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The earliest record of pylochelid hermit crabs from the Late Jurassic of southern Poland, with notes on paguroid carapace terminology

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Strata with cyanobacterial-sponge buildups of Middle to Late Oxfordian (Late Jurassic) age in the southern Polish Uplands document the earliest known members of the Pylochelidae. Two new Late Jurassic species of “symmetrical” hermit crabs, *Ammopylocheles robertboreki* and *Jurapylocheles iwona*, are described. A new term, the massetic region, is introduced to describe the equivalent in paguroids of the hepatic region in brachyuran carapaces, because in the former, this region does not reflect the position of the liver but rather an attachment zone of the mandibular muscles.

Key words: Paguroidea, Pylochelidae, new species, massetic region, evolution, Oxfordian, Poland.

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Introduction

At the present day, pylochelid hermit crabs inhabit the Indo-West Pacific with the western Atlantic oceans, their vertical distribution in subtropical to tropical waters ranging from 30 to 2,149 metres. Occurrences above 100 metres are rare with the maximum number of species having been recorded from depths between 200 and 500 metres (Forest 1987b; McLaughlin and Lemaitre 2009). Unlike most paguroids, all extant pylochelids have well-calcified carapaces and abdominal tergites, in particular the sixth abdominal tergite. This group of “symmetrical” paguroids, so named because their chelipeds are of near-similar size, seek protection in hollow objects, with the sixth abdominal tergite functioning as an operculum to close off the posterior opening of their abode. Dependent of availability, pylochelids use cavities in pieces of wood (e.g., bamboo), rock (conglomerate, limestone and tuff/pumice) or empty shells of molluscs (mainly scaphopods, but also gastropods) and serpulid worms, while some species carry living sponges. A number of species of the genera *Trizoecheles* Forest, 1987a and *Pylocheles* Milne-Edwards,

1880 demonstrate a mutualistic relationship with thin-walled dictyonin hexactinellids or more massively built lithistid and haplosclerid demosponges (Forest 1987b; McLaughlin and Lemaitre 2009).

In general, there are only few studies on Late Jurassic decapod crustaceans from Poland, and most of them are devoted to brachyuran crabs, e.g., Radwański (1972), Collins and Wierzbowski (1985), Krobicki and Müller (2000), Müller et al. (2000), Krobicki and Zatoń (2008) and Starzyk et al. (2011), or describe remains of macrurans, e.g., Förster and Matyja (1986) and Garassino and Krobicki (2002). The first paper in which anomurans from Jurassic strata in Poland were recorded was that by Van Bakel et al. (2008), in which a species of the gastrodorid genus *Gastrodorus* von Meyer, 1864 (see also Klompmaker et al. 2011) was described and illustrated. Van Bakel et al. (2008) were the first to recognise and document a wide range of paguroid carapaces, including two species of pylochelid, from the Late Jurassic of southern Germany. They also were able to place these specimens within the present classification of the Paguroidea. For reasons unknown to us, Schweitzer et al. (2010: 53) listed the four new genera

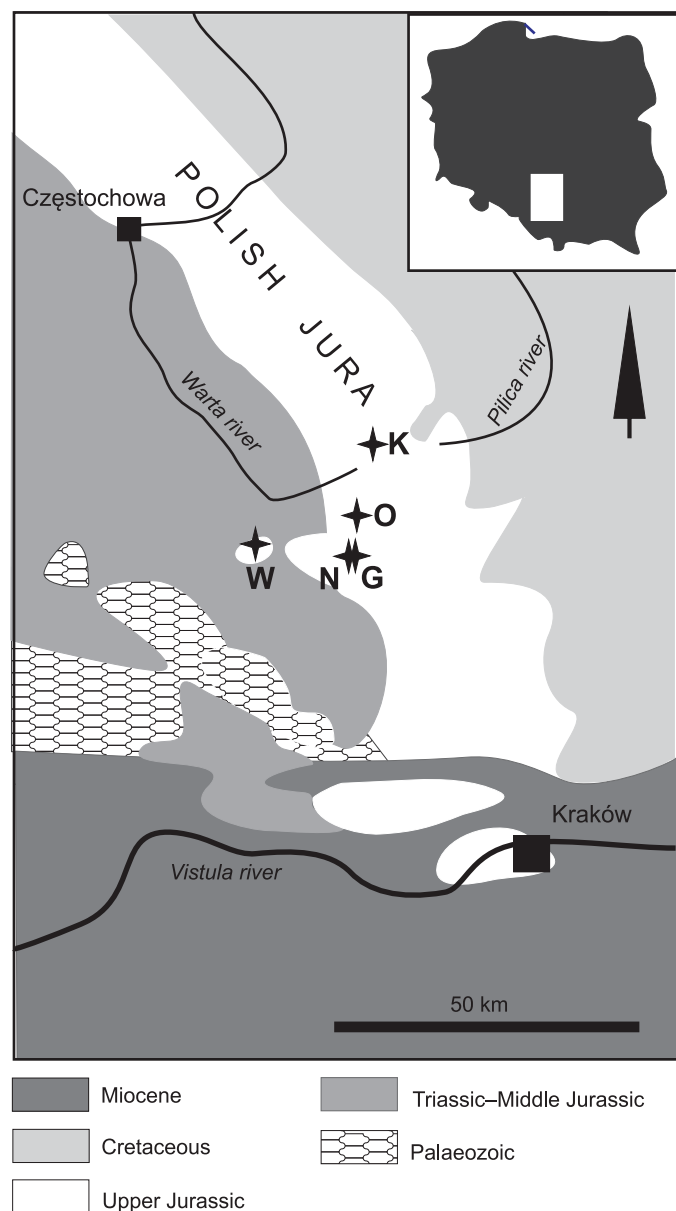


Fig. 1. Localities with paguroid-bearing strata of Middle–Late Oxfordian age in southern Poland (see inset), as follows: G, Grabowa; K, Kroczyce; N, Niegowonice; O, Ogrodzieniec; W, Wysoka (modified after Główniak 2006: fig. 2).

erected by Van Bakel et al. (2008) as “Family uncertain” within the superfamily Paguroidea Latreille, 1802.

Following this, the Borek family from the village of Dąbrowa Górnicza (southern Poland) succeeded in collecting, over a period of two years, in excess of 7,000 specimens of decapod crustaceans from six localities within the southern Polish Uplands, northwest of Kraków (Fig. 1). This impressive collection now forms the basis of the present note as well as of several ongoing studies on anomurans, brachyurans (Starzyk et al. 2011) and macrurans.

Microfossil assemblages from the Oxfordian sponge facies of the Kraków Upland comprise mainly foraminifera, ostracods and sponge spicules. The commonest spicules can be as-

signed to the Choristida, Lithistida, and Lyssakida (Olszewska and Wieczorek 1988). Other associated macrofossil groups in this facies are ammonites, belemnites, echinoids, crinoids, and brachiopods, while bivalves, gastropods, and fish remains occur rather sporadically.

Institutional abbreviations.—ISEA, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland; MAB, Oertijdmuseum De Groene Poort, Boxtel, the Netherlands.

Geographic and stratigraphic setting

The paguroids described below most probably lived between and/or within sponge buildups, which formed in neritic environments along the southernmost part of the epicontinental Peri-Tethyan sea, which was connected with the northernmost shelf of the Tethys Ocean during Oxfordian times. Originally, sponge accumulations formed sponge-microbial bioherms surrounded by soft muddy bottoms, the latter now represented by thin-bedded, micritic, chert-free, platy limestone with thin marly intercalations, full of nektonic ammonites and rare decapod crustaceans (Müller et al. 2000; Garassino and Krobicki 2002; Krobicki and Krzemiński 2010). The Upper Oxfordian massive limestone and thick-bedded, sponge-microbial chert-bearing limestone are relatively decapod-rich deposits as typical type of sponge megafacies limestone across the whole of Europe, in particular the Jurassic of the Fränkische and Schwäbische Alb in southern Germany (see Wehner 1988; Müller et al. 2000). The depth of deposition of these Oxfordian limestone rocks has been hotly disputed (Matyja and Wierzbowski 1996, 2004; Matyszkiewicz 1999), which is related to the lack of both bathymetrically diagnostic fossils and sedimentary structures, but most probably carbonate buildups originated at depths of one to a few hundred metres (Leinfelder 1993; Leinfelder et al. 1994; Matyja and Wierzbowski 1996, 2004; Matyszkiewicz 2008). After the global Callovian transgression, which allowed the formation of bioherms and reefs in Late Jurassic Peri-Tethyan basins, this created a palaeoenvironment which was conducive to the rapidly evolving decapod crustaceans (Müller et al. 2000; Van Bakel et al. 2008). When the first Oxfordian cyanobacteria-sponge buildups appeared in Europe, decapod crustaceans began to flourish and inhabited these biostructures in great numbers, expanded practically over the whole of Europe during the Oxfordian, from Portugal through Spain and France and to Germany, Poland, and Romania (Müller et al. 2000; Feldmann et al. 2006; Krobicki and Zatoń 2008). In turn, the latest Jurassic regression in the Peri-Tethyan area resulted in the disappearance of the sponge megafacies and led to changes of habitat, migration and colonisation of primitive crabs, for instance in the Štramberk coral reefs along the northernmost margin of the Tethys

Ocean, where these crabs probably reached an acme (Müller et al. 2000; Krobicki and Zatoń 2008).

The material described below originates from six localities in the southern Polish Uplands, northwest of Kraków (Fig. 1), as follows:

Ogrodzieniec.—On ammonite evidence, the section exposed at Ogrodzieniec Quarry can be dated as Early and Middle Oxfordian. With the exception of the discontinuous *Quenstedtoceras mariae* Zone, all zones and subzones from the *Cardioceras cordatum* to the *Gregoriceras transversarium* zones, have been documented (Główniak 2006).

Bzów.—This pit, the northerly portion of which is in the village of Bzów, represents a prolongation of the large quarry at Ogrodzieniec. Ammonites (*Ochetoceras canaliculatum* [von Buch, 1831], *Trimarginites trimarginatus* [Oppel, 1863], *Dichotomosphinctes* sp., *Glochineras subclausum* [Oppel, 1863]) collected at this locality have recently been identified by Günter Schweigert (personal communication 2011) (Staatliches Museum für Naturkunde, Stuttgart, Germany) and indicate the *Gregoriceras transversarium* Zone of the Middle Oxfordian. A single specimen in this lot might represent *Cardioceras tenuiserratum* Oppel, 1863, which would indicate the upper *Perisphinctes plicatilis* Zone (see also Matyja and Wierzbowski 1994).

Niegowonice.—The sequence exposed at this quarry ranges from the upper *Peltoceratoides elisabethae* Subzone to the upper *Dichotomoceras wartae* Subzone, i.e., is of Middle and Late Oxfordian age (Główniak 2006).

Grabowa.—The quarry is east to the quarry of Niegowonice and very close to it. The age of these sediments was until now not known from the literature. One accompanying ammonite was recently determined by Ewa Główniak and Andrzej Wierzbowski (personal communication 2011) as *Taramelliceras externodosum* (Dorn, 1930), which correlates with the Upper Oxfordian zone of the uppermost *Perisphinctes bifurcatus* to the lowermost *Epipeltoceras bimammatum* (*Euspidoceras hypselum* Subzone) (according to Główniak and Wierzbowski 2007: fig. 2).

Kroczyce.—As above, the age of these sediments has been recently determined by Główniak and Wierzbowski (2007) as Late Oxfordian (uppermost *Perisphinctes bifurcatus* to the lowermost *Epipeltoceras bimammatum* (Subzone: *Euspidoceras hypselum*) zones, on the basis of accompanying ammonites: *Taramelliceras externodosum*, *Glochiceras* (*Glochiceras*) *tectum* Ziegler, 1958, *Glochiceras* (*Coryceras*) aff. *canale* (Quenstedt, 1848) and *Taramelliceras* (*Richeiceras*) *jaeggii* Quereilhac, 2009. The biohermal basin of Kroczyce is c. 20 km long and extends in a NE-SW direction. It belongs to a complex of bioherms occupying over c. 100 km from NW to SE of the Polish Jurassic Chain (Matyja and Wierzbowski 2004).

Wysoka.—Główniak (2002) documented the *Perisphinctes plicatilis* Zone and the base of the *Gregoriceras transversarium* Zone at this quarry, i.e., the Middle Oxfordian.

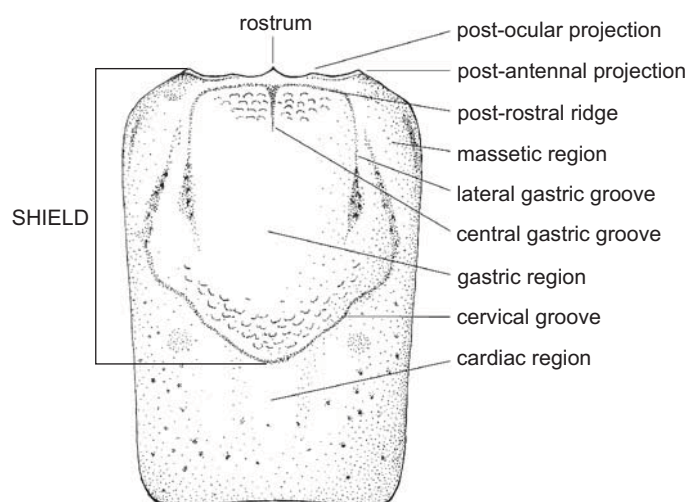


Fig. 2. Pylochelid carapace terminology employed in the present paper.

Paguroid carapace terminology

Despite the fact that paguroid carapaces very often display clearly developed and diverse morphological features, comparatively little attention has been paid to these features by neontologists. Carapace morphology amongst pylochelids is highly diagnostic (Fig. 2), as was demonstrated in a landmark study of this family by Forest (1987a: 17), who noted [translated from French], “The definitions and descriptions of the different taxa of Pylochelidae are based on numerous characters of external morphology. The shape, the proportions, and the lines and grooves of the cephalothoracic carapace and of the abdomen are probably the elements allowing an immediate generic identification...”. Unfortunately, in that particular paper, as well as in all subsequent work on pylochelids, descriptions of shield and carapace merely mention their size and the presence of a cervical groove and linea transversalis. Even in the most recent classification of the Pylochelidae (McLaughlin and Lemaître 2009: 162), the part of the diagnosis of the family which deals with carapace features is very meagre, “Carapace usually well calcified, at least anteriorly; incompletely or completely divided into shield and posterior carapace by linea transversalis; cervical groove contiguous or not with linea transversalis. Rostrum present or absent.”

In recent years, the number of fossil paguroid carapaces on record has steadily grown (e.g., Fraaije et al. 2008; Van Bakel et al. 2008; the present study). Data obtained from the study of these carapaces are a welcome addition to our understanding of phylogenetic relationships within the Paguroidea (Lemaître and McLaughlin 2009). In order to assess properly the phylogenetic “signal” preserved in these carapaces, a uniform descriptive terminology is called for and this would also allow the recognition of homologous structures or carapace regions. However, a survey of the biological literature has revealed an omission in the standard terminology of a particular region in a

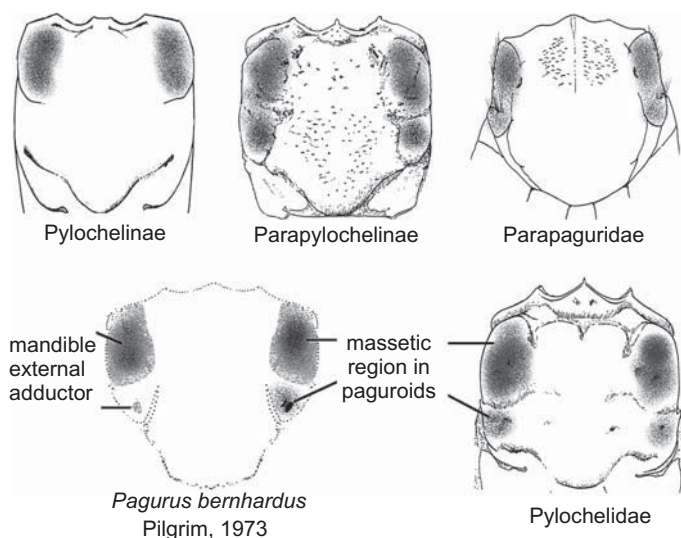


Fig. 3. The position of the massetic region (new term) in various paguroid families and subfamilies.

paguroid carapace, which is often very pronounced. In brachyuran crabs, the equivalent of this is referred to as the hepatic region, this area more or less reflecting the position of the underlying hepatic caeca (Stachowitsch 1992). In a detailed study of the internal muscular anatomy of the Recent *Pagurus bernhardus* (Linnaeus, 1758), Pilgrim (1973) demonstrated the presence of two areas of attachment of mandible muscles to the carapace. A large, powerful external adductor occupies and is attached to a large elongated-oval area of the anterolateral gastric region, whereas the much smaller external abductor is located posteriorly of the adductor within the same area. This region is at the same position of the hepatic region in brachyurans, but, in view of the fact that it does not reflect the location of the liver in paguroids, this should be named differently. Here we introduce the term “massetic region” (New Latin *massētēr*, from Greek *masētēr*, *massētēr*, to masticate or chew) for this morphologically clearly distinct region on the carapace, which constitutes the site of attachment of the mandibular adductor and abductor muscles.

This homologous region cannot be overlooked in representatives of nearly all paguroid families (Fig. 3). In some groups, it usually appears as an undivided, elongated-oval region (e.g., in the Pylochelinae), whereas in others (e.g., in the Parapylochelinae and Parapaguridae) there is a markedly larger anterior and a smaller posterior portion which are divided by a clear groove. It would appear that in all major taxonomic studies of the Pylochelidae, drawings rather than photographs are contained to illustrate the species described. While comparing line drawings of the same species in different studies, it seems that the massetic region was either interpreted differently, or even ignored, by the artist. For that rea-

son, we strongly recommend the use of photographs in all future studies of paguroids, and of pylochelids in particular. To stress this fact, one example will suffice here: compare e.g., *Trizacheles s. spinosus* in Forest (1987a: 203, fig. 70) and Forest et al. (2000: 46, fig. 11).

Amongst other extinct decapod crustaceans, there is only one group which has pronounced massetic regions. This is the closely related family Gastrodoridae (see Van Bakel et al. 2008: 149, figs. 9, 10b, d; Klompmaker et al. 2011: fig. 6). This observation also makes it highly probable that in the equally closely related Galatheoidea (e.g., Klompmaker et al. 2011), the term hepatic should also be replaced by massetic. Thorough studies, along the lines of Pilgrim's 1973 paper, are needed to resolve this matter.

Systematic palaeontology

The classification proposed by McLaughlin et al. (2010) is adopted here pending further refinements.

Anomura MacLeay, 1838

Paguroidea Latreille, 1802

Pylochelidae Bate, 1888

Trizochelinae Forest, 1987a

Genus *Ammopylocheles* Van Bakel, Fraaije, Jagt, and Artal, 2008

Type species: Ammopylocheles mclaughlinae Van Bakel, Fraaije, Jagt, and Artal, 2008 (by original designation); reefal limestone interfingering with the Felsenkalke Formation (“Weißjura delta”, *Aulacostephanoides mutabilis*/*Aspidoceras acanthicum* Zone; early Late Kimmeridgian) exposed in a quarry north of the village of Geisingen, southern Germany.

Ammopylocheles robertboreki sp. nov.

Fig. 4A–D.

Etymology: Named after Robert Borek, who collected the majority of specimens used in the present study, in the company of his wife Iwona and daughter Karolina.

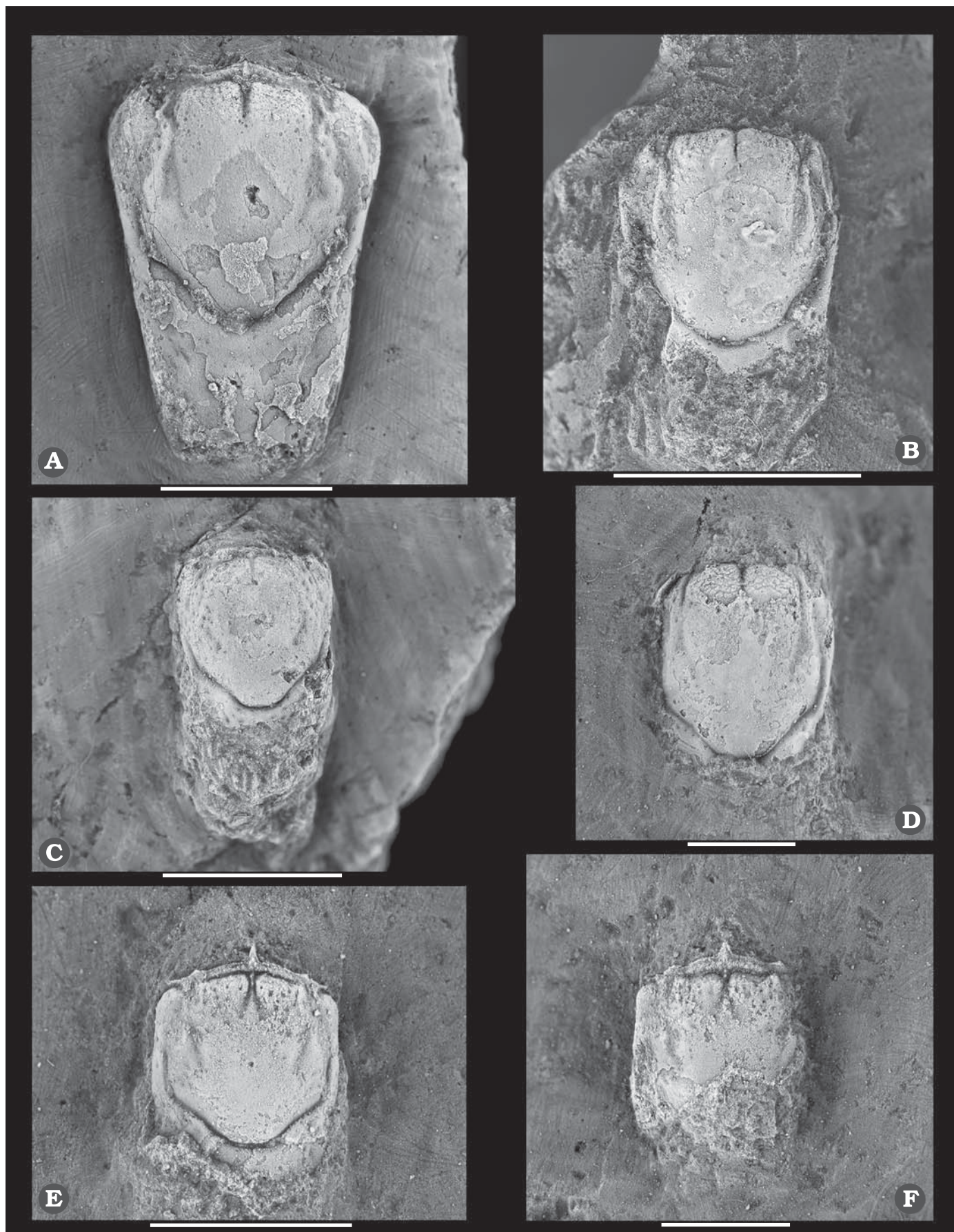
Holotype: ISEA I-F/MP/2745/1530/08 is a near-complete carapace (maximum length 11.5 mm, maximum width 8 mm).

Type locality: Wysoka, southern Poland.

Type horizon: *Perisphinctes plicatilis* Zone and base of *Gregoriceras transversarium* Zone (Middle Oxfordian; see Główniak 2002).

Referred material.—ISEA I-F/MP/6199/1577/10, a near-complete shield (maximum length 3.5 mm, maximum width 3 mm) from Ogrodzieniec; ISEA I-F/MP/6198/1577/10, a near-complete shield (maximum length 5 mm, maximum width 4 mm) from the same locality; ISEA I-F/MP/6197/1577/10, a near-complete shield (maximum length 7 mm, maximum width 4.5 mm) from Kroczyce.

Fig. 4. Pylochelid hermit crabs from Oxfordian (Jurassic) of southern Poland. **A–D.** *Ammopylocheles robertboreki* sp. nov. **A.** Holotype, ISEA I-F/MP/2745/1530/08 from Wysoka. **B.** ISEA I-F/MP/6198/1577/10 from Ogrodzieniec. **C.** ISEA I-F/MP/6197/1577/10 from Kroczyce. **D.** ISEA I-F/MP/6199/1577/10 from Ogrodzieniec. **E–F.** *Jurapylocheles iwona* sp. nov. **E.** Holotype, ISEA I-F/MP/3956/1533/08 from Bzów. **F.** Paratype, ISEA I-F/MP/6193/1577/10 from Ogrodzieniec. Scale bars: A–C 5 mm, D–F 2 mm.



Diagnosis.—Carapace longer than broad, shield as long as wide, broadest at centre of undivided massetic regions and clearly tapering posteriorly; small rostrum; distinct sinuous cervical furrow, central gastric groove and post-frontal ridge.

Description.—Carapace markedly longer than broad (W/L ratio 0.68), strongly convex in transverse section, convex in longitudinal section, markedly tapering posteriorly. Shield width and length approximately equal (W/L ratio 1.03); cervical groove prominent, a separate linea transversalis is absent; ornament of dorsal surface of gastric region consisting of small, imbricated granules on anterior and posterior sides; long longitudinal ridges at sides, bounded by lateral gastric grooves which tend to converge axially.

Small transverse post-rostral region with obscure rostrum; transverse, markedly convex, post-rostral ridge medially subdivided by a deep, central gastric groove; post-antennal projections obtuse. Lateral margins sloping, with highly globose, undivided massetic region. Posterior carapace shorter than shield, less well calcified, smooth, strongly tapering posteriorly.

Remarks.—The new species, of Middle Oxfordian age, differs from its Kimmeridgian congener, *Ammopylocheles mclaughlinae* (holotype: MAB k.2454), in having a transversely more convex, cylindrical and markedly posteriorly tapering carapace. The shift from a more cylindrical towards a more flattened carapace could be indicative of a change in hiding strategy. Currently, *A. robertboreki* sp. nov. is known from three localities at which the deeper, intra-reefal layered sponge limestone (Förster and Matyja 1986; Krobicki and Zatoń 2008) are exposed, while *A. mclaughlinae* inhabited areas closer to and within the shallower sponge reefs (Van Bakel et al. 2008). The absence of fragments of wood, scaphopods, larger serpulids and rock fragments at the type locality would suggest a possible mutualistic mode of life (pylochelid/ sponge) for *A. robertboreki* sp. nov., while *A. mclaughlinae* also had reefal debris available to hide in as well as under.

Geographic and stratigraphic range.—To date, known only from the southern Polish Uplands, northwest of Kraków, all material stemming from the Middle to Late Oxfordian.

Mixtopagurinae Forest, 1987a

Genus *Jurapylocheles* Van Bakel, Fraaije, Jagt, and Artal, 2008

Type species: *Jurapylocheles malutka* Van Bakel, Fraaije, Jagt, and Artal, 2008 (by original designation). Algal limestone of the “Riff-fazies” of the Kimmeridgian Untere Felsenkalke Formation (“Weißjura delta”, early Late Kimmeridgian, *Aulacostephanoides mutabilis*/*Aspidoceras acanthicum* Zone) exposed in a quarry north of the village of Geisingen, southern Germany.

Jurapylocheles iwona sp. nov.

Fig. 4E, F.

Etymology: Named after Iwona Borek, who, together with her husband

and daughter, collected numerous new decapod crustaceans from Oxfordian strata in the southern Polish Uplands.

Type material: The holotype (ISEA I-F/MP/3956/1533/08) is a near-complete shield (maximum length 2.0 mm, maximum width 1.9 mm) from Bzów; the single paratype (ISEA I-F/MP/6193/1577/10) also represents a near-complete shield (maximum length 3.0 mm, maximum width 2.8 mm) from Ogrodzieniec.

Type locality: Bzów, southern Poland.

Type horizon: *Gregoriceras transversarium* Zone and upper *Perisphinctes plicatilis* Zone (Middle Oxfordian; see above).

Diagnosis.—Shield as broad as long; small, sharp triangular rostrum; well-defined cervical groove effacing anteriorly, central gastric groove extending posteriorly into a distinct gastric process, pronounced postfrontal ridge with spine closely behind post-antennal projections.

Description.—Well-calcified shield, width equalling length, excluding rostrum; cervical groove most prominent centrally, initially convex posteriorly, proceeding slightly concavely and oblique forwardly and continuing almost parallel to the lateral border, effacing towards the post-antennal projections; dorsal surface of anterior part covered by coarse pits. A small, yet sharp and salient, triangular spine forming rostrum, with a short median crest; post-antennal projections small, each forming a blunt triangular spine faintly directed outwards; frontal ridge slightly concave and covered with granules; lateral regions straight and elongated, anteriorly with a globose, undivided massetic region; margins sloping and arched. Posterior margin of shield straight in centre and, following concave lateral curvature, extending longitudinally towards outermost post-antennal projections. Dorsal surface of shield with some swellings and additional faint furrows, anteriorly covered with coarse pits. Anterior central gastric groove extending posteriorly into a small gastric process; anterior portion of gastric region elevated, forming post-frontal ridge, curving backwards at level between post-antennal projections, having a triangular spine just behind post-antennal projections. Posterior carapace less well calcified and smooth, where preserved.

Remarks.—The new species is distinguished from the type species, *J. malutka* (Kimmeridgian, southern Germany; holotype MAB k.2453), by having post-frontal spines, a less angular cervical furrow and a more coarsely pitted anterior part of the shield.

Geographic and stratigraphic range.—To date, known solely from the southern Polish Uplands, northwest of Kraków, all material being of Middle to Late Oxfordian age.

Conclusions

The present pylochelid faunule from the Oxfordian of the southern Polish Uplands matches well that of the Kimmeridgian in southern Germany (see Van Bakel et al. 2008), with the same subfamilies and genera being represented. Probably as a result of the rise of brachyuran crabs and galatheid ano-

murans, which led to increased competition within shallow-marine near-reefal environments, pylochelids migrated from near-reefal environments to deeper-water settings during the Late Jurassic and have remained there ever since.

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