Netherlands Journal of Geosciences — Geologie en Mijnbouw | 92 – 2/3 | 109-117 | 2013

An array of sixth abdominal tergite types of paguroid anomurans (Crustacea) from the mid-Cretaceous of Navarra, northern Spain•

R.H.B. Fraaije[1,*], P. Artal[2], B.W.M. van Bakel[3], J.W.M. Jagt[4] & A.A. Klompmaker[5]

1 Oertijdmuseum De Groene Poort, Bosscheweg 80, 5283 WB Boxtel, the Netherlands
2 Museo Geológico del Seminario de Barcelona, Diputación 231, 08007 Barcelona, Spain
3 Oertijdmuseum De Groene Poort, Bosscheweg 80, 5283 WB Boxtel, the Netherlands; and Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, the Netherlands
4 Natuurhistorisch Museum Maastricht, De Bosquetplein 6-7, 6211 KJ Maastricht, the Netherlands
5 Florida Museum of Natural History, University of Florida, 1659 Museum Road, P.O. Box 117800, Gainesville FL 32611, USA
* Corresponding author. Email: info@oertijdmuseum.nl

Manuscript received: January 2013, accepted: April 2013

Abstract

In recent years, a range of operculate sixth abdominal tergite types of pylochelid and parapylochelid hermit crabs (Anomura, Paguroidea) have been recorded from Upper Jurassic (Oxfordian and Kimmeridgian) strata in southern Poland and southern Germany. Here we add two new genera (*Parapylochelitergites*, *Paguritergites*) and four new late Early Cretaceous species (*Parapylochelitergites pustulosus*, *Pylochelitergites alatus*, *Pylochelitergites rugosus* and *Paguritergites yvonnecooleae*) from Navarra, northern Spain. In the reefal limestones at Koskobilo quarry near Alsasua, of late Albian age, the number of sixth abdominal paguroid tergite taxa approximates that of paguroid carapace types. Thus, linking fossil paguroid carapaces to tergites can now be attempted. Assemblages of symmetrical hermit crabs (parapylochelids and pylochelids) in reefal settings appear to have changed drastically from the late Albian onwards, with asymmetrical forms (Diogenidae, Paguridae) becoming predominant.

Keywords: Paguroidea, Pylochelidae, Parapylochelidae, Paguridae, new taxa, Albian

Introduction

Amongst decapod crustaceans, hermit crabs are classified in the superfamily Paguroidea. The majority of extant species, 1,106 in total (see McLaughlin et al., 2010), possess an asymmetrical, spirally curved, soft abdomen which is concealed in empty gastropod shells that are carried around by the paguroid. Most of these asymmetrical, spirally curved abdomina have asymmetrical sixth abdominal tergites, while only 42 species (see De Grave et al., 2009) within the extant paguroid families Pylochelidae and Parapylochelidae have exclusively symmetrical abdomina with symmetrical sixth abdominal tergites. A few genera within the families Paguridae (e.g., *Xylopagurus* A. Milne-Edwards, 1880) and Diogenidae (e.g., *Cancellus* H. Milne Edwards, 1836) also have symmetrical sixth abdominal tergites (Lemaitre, 1995). These pylochelid and parapylochelid symmetrical sixth abdominal tergites serve as opercula. Inhabitation of pieces of wood, rock and coral, as well as polychaete worm tubes and scaphopod molluscan shells, with openings at both ends, has led to the development of strongly calcified operculate chelae and operculate tergites to protect the vulnerable paguroid body (Fig. 1; see Ďuriš, 1992; McLaughlin & Lemaitre, 1997). Only recently have fossil examples of such abdominal tergites been recognised and formally described (Fraaije et al., 2012d). In the meantime, additional Oxfordian and Kimmeridgian (Late Jurassic) taxa have been collected in southern Germany, southern Poland and the Czech Republic (Guenter Schweigert, pers. comm., November 2012; Fraaije et

• *In:* Mulder, E.W.A., Jagt, J.W.M. & Schulp, A.S. (eds): The Sunday's child of Dutch earth sciences – a tribute to Bert Boekschoten on the occasion of his 80th birthday.

https://doi.org/10.1017/S0016774600000032 Published online by Cambridge University Press

Fig. 1. Extant Pylocheles mortensenii *Boas, 1926 (MNHN-Pg 3437), Tosa Bay, southern Japan, showing the entire animal in lateral aspect (A) and morphology of the sixth abdominal operculate tergite (B). Not to scale.*

al., 2013). This clearly documents the high fossilisation potential of such tergites. All currently known taxa of Late Jurassic tergites exhibit the closest similarities to members of the families Pylochelidae Bate, 1888 (Fig. 1) and Parapylochelidae Fraaije, Klompmaker & Artal, 2012; they are thus assigned to these families.

The calcified symmetrical sixth tergites of extant paguroids all show groove-like structures and/or lateral notches. Characteristic of some members of the families Paguridae Latreille, 1802 (e.g., *Xylopagurus*, *Discorsopagurus* McLaughlin, 1974 and *Orthopagurus* Stevens, 1927) and Diogenidae Ortmann, 1892 (e.g., *Cancellus*) is a distinct transverse depression or groove which divides the tergite into more or less equal-sized anterior and posterior parts (see Lemaitre, 1995, figs 7, 16, 17c). The tergites of those pagurid genera are rectangular in outline, and length exceeds width. The tergites of *Cancellus* are subhexagonal, width exceeding length. For morphological terminology of calcified symmetrical tergites of pagurids and diogenids, reference is made to Lemaitre (1995) and to Figure 2 here.

Sixth abdominal tergites of extant members of the Pylochelidae differ considerably from those of other families in being subquadrate to subhexagonal or subcircular in outline, convex in cross-section and in having groove- and furrow-like structures and/or lateral notches. They invariably lack a distinct median transverse groove (e.g., Forest, 1987a, fig. 42b). Tergites of the family Parapylochelidae are elongate and suboval; they also lack such a median groove (Fig. 2).

The goal of the present paper is to describe and name the first sixth abdominal tergites from the mid-Cretaceous. Furthermore, an attempt is made to link associated paguroid carapace types, all found isolated (see Fraaije et al., 2012a), with these tergites.

Systematic palaeontology

Institutional abbreviations

MAB – Oertijdmuseum De Groene Poort, Boxtel, the Netherlands; MNHN-P – Muséum national d'Histoire naturelle, Paris, France; MGSB – Museo Geológico del Seminario de Barcelona, Barcelona, Spain.

Order Decapoda Latreille, 1802
Infraorder Anomura MacLeay, 1838
Superfamily Paguroidea Latreille, 1802
Family ?Parapylochelidae Fraaije, Klompmaker & Artal, 2012
Genus Parapylochelitergites *nov.*

Type species
Parapylochelitergites pustulosus nov. sp.

Derivation of name
A combination of the word 'tergite' and the family name, Parapylochelidae.

Diagnosis
Subhexagonal, convex tergite, width and length approximately equal. Prominent longitudinal median groove. Distinct lateral bulges, bordered anteriorly by lateral groove and posteriorly by posterior notch. Fine, uniformly pustulose ornament.

Parapylochelitergites pustulosus *nov. sp.*

Figs 2, 3D, 5C.

Types
Holotype is MGSB 79776, a complete tergite (maximum length and width 3.0 mm and 3.0 mm, respectively); paratypes are MAB k. 2648, a near-complete tergite (maximum length and width 3.5 mm and 3.5 mm, respectively); MAB k. 2664, a complete

https://doi.org/10.1017/S0016774600000032 Published online by Cambridge University Press

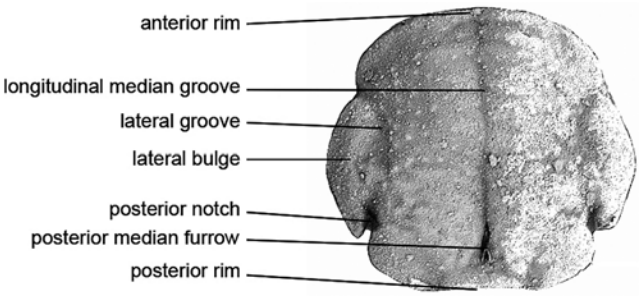

Fig. 2. Paguroid sixth abdominal tergite morphology exemplified by Parapylochelitergites pustulosus *nov. gen., nov. sp. (see also Figs 3D, 5C; modified from Fraaije et al., 2012d, fig. 3B).*

tergite (maximum length and width 2.5 mm and 2.5 mm, respectively); MAB k. 2665, a complete tergite (maximum length and width 3.0 mm and 3.0 mm, respectively), and MAB k. 3125, a complete tergite (maximum length and width 2.0 mm and 2.0 mm, respectively).

Derivation of name

In allusion to the pustulose ornament.

Type locality and horizon

Koskobilo quarry (co-ordinates: N 42.8823°, W 2.1990°), 3 km southwest of the village of Alsasua, Navarra (northern Spain). All specimens originate from the uppermost reefal sediments of the Albeniz Unit (Eguino Formation), which has been dated as late Albian (see Klompmaker, 2013).

Diagnosis

As for genus (see above).

Description

Tergite subhexagonal, convex transversely and longitudinally, width and length approximately equal. Convex anterior rim extending towards anterior part of lateral groove parallel to lateral bulges. Longitudinal median groove extending from

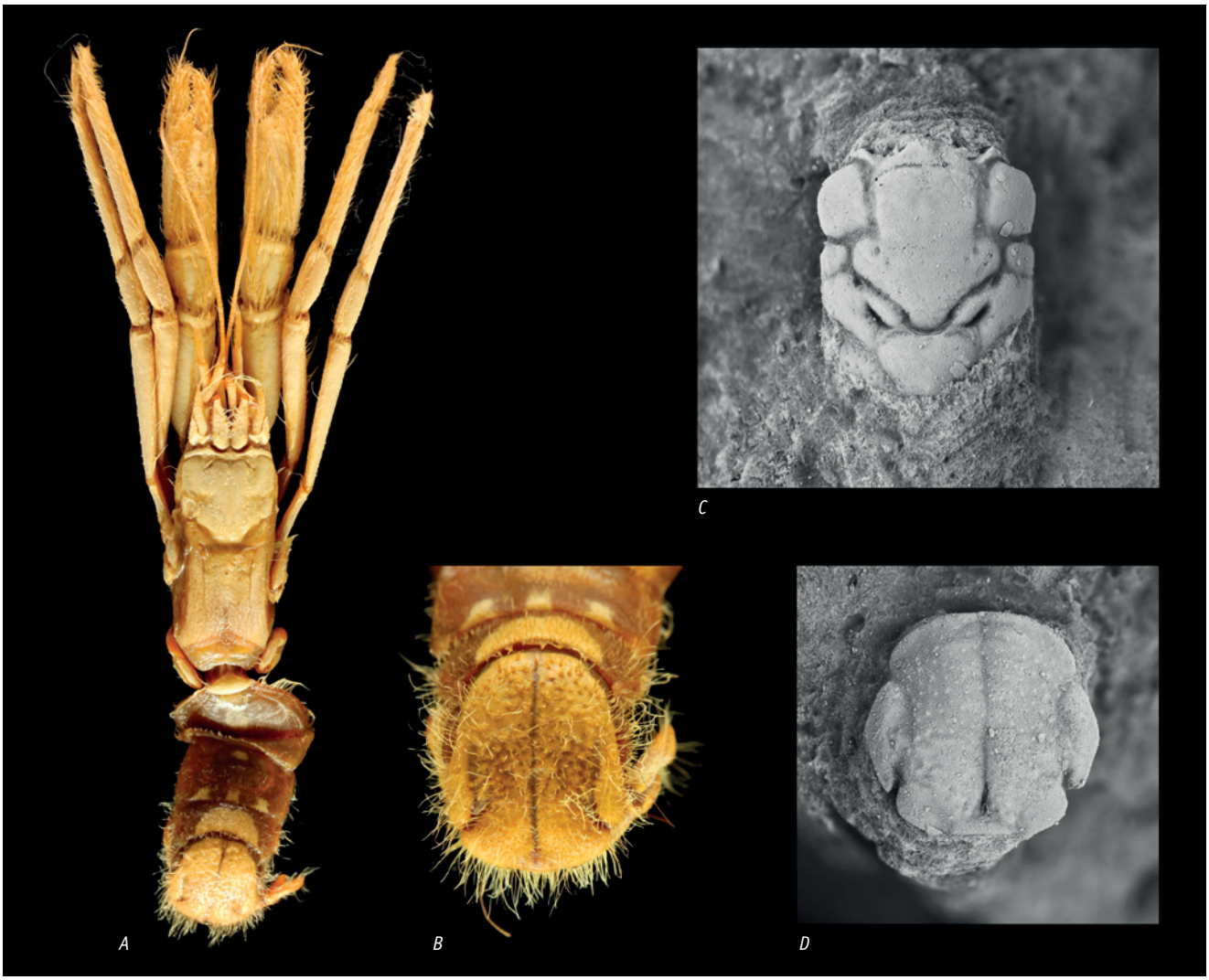

Fig. 3. Comparison of extant (A, B) and mid-Cretaceous parapylochelid paguroids; A, B. Parapylocheles scorpio *(Alcock, 1894) (MNHN-Pg 2733), MUSORSTOM II, Philippines; C.* Mesoparapylocheles michaeljacksoni *Fraaije, Klompmaker & Artal, 2012 (holotype, MGSB 78333; carapace); D.* Parapylochelitergites pustulosus *nov. gen., nov. sp. (holotype, MGSB 79776; tergite). Not to scale.*

https://doi.org/10.1017/S0016774600000032 Published online by Cambridge University Press

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 uniformly covered with fine pustules, except for smooth lateral bulges and areas posteriorly and postero-laterally of posterior median furrow.

Discussion

Studies of sixth abdominal tergites of pylochelids have revealed a considerable range of variation (see e.g., Forest, 1987a; McLaughlin & Lemaitre, 2009). Tergites of members of the subfamilies Pylochelinae and Pomatochelinae Stebbing, 1914, lack a longitudinal median ridge that extends to the anterior rim (Figs 1B, 4A, B), and mixtopagurine tergites have a spinose posterior margin (Forest, 1987a, fig. 77a-j). Tergites of the pylochelid subfamilies Cancellochelinae Forest, 1987a and Trizochelinae Forest, 1987a (Fig. 4C, D) resemble those of the Parapylochelidae (Fig. 5C). However, cancellocheline tergites lack a pustulose ornament, whereas trizochelines have less pronounced and less elongated lateral bulges, in combination with a wider straight central part of the posterior rim. This leaves the Parapylochelidae as the most probable candidate for the new fossil tergite genus described here, although assignment is tentative. This suggestion is supported by the similar abundance of carapaces of the parapylochelid *Mesoparapylocheles* Fraaije, Klompmaker & Artal, 2012 and this tergite type from Koskobilo (Fig. 3C; Table 1).

Family ?Pylochelidae Bate, 1888

Genus Pylochelitergites *Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2012d.*

Table 1. Carapace- and abdominal tergite-based paguroid taxa from the upper Albian of Koskobilo quarry, provisionally paired, as based on current MAB and MGSB collections.

Taxon	Number of specimens	Reference
Mesoparapylocheles michaeljacksoni Fraaije, Klompmaker & Artal, 2012	35 (herein)	Fraaije et al. (2012a)
Parapylochelitergites pustulosus nov. gen., nov. sp.	17	herein
Cretatrizocheles olazagutiensis Fraaije, Klompmaker & Artal, 2012	7 (herein)	Fraaije et al. (2012a)
Pylochelitergites alatus nov. sp.	8	herein

Pylochelitergites alatus *nov. sp.*

Fig. 5D-F.

Types

Holotype is MGSB 79777, a near-complete tergite (maximum length and width 2.0 mm and 2.5 mm, respectively); paratypes are MAB k. 2789, a near-complete tergite (maximum length and width 2.5 mm and 3.0 mm, respectively), MAB k. 3278, a complete tergite (maximum length and width 1.5 mm and 2.0 mm, respectively), and MAB k. 3294, a complete tergite (maximum length and width 3.1 mm and 3.3 mm, respectively).

Derivation of name

From Latin *ala* (*alatus*), meaning 'wing(ed)', in allusion to the wing-like lateral bulges.

Type locality and horizon

Koskobilo quarry (co-ordinates: N 42.8823°, W 2.1990°), 3 km southwest of the village of Alsasua, Navarra (northern Spain).

Fig. 4. Types of sixth abdominal tergites in Recent pylochelid paguroids; A. Bathycheles crosnieri *(Forest, 1985) (MNHN-Pg 2847), Indian Ocean; B.* Pomatocheles jeffreysii *Miers, 1879 (MNHN-Pg 3491), Tosa Bay, southern Japan; C.* Cancellocheles sculptipes *(Miyake, 1978) (MNHN-Pg 3436), Tosa Bay, southern Japan; D.* Trizocheles *sp. (MNHN unregistered). Not to scale.*

https://doi.org/10.1017/S0016774600000032 Published online by Cambridge University Press

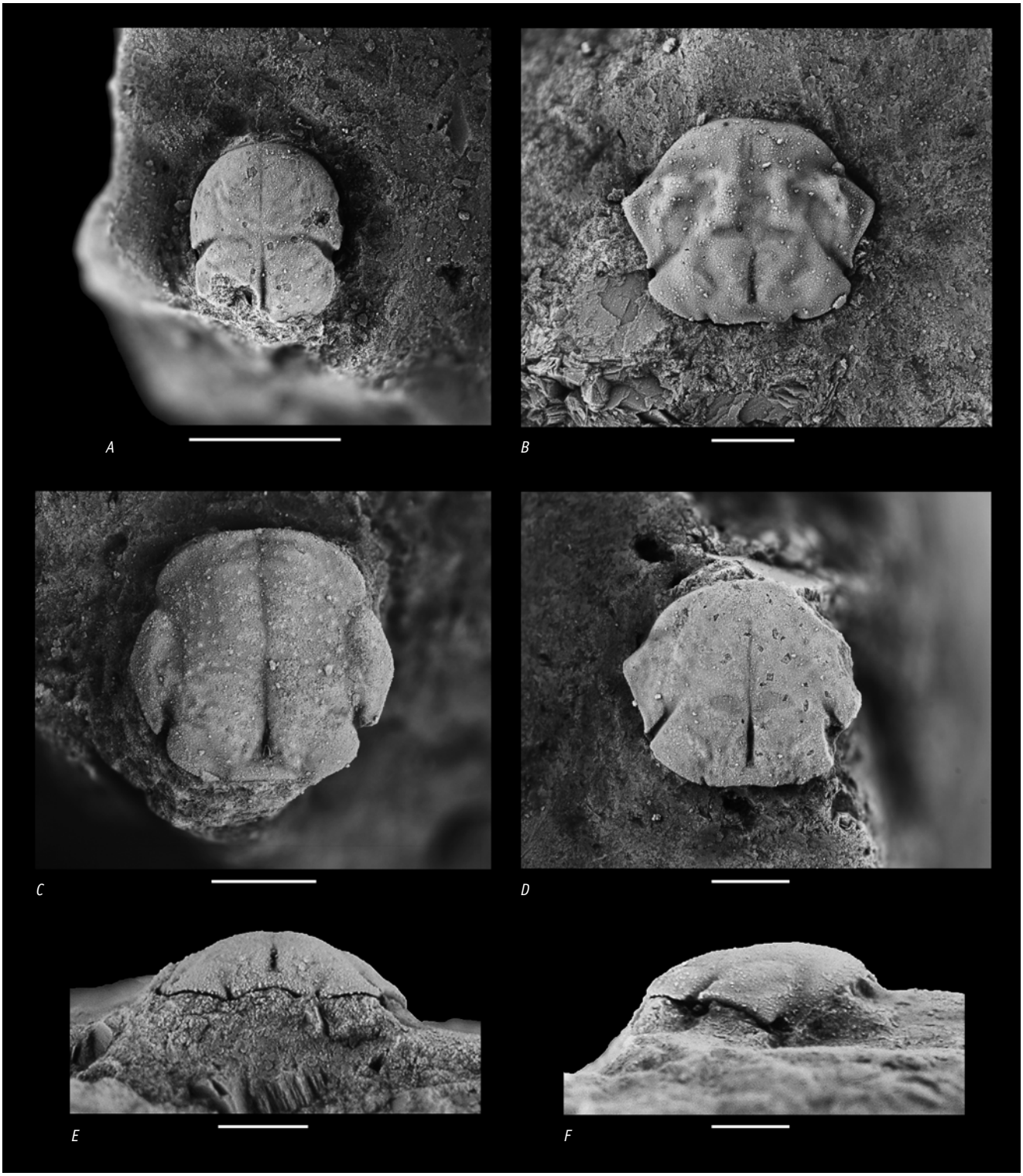

Fig. 5. Paguroid abdominal tergite types from the upper Albian of Koskobilo quarry (Navarra, northern Spain); A. Paguritergites yvonnecooleae *nov. gen., nov. sp. (MGSB 79779; holotype); B.* Pylochelitergites rugosus *nov. sp. (MGSB 79778; holotype); C.* Parapylochelitergites pustulosus *nov. gen., nov. sp. (MGSB 79776; holotype); D.* Pylochelitergites alatus *nov. sp. (MGSB 79777; holotype), in dorsal aspect; E-F.* Pylochelitergites alatus *nov. sp. (MAB k. 3294; paratype), in posterior and right lateral aspect, respectively. All scale bars equal 1 mm.*

All specimens originate from the uppermost reefal sediments of the Albeniz Unit (Eguino Formation), which has been dated as late Albian (see Klompmaker, 2013).

Diagnosis

Smooth, hexagonal pylochelid sixth abdominal tergite, with flat, wing-like lateral bulges, a faint longitudinal median groove and deep, oblique posterior notches.

https://doi.org/10.1017/S0016774600000032 Published online by Cambridge University Press

Description
Tergite smooth, hexagonal, width exceeding length, widest slightly anterior of mid-length. Convex in longitudinal and transverse sections. Faint longitudinal median groove on anterior half, extending posteriorly, developing into deep, elongate cleft. Flat, wing-like lateral bulges representing widest part of tergite. Deep, oblique, incisive posterior notches. Posterior rim slightly concave and finely spinose centrally ending in small incisions, laterally protruding convexly and smooth, ending at posterior notches.

Discussion
This new form differs from all other species referred to this tergite-based genus to date (compare Fraaije et al. 2012d, 2013) in being of lesser width and with the maximum width in the anterior half, and in having more oblique posterior notches. Based on a comparison of the general morphology with extant pylochelids and the near-equal number of carapaces and tergites collected at Koskobilo quarry (see Table 1), *Pylochelitergites alatus* nov. sp. seems best paired with *Cretatrizocheles olazagutiensis* Fraaije, Klompmaker & Artal, 2012.

Pylochelitergites rugosus *nov. sp.*

Fig. 5B.

Type
Holotype, and sole specimen known, is MGSB 79778, a near-complete tergite (maximum length and width 2.5 mm and 3.0 mm, respectively).

Derivation of name
From Latin *ruga* (*rugosus*, *-a*) in reference to the wrinkled surface.

Type locality and horizon
Koskobilo quarry (co-ordinates: N 42.8823°, W 2.1990°), 3 km southwest of the village of Alsasua, Navarra (northern Spain). All specimens originate from the uppermost reefal sediments of the Albeniz Unit (Eguino Formation), which has been dated as late Albian (see Klompmaker, 2013).

Diagnosis
Hexagonal pylochelid sixth abdominal tergite, with wrinkled surface, a broad longitudinal median groove, extending into a deep posterior cleft, flat, wing-like lateral bulges and and deep, oblique posterior notches.

Description
Tergite hexagonal, with wrinkled surface, width exceeding length, maximum width slightly anterior of mid-length. Convex in longitudinal and transverse sections. A faint, broad longitudinal median groove on anterior part ends in transverse, wide groove centrally and extends posteriorly into deep, elongated cleft. Flat, wing-like lateral bulges form widest part of tergite. Deep, oblique, incisive posterior notches. Convex and smooth anterior rim. Posterior rim slightly concave and finely spinose centrally, ending in small incisions and protruding convexly and smooth, laterally ending at posterior notches.

Discussion
The present form is easily distinguished from *Pylochelitergites alatus* nov. sp. and all other known congeners on account of its wrinkled surface and the deep, oblique, incisive posterior notches which are more centrally oriented than in the other species.

Family ?Paguridae Latreille, 1802
Genus Paguritergites *nov.*

Type species
Paguritergites yvonnecooleae nov. sp.

Derivation of name
A combination of the word 'tergite' with the family name Paguridae.

Diagnosis
Small, elongated tergite, with distinct longitudinal median and transverse median grooves forming a cross at the centre. Surface with fine, uniformly rugose ornament. Smooth, subrounded anterior rim; posterior rim slightly convex.

Paguritergites yvonnecooleae *nov. sp.*

Fig. 5A.

Type
Holotype, and sole specimen known, is MGSB 79779, a near-complete tergite (maximum length and width 1.5 mm and 1.0 mm, respectively).

Derivation of name
Named after Mrs Yvonne Coole, who collected and donated the type specimen.

Type locality and horizon
Koskobilo quarry (co-ordinates: N 42.8823°, W 2.1990°), 3 km southwest of the village of Alsasua, Navarra (northern Spain). All specimens originate from the uppermost reefal sediments of the Albeniz Unit (Eguino Formation), which has been dated as late Albian (see Klompmaker, 2013).

Diagnosis
As for genus (see above).

https://doi.org/10.1017/S0016774600000032 Published online by Cambridge University Press

Description

Tergite small and elongate, with smooth, subrounded anterior rim and smooth, subrectangular posterior part. Longitudinal median groove extending from anterior rim and deepening into furrow posteriorly. Transverse depression submedially extending towards deep, postero-laterally oblique, posterior notches. Fine, uniformly rugose ornament.

Discussion

The presence of a heavily calcified, symmetrical tergite with four subequal quadrants formed by anterior and posterior longitudinal median grooves and a submedian transverse depression is characteristic of extant species of the genera *Xylopagurus*, *Discorsopagurus* and *Orthopagurus*, all members of the *Pylopaguropsis* group within the family Paguridae (see Lemaitre, 1995). Some diogenids, such as *Cancellus*, also show this clear 4-quadrant arrangement, but the general outline differs markedly (e.g., Lemaitre, 1995, fig. 17c).

Discussion

It is worthy of note that, to date, abdominal tergites of paguroids have been recorded exclusively from reefal strata of Middle and Late Jurassic and latest Early Cretaceous age (Fraaije et al., 2012d; herein); Late Cretaceous and younger forms have yet to be found. Naturally, this can, in part, be explained by collection bias, but it could also illustrate that pylochelid and parapylochelid abundance in relatively shallow-water reefal settings dropped markedly from the mid-Cretaceous onwards. Alternatively, sixth abdominal tergites may not have been preserved, due either to unfavourable physical and chemical conditions prior to and during fossilisation, or to (partial) decalcification of the tergites themselves. Despite extensive collecting by ourselves and by colleagues in comparable reefal strata of Late Cretaceous, Paleogene and Neogene age (e.g., the upper Maastrichtian of the southeast Netherlands and northeast Belgium; the lower Paleocene (Danian) of central Poland; the Eocene of Hungary (P. Müller, pers. comm., June 2009) and of northern Italy (A. de Angeli & A. Garassino, pers. comm., December 2012) and the Miocene of Spain, Hungary and Cyprus, we are not aware of any calcified paguroid tergites from these levels. This is even more puzzling because from a number of these localities paguroid carapaces are now known.

The abundance and diversity of paguroid carapaces and sixth abdominal tergites in strata of Late Jurassic (Oxfordian-Kimmeridgian) to mid-Cretaceous age are indicative of markedly different faunal assemblages (Table 2) in comparison with Recent marine paguroid faunal diversity and composition (e.g., De Grave et al., 2009; McLaughlin et al. 2010). Nowadays, in terms of species numbers, less than four percent of paguroids in all habitats belong to the Pylochelidae and/or Parapylochelidae (De Grave et al., 2009).

Table 2. Carapace- (in bold print) and abdominal tergite-based paguroid genera of Late Jurassic and mid-Cretaceous age, arranged alphabetically and with number of species currently assigned to them and family placement favoured (data from Van Bakel et al. 2008; Fraaije et al. 2009, 2012a-d, 2013).

Taxon	Number of species referred	Family assignment
Ammopylocheles	2	Pylochelidae
Annuntidiogenes	2	Diogenidae
Cretatrizocheles	1	Pylochelidae
Diogenicheles	1	Parapylochelidae
Eopaguropsis	2	Diogenidae
Eotylaspis	1	?Diogenidae
Jurapylocheles	2	Pylochelidae
Liocaris	1	?Pylochelidae
Masticacheles	1	Parapylochelidae
Mesoparapylocheles	1	Parapylochelidae
Paguritergites nov. gen.	1	?Paguridae
Parapylochelitergites nov. gen.	1	Parapylochelidae
Pilgrimcheles	1	Parapylochelidae
Pylochelitergites	5	?Pylochelidae
Stagmacaris	3	?Pylochelidae

The above data, coupled with field observations during recent years, are indicative of a clear predominance of the families Pylochelidae and Parapylochelidae (80 per cent, or more; based on specimens collected) in reefal settings during the Late Jurassic to mid-Cretaceous, in co-occurrence with far less diverse and numerous diogenids. A radiation during the Jurassic of the families Pylochelidae and Diogenidae, followed by a proliferation of pagurids (family Paguridae) during the Cretaceous, would match the maximum likelihood ancestral state reconstruction of the various body forms within anomuran lineages as envisaged by Tsang et al. (2011). The fossil record is in support of views expressed by Forest (1987b) that the Diogenidae and Pylochelidae probably had a common ancestor. It would appear that the faunal turnover from the predominantly symmetrical paguroids to asymmetrical ones and from pylochelid/parapylochelid-dominated faunas to those in which members of both families were absent in shallow-marine, reefal settings did not come about earlier than sometime during the Late Cretaceous. At present, not a single pylochelid or parapylochelid occurs in shallow-marine reefal habitats (Forest, 1987b).

In their new classification for the family Pylochelidae, McLaughlin & Lemaitre (2009) noted the morphological diversity of the sixth abdominal tergites. When additional material of extinct taxa becomes available and more detailed attention is paid to the external morphology of extant forms, these sixth abdominal tergites may be expected to constitute useful tools in unravelling the phylogenetic relationships, even in the absence of paguroid carapaces. Symmetrical, operculate sixth

https://doi.org/10.1017/S0016774600000032 Published online by Cambridge University Press

abdominal tergites within extant species of the families Paguridae and Diogenidae would appear to constitute synapomorphic relics rather than cases of convergent adaptation.

For the first time, sixth abdominal tergite and carapace types of fossil paguroids are linked to one another on the basis of abundance patterns (Table 1). The assumption is that conspecific carapaces and tergites are equally well calcified. *Pylochelitergites rugosus* nov. sp. and *Paguritergites yvonnecooleae* nov. gen., nov. sp. cannot be linked to any carapace type collected so far, which implies that at least two paguroid carapace types have yet to be found. These two tergites add to the decapod crustacean diversity of the Koskobilo quarry (see Klompmaker, 2013); the total number of decapod crustacean species known now is 38. In general, we may conclude that tergite types may be used to reveal some of the hidden paguroid diversity in the fossil record.

Acknowledgements

We thank the Cementos Portland Valderrivas Company (Olazti, Navarra) for their kind permission and hospitality to do fieldwork at the disused Koskobilo quarry, Thea Fraaije-van Boom (Boxtel, the Netherlands), Carrie Schweitzer (Kent, Ohio, USA), Rodney Feldmann (Kent, Ohio, USA) and Yvonne Coole (Stramproy, the Netherlands) for assistance during fieldwork at Koskobilo quarry and the last-named for donating important specimens. Fieldwork at Koskobilo was in part supported by the Molengraaff Fonds, an Amoco Alumni Scholarship, a Graduate Student Senate (Kent State University) research grant, a Sigma Gamma Epsilon (Gemma Zeta Chapter) research grant to Klompmaker, as well as an NSF grant (EF-0531670) to Feldmann and Schweitzer. This work was further supported by the Jon L. and Beverly A. Thompson Endowment Fund to Klompmaker. Lastly, we acknowledge the assistance given by Danièle Guinot and Danielle Defaye (MNHN, Paris) while consulting collections, and the pertinent comments made by the journal reviewers, Guenter Schweigert (Staatliches Museum für Naturkunde, Stuttgart) and Rafael Lemaitre (Smithsonian Institution, National Museum of Natural History, Washington DC). This is University of Florida Contribution to Paleobiology 655.

References

Alcock, A., 1894. Natural history notes from H.M. Royal Indian Marine Survey Steamer 'Investigator', commander R.F. Hoskin, R.N., commanding; Series II, No. 1. On the results of deep-sea dredging during the season of 1890-91 (continued). Annals and Magazine of Natural History (6)13: 321-334.

Bate, C.S., 1888. Report on the Crustacea Macrura collected by H.M.S. Challenger during the years 1873-76. *In:* Murray, J. (ed.): Zoology. Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873-76 under the command of Captain George S. Nares, R.N., F.R.S. and the Late Captain Frank Tourle Thomson, R.N. 24(52): xc + 942 pp.

Boas, J.E.V., 1926. Zur Kenntnis symmetrischer Paguriden. Kongelige Danske Videnskabernes Selskabs Skrifter, Biologiske Meddelelser 5(6): 1-52.

De Grave, S., Pentcheff, N.D., Ahyong, S.T., Chan, T.-Y., Crandall, K.A., Dworschak, P.C., Felder, D.L., Feldmann, R.M., Fransen, C.H.J.M., Goulding, L.Y.D., Lemaitre, R., Low, M.L., Martin, J.W., Ng, P.K.L., Schweitzer, C.E., Tan, S.H., Tshudy, D. & Wetzer, R., 2009. A classification of Recent and fossil genera of decapod crustaceans. The Raffles Bulletin of Zoology, Supplement 21: 1-109.

Ďuriš, Z., 1992. On a small collection of Crustacea Decapoda from the Bellsund region, Spitsbergen. *In:* Repelewska-Pekalowa, J. & Pekala, K. (eds): Wyprawy geograficzne na Spitsbergen. UMCS, Lublin: 121-154.

Forest, J., 1985. La campagne MUSORSTOM II (1980). Compte rendu et liste des stations. Mémoires du Muséum national d'Histoire naturelle de Paris A133: 9-30.

Forest, J., 1987a. Les Pylochelidae ou 'Pagures symétriques' (Crustacea Coenobitoidea). *In:* Crosnier, A. (ed.): Résultats des Campagnes MUSORSTOM, Volume 3. Mémoires du Muséum national d'Histoire naturelle A137: 1-254.

Forest, J., 1987b. Ethology and distribution of Pylochelidae (Crustacea Decapoda Coenobitoidea). Bulletin of Marine Science 41: 309-321.

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., Krzemiński, W., Van Bakel, B.W.M., Krzemińska, E. & Jagt, J.W.M., 2012d. The sixth abdominal tergites of paguroid anomurans – a newly recognized crustacean macrofossil type. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 266: 115-122.

Fraaije, R.H.B., Krzemiński, W., Van Bakel, B.W.M., Krzemińska, E. & Jagt, J.W.M., 2013. New Late Jurassic symmetrical hermit crabs from the southern Polish Uplands and early paguroid diversification. Acta Palaeontologica Polonica, dx.doi.org/10.4202/app.2012.0022

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.

Klompmaker, A.A., 2013. Extreme diversity of decapod crustaceans from the mid-Cretaceous (late Albian) of Spain: implications for Cretaceous decapod paleoecology. Cretaceous Research 41: 150-185.

Latreille, P.A., 1802-1803. Histoire naturelle, générale et particulière, des Crustacés et des Insectes 3. F. Dufart (Paris), xiii + 568 pp.

Lemaitre, R., 1995. A review of the hermit crabs of the genus *Xylopagurus* A. Milne Edwards, 1880 (Crustacea: Decapoda: Paguridae). Smithsonian Contributions to Zoology 570: 1-27.

https://doi.org/10.1017/S0016774600000032 Published online by Cambridge University Press

MacLeay, W.S., 1838. On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith. *In:* Smith, A. Illustrations of the zoology of South Africa; consisting chiefly of figures and descriptions of the objects of natural history collected during an expedition into the interior of South Africa, in the years 1834, 1835, and 1836; fitted out by 'The Cape of Good Hope Association for Exploring Central Africa': together with a summary of African zoology, and an inquiry into the geographical ranges of species in that quarter of the globe. Invertebratae. Smith, Elder & Co. (London): 53-71.

McLaughlin, P.A., 1974. The hermit crabs (Crustacea, Decapoda, Paguridea) of northwestern North America. Zoologische Verhandelingen 130: 1-396.

McLaughlin, P.A. & Lemaitre, R., 1997. Carcinization in the Anomura – fact or fiction? Evidence from adult morphology. Contributions to Zoology 67: 79-123.

McLaughlin, P.A. & Lemaitre, R., 2009. A new classification for the Pylochelidae (Decapoda: Anomura: Paguroidea) and descriptions of new taxa. The Raffles Bulletin of Zoology, Supplement 20: 159-231.

McLaughlin, P.A., Komai, T., Lemaitre, R. & Rahayu, D.L., 2010. Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostylidae and Galatheidae of the Galatheoidea). Part I – Lithodoidea, Lomisoidea and Paguroidea. *In:* Low, M.E.Y. & Tan, S.H. (eds.): Checklists of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostylidae and Galatheidae of the Galatheoidea) and marine lobsters of the world. Zootaxa, Supplement 23: 5-107.

Miers, E.J., 1879. On a collection of Crustacea made by Capt. H.C. St. John, R.N., in the Corean and Japanese Seas. Part I. Podophthalmia. With an appendix by Capt. H.C. St. John. Proceedings of the Zoological Society of London 1879: 18-61.

Milne-Edwards, A., 1880. Report on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, 78, 79, by the United States Coast Survey Steamer 'Blake', Lieut.-Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. VIII. Études preliminaries sur les Crustacés. Bulletin of the Museum of Comparative Zoology, Harvard College 8: 1-68.

Milne Edwards, H., 1836. Observations zoologiques sur les Pagures et description d'un nouveau genre de la tribu des Paguriens. Annales des Sciences naturelles, Zoologie (2)6: 257-288.

Miyake, S., 1978. The crustacean Anomura of Sagami Bay. Biological Laboratory, Imperial Household (Tokyo), 1-200 (English) + 1-161 (Japanese).

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.

Stebbing, T.R.R., 1914. South African Crustacea (Part VII of S.A. Crustacea, for the Marine Investigations in South Africa). Annals of the South African Museum 15: 1-55.

Stevens, B.A., 1927. Orthopagurus, a new genus of Paguridae from the Pacific coast. Publications of the Puget Sound Biological Station 5: 245-252.

Tsang, l.M., Chan, T.-Y., Ahyong, S.T. & Chu, K.H., 2011. Hermit to king, or hermit to all: multiple transitions to crab-like forms from hermit crab ancestors. Systematic Biology 60: 1-14.

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.

https://doi.org/10.1017/S0016774600000032 Published online by Cambridge University Press