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The earliest record of a diogenid hermit crab from the Late Jurassic of the southern Polish Uplands, with notes on paguroid carapace terminology

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A new species of diogenid paguroid, *Eopaguropsis nidiaquilae*, the earliest known member of the family to date, is recorded from sponge-reefal strata of Oxfordian (Late Jurassic) age in the southern Polish Uplands. Morphological features of the carapace suggest that the family Diogenidae diverged from other paguroid lineages such as the Pylochelidae and Parapaguridae, long before the Oxfordian Stage (161.2–155.7 Ma). The typically deep, V-shaped cervical groove of diogenids most likely was the product of fusion of the branchiocardiac and cervical grooves of their predecessors.

Key words: Paguroidea, Diogenidae, carapace morphology, evolution, Late Jurassic, Oxfordian, Poland.

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Introduction

At present, the family Diogenidae, commonly referred to as the “left-handed hermit crabs”, includes some of the largest, most colourful and most conspicuous marine paguroids. In number of species it comes second after the family Paguridae. In a recent overview (McLaughlin et al. 2010), twenty diogenid genera have been distinguished worldwide, except for Arctic and Antarctic seas. They are found in a wide range of habitats, ranging from fresh water and intertidal mangrove swamps to coral reefs and deeper offshore waters. Their acme of distribution lies in intertidal, subtidal, sublittoral, littoral and reefal environments, but they are known to extend to depths of around 300 metres on the continental shelf (Davie 2002).

Currently, eleven extinct diogenid genera, eight of them based exclusively on cheliped morphology (Schweitzer et al. 2010) and three on carapaces (Van Bakel et al. 2008; Fraaije et al. 2008, 2009; Garassino et al. 2009) have been described. Prior to the present note, the oldest diogenid on record was *Eopaguropsis loercheri* Van Bakel, Fraaije, Jagt, and Artal,

2008 from the Submediterranean Late Oxfordian (*Idoceras planula* Zone) of southern Germany. Other paguroids, recently recorded from the Middle to Late Oxfordian of southern Poland, include two species of pylochelid (Fraaije et al. 2012). The new diogenid described herein brings the total count of carapace-based paguroid taxa from the Polish Oxfordian to three.

Over a period of two years, the Borek family of the village of Dąbrowa Górnicza (southern Poland) succeeded in collecting in excess of 7,000 specimens of decapod crustaceans from about a dozen localities within the southern Polish Uplands, west of Kraków. This impressive collection, of which only less than one percent consist of paguroids, forms the basis of the present note as well as of several ongoing studies on anomurans, brachyurans (Starzyk et al. 2011), and macrurans.

Institutional abbreviation.—ISEA, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland.

Other abbreviations.—L, length; W, width.

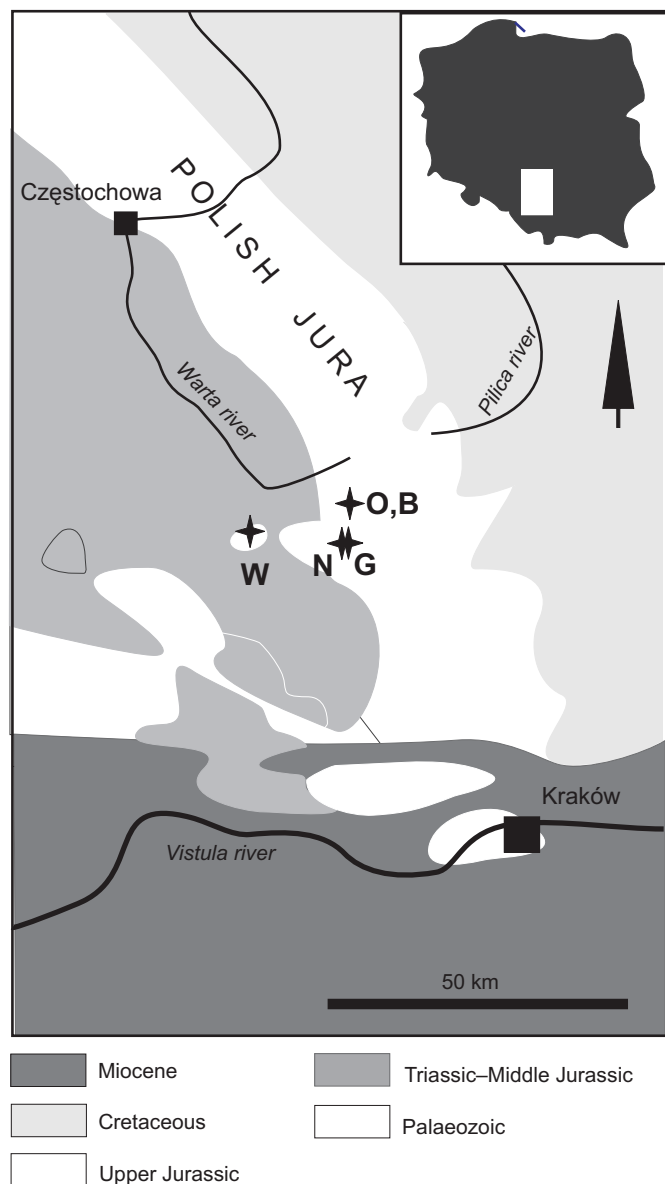


Fig. 1. Localities with diogenid-bearing strata of Middle–Late Oxfordian age in southern Poland (see inset), as follows: B, Bzów; G, Grabowa; N, Niegowonice; O, Ogrodzieniec; W, Wysoka (modified after Główniak 2006: fig. 2).

Geographic and stratigraphic setting

The material described below originates from five localities in the southern Polish Uplands (known as Polish Jura), north-west of Kraków (Fig. 1), whose age and geographical position was given in detail by Fraaije et al. (2012).

Ogrodzieniec.—Lower and Middle Oxfordian (according to 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 accompanying indicate the Mid-

dle Oxfordian *Gregoriceras transversarium* 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 uppermost *Perisphinctes bifurcatus* to lowermost *Epipeltoceras bimammatum* (*Euaspidoceras hypselum* Subzone) zones of Late Oxfordian age (compare Główniak and Wierzbowski 2007: fig. 2).

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

Systematic palaeontology

For the time being, we here adopt the classification proposed by McLaughlin et al. (2010).

Anomura MacLeay, 1838

Paguroidea Latreille, 1802

Diogenidae Ortmann, 1892

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

Type species: *Eopaguropsis loercheri* Van Bakel, Fraaije, Jagt and Artal, 2008. Quarry southeast of Gosheim, southern Germany, Late Oxfordian, Late Jurassic.

Eopaguropsis nidiaquilae sp. nov.

Fig. 2A–E.

Etymology: From Latin *nidi aquilae*, an eagle's nest; in reference to the medieval castle of Ogrodzieniec, which was called eagle's nest, like other surrounding castles.

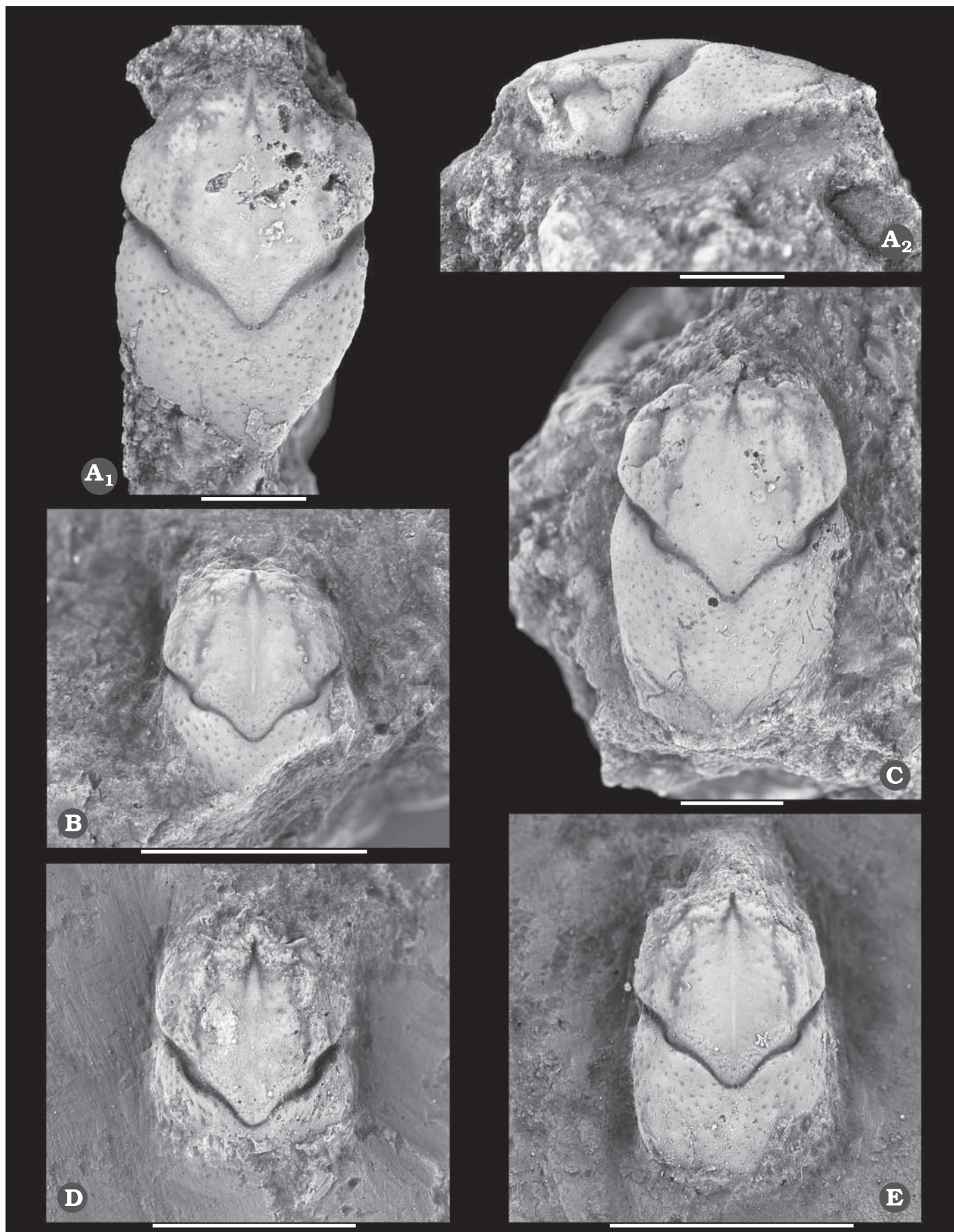
Type material: The holotype (ISEA I-F/MP/2747/1530/08) is a near-complete carapace (maximum length 19 mm, maximum width 12 mm) from Niegowonice; paratype is ISEA I-F/MP/2744/1530/08, a near-complete carapace (maximum length 19 mm, maximum width 12 mm) from Ogrodzieniec.

Type locality: A limestone quarry near Niegowonice.

Type horizon: Upper *Peltoceratoides elisabethae* Subzone to the upper *Dichotomoceras wartae* Subzone (Middle and Late Oxfordian) (Główniak 2006).

Additional material.—ISEA I-F/MP/5343/1543/09, a near-complete shield (maximum length 5 mm, maximum width 4.5 mm) from Grabowa; ISEA I-F/MP/2811/1530/08, a near-complete shield (maximum length 4 mm, maximum width 3.5 mm) from Wysoka, and ISEA I-F/MP/4626/1534/08, a

Fig. 2. Diogenid hermit crab *Eopaguropsis nidiaquilae* sp. nov. **A.** Holotype ISEA I-F/MP/2747/1530/08, a near-complete carapace (maximum length 19 mm, maximum width 12 mm) from Niegowonice, in dorsal (A_1) and lateral (A_2) views. **B.** ISEA I-F/MP/5343/1543/09 from Grabowa. **C.** Paratype ISEA I-F/MP/2744/1530/08 from Ogrodzieniec. **D.** ISEA I-F/MP/2811/1530/08 from Wysoka. **E.** ISEA I-F/MP/4626/1534/08 from Bzów. Scale bars 5 mm.



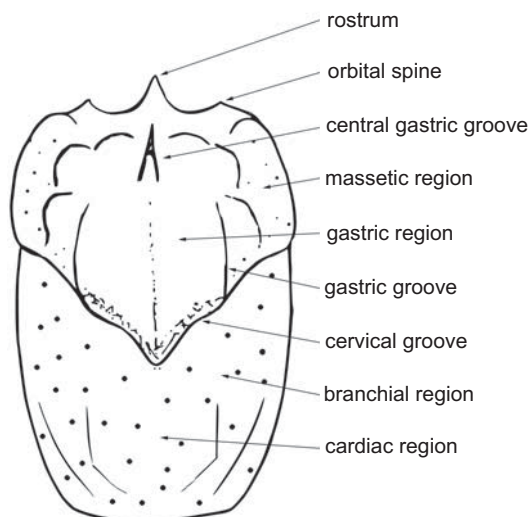


Fig. 3. Drawing of diogenid hermit crab carapace, illustrating morphological terms used herein.

near-complete carapace (maximum length 6 mm, maximum width 4 mm) from Bzów.

Diagnosis.—Carapace longer than wide, shield slightly longer than wide, broadest at centre of massetic regions; distinct triangular rostrum; deep, V-shaped, sinuous cervical groove; central gastric process.

Description.—Carapace markedly longer than wide (L/W ratio 1.58), strongly convex in transverse section, convex in longitudinal section. Shield slightly longer than wide. Triangular rostrum. Subcircular orbital rim ending in blunt outer orbital spine. Prominent central gastric process ending in a deep incision at base of rostrum. Frontal region and elongated massetic region covered with coarse pits and tubercles. In between the massetic and gastric regions, starting just anteriorly of the cervical groove, a row of three oval, tuberculate elevations curve towards the mesogastric process. Especially in juvenile specimens (Fig. 2B, E), the gastric region shows a thin mid-line which extends from the gastric process to the base of the cervical groove. Prominent V-shaped, very deep, sinuous cervical groove, widest and deepest anterolaterally; where it joins the gastric grooves, a typical kink is formed. The cervical groove is bordered anteriorly by a small row of crenulations between the gastric grooves. Two close-set pits occur just posterior of the most acute point of the cervical groove. Anterior part of dorsal carapace is less calcified and regularly covered with very coarse pits. Thin cardiac grooves delineate the cardiac region laterally and posteriorly, while two thin branchial grooves occur in the posterobranchial corners.

Remarks.—*Eopaguropsis nidiaquilae* sp. nov. differs from the type and only other known species of the genus, *E. loercheri* (Submediterranean Late Oxfordian, southern Germany), in having a less pronounced kink where the gastric and cervical grooves meet and a more subdued ornament of the frontal and lateral portions of the shield. The new species is now known from five localities at which the intrabuildups layered sponge limestone (Förster and Matyja 1986; Krobicki and

Zatoń 2008) are exposed, which makes it the commonest paguroid in Middle Oxfordian deposits of the Kraków area.

Discussion

In composition, paguroid faunules from the Oxfordian of southern Poland are nearly identical to those recorded from the Late Oxfordian–Early Kimmeridgian of southern Germany (Van Bakel et al. 2008). Garassino and Schweigert (2006: 24, pl. 15: 2) illustrated *Orhomalus deformis* (Oppel, 1862) from the Tithonian (Late Jurassic, 150.8–145.5 Ma) of Solnhofen, southern Germany. The type, and sole specimen known to date, was assigned by those authors to an “Indeterminate Family”. We consider this to be a possible diogenid that, in view of the fact that it preserves a near-complete carapace as well as several pereiopods, warrants a detailed redescription.

Concluding remarks

Feldmann and Schweitzer (2010) noted that identification of the various grooves and lineae in fossil decapod crustaceans was a more or less subjective matter, despite the fact that such have commonly been used in cladistic analyses and assumed homologous. Carapace terminology in paguroids is certainly not consistent either; compare, for instance, the location of cervical grooves and the linea transversalis in McLaughlin and Lemaitre (2001: 1065, fig. 2) and McLaughlin (2003: 230, fig. 1) with that of the linea anomurica in Forest (1987: 19, fig. 1) and Lemaitre (1995: 2, fig. 1). Even interpretations of carapace shape differ amongst authors (e.g., McLaughlin et al. 2007). Moreover, some species are discriminated primarily on colour pattern, with only subtle morphological differences noted (Hirose et al. 2010). It is striking that since Mayo’s (1973) landmark study of the diogenid genus *Cancellus* Milne Edwards, 1836, no clear and detailed diagrammatic illustrations of carapaces have been included in any paper on extant diogenids. To complicate matters further, in all subsequent descriptive studies of diogenids that we have been able to consult, there is no reference to Mayo (1973). Instead, reference is made either to McLaughlin (2003), which lacks any illustration of a diogenid carapace (see Osawa and Fujita 2008), to other studies which suffer from these same shortcomings (McLaughlin 1974; Forest et al. 2000; see also Asakura 2002), or to more extensive work in which carapace morphology is not considered in generic and specific diagnoses (e.g., Morgan 1991).

Fossil carapaces such as the ones described herein are thus of note in helping unravel the origin of carapace regions and grooves and, thus, the phylogeny within the Paguroidea. In this respect, Fraaije et al. (2012) introduced a new term to describe a homologous paguroid carapace feature, the massetic region. In attempting to understand the carapace morphology of the earliest known paguroid, we have com-

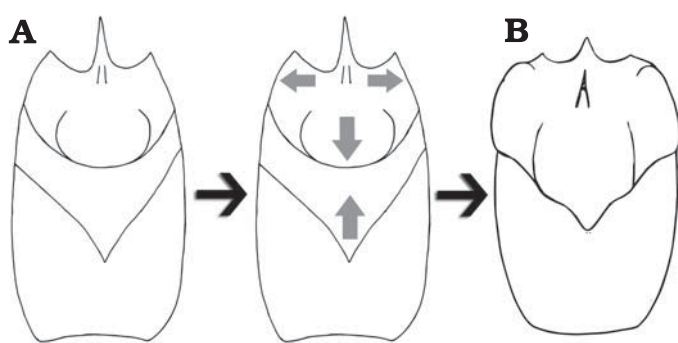


Fig. 4. Explanation of the hypothesised origin (centre) of the cervical groove and massetic region, in transition from the Triassic anomuran *Platykotta akaina* (A) to *Eopaguropsis nidiaquilae* sp. nov. (B).

pared it to the recently discovered Late Triassic anomuran *Platykotta akaina* from the United Arab Emirates (Chablais et al. 2011). The possible origination of the single (cervical) groove in extant diogenids is illustrated in Fig. 4. The carapace morphology of *Eopaguropsis* shows two major novelties; the most striking of which is the fusion of the V-shaped branchiocardiac and the subcircular cervical groove (as seen in *Platykotta*) to a fused sinuous groove (cervical groove) in *Eopaguropsis*. Secondly, the frontolateral region is widened to form the massetic region. Interestingly, juvenile specimens (Fig. 2B, E) of *E. nidiaquilae* sp. nov. reveal a clear midline along the axis of the shield. This could be a relict of even earlier macruran roots. Altogether, the anterior part (shield) of the carapace in *Eopaguropsis* is much enlarged, which probably is the result of making room for the strong mandibular muscles (reflecting diet) and the first three pairs of pereopods (reflecting movement). The less calcified anterior carapace is covered with numerous coarse (setal?) pits. *Eopaguropsis* probably relied on epibionts for camouflage and protection, in a fashion similar to many extant paguroids (Fernandez-Leborans 2010). For instance, *Paguropsis typica* is well known for its symbiosis with cnidarians (Ates 2003; Williams and McDermott 2004) which are held directly by the hermit crab itself, thus covering its abdomen, and are not attached to a gastropod shell.

Only a single example of sea anemone/juvenile hermit crab association has ever been recorded. The megalopae of *Paguropsis typica* in the Indo-West Pacific host an unidentified nyanthean actinian that attaches singly to the abdomen (Schäfer et al. 1983). Those authors noted that the dumb-bell-shaped anemones might feed on food dropped by the megalopae. Such “advanced” symbiotic relationships and the fact *Paguropsis* has semi-symmetric chelae and abdomen (rare amongst diogenids; see Morgan 1990) appear indicative of a long geological record. The common occurrence of *P. typica* at depths of 350 metres (Thomas 1989) illustrates the same evolutionary/ecological pathway, i.e., from shallow to deeper waters, as that documented for pylochelids from the Oxfordian onwards (Fraaije et al. 2012).

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