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New Late Jurassic symmetrical hermit crabs from the southern Polish Uplands and early paguroid diversification

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On the basis of carapaces, three new genera and species of symmetrical paguroid anomurans are described. *Diogenicheles theodora*, *Masticacheles longirostris*, and *Pilgrimcheles karolinae* constitute the oldest known members of the family Parapylochelidae. As noted previously, assemblages from sponge-reefal strata of Oxfordian (Late Jurassic) age in the southern Polish Uplands document an important radiation event amongst paguroids. Compared to the present day, the Parapylochelidae were more diverse during the mid-Mesozoic; they appear to have withdrawn from shallow, reefal waters to deep-water settings from the Late Jurassic onwards. Paguroid faunas from the Oxfordian of Europe already are highly diverse, both morphologically and phylogenetically, and comprise early members of the families Diogenidae, Pylochelidae, and Parapylochelidae. This suggests that the evolutionary history of paguroids started much earlier (i.e., in pre-Jurassic times) than previously assumed. New terms for several typical paguroid carapace regions are introduced and on the basis of carapace morphology and ecological shifts hypotheses on the early speciation of hermit crabs are put forward.

Key words: Anomura, Paguroidea, Parapylochelidae, carapace morphology, evolution, Oxfordian, Jurassic, Poland.

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Introduction

At the present day, only a single living parapylochelid hermit crab is known, *Parapylocheles scorpio* (Alcock, 1894) from the Indo-West Pacific, at depths between 200 and 1,000 metres (Forest 1987b; McLaughlin and Lemaitre 2009). Forest (1987b) was unable to find any characters that might have hinted at affinities with other genera then contained in the family Pylochelidae Bate, 1888, which is why he suggested that subfamily rank was appropriate for the monotypic genus *Parapylocheles* Alcock, 1901. Fraaije et al. (2012a) raised this taxon to family rank and recorded also a new genus and species within this family, *Mesoparapylocheles michaeljacksoni*,

from the mid-Cretaceous (Albian–Cenomanian) of Navarra (northern Spain). The new Late Jurassic taxa described herein illustrate an even more diverse array of parapylochelids in the fossil record. Co-occurring pylochelids, diogenids, and sixth abdominal tergites of unassigned paguroids from the southern Polish Uplands have previously been described by Fraaije et al. (2012b, c), and Fraaije et al. (2012d), respectively. For an overview of previous studies of Late Jurassic decapod crustaceans from Poland, reference is made to Collins and Wierzbowski (1985), Krobicki and Zatoń (2008), Starzyk et al. (2011, 2012), and Fraaije et al. (2012b–d).

An impressive collection of over 7,000 specimens of decapod crustaceans from about a dozen localities within the

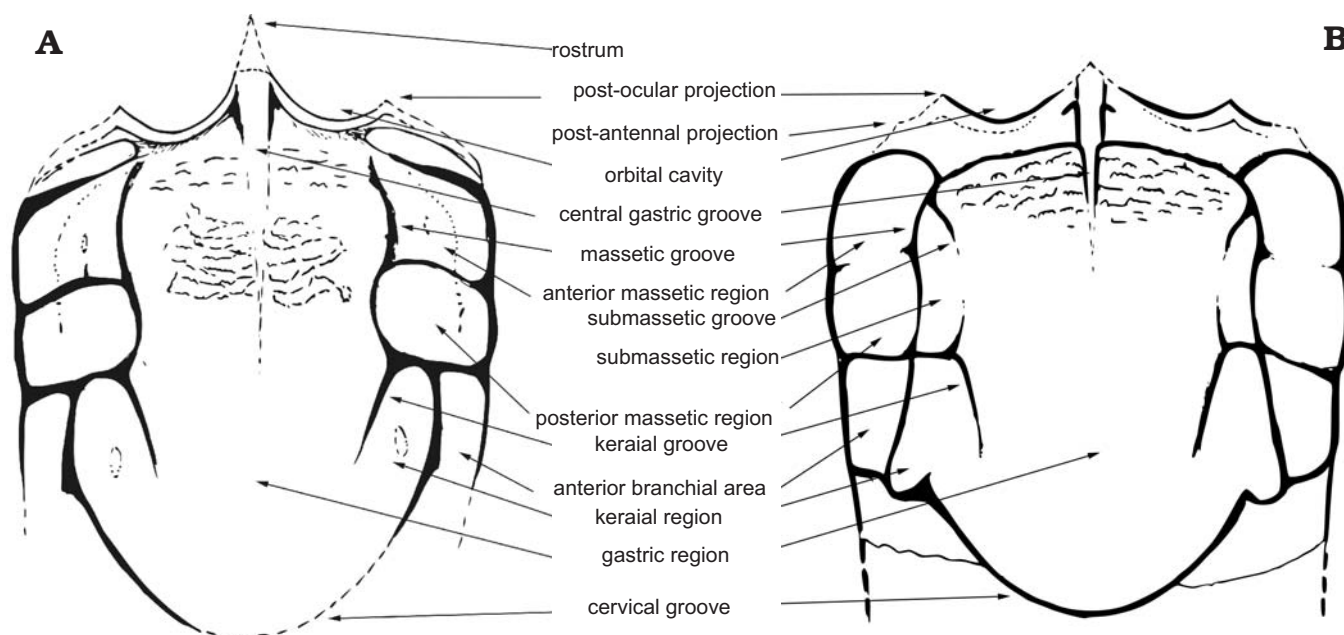


Fig. 1. Carapace terms for pylochelid (A) and parapylochelid (B) paguroids as employed in the present paper.

southern Polish Uplands, west of Kraków, was amassed by the Borek family of Dąbrowa Górnicza (southern Poland), over a period of two years. It is from this collection that the present parapylochelid material originates. Types have been transferred to the collections ISEA and MAB.

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

Introduction of new terminology

Unfortunately, carapace terminology (in particular of grooves and lineae) is subjective and rather inconsistent within macruran and brachyuran decapod crustaceans (Feldmann and Schweitzer 2010). In paguroids, terms for carapace features are rarely used, and if used, are inconsistently applied (discussed also by Fraaije et al. 2012b, c). Data obtained from studies of fossil carapaces are a welcome addition to the understanding of phylogenetic relationships within the Paguroidea, as indicated by Lemaitre and McLaughlin (2009). However, in order to assess properly the phylogenetic “signal” preserved in these fossil carapaces, a uniform descriptive terminology is needed. This would also allow the recognition of homologous structures or carapace regions (Fraaije et al. 2012c). In Fig. 1, we indicate and name all grooves and regions so that symmetrical hermit crab carapaces of the families Pylochelidae and Parapylochelidae can be described uniformly. Several new terms are introduced, namely the keraial and submassetic regions, and the keraial, massetic and submassetic grooves. An antero-medially forking groove extending from the cervi-

cal groove (= massetic groove as understood here) has previously been indicated by Boas (1880: fig. 141) and Pilgrim (1973: 366, fig. 1) and preliminarily referred to by them as “?linea d”, without further explanation.

For the oval to reniform area at the lateral anterior corners of the cervical groove we here introduce the name keraial region (from Greek *keraia*, antenna). In this specific area, the attachment of the muscle which led up to the antenna is situated (compare Pilgrim 1973: 388, fig. 7). For the small gastric region, parallel and central to the anterior massetic region, we here use the term submassetic region. Another region important for unravelling the phylogenetic history of the paguroids is located posterior of the massetic region and lateral of the keraial region. This was referred to as the anterior branchial area by Martin and Abele (1988: fig. 2).

Systematic palaeontology

Anomura MacLeay, 1838

Paguroidea Latreille, 1802

Parapylochelidae Forest, 1987b

Genus *Diogenicheles* nov.

Type species: Diogenicheles theodora sp. nov.; see below.

Etymology: In reference to the admixture of diogenid and parapylochelid carapace features.

Diagnosis.—Shield well calcified, length exceeding width, areolated, with distinct regions, including a large, undivided massetic region. Anterior portion of gastric region crenulate, with broad, crescentic post-rostral ridge medially indented by a central gastric groove; posterior part of cervical groove

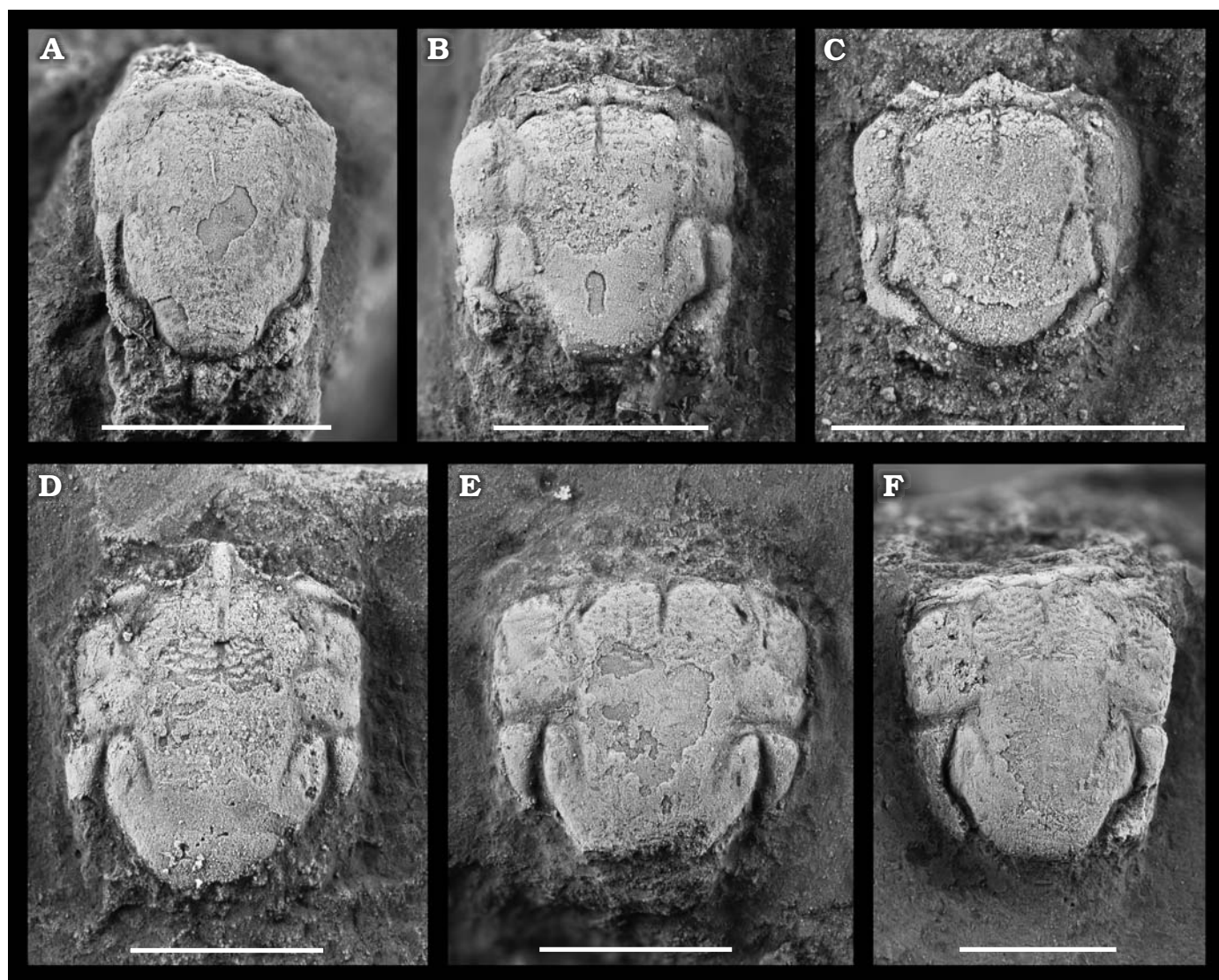


Fig. 2. Paguroid hermit crabs from the Oxfordian (Late Jurassic) of Bzów (A, B, E, F) and Ogródzieniec (C, D). **A.** *Diogenicheles theodora* gen. et sp. nov., holotype; I-F/MP/3957/1533/08(ISEA). **B, C.** *Pilgrimcheles karolinae* gen. et sp. nov. **B.** Holotype; I-F/MP/3953/1533/08(ISEA). **C.** Paratype MAB k. 3205. **D–F.** *Mastigacheles longirostris* gen. et sp. nov. **D.** Holotype; I-F/MP/6194/1577/10 (ISEA). **E.** Paratype; I-F/MP/3958/1533/08(ISEA). **F.** Paratype; MAB k. 3204. Scale bars 2 mm.

U-shaped. Distinct keraial region laterally bordered by elongated anterior branchial area.

Diogenicheles theodora sp. nov.

Figs. 2A, 3A.

Etymology: Named after Theodora van Boom, wife of the senior author, in acknowledgement of her patience and companionship during research of fossil paguroids.

Holotype: I-F/MP/3957/1533/08 (ISEA), a near-complete shield (maximum length 3.0 mm, maximum width 2.5 mm).

Type locality: Abandoned quarry at Bzów, a prolongation of the huge quarry at Ogródzieniec, southern Poland.

Type horizon: Ammonites [*Ochetoceras canaliculatum* (von Buch, 1831), *Trimarginites trimarginatus* (Oppel, 1863), *Dichotomosphinctes* sp. and *Glochioceras subclausum* (Oppel, 1863)] collected at this locality have recently been identified by Günter Schweigert (personal communication 2011). They 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).

Diagnosis.—As for the genus, by monotypy.

Description.—Well-calcified and areolated shield, length slightly exceeding width, subcylindrical transversely, slightly convex longitudinally. Relatively broad post-rostral area centrally covered by a ridge forming the base of the rostrum and posteriorly passing into shallow central gastric groove. Broad crescentic post-rostral ridge. Gastric region bounded laterally by massetic grooves, posteriorly by deep wavy U-shaped cervical groove; anterior part delimited by and covered by faint transverse crenulations. Mesogastric process absent. Elongated and undivided massetic region forming widest part of shield. Posterior part of wavy U-shaped cervical groove pro-

nounced and very deep, anterolaterally curving around reniform keraial region area. Distinct, elongated anterior branchial area present lateral to keraial region and posterior of massetic region. Cardiac region not preserved.

Remarks.—*Diogenicheles theodora* gen. et sp. nov. reveals certain similarities to the mid-Cretaceous (Albian–Cenomanian) diogenid *Annuntidiogenes worfi* Fraaije, Van Bakel, Jagt, Klompmaker, and Artal, 2009 (see also Fraaije et al. 2012a). Both forms have an elongated shield that becomes narrower posteriorly, anterior gastric crenulations, and an undivided, elongated and smooth massetic region. The typical distinct threefold junction of keraial, massetic and anterior branchial areas is observed only in the Parapylochelidae and therefore we assign *Diogenicheles theodora* to this family. It is distinguished from all other known parapylochelids by its elongated and undivided massetic region. The broad post-frontal ridge and the morphology of the gastric and keraial regions suggest a close relationship with *Pilgrimcheles karolinae* sp. nov. Unfortunately, the rostrum and frontal details are not preserved in the sole specimen known to date.

Genus *Masticacheles* nov.

Type species: *Masticacheles longirostris* sp. nov., see below.

Etymology: In reference to the pronounced massetic regions formed by several muscle attachment areas.

Diagnosis.—Shield well calcified, length slightly exceeding width, well areolated, with distinct regions, including more or less equal-sized anterior and posterior massetic regions, both wider than long. Rostrum prominent, triangular. Post-ocular spines distinct, triangular. Post-rostral ridge turning into central gastric groove. Anterior part of gastric region vermiculate, posterior part bluntly arrowhead-shaped to obtuse.

Masticacheles longirostris sp. nov.

Figs. 2D–F, 3B.

Etymology: In reference to the distinct rostrum.

Type material: Holotype is I-F/MP/6194/1577/10(ISEA), a near-complete shield (maximum length 3.0 mm, maximum width 2.5 mm), from Ogródzieniec; paratypes are I-F/MP/3958/1533/08 (ISEA), a near-complete shield (maximum length 3.5 mm, maximum width 3.0 mm), from Bzów, and MAB k. 3204, a near-complete shield (maximum length 4.0 mm, maximum width 3.5 mm), from the same locality.

Type locality: Large abandoned quarry at Ogródzieniec, southern Poland.

Type horizon: On ammonite evidence, the section exposed at Ogródzieniec can be dated as early to 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). The specimens most probably originated from the upper levels exposed at this locality.

Diagnosis.—As for the genus, by monotypy.

Description.—Well-calcified and clearly areolated shield, slightly longer than wide, strongly convex transversely, slightly convex longitudinally. Pronounced, slightly downturned, triangular rostrum, with a broad median ridge that extends towards the gastric region into a smaller central gastric groove. Orbital cavities rimmed and subcircular, bounded by triangular, forwardly directed, post-ocular spines. Ocular-frontal area equalling about 60% of maximum shield width. Antennal area bordered by elevated, elongated ridge. Posteriorly pointed, bluntly arrowhead-shaped to obtuse gastric region, bounded laterally by massetic grooves, posteriorly by deep V-shaped cervical groove; anterior part covered by transverse crenulations. Mesogastric process absent. Prominent, globose and rhomboidal anterior massetic region forming widest part of shield. Posterior massetic region of more or less equal size, but more elongated transversely. Both anterior and posterior massetic regions wider than long. V-shaped cervical groove pronounced and very deep, especially around the keraial region where the cervical groove has a typical crook on both sides. Lateral of the keraial region the major portion of an elongated anterior branchial area is present. Cardiac region or other more posterior parts are not preserved.

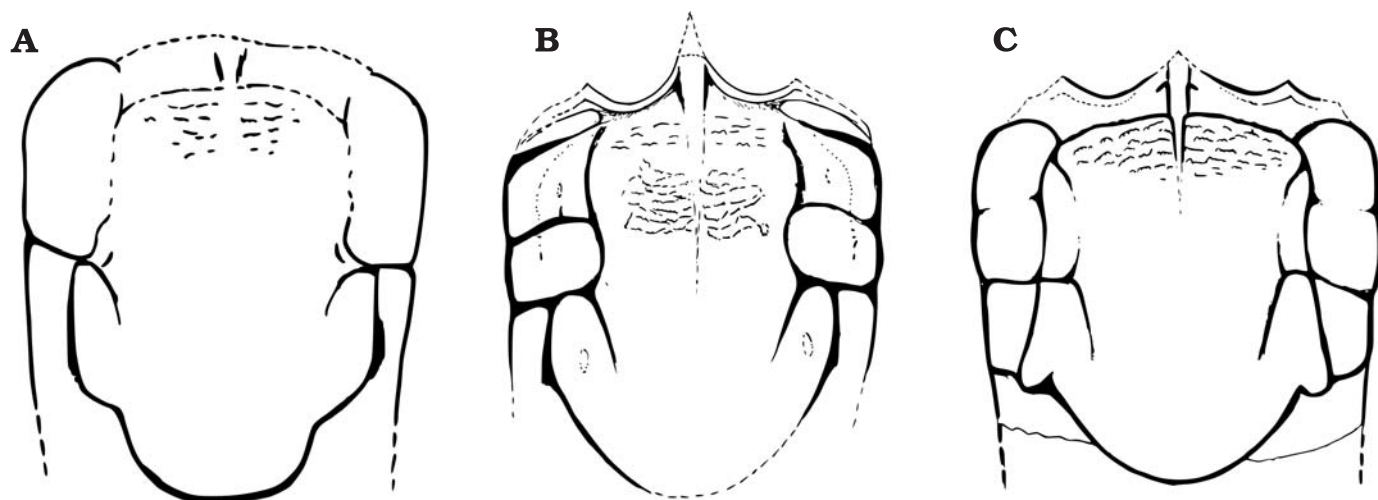


Fig. 3. Schematic dorsal views of shields of Late Jurassic (Oxfordian) hermit crabs. **A.** *Diogenicheles theodora* gen. et sp. nov. **B.** *Masticacheles longirostris* gen. et sp. nov. **C.** *Pilgrimcheles karolinae* gen. et sp. nov.

Remarks.—*Masticacheles longirostris* gen. et sp. nov. is yet another new member of the Parapylochelidae. Prior to this study only two species were known: *Mesoparapylocheles michaeljacksoni* Fraaije, Klompmaker, and Artal, 2012a (mid-Cretaceous; Navarra, northern Spain) and *Parapylocheles scorpio* (extant; Indo-Pacific Ocean, between 200 and 1,000 m; compare Forest 1987a). The new taxon can be distinguished by having a ridged rostrum, rimmed orbital cavities, more or less equal-sized massetic regions and a much less angular cervical groove. *Masticacheles longirostris* sp. nov. and *Mesoparapylocheles michaeljacksoni* are found, without any clue as to their ethology, in deposits laid down in relatively shallow-water, reefal settings, whereas *P. scorpio* is xylicolous, preferring mainly hollow pieces of bamboo, in relatively deep-marine environments. Thus, based on current data, parapylochelids appear to have migrated into deeper waters during the course of their evolution. The absence of suitable and transportable straight, hollow and firm shelters in Upper Jurassic and mid-Cretaceous sediments from which the material described originates (e.g., no dentaliid molluscs, serpulid tubes or wood fragments), allows to conclude that parapylochelids changed their ethology also, possibly preferring a mutualistic lifestyle with sponges. Several types of sponges are common in Mesozoic reefs. Such a mutualistic lifestyle, with hexactinellids and demosponges, is known for modern pylochelids (Forest 1987a).

Genus *Pilgrimcheles* nov.

Type species: *Pilgrimcheles karolinae* sp. nov.; see below.

Etymology: Named after Robert L.C. Pilgrim (1921–2010), whose seminal 1973 paper on the extant *Pagurus bernhardus* (Linnaeus, 1758) helped us understand fossil paguroid carapace morphologies.

Diagnosis.—Shield well calcified, length slightly exceeding width, well areolated, with distinct regions, including an anterior and posterior massetic region of equal size, paralleled by a adjacent submassetic region. Rostrum broad based, triangular. Post-ocular spines distinct, triangular. Anterior portion of gastric region delimited by post-rostral ridge, partially crenulate and with central gastric groove; posterior part shaped like a blunt arrowhead. Typically reniform keraial regions anteriorly at widest part of cervical groove, laterally bordered by the anterior branchial areas.

Pilgrimcheles karolinae sp. nov.

Figs. 2B, C, 3C.

Etymology: Named in honour of Karolina Borek, who, together with her parents, collected the majority of specimens used in the present study.

Types: Holotype is I-F/MP/3953/1533/08(ISEA), a near-complete shield (maximum length 3.0 mm, maximum width 2.5 mm), from Bzów; paratypes are MAB k.3205, a near-complete shield (maximum length 2.0 mm, maximum width 1.5 mm) from Ogrodzieniec and I-F/MP/6266/1599/12(ISEA), a near-complete carapace (maximum length 4.0 mm and maximum width 3.3 mm), from Niegowonice.

Type locality: Abandoned quarry at Bzów, a prolongation of the huge quarry at Ogrodzieniec, southern Poland.

Type horizon: Ammonites (*Ochetoceras canaliculatum*, *Trimarginites trimarginatus*, *Dichotomosphinctes* sp., and *Glochioceras subclausum*)

collected at this locality, have recently been identified by Günter Schweigert (personal communication 2011). They indicate the *Gregoriceras transversarium* Zone of the middle Oxfordian. A single specimen in this lot might represent *Cardioceras tenuiserratum*, which would indicate the upper *Perisphinctes plicatilis* Zone (see also Matyja and Wierzbowski 1994).

Diagnosis.—As for genus, by monotypy.

Description.—Well-calcified and clearly areolated shield, length slightly exceeding width, subcylindrical transversely, slightly convex longitudinally. Small, broad-based, triangular rostrum, with a broad, median ridge which towards the gastric region turns into a central gastric groove. Orbital cavity rimmed and subovate, bounded by triangular, forwardly directed, post-ocular spine. Ocular-frontal area equaling about 55% of total maximum width. Posterior pointed, bluntly arrowhead-shaped gastric region, bounded laterally by the massetic grooves, posteriorly by deep V-shaped cervical groove; anterior part delimited by prominent crescentic post-rostral ridge and covered by transverse crenulations. Mesogastric process absent. Prominent, globose and elongated anterior and posterior massetic regions forming widest part of shield. Central part of V-shaped cervical groove pronounced and very deep, curving around reniform keraial region, extending through massetic grooves almost linearly towards postfrontal ridge. Anterior of keraial region and paralleling the posterior massetic region occurs an elongated submassetic region. Lateral of keraial region a similar-sized anterior branchial area. Cardiac region or other posterior parts not preserved.

Remarks.—*Pilgrimcheles karolinae* gen. et sp. nov. can be distinguished from *Masticacheles longirostris* gen. et sp. nov. in having more elongated massetic regions instead of globose rhomboidal ones, and in having submassetic and keraial regions of reniform shape. *Mesoparapylocheles michaeljacksoni* and *Diogenicheles theodora* gen. et sp. nov. both have undivided massetic regions. Overall carapace morphology of *Pilgrimcheles karolinae* most closely resembles that of the extant *Parapylocheles scorpio* but differs in having a robust and ridged rostrum, broader orbital cavities and a divided massetic region.

Remarks on paguroid evolution

In recent years, numerous fossil paguroid carapaces have been recorded (Fraaije et al. 2008, 2009, 2012a–c; Van Bakel et al. 2008; Garassino et al. 2009). Based on these data, and on the present material, several preliminary ideas may be put forward. Firstly, during the Late Jurassic already a substantial diversity in carapace morphology is documented, with members of the families Diogenidae, Parapylochelidae, and Pylochelidae (and possibly Parapaguridae) being represented. The diogenids (one genus) reveal an evolutionary novelty in that an acute, V-shaped branchiocardiac and a subcircular cervical groove (as seen in the Triassic anomuran *Platykotta* Chablais, Feldmann, and Schweitzer, 2010) becomes fused to a single, sinuous groove (i.e., cervical groove) (Fraaije et al. 2012b).

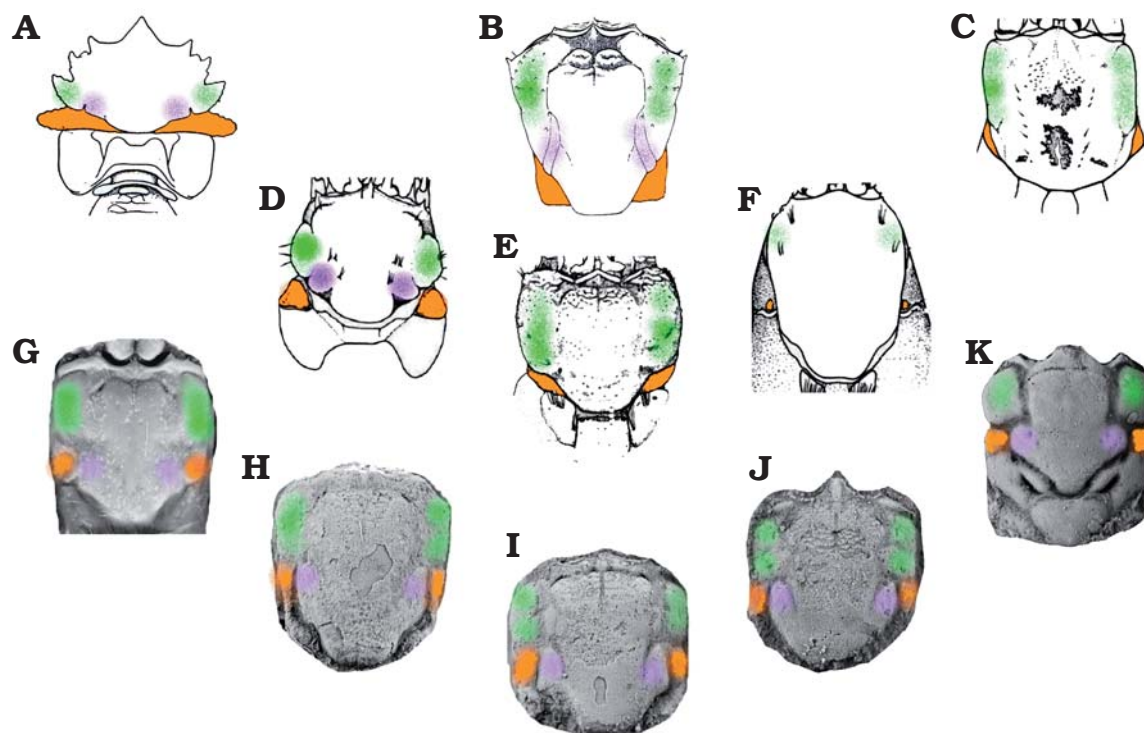


Fig. 4. Schematic dorsal carapace views, with the position of the massetic (green), keraial (purple), and lateral branchial (orange) regions in Paguridae (A, B), Diogenidae (C, D), Pylojacqueidae (E), Parapaguridae (F), and Parapylochelidae (G–K).

The Pylochelidae and Parapylochelidae are the most diverse and speciose paguroid families during the Late Jurassic, with two and three genera, respectively (Van Bakel et al. 2008; Fraaije et al. 2012c; the present study). One species, *Eotylaspis wehnerae*, was tentatively assigned to the Parapaguridae by Van Bakel et al. (2008), but this form might also turn out to be a parapylochelid. Better-preserved material is needed to substantiate this identification.

The marked morphological diversity based on paguroid carapaces from the Upper Jurassic, combined with the common occurrence of a wide array of paguroid cheliped remains in Lower and Middle Jurassic deposits (e.g., Van Straelen 1925; Jagt et al. 2006), hint at a Triassic, rather than a Late Jurassic, origin of the Paguroidea. This is consistent with recent phylogenetic studies that see hermit crabs as having a very early origin, out of which other groups such as squat lobsters (Galatheoidea) have arisen (e.g., Tsang et al. 2011; Ah Yong et al. 2011). Records of paguroids from the Upper Triassic or Lower Jurassic may thus be expected in the near future, provided that reefal sediments of this time interval are targeted and material properly assessed. A recent example concerns *Venipagurus mariae* Collins, 2011 from the Lower Jurassic (Black Ven Marls, lower Sinemurian) of Dorset, southwest England; this was described as the oldest (pylochelid) paguroid. To accommodate this form, Collins (2011) erected a new superfamily, Venipaguroidea, within the Anomura, yet failed to compare this with other anomuran superfamilies. However, carapace morphology of *Venipagurus mariae* reveals a much closer resemblance to that of a thalassinidean decapod, with

the longitudinal sutures representing the linea thalassinica, suggesting that this form was incorrectly assigned.

A number of primitive characters amongst various early paguroids involve an axial mid-line, a broad-based and pronounced rostrum, (bifid) spiny post-ocular projections and remains of a triangular cardiac region (Fraaije et al. 2012a–c).

The diogenids, pylochelids, and parapylochelids noted above all have clear massetic regions, a novelty which they share with the Gastrodoridae (see Klompmaker et al. 2011). Two groups, the Pylochelidae and Parapylochelidae, reveal another new feature, i.e., the keraial region and amongst early parapylochelids a clearly defined, twofold massetic region evolved. A threefold junction with a lateral branchial area bordered centrally by the keraial region and anteriorly by the massetic region is observed only within the Parapylochelidae. Schematic dorsal carapace views, with the position of the massetic (green), keraial (purple), and lateral branchial (orange) regions in Parapylochelidae, Paguridae, Diogenidae, Pylojacqueidae, and Parapaguridae are shown in Fig. 4.

Interestingly, the reproductive strategy of extant pylochelids, the single parapylochelid and certain diogenids (e.g., the genera *Cancellus* Milne Edwards, 1836 and *Paguristes* Dana, 1851) involves having few (maximum 20) large eggs with abbreviated larval stages. This type of reproduction (so-called “K-strategy” of reproduction) favours a high survival rate in places where appropriate shelters exist, but the absence or brevity of a larval stage considerably limits the capacity for dispersal for these species (Forest and McLay

2001). The evolutionarily younger pagurids and many diogenids produce numerous small eggs with many and long-lived, free-swimming larval stages (“R-strategy”), resulting in a more effective dispersal and radiation.

Extant pylochelids more often inhabit solid shelters, heavier than gastropod shells, and less mobile or even fixed, including fragments of wood or rock, calcareous algae or sponges. The habitats of “primitive” diogenids, such as *Cancellus*, are very close to those of the Pylochelidae. They either use existing cavities or hollow out new ones, in fragments of algae, bryozoans, coral, and rock. Some pylochelids and “primitive” diogenids inhabit sponges with which they may live symbiotically, since the sponges continue their growth and form a sheath around the carapace.

When field observations (i.e., absence of gastropod shells, presence of reef rubble, algae and sponges) are combined with the preservational state of the posterior carapace, the mode of life of Late Jurassic pylochelids and diogenids appears to have been closely comparable to extant members of these families. Parapylochelids have less well-preserved posterior carapaces and possibly covered their (posterior) carapaces already with or within soft-tissued symbiotic organisms. Parapylochelids were less widely distributed in Late Jurassic reefal settings, with but a few localities from southern Poland so far, while diogenids and pylochelids have been recorded from numerous localities in southern Poland and Germany (Fraaije et al. 2012b, c).

There is a general decreasing trend in size and complexity, in both the massetic and keraial regions, from the Jurassic onwards. Assuming that increase in size and complexity of these regions can be correlated with an increase in muscle strength, it would appear that Jurassic paguroids had dietary requirements which needed more mandibular cutting strength. In addition, for proper antennal function, more muscle power was called for the presumably longer and heavier antennae.

The transition from the Jurassic to the Cretaceous saw the radiation of (partially) new groups of marine phytoplankton and zooplankton, such as dinoflagellates, radiolarians, calpionellids, and planktonic foraminifera. The post-mortem accumulation of these microfossils enriched all marine environments with finely dispersed food particles and created many new benthic niches. Apparently, like other groups, such as bilaterally symmetrical echinoids, raninoidian brachyurans, and saccocomid crinoids, paguroids benefitted from this new food supply. In short, having been distributed within the Jurassic mainly in shallow reefal environments, hermit crabs relocated into both deeper and shallower marine environments. Changes in the availability of food items, detection of food source and a shift from immobile, or less mobile, solid shelters to empty, easily carried ammonite and gastropod shells, all had an impact on the development of the massetic and keraial regions in paguroids. Worthy of note is the fact that the mandibular cutting edge is chitinous in extant *Parapylocheles* but calcified in modern pylochelids; this possibly is an early (Mesozoic?) adaptation to different food sources.

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