



A new hermit crab out of its shell from the Eocene Arguis Formation, Huesca, Spain

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Semi-articulated paguroids are rare fossils, and there are only few records from Cenozoic strata. Here we present a new and exceptionally preserved hermit crab (Diogenidae) from the Eocene of Huesca (Spain) that preserves the anterior part of the carapace, together with appendages. *Diogenes augustinus* sp. nov. represents one of most completely preserved hermit crabs known to date, providing crucial information to understand the evolution of the family Diogenidae. It is characterized by poorly marked regions of shield, absence of Y-line and markedly unequal and robust chelipeds. The specimen is preserved out of its host shell suggesting rapid burial in siliciclastic strata of a prodeltaic environment.

Introduction

Hermit crabs (superfamily Paguroidea Latreille, 1802) are an iconic group of decapod crustaceans with very specialized characteristics that usually include a poorly mineralized and asymmetric abdomen. This is the result of a life confined to empty gastropod shells (e.g., Walker 1992), or in cavities of sponges, corals and plant remains (e.g., De Forges et al. 2001). Due to the weakly mineralised body and articulations, the fossil record of paguroids is poor and often dominated by isolated chelipeds and other dissociated remains (e.g., Hyžný et al. 2016; Fraaije et al. 2020, and references therein).

Examples of articulated hermit crabs in the fossil record are rare, and only few nearly complete specimens are known; in most cases preserved in situ, inside gastropods or other shells (see Fraaije and Polkowsky 2016 and Pasini et al. 2020, who summarized main records). Because they hide naturally inside shells, hermit crabs usually reveal only a small part of their anatomy (for instance, chelipeds and sectioned pereopods) or occur as incomplete remains with articulated chelipeds (e.g., Schweitzer and Feldmann 2001; Fraaije et al. 2011). So far, for only seven specimens, the anterior part of the carapace (shield), in association with, chelipeds have been recorded (Jagt et al. 2006; Garassino and Schweigert 2006; Fraaije et al. 2008; Garassino et al. 2009; Schweigert et al. 2013; Fraaije and Polkowsky 2016; Pasini et al. 2020). This information allows a better understanding of how chelipeds are associated with body fossils. Here we describe an extraordinary example of a paguroid from the Eocene Arguis Formation (South Pyrenean Basin, northeast Spain) that is

preserved out its host shell and retains a partial carapace, plus chelipeds and walking legs.

Institutional abbreviations.—MPZ, Museo de Ciencias Naturales de la Universidad de Zaragoza, Spain.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in Zoobank: urn:lsid:zoobank.org:pub:1B4F2880-02E2-4D94-958F-4E30C973536F

Geological setting

The present material comes from sandstone and marly beds in the lower part of the Arguis Formation (middle–upper Eocene), as exposed along the southern margin of the Jaca-Pamplona Basin, between the villages of Belsué and Lúsera (Huesca) (co-ordinates 42°18'54" N, 0°20'41" W). This basin, located in the south-central Pyrenean zone (Sierras Exteriores), formed in consequence of the propagation of the Pyrenean tectonic structures during the Paleogene (Millán et al. 1994; Huyghe et al. 2009). This propagation during the middle and late Eocene resulted in the formation of reliefs that became part of sediment source areas for deltaic complexes (Dreyer et al. 1999).

The Arguis Formation (latest Lutetian–early Priabonian) consists of four deepening–shallowing third-order sequences, I to IV (Millán et al. 1994). Specifically, the paguroids described come from prodeltaic sandstone found in the lower part of Sequence II as described by Millán et al. (1994). The late Bartonian age of Sequence II is well constrained by magnetostratigraphical and palaeontological data (Pueyo et al. 2002; Silva-Casal et al. 2019). The Arguis Formation includes highly fossiliferous intervals, with benthic foraminifera, decapod crustaceans, echinoderms, and molluscs (e.g., Ferratges et al. 2020).

Systematic palaeontology

Systematic classification follows McLaughlin (2003) and carapace terminology follows Fraaije et al. (2019).

Order Decapoda Latreille, 1802

Infraorder Anomura MacLeay, 1838

Superfamily Paguroidea Latreille, 1802

Family Diogenidae Latreille, 1802

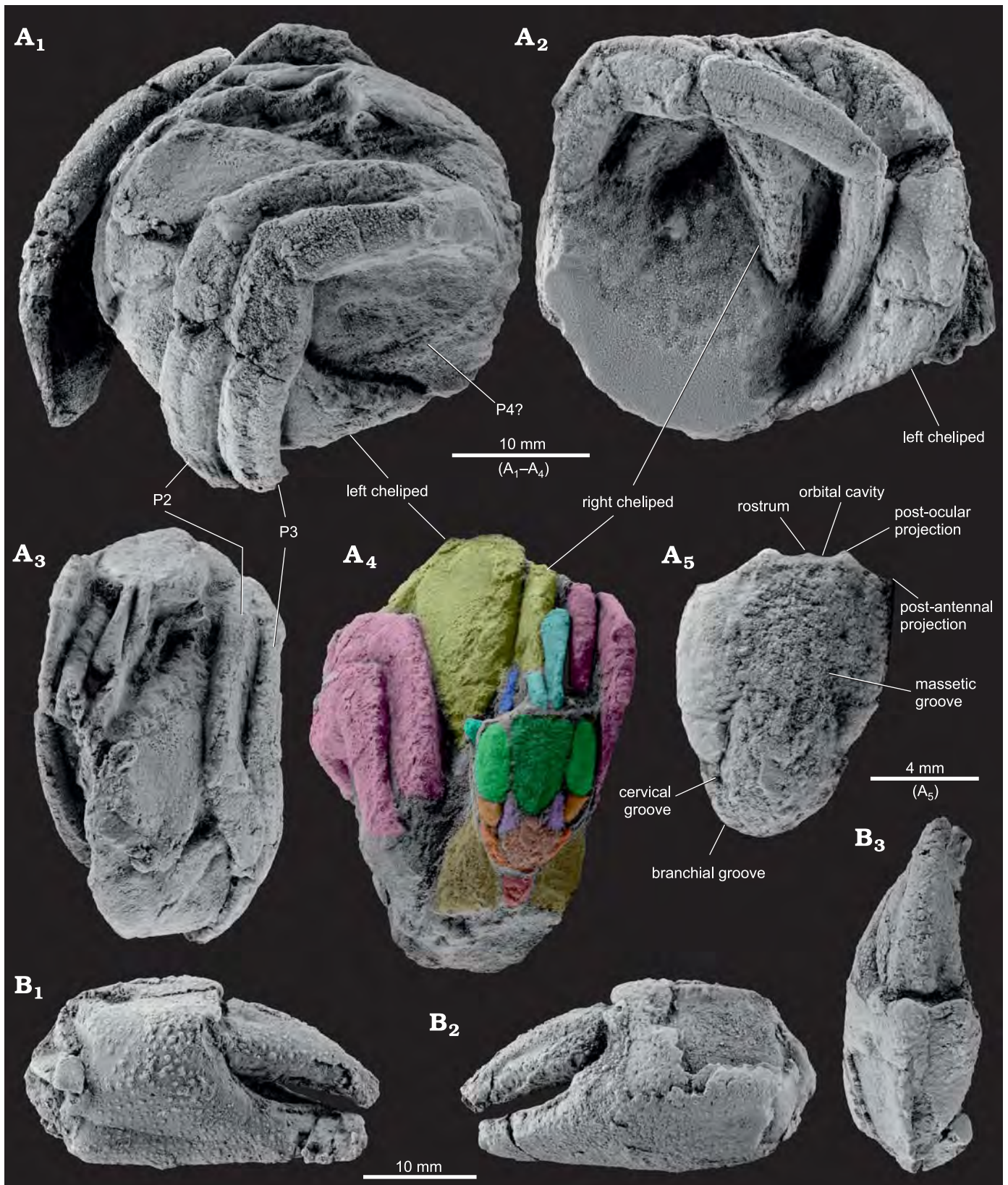


Fig. 1. Paguroid crab *Diogenes augustinus* sp. nov. from the upper Bartonian of Arguís Formation, Eocene, Lúsera, Huesca, Spain. **A.** Holotype (MPZ2020/54), in left lateral (A_1), right lateral (A_2), and frontal (A_3) views. Dorsal region details (A_4): light blue, eyestalk; dark blue, maxilliped?; turquoise, antenna; light green, massetic; dark green, anterior gastric; orange, lateral branchial; purple, keraial; light orange, anterior branchial; dark orange, mesobranchial; dark yellow, metabranchial; red, cardiac. Shield details (A_5): P_2 , P_3 , $P_4?$, pereiopods. **B.** MPZ2020/55, paratype, isolated left cheliped in mesial (B_1), outer (B_2), and dorsal (B_3) views. Specimens have been photographed dry and coated with an ammonium chloride sublimated.

Genus *Diogenes* Dana, 1851

Type species: *Pagurus miles* Fabricius, 1787, by subsequent designation of Stimpson (1859); Eocene–Recent.

Diogenes augustinus sp. nov.

Figs. 1, 2.

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Etymology: In honour of Agustín Gálvez (Zaragoza, Spain) who found and donated the specimen.

Type material: Holotype: MPZ2020/54, articulated specimen, partial carapace, plus chelipeds and walking legs. Paratypes: MPZ2020/55 and MPZ2020/56, isolated chelipeds. From the type locality and horizon.

Type locality: Village of Lúsera, Huesca Province, Spain.

Type horizon: Arguis Formation, upper Bartonian, middle–upper Eocene.

Material.—Type material only.

Diagnosis.—Shield longer than wide, length/width ratio 1.32, slightly convex transversely and longitudinally; rostrum not prominent. Orbital cavity concave, shallow antennal cavities. Regions of shield poorly marked; massetic region elongated, with perpendicular striate. Anterior branchial area globose, subtriangular. Eyestalks smooth, shorter than shield, diameter 1.42 mm. Chelipeds markedly unequal, left largest; palm quadrate, without stridulatory mechanism on mesial face of palm. Carpus triangular; axis of carpal-propodal articulation oblique in relation to sagittal plane. P2 merus depressed on outer side. Dorsolateral faces of propodus covered with small granules. Dactyls of P2 and P3 about same length as propodus, margin smooth.

Measurements (in mm).—MPZ2020/54: shield length 10.74; shield width 8.08; eyestalk length 7.63; left manus length 15.12; left manus height 14.29; right manus length 8.01; right manus height 7.05. MPZ2020/55: major cheliped height 19.35; length 17.74. MPZ2020/56: major cheliped height 17.33.

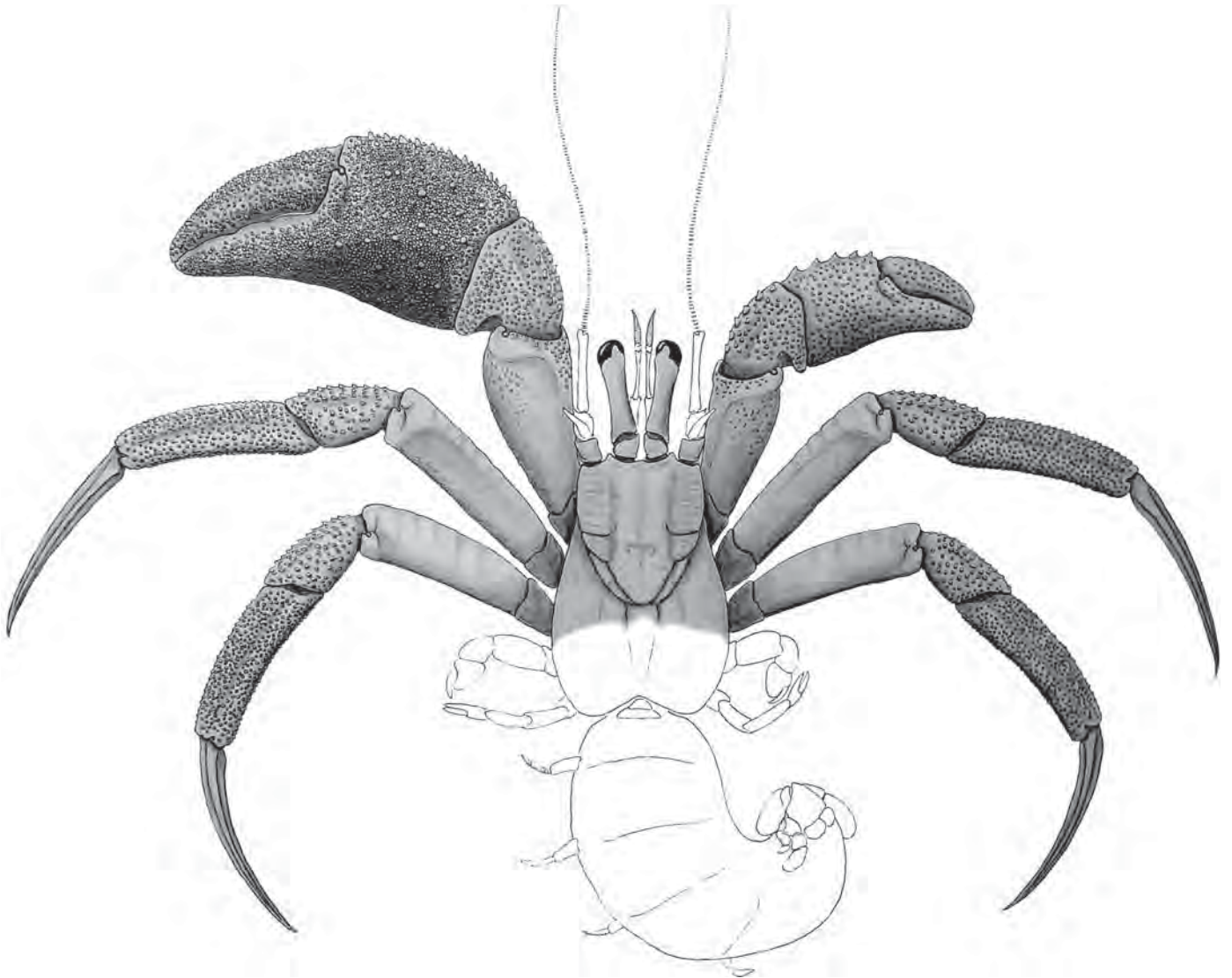


Fig. 2. Reconstruction of *Diogenes augustinus* sp. nov. Parts shown in grey are those preserved in the fossil material available. Other parts have been reconstructed from the most closely related modern taxa.

Description.—Shield longer than wide, slightly domed; surface roughened by shallow grooves, except for most of gastric region which is smooth with a subtle longitudinal ridge; rostrum weakly developed; anterior margin weakly convex; orbital cavity shallow; post-ocular projection acute; post-antennal projection slightly rounded; central gastric furrow present, but weakly developed; massetic groove weakly marked; massetic region elongated, with perpendicular stretch marks; keraial region poorly differentiated; gastric regions flat; U-shaped cervical groove; posterior carapace not well preserved (Fig. 1A). Eystalks slightly longer than half length of shield. Chelipeds markedly unequal, with the left considerably larger; without stridulatory mechanism developed on the mesial face of the palm. Major cheliped: palm longer than broad, lateral surface of carpus covered with densely small granules; upper margin with pointed conical granules; weakly granulated dorso-ventrally (Fig. 1). Minor cheliped: palm covered by small and conic wide-spaced granules, upper margin with five pointed teeth. Merus and carpus of both chelipeds less granulated than palm; subtriangular fixed finger broad at base, with rounded distal extremity; fingers curved ventromesially; moveable finger longer than mesial margin of palm. Ambulatory legs symmetrical; merus subrectangular and elongate, upper margin convex, less ornamented than carpus and propodus; outer side of P2 merus depressed to accommodate P3; carpus subtriangular; carpus and propodus of P2–P3 with slightly serrated dorsal margins. Dactylus of ambulatory legs as long as propodus, broadly curved (Figs. 1, 2).

Remarks.—Reconciliation of fossils and neontologist classifications are problematic, because most of the taxonomic features to differentiate between modern genera are not preserved in extinct material (e.g., Jagt et al. 2006; Fraaije 2014; Fraaije et al. 2014). This drawback is exacerbated by the fact that the majority of fossil paguroids are found as disarticulated elements or, in the best cases, they are hidden inside gastropod shells; and this hampers our ability to provide a complete description of specimens. This explains why the systematic placement of fossil paguroids is fraught with difficulties (Fraaije and Polkowsky 2016). Fortunately, the material described herein includes both the chelipeds and the carapace and represents one of the few examples in which all of the anterior portion of the animal is available.

Despite these drawbacks, McLaughlin (2003) listed important morphological characters to distinguish between different modern taxa that can also be recognised in fossil species. For instance, Fraaije et al. (2019), among others, included detailed data on shields of extant taxa that can be seen in fossils.

The material studied retains delicate diagnostic characteristics, such as the morphology of the shield, cheliped ornamentation, ocular peduncles and ambulatory legs. This allows its definite assignment to the family Diogenidae. We include the new taxon in *Diogenes* on the basis of similarities in features of chelipeds, pereopods and distribution of dorsal carapace regions. Our material also shows corrugated and poorly defined massetic regions, a gastric region without Y-line and eystalks that are long and thin (Fig. 2). Diogenids of Eocene age include nine genera that have been described on the basis of isolated

chela only (Garassino et al. 2009; De Angeli and Caporiondo, 2017), making comparison with our material difficult.

The modern genera *Dardanus* Paul'son, 1875 and *Calcinus* Dana, 1851, show similar characteristics to those observed in the studied specimen. However, *Diogenes augustinus* sp. nov. differs from both genera in having a near-straight frontal area, a less well-developed rostrum, a well-defined anterior branchial region (triangular in shape), much larger ambulatory dactyli; in addition, it lacks a Y-line on the posterior part of the shield. The genus *Petrochirus* Stimpson, 1858 has a characteristic squamose ornamentation; moreover, the anterior branchial region is not clearly defined.

Stratigraphic and geographic range.—Type locality and horizon only.

Concluding remarks

Articulated hermit crabs are rare fossils; mostly only isolated chelipeds are available that offer little information on the overall build of the animals. The depositional setting from which the present articulated specimen was recovered corresponds to a deltaic complex, some few kilometres away of the sediment source area (Millán et al. 1994; Dreyer et al. 1999). The matrix is a fine sandstone, with rare associated molluscs and irregular echinoids. Field observations suggest that bioturbation was rare at these levels except for vertical burrows assigned to *Skolithos*.

Based on taphonomic experiments, Klomp maker et al. (2017) have recently demonstrated that hermit crabs decay and disarticulate rapidly, only a few days after death. Articulated specimens will be preserved only under certain environmental conditions such as anoxic sea floors (e.g., Garassino et al. 2009) or in areas where sedimentation rates are high (e.g., Shives and Dunbar 2010). With this in mind, we consider the present specimens to have been transported and buried rapidly after the animals abandoned their host shells. High sedimentation rates in the study area were probably responsible for keeping at least one specimen intact by avoiding post-mortem interactions with scavengers. The specimen is preserved out of its host shell; there is no trace of shell material around the crab. This agrees with observations on modern representatives that suggest shell abandonment occurs in 46% of hermit crabs that are smothered after sudden episodic sedimentation (Shives and Dunbar 2010). In fact, episodic high-hydrodynamic pulses associated with a deltaic environment increase sedimentation rate and can bury benthic organisms even alive (e.g., Nichols et al. 1978; Hinchey et al. 2006; Shives and Dunbar 2010). In the study area this is also emphasised by the creation of tectonically induced, large spaces open to sedimentation (Millán et al. 1994).

The data provided by the present material reinforces the ideas previously documented that an increase in sedimentation rate, sudden sedimentary events and absence of scavengers favour the preservation of articulated hermit crabs. The fact that the new material is articulated and occurs outside of the host shells supports the fact that sedimentation rates were very high in this area, probably because it was close to the source area and local tectonics were conducive to such events.

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