k.3357, a near-complete tergite with maximum length and width 2.0 mm and 2.0 mm respectively.

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Diagnosis: As for genus (monotypic).

Description: Subhexagonal, convex tergite, wider than long. Longitudinal median groove, shallowest centrally and deepest at indentation of anterior margin and close to posterior margin. Distinct deep lateral posterior notches. Short wing-like lateral bulges. Broadly pointed posterior margin.

Remarks: *Scututergites* n. gen. differs from all other known fossil tergites in having a pointed posterior margin and an indented anterior margin. This typical morphology is not known by the author for any fossil and extant paguroid.

Genus *Stagmacaris* Schweigert, 2006

Type species: *Stagmacaris quenstedti* Schweigert, 2006.

Stagmacaris subcircularis n. sp.
Fig. 13C

Etymology: Named after its almost circular.appearance.

Holotype: MAB k.3356, a tergite, maximum length 1.5 mm and width 1.5 mm.

Locality and horizon: Small local quarry at the Westerberg, with well-bedded sponge-microbial limestones and marls of the *Aulacostephanus pseudomutabilis* Zone of late Kimmeridgian (= 'Malm delta 3-4') age.

Diagnosis: Subcircular tergite; distinct longitudinal, broad median furrow, terminating before reaching margins. Posteriorly, longitudinal median furrow bordered laterally by two pairs of oblique irregular ridges.

Description: Subcircular tergite; broad, serrated, longitudinal median furrow over entire tergite, widest and most serrated in anterior half, effacing before reaching margins. Posterior part bordered laterally by two square, irregular wavy ridges almost reaching the posterior notch. Smooth, narrow and long lateral bulges.

Remarks: *Stagmacaris subcircularis* n. sp. differs from all other known species of the genus in having transverse, almost straight ridges, on the posterior half between the median furrow and lateral bulges, instead of arched crescent ones.

4. Mesozoic anomuran evolution

In recent years our insights into the diversity and evolutionary history of Mesozoic anomurans has increased considerably. Robins et al. (2013) documented a galatheoid fauna of 28 species of munidopsid and a large number of undescribed galatheids from the Tithonian coralgal reef limestones of Ernstbrunn (Austria). According to those authors, the Štramberk Limestones of Moravia (Czech Republic) and southern Poland, which also represent Tithonian coralgal reef-

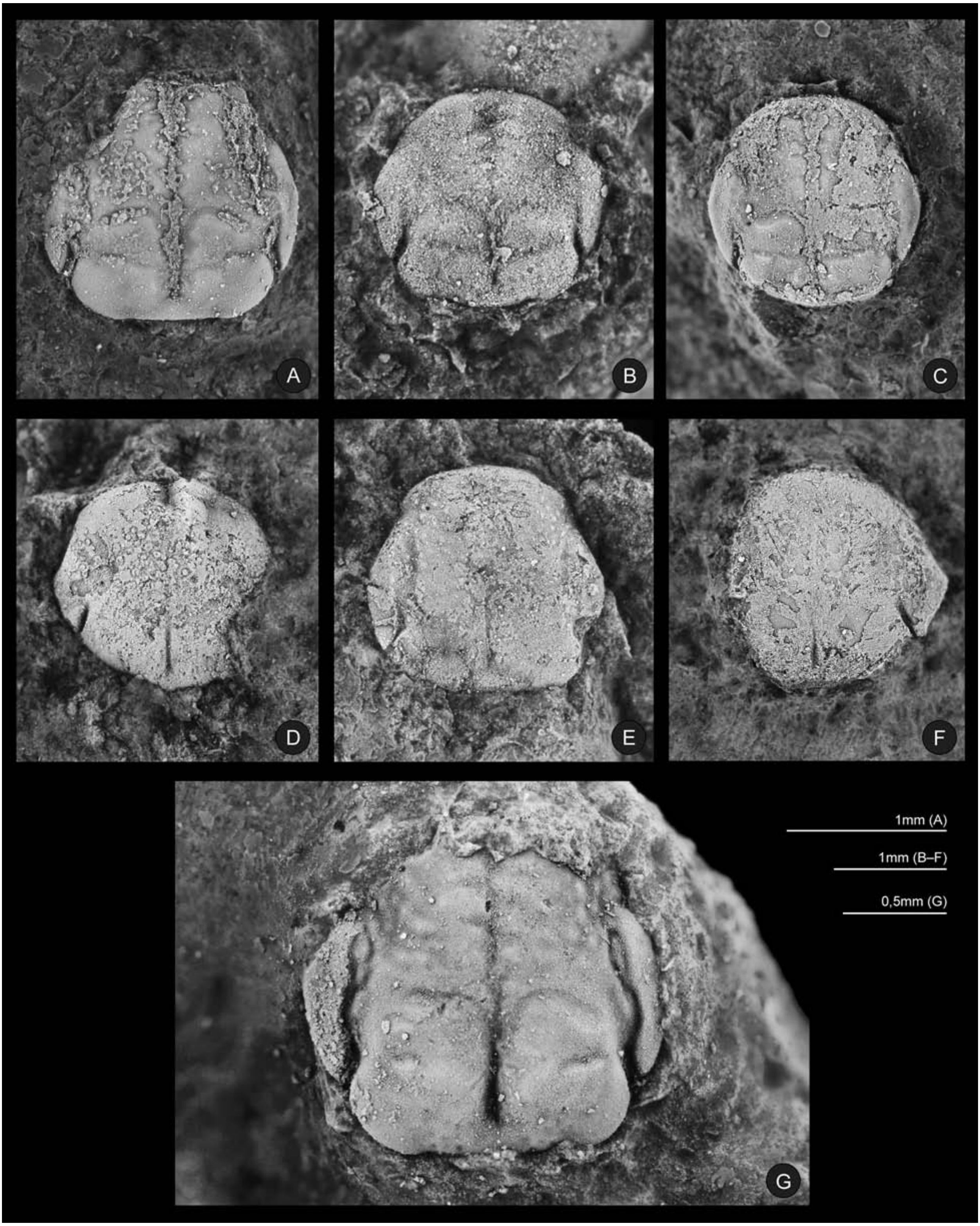

Fig. 13. A, B, G – *Parapylochelitergites deductio* n. sp., paratypes MAB k. 3360, 3382, holotype MAB k. 3256, **C** – *Stagmacaris subcircularis* n. sp., holotype MAB k. 3356, **D** – *Scututergites biindentata* n. sp., holotype MAB k. 3357, **E** – *Parapylochelitergites prepustulosus* n. sp., holotype MAB k. 3364, **F** – *Pylochelitergites westerbergensis* Fraaije et al., 2012d, MAB k. 3382.

type deposits, most likely are characterised by similarly high diversities amongst munidopsids and galatheids. Klompmaker et al. (2012) recorded from Albian reefal deposits in northwest Spain ten species of galatheid, this being the richest Cretaceous galatheid fauna known. Both Tithonian and Albian faunas also comprise porcellanids and paguroids. The Kimmeridgian anomuran fauna of the present study includes a single galatheoid and 17 paguroid taxa. These data, together with personal observations during several decades of fieldwork in Mesozoic reefal outcrops across Europe, illustrate successive predominance by different anomuran groups within reef settings.

Within those of Oxfordian and Kimmeridgian age paguroids flourished, in addition to primitive brachyurans (Podotremata Guinot, 1977). During the Tithonian, galatheoids took over the paguroid niche. In Albian times, reef-inhabiting galatheoids were still abundant, but their diversity decreased considerably. Paguroids were present, albeit in relatively low abundance and diversity. From that time onwards, the majority of Mesozoic paguroids migrated into deeper-water environments or went extinct. The same holds true for the majority of Mesozoic galatheoids, i.e., the munidopsids. From the mid-Cretaceous onwards the better-adapted eubrachyurans occupied most of the niches favoured by early anomurans and podotreme brachyurans within reef settings. The shift of a reefal to a deep-sea habitat by early paguroids and anomurans was made possible by a huge increase in the diversity and biomass of planktonic organisms with mineralised skeletons from the Aptian onwards. An enormous radiation of planktonic foraminifera, coccolithophores and other armoured algae (e.g., silicoflagellates) and diatoms occurred; this enriched the deeper ocean floors with food and allowed abundant, diverse benthic animal life. Most modern paguroids have considerably less developed massetic and keraial regions, which indicates a change of food-gathering from the Late Jurassic onwards. This is clear when comparing *Annuntidiogenes*, parapylochelids and pylochelids with modern pagurids.

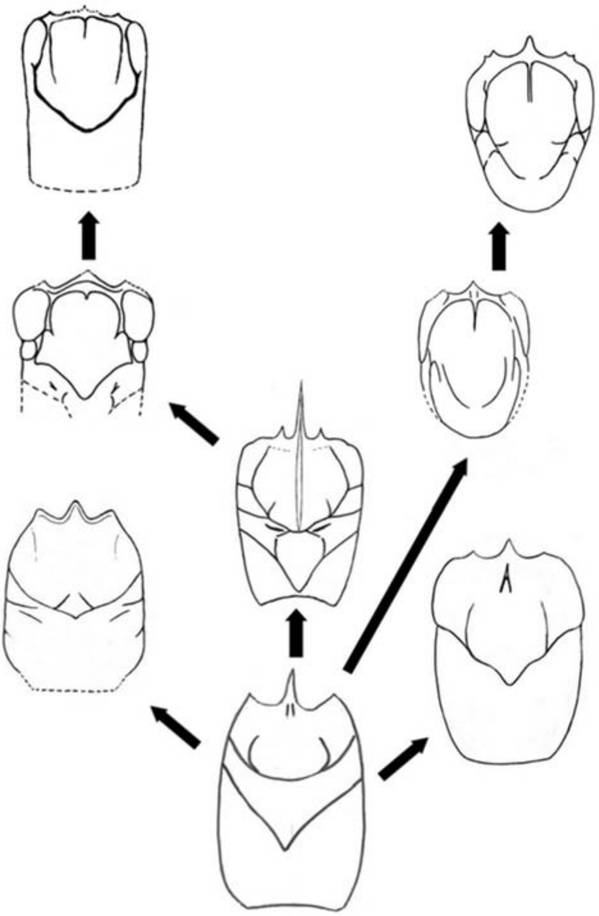

Fig. 14. Jurassic paguroid evolution showing different pathways in the fusion of branchiocardiac and cervical grooves.

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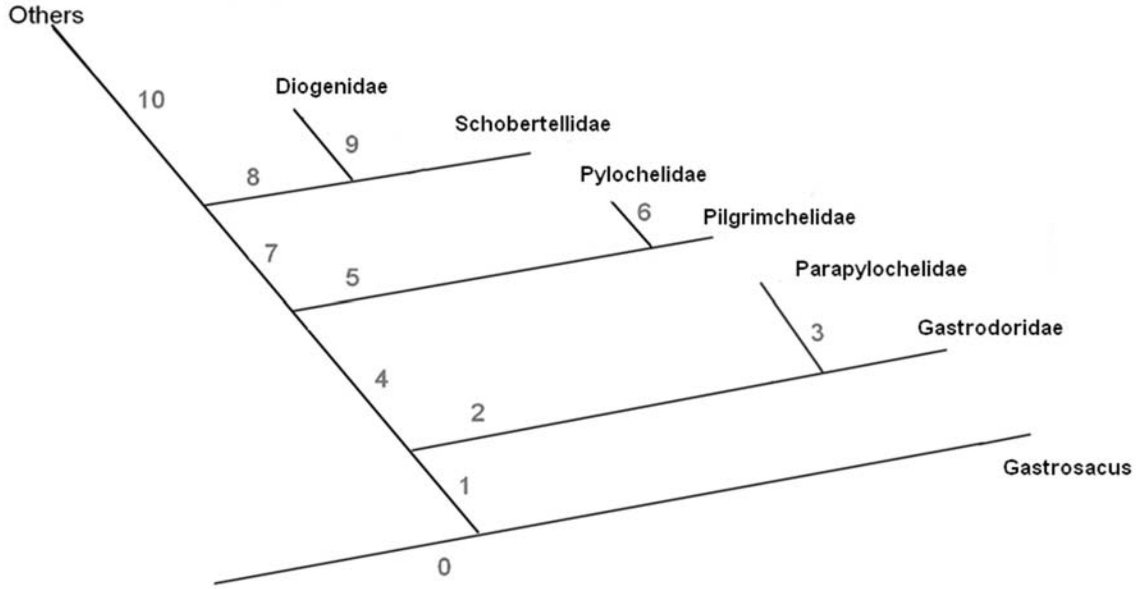

Fig. 15. Cladogram of Mesozoic paguroid families adapted from Fraaije et al. (2013c). Characters: 0. cervical = circumgastric groove; 1. inflated massetic and anterior branchial area; 2. branchiocardiac and postcervical grooves; 3. arrowhead-shaped gastric and globose massetic; 4. confluence of branchiocardiac and cervical grooves, plus loss of delineated cardiac; 5. elongated keraial region; 6. loss of anterior branchial area; 7. cervical groove reaching lateral sides; 8. broad subcircular 'orbits', no post-antennal spines; 9. coarse pores on shield; 10. loss of calcified posterior carapace.

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