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Filling the early Eocene gap of paguroids (Decapoda, Anomura): a new highly diversified fauna from the Spanish Pyrenees (Serraduy Formation, Graus-Tremp Basin)

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Abstract.—A highly diversified fauna of hermit crabs associated with reef environments from the Serraduy Formation (lower Eocene) in the southern Pyrenees (Huesca, Spain) is described. Other European Eocene outcrops have yielded paguroids associated with a single environment; however, the studied association represents one of the highest paguroid diversities in a single Eocene outcrop worldwide. The new material increases the diversity of known fossil paguroids, including eight species from which six are new: *Clibanarius isabenaensis* n. sp., *Parapetrochirus serratus* n. sp., *Dardanus balaitus* n. sp., ?*Petrochirus* sp., *Eocalcinus veteris* n. sp., ?*Pagurus* sp., *Paguristes perlatus* n. sp., and *Anisopagurus primigenius* n. sp. We erected a new combination for *Paguristes sossanensis* De Angeli and Caporiondo, 2009 and *Paguristes cecconi* De Angeli and Caporiondo, 2017 and transfer them to the genus *Clibanarius*. This association contains the oldest record of the genera *Eocalcinus* and *Anisopagurus*. Our data demonstrate that paguroids were diverse by the early Eocene in coral-reef environments and fill an important gap between the poorly known Paleocene assemblages and the more diverse mid- to late Eocene ones.

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Introduction

Hermit crabs (superfamily Paguroidea Latreille, 1802) are an interesting and diverse group of decapod crustaceans with a widely distributed but fragmentary fossil record (i.e., Via, 1959; Beschin et al., 2002, 2005, 2010, 2012; De Angeli et al., 2009; Garassino et al., 2009a, b; Pasini and Garassino, 2010a, b, 2011; Fraaije et al., 2011, 2015, 2020; Schweigert et al., 2013; Fraaije, 2014; Garassino et al., 2014; Hyžný et al., 2016; De Angeli and Caporiondo, 2017; Ferratges et al., 2020, 2021a; Mironenko, 2020; Ossó, 2020; Pasini et al., 2020) that extends back to the Jurassic (see Fraaije et al., 2022). This is due in part to their highly specialized morphology with poorly mineralized pleon adapted to life inside empty shells or other cavities (e.g., Lemaitre, 1989, 1990; Walker, 1992; de Forges et al., 2001). After death, disarticulation occurs rapidly, and the fossil record of this group is represented mostly by isolated propodi and chelae, which are the harder and more resistant parts (see Klompmaker et al., 2017).

Eocene outcrops in Europe have provided a rich diversity of hermit crabs, especially in the middle and late Eocene, concentrated in reef environments from Italy (Beschin et al., 2007, 2015, 2018, 2019; Tessier et al., 2011) and Hungary (Müller and Collins, 1991) and siliciclastic prodelta environments from Italy (De Angeli and Caporiondo, 2017). By contrast, early Eocene material is rarer and concentrated in only a few localities (see Fraaije et al., 2011; Beschin et al., 2016; Fraaije and Polkowsky, 2016; Ferratges et al., 2021b). However, Paleocene records of paguroids are scarce, and hermit crab assemblages of this age remain largely understudied (see Jakobsen et al., 2020 and references therein).

During the Paleocene–Eocene, the southern Pyrenean basin corresponded to an elongated gulf located in tropical latitudes (Hay et al., 1999), resulting in a biodiversity hotspot of several marine invertebrates, including decapod crustaceans, and the development of coral-reef environments (Ferratges et al., 2021b). In this sense, the early Eocene seems to be an important period of diversification of hermit crabs, with the appearance of several modern families. Here we describe eight taxa of paguroids from the middle Ypresian (lower Eocene) associated with reef environments from the Ramals outcrop in the Pyrenees of Huesca, Spain. This locality has provided a great diversity of other decapod crustaceans (Artal and Via, 1989; Artal and Castillo, 2005; Artal and van Bakel, 2018a, b; Ferratges et al., 2019, 2021b; Artal et al., 2022), but paguroids remained undescribed until the present study.

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The aim of the present study includes the description of new paguroids discovered in the Serraduy Formation (Ypresian, lower Eocene) from the southern Pyrenees (Spain). This important association shows diverse paguroids associated with a reef environment. The presence of complete chelae allows comparison with both modern and fossil representatives of the group and enlarges the general knowledge of the European fossil record of Paguridae.

Locality, materials, and methods

Locality.—The material described herein was collected from the lower Eocene (middle Ypresian) Serraduy Formation of the Tremp-Graus Basin. All specimens were collected from the same levels described by Ferratges et al. (2021b) and Artal et al. (2022).

Materials.—The studied material comprises 130 specimens represented by isolated left and right propodi belonging to eight genera and eight species, from which six are formally named. The material included in the present study was collected from the outcrop that exposes the transition between the reef limestones and the overlying Riguala Marls at a locality known as "Barranco de Ramals" (see Ferratges et al., 2021b for further information).

Some of this material (50 isolated propodi, 5.49% of the total decapod crustacean assemblage) was recovered during a paleoecological study of the area (see Ferratges et al., 2021b). The remaining specimens (80 isolated propodi and chelae) were studied in historical museum collections (MGSB). The studied chelae are well preserved, usually with their cuticle and without deformation.

Left and right chelae showing apparent homochely, as in the new species included in *Clibanarius*, *Parapetrochirus*, and *Dardanus*, have been considered to belong to the same taxon. In the case of taxa with probably asymmetric chelae (heterochely), assignment to the same taxon has been discarded due to very different ornamentations between different genera and to the fact that none of the known representatives of these genera fit with the other chelae collected in the same area. This is the case of the genera *Petrochirus* Stimpson, 1859, *Eocalcinus* Via, 1959, *Pagurus* Fabricius, 1775, *Paguristes* Dana, 1852, and *Anisopagurus* McLaughlin, 1981.

Methods

The specimens were prepared using a Micro Jack 2 air scribe (Paleotools) and binocular magnifying. They were later photographed dry and coated with ammonium chloride sublimate. Detailed photography of the cheliped surfaces was made using a Nikon d7100 camera (Nikon, Tokyo, Japan) with a 60 mm macro lens.

Repositories and institutional abbreviations.—The specimens are deposited in the Museo Geológico del Seminario de Barcelona (MGSB) and the Museo de Ciencias Naturales de la Universidad de Zaragoza (Spain) (MPZ). The material deposited in MPZ was collected under permit EXP: 032/2018 from the Servicio de Prevención, Protección e Investigación del Patrimonio Cultural (Gobierno de Aragón). The material deposited in MGSB was collected in the early 1980s and is housed within the historical collection of the Seminario Conciliar de Barcelona.

Systematic paleontology

Systematic classification follows McLaughlin (2003), McLaughlin et al. (2007; 2010), and Fraaije et al. (2022). For the morphological terminology of chelipeds, see Figure 1.

Order Decapoda Latreille, 1802
Infraorder Anomura MacLeay, 1838
Superfamily Paguroidea Latreille, 1802
Family Diogenidae Ortmann, 1892
Genus *Clibanarius* Dana, 1852

Type species.—*Cancer clibanarius* Herbst, 1791 (Herbst, 1791–1796).

Fossil species included.—*C. sossanensis* (De Angeli and Caporiondo, 2009); *C. cecconi* (De Angeli and Caporiondo, 2017); *C. isabenaensis* n. sp.

Clibanarius isabenaensis new species
Figure 2

Type material.—The holotype is MGSB77625, a near-complete, well-preserved left chela retaining cuticle. There are three paratypes (MGSB85955, MPZ 2021/30, MPZ 2022/1), which lack the dactylus.

Diagnosis.—Small left and right chela. Right and left propodus with slightly tilted carpo-propodus articulation, oriented at angle over 50°. Palm anteriorly convergent. Both propodi of similar size and shape (homochely). Two rows of conical spines on upper margin. Four rows of spiny granules on outer surface of palm. Inner surface of palm smooth. Fingers slender, rounded, elongated, bearing granules and setal pits of large size. Occlusal margin with acute outer sides.

Description.—Small left and right chelae of presumably similar shape and size. Palm subrectangular, somewhat longer than high. Complete propodus about 13.0 mm long, 7.0 mm palm length, and 6 mm palm height. Oval cross section. Inner surface fairly convex, nearly smooth. Outer surface densely granular, bearing four principal rows of spinose tubercles with setal pits near the base, directed upward. Upper margin with two rows of conical spines. Lower margin straight, rounded, with small conical granules directed forward. Posterior part of palm with prominent groove on both inner and outer surfaces, probably related to the articulation with the carpus. Fingers long, circular in cross section, slender, curved, with broad space between their occlusal margins. Large setal pits on fixed finger, of similar size and randomly distributed (Fig. 2).

Etymology.—The specific name comes from Isábena, the municipality of the province of Huesca where the material was collected.

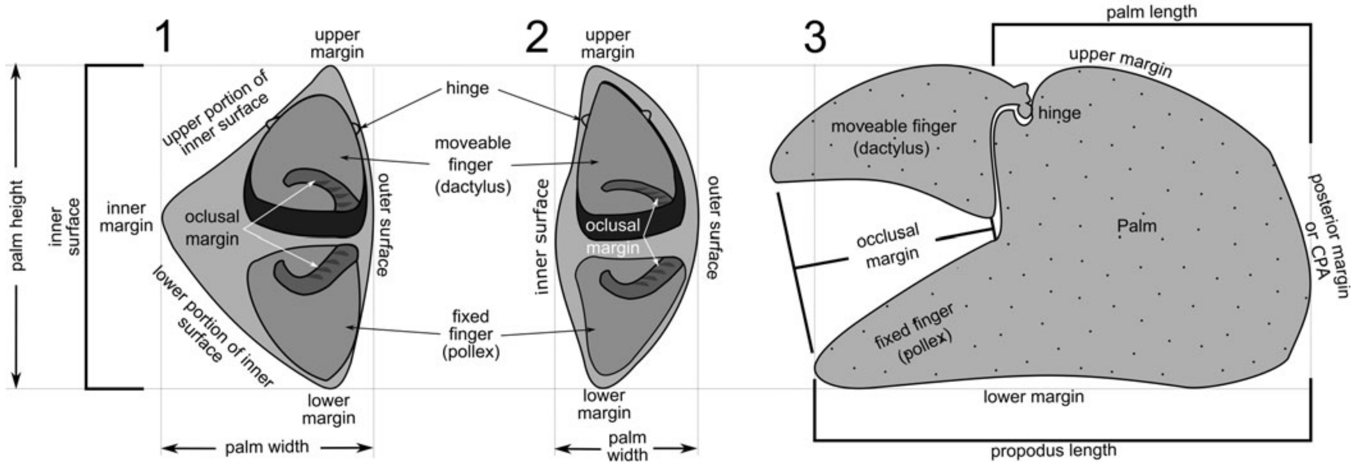

Figure 1. Simplified anatomical scheme of cheliped morphotypes of paguroids. (**1**, **2**) Frontal view of two different morphotypes. (**3**) Lateral view. CPA = carpo-propodus articulation.

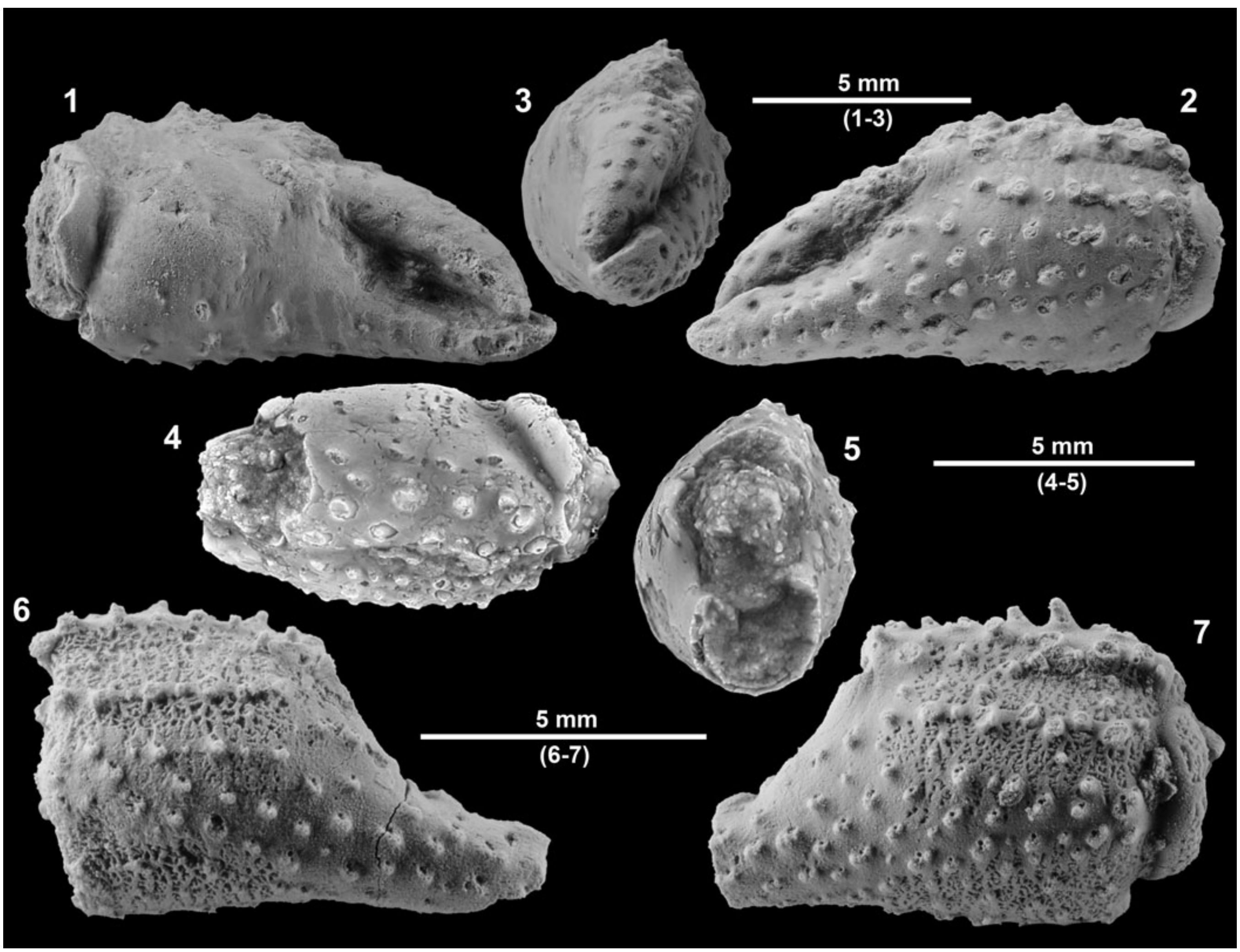

Figure 2. *Clibanarius isabenaensis* n. sp. (**1–3**) Holotype MGSB77625: (**1**) lateral view of inner side of left chela; (**2**) frontal view; (**3**) outer side lateral view of left chela. (**4, 5**) Paratype (MGSB85955), left chela: (**4**) upper view (**5**) frontal view. (**6**) Paratype MPZ 2021/30, lateral view of outer side of right chela. (**7**) Paratype MPZ 2022/1, lateral view of outer side of left chela.

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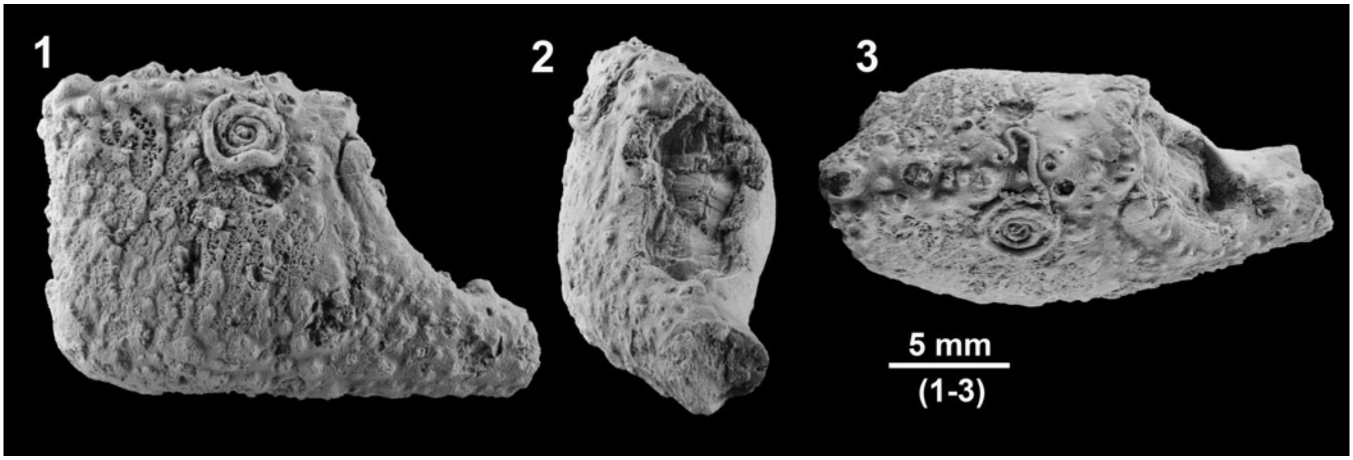

Figure 3. ?*Petrochirus* sp. (**1–3**) Right cheliped (specimen MPZ 2022/10): (**1**) lateral view of outer side; (**2**) frontal view; (**3**) upper view.

Other material examined.—Ten additional specimens MGSB85956a–j and five additional specimens at MPZ 2022/2–6. All the examined materials have a similar size.

Remarks.—The new species shows characteristics of the palm typical of the genus *Clibanarius*, as well as the presumed homochely, the small and similar size of both chelae, and the outer surface covered by small spines. Nevertheless, some taxonomic doubts exist with respect to species of the genus *Clibanarius* that are closely related to each other, and in some cases, this strong morphological similarity has raised questions about their status as separate species (McLaughlin et al., 2010). In most extant species, the fingers present a robust, stout shape, being strongly thick and clearly short (Sánchez and Campos, 1978; McLaughlin, 2003; McLaughlin et al., 2007, 2010; Negri et al., 2014). In almost all modern species included in the genus *Clibanarius*, the occlusal margins of the fingers are straight, with no gap between them (with some exceptions such as *C. antillensis* Stimpson, 1859 and *C. ambonensis* Rahayu and Forest, 1992). *Clibanarius isabenaensis* n. sp. exhibits longer and thinner fingers than the most modern representatives of the genus *Clibanarius*, with a curved dactylus and pollex, occlusal margin curved, with a wide gap between the fingers. However, we consider that the similarities presented by the new species justify inclusion in this genus.

Some species included in the genus *Paguristes* are similar to the new species, including several modern and fossil species (i.e., Müller and Collins, 1991; Blow and Manning, 1996; Beschin et al., 2005, 2007, 2018; De Angeli and Caporiondo, 2009, 2017; Garassino et al., 2009b). However, modern representatives of the genus *Paguristes* originally included a large number of morphologically different taxa, and currently, the genus has been split into several less-variable genera (see McLaughlin et al., 2010). Unfortunately, most diagnostic criteria used for modern species are not preserved in the fossil record. In any case, extant species assigned to *Paguristes* show certain differences from the new species: (1) heterochely; (2) shorter and more robust fingers; (3) setal pits tend to show a different distribution from that of the material assigned to *Clibanarius isabenaensis* n. sp. (grouping of several setal pits in front of the tubercles, oriented distally, instead of a large setal pit oriented obliquely upward). Furthermore, the extant species of *Paguristes* do not present tubercle alignment as in the new species (i.e., Rahayu and McLaughlin, 2006; Rahayu, 2007; Komai, 2010; McLaughlin et al., 2010). The fossil species *Paguristes cecconi* De Angeli and Caporiondo, 2017 shows a clear affinity with the material studied here. Nevertheless, *P. cecconi* differs from *C. isabenaensis* n. sp. by having a less elongate shape and fewer and more robust spiny tubercles on the upper margin (see De Angeli and Caporiondo, 2017, p. 15–16, fig. 7, t. 3). Furthermore, *C. isabenaensis* n. sp. has slightly less convergent upper and lower margins than *P. cecconi*. The species *Paguristes sossanensis* De Angeli and Caporiondo, 2009 also shows similarities with *C. isabenaensis* n. sp. in the general shape of the chela and distribution of the tubercles (see De Angeli and Caporiondo, 2009, p. 24–25, figs. 2, 3). However, *P. sossanensis* shows a more globose morphology, smaller tubercles on the outer surface, reduced spines on the upper margin, and a shorter and more robust fixed finger. For these reasons, we consider that the species *P. cecconi* and *P. sossanensis* should be assigned to the genus *Clibanarius*.

Genus *Petrochirus* Stimpson, 1859

Type species.—*Pagurus granulatus* Olivier, 1811 (= *Cancer bahamensis* Herbst, 1796 (for 1791 in Herbst, 1782–1804]), by original designation.

Fossil species included.—*Petrochirus bahamensis* (Herbst, 1791); *P. bouvieri* Rathbun, 1919a; *P. diogenes* (Linnaeus, 1758); *P. inequalis* Rathbun, 1919b; *P. mezi* (Lőrenthey, 1909); *P. minutus* Beschin et al., 2016; *P. poscolensis* Beschin et al., 2006; *P. priscus* (Brocchi, 1883); *P. sanctilazzari* Baldanza et al., 2014; *P. savii* Beschin et al., 2012; *P. taylori* Rathbun, 1935.

?*Petrochirus* sp.
Figure 3

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Description.—Propodus length: 22.0 mm; palm length: 14.7 mm; palm height: 14.0 mm. Palm subrectangular, outer surface of palm densely coarsely granulate; inner surface less ornamented with granules. On the outer surface, more dense and coarse tubercles; on the inner surface, more numerous in the upper portion; lower portion nearly smooth. Both surfaces convex. Palm sigmoidal in cross section. Upper margin with four prominent spines surrounded by other smaller spines, irregularly distributed. Upper and lower margins of propodus straight (Fig. 3). Incomplete remains of fixed finger exhibit a robust construction and strong occlusal molariform teeth.

Material examined.—Four specimens corresponding to one isolated propodus (MPZ 2022/10) and three movable fingers (MPZ 2022/11–12, MPZ 2022/59).

Remarks.—This taxon is characterized by a subquadrate palm, with fairly convex inner and outer surfaces and densely covered by unevenly spaced granules. The fixed finger is not complete, but the first portion suggests it is robust, rounded, and elongated. Numerous incomplete or badly preserved chelae (Portell and Agnew, 2004; Vega et al., 2008; Collins et al., 2009a, b; Bermudez et al., 2017; Luque et al., 2020) have been traditionally assigned to *Petrochirus* mainly on the basis of a subrectangular shape and the squamous or pavement-like ornamentation (see Beschin et al., 2002; Todd and Collins, 2005; Vega et al., 2009; De Angeli and Caporiondo, 2017; Luque et al., 2017). The most similar fossil remains are from *P. savii* from Italy. Major differences are the coarser, larger granules on the outer surface and the bigger, more numerous granules on the inner surface of the palm in the Spanish form. The Italian form is characterized by a more elongate, subrectangular palm; an outer surface with smaller granules; an inner surface of the palm smooth, reticulate, with very few granules (De Angeli and Caporiondo, 2017).

Genus *Parapetrochirus* Ferratges, Artal, and Zamora, 2021a

Type species.—*Parapetrochirus robustus* Ferratges, Artal, and Zamora, 2021 (Ferratges et al., 2021a).

Fossil species included.—*P. robustus* Ferratges, Artal, and Zamora, 2021; *P. serratus* n. sp.

Parapetrochirus serratus new species
Figure 4

Type material.—The holotype is MPZ 2022/7, a well-preserved left propodus, with cuticle preserved; there are also three paratypes (two right propodi and one isolated dactylus): MGSB77621a–c.

Diagnosis.—Upper and lower margins of the palm notably ridged; oblique strong ridge on the medial portion of the inner surface of the palm; occlusal margin of the fixed finger bearing three molariform teeth, various small setal pits, and two relatively large elliptical depressions with numerous setal pits. The propodi are of similar size and shape (homochely).

Description.—Propodus length: 19.5 mm; palm length: 12.8 mm; palm height: 13.9 mm of holotype. Upper and lower margins of the palm strongly ridged, angular, developed as a strong oblique ridge in the inner margin. Upper margin straight, becoming higher proximally; lower margin straight, also higher proximally. Both margins with dentiform tubercles. Inner and outer surface of palm densely tuberculated, covered with closely spaced squamose granules. Palm with convex upper and lower margins, triangular in cross section, longer than high, with the upper and lower margins straight, subparallel, somewhat inclined, outer portion only somewhat convex, nearly flat; both margins angular, keeled, with notable conical denticles directed forward. Propodi are of similar size and shape (homochely), forming a circular shield when joined (Fig. 4.1, 4.5). The ornamentation of the inner and outer surfaces consists of squamose closely spaced tubercles. Fixed finger robust, triangular in cross section, straight. Dactylus robust; the occlusal edge is concave, smooth, bearing up to three molariform teeth, about four small setal pits, and two large depressions near the tip that exhibit multiple, numerous small setal pits (Fig. 4.10, 4.11).

Etymology.—From the Latin *serratus,* referring to its serrated margins.

Other material examined.—Eleven additional specimens at MGSB85957a–k, and three specimens at MPZ (one left dactylus: MPZ 2021/37; two fragments: MPZ 2022/8–9. All the examined material has similar size to the type material.

Remarks.—Incomplete remains of fossil paguroids with squamous ornamentation have usually been assigned to the genus *Petrochirus* (i.e., Portell and Agnew, 2004; Todd and Collins, 2005; Vega et al., 2008; Bermúdez et al., 2017; Luque et al., 2017, 2020). Some are recorded as extant species (i.e., Todd and Collins, 2005; Collins et al., 2009a, b; Luque et al., 2017). *Petrochirus* Stimpson, 1859 is characterized by globular chelipeds with elongate and subrectangular palms covered by numerous granules on the inner and outer surfaces. However, the genus *Parapetrochirus* is characterized by angular, strongly ridged upper and lower margins of the palm and a strong oblique ridge situated in the medial portion of the inner surface and margins bearing strong conical teeth. Some rather complete chelae from Italy identified as *Petrochirus savii* (De Angeli and Caporiondo, 2017) and *Petrochirus sanctilazzari* Baldanza et al., 2014 appear morphologically similar to the Spanish genus *Parapetrochirus*. *Petrochirus savii* presents striking similarities, mainly in the occlusal margins. The lower occlusal margin of *Petrochirus savii* presents some characters that are nearly identical to *Parapetrochirus serratus* n. sp., such as molariform teeth and deep elliptical depressions (De Angeli and Caporiondo, 2017). Differences in *Petrochirus savii* from *Parapetrochirus serratus* are palm more elongate; subrectangular; upper and lower margin of palm rounded, not crested; different ornamentation; near absence of granules on the inner portion; smaller granules, not pavement-like, on the outer portion. Main differences in *Petrochirus sanctilazzari* from *Parapetrochirus serratus* are a

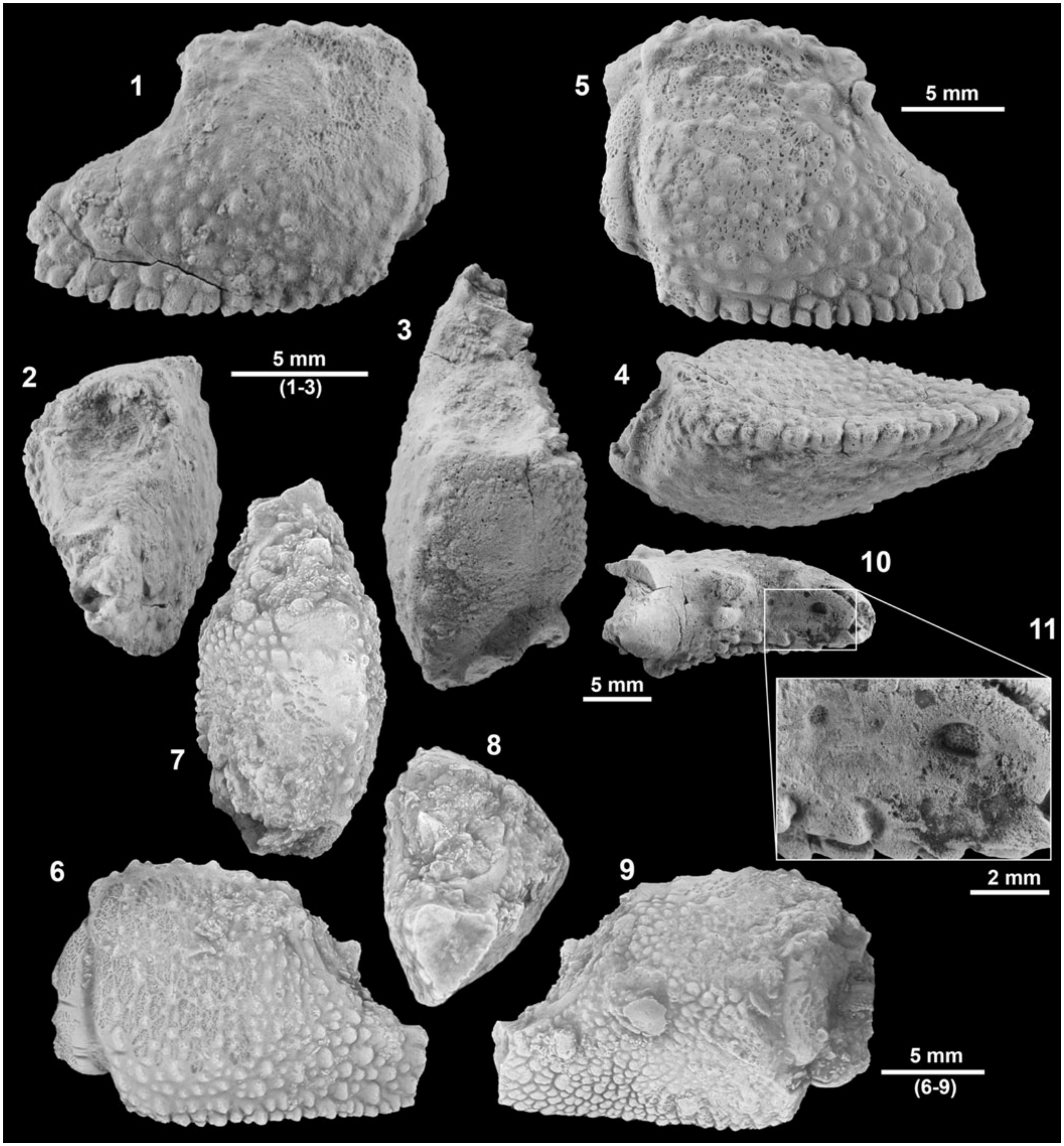

Figure 4. *Parapetrochirus serratus* n. sp. (**1–4**) Holotype MPZ 2022/7, left chela: (**1**) lateral view of outer side; (**2**) frontal view; (**3**) upper view; (**4**) lower view. (**5**) Paratype MGSB77621a, lateral view of outer side of right cheliped. (**6–9**) Paratype MGSB77621b, right chela: (**6**) lateral view of outer side; (**7**) upper view; (**8**) frontal view; (**9**) inner side lateral view. (**10**) Occlusal margin of isolated dactylus (paratype MGSB77621c). (**11**) Detail of the capsulated setal pits of the occlusal margin of dactylus.

more elongated palm and more rounded lower and upper margins in the former.

The Mexican *Petrochirus* sp. from the lower Eocene (Vega et al., 2008) shows some similarities to *Parapetrochirus serratus* n. sp. such as upper and lower margins bearing conical teeth, dense ornamentation, and a subrectangular propodus. The main differences in the Mexican specimen are: (1) absence of a strong oblique ridge on the inner surface; (2) lower margin strongly arched; (3) outer surface of the palm scarcely granulated (see Vega et al., 2008).

Parapetrochirus serratus n. sp. shows similarities to *Calcinus agonensis* Beschin et al., 2005 in the general outline and ornamentation of the chela. However, the new species presents more weakly developed tubercles on the upper margin and a more serrated lower margin. In addition, modern representatives of the genus *Calcinus* show a great diversity of shapes and need deep systematic review. In any case, the modern forms assigned to the genus *Calcinus* present clear differences from *P. serratus* n. sp. such as: (1) evident heterochely and (2) globose chelae, not rounded or opercular as is the case with fossil material (i.e., Forest, 1958, p. 4–7, 9–12, figs. 6–12; Haig and McLaughlin, 1984, p. 109–110, 112, 117, figs. 1, 2; Poupin, 1997, figs. 4–7; Asakura and Tachikawa, 2000, p. 270, 275, figs. 2, 6; Asakura, 2002, p. 29, 32, 34–35, 37, 41, 47, 51–52, 56–57, 59, 64–65, figs. 2–6, 8, 10, 13–16, 18–21; Poupin and Lemaitre, 2003, p. 5, 7, figs. 1–3, 5).

The species *Parapetrochirus robustus* from the upper Ypresian of Huesca (Spain) also shows similarities with the new species in the ornamentation; inner and outer surface of the palm densely tuberculated, covered with squamose granules; robust fixed finger; lower margin arched proximally, and keeled in the distal portion (see Ferratges et al., 2021a). However, *P. serratus* n. sp. has a much more compact shape, with an oval outline, less compressed in the lower zone, convergent upper and lower margins, not divergent as in *P. robustus*, and less dense ornamentation. In addition, the new species presents both chelipeds with very similar morphology.

Family Annuntidiogenidae Fraaije, 2014
Genus *Paguristes* Dana, 1852

Type species.—*Paguristes hirtus* Dana, 1852 by subsequent designation of Stimpson, 1859.

Fossil species included.—*Paguristes baldoensis* Garassino, De Angeli, and Pasini, 2009 (Garassino et al., 2009b); *P. cecconi* De Angeli and Caporiondo, 2017; *P. chipolensis* Rathbun, 1935; *P. clampensis* De Angeli and Caporiondo, 2017; *P. cserhatensis* Müller, 1984; *P. florae* Collins, Fraaye, and Jagt, 1995; *P. hokoensis* Schweitzer and Feldmann, 2001; *P. johnsoni* Rathbun, 1935; *P. lineatuberculatus* Beschin et al., 2006; *P. liwinskii* Fraaije, Van Bakel, and Jagt, 2015; *P. mexicanus* (Vega et al., 2001); *P. michikoae* Karasawa and Fudouji, 2018; *P. oligotuberculatus* Müller and Collins, 1991; *P. ouachitensis* Rathbun, 1935; *P. paucituberculatus* Beschin, Busulini, and Tessier in Beschin et al., 2016; *P. prealpinus* Beschin et al., 2005; *P. santamartaensis* Feldmann, Tshudy, and Thomson, 1993; *P. sossanensis* De Angeli and Caporiondo, 2009; *P. subaequalis* (Rathbun, 1926); *P. teruakii* Karasawa and Fudouji, 2018; *P. wheeleri* Blow and Manning, 1996; *P. whitteni* Bishop, 1983 (modified from Schweitzer et al., 2010 and Fraaije et al., 2015).

Remarks.—The genus *Paguristes* Dana, 1852 was previously considered in the family Diogenidae (sensu lato), a position that was revised by Fraaije (2014) and Fraaije et al. (2017). These authors proposed its inclusion in a new family (Annuntidiogenidae Fraaije, 2014). Paguroid phylogeny is not in the scope of this paper, and we follow at this moment placement of the genus *Paguristes* in the Annuntidiogenidae as proposed by Fraaije (2014) and Fraaije et al (2017, 2022).

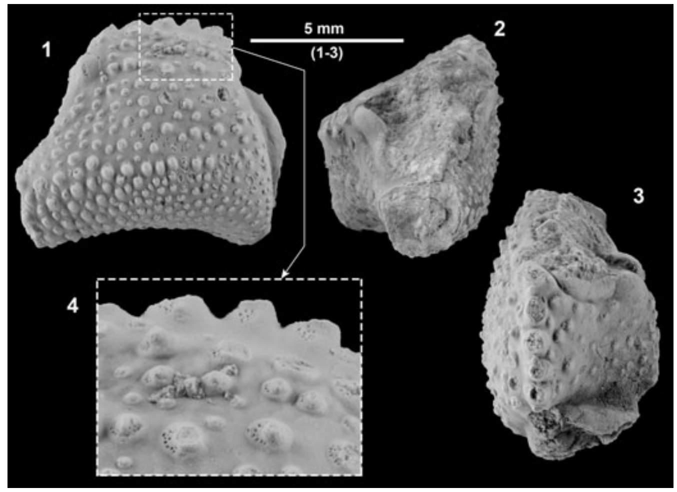

Figure 5. *Paguristes perlatus* n. sp. (**1–4**) Holotype (MPZ 2022/38), left chela: (**1**) lateral view of outer side; (**2**) frontal view; (**3**) upper view. (**4**) Detail of the distribution of the setal pits. Specimens whitened with ammonium chloride sublimate.

Paguristes perlatus new species
Figure 5

Type material.—The holotype, MPZ 2022/38, is a left propodus (propodus length without fixed finger: 8.0 mm; palm length: 7.2 mm; palm height: 7.0 mm).

Diagnosis.—Palm subquadrate; upper margin short, with strong conical teeth; lower margin fairly concave. Outer surface convex, densely granular. Inner surface with strong ridge. Upper portion of the inner surface concave; lower portion concave. Carpo-propodus articulation oblique. Fingers curving inward laterally when seen from dorsal view.

Description.—Chela of small size, palm subquadrate, slightly higher than long; outer surface concave, densely covered by evenly spaced perliform granules; inner surface bearing a strong medial ridge (inner margin), the lower portion densely granular. Inner margin rounded, strongly concave. Propodus with concavity on the upper portion of inner surface when seen from frontal view, fingers curving laterally. Lower portion of the inner surface concave. Upper margin short, bearing strong conical teeth. Lower margin longer, notably concave. Carpo-propodus articulation fairly oblique, short (Fig. 5).

Etymology.—The name refers to the characteristic perlated tubercles on the outer surface of the palm.

Remarks.—The genus *Paguristes* is morphologically diverse in modern ecosystems (Rahayu, 2006). Members of *Paguristes* in the fossil record are diagnosed by various characteristics (i.e., Beschin et al., 2012, 2016): carpus short, highest distally, with concave, arcuate lower margin and ornamented with spines and nodes; palm short, shortest along the upper margin, ornamented with numerous tubercles and spines; fixed finger stout and very high proximally. Because the features of the chelipeds of the fossil material are similar to members of *Paguristes*, the new material is placed tentatively within this genus.

Paguristes perlatus n. sp. exhibits a short upper margin of the palm bearing strongly marked conical teeth. The lower margin is fairly concave with a marked convexity in the proximal portion. Palm robust, globular, somewhat higher than long. Both surfaces are convex, the outer surface densely covered by pearled granules, the inner surface with an oblique ridge, the lower portion with numerous granules. Carpo-propodus articulation oblique. All the characters fit with the general morphological characteristics of the genus *Paguristes.* Major differences from the extant species are the ornamentation of the palm, which exhibits conical spines and the usually less concave lower margin of palm (Provenzano, 1965; Campos and Sanchez, 1995; Manjón et al., 2002; Lima and Santana, 2017). The morphologically closest fossil form is *Paguristes prealpinus*, which shares the main morphological characteristics described here. Major differences from the new species are the more subrectangular shape of the palm, the upper margin with less marked conical teeth; the concavity in the lower margin distally situated; granulation in the outer surface less marked and more irregularly distributed (Beschin et al., 2012; De Angeli and Caporiondo, 2017). *Paguristes cecconi* is assigned in this study to *Clibanarius*, as indicated in the preceding.

The fossil species *Paguristes hokoensis*, *P. liwinskii*, and *P. teruakii* exhibit the characteristic lateral curvature of the fingers from dorsal view, the conical teeth in the upper margin, and the granulated outer surface. However, *P. hokoensis* and *P. teruakii* have different ornamentation, a more elongated outline, strongly convergent upper and lower margins, and more rounded proximal lower margin (see Schweitzer and Feldmann, 2001, p. 193–195, fig. 13; Karasawa and Fudouji, 2018, p. 26, fig. 2). Major differences in *P. liwinskii* are the coarse granulation of the palm, the oval outline with markedly convex lower margin, and the smoother inner surface (Fraaije et al., 2015, p. 590, fig. 1C).

Extant *Paguristes* consists of over 120 species (McLaughlin et al., 2010; Komai et al., 2015). Several authors suggested extant *Paguristes* are mainly distributed in shallow-water areas of the temperate–tropical waters (i.e., Rahayu, 2006; Rahayu and Forest, 2009; Trivedi and Vachhrajani, 2017).

Family Calcinidae Fraaije, Van Bakel, and Jagt, 2017
Genus *Dardanus* Paul'son, 1875

Type species.—*Dardanus hellerii* Paul'son, 1875 by monotypy.

Fossil species included.—*D. arnoldi* Rathbun, 1926; *D. arrosor* (Herbst, 1796) (Herbst, 1782–1804); *D. balaitus* n. sp.; *D. bayani* Beschin et al., 2016; *D. biordines* Collins in Todd and Collins, 2005; *D. braggensis* Beschin, Busulini, and Tessier, 2015; *D. curtimanus* Müller and Collins, 1991; *D. gemmatus* (Milne Edwards, 1848); *D. hungaricus* (Lörenthey in Lörenthey and Beurlen, 1929); *D. impressus* (De Haan, 1833–1850); *D. lauensis* Rathbun, 1945; *D. mediterraneus* (Lörenthey, 1909); *D. mexicanus* Vega et al., 2001; *D. muelleri* Karasawa and Inoue, 1992; *D. squamatus* Collins in Collins et al., 2009 (Collins et al., 2009b); *D. substriatiformis* (Lörenthey in Lörenthey and Beurlen, 1929).

Remarks.—The genus *Dardanus* Paul'son, 1875 was previously considered in the family Diogenidae (sensu lato), and its position was revised by Fraaije et al. (2017). However, paguroid phylogeny is not in the scope of this paper; for consistency, we here follow Fraaije et al. (2017, 2022).

Dardanus balaitus new species
Figure 6

Type material.—The holotype, MGSB77622, is a near-complete, well-preserved right propodus, retaining cuticle. There are two paratypes, one left propodus without dactylus, MGSB77623, and one isolated finger, MPZ 2021/36.

Diagnosis.—Elongated propodus; palm globular. Inner surface convex, lower portion with notable arched lobes, upper portion nearly smooth; lower portion with notable arched lobes bearing numerous setal pits. Outer surface convex, densely granulated, with spaced granules and tubercles, all of them bearing numerous setal pits on tips and in anterior portion.

Description.—Propodus length: 20.0 mm; palm length: 12.0 mm; palm height: 13.0 mm of the holotype. Elongated propodus; palm globular, with rounded sides and margins. The inner surface bears an oblique inflation in the medial portion. Outer surface of the palm convex, ornamented with obliquely situated tubercles and oblique short or elongated raised lobes. The tubercles in the upper portion bearing one, two, three, or four setal pits, with several small setal pits in the anterior side. The lower portion of the outer surface with raised oblique lobes, the larger ones bearing about seven or eight setal pits on the tip and numerous, irregular, smaller setal pits on the anterior side. The setal pits on the anterior side are numerous and of irregular size; in the larger lobes, up to 18 smaller pits and up to eight larger pits. Inner surface smoother, less ornamented, but with large oblique rows of setal pits in the lower portion; the larger ones up to 20 irregular setal pits. Upper margin of palm with two rows of small conical teeth. Fixed finger with depressed, smooth occlusal margin; outer side of the finger with one strong, molariform tooth (Fig. 6).

Etymology.—The specific name refers to the pre-Roman mythological character "*Balaitús*," who lived in the Pyrenees and was dedicated to causing storms in the mountains.

Other material examined.—Nineteen additional specimens (isolated propodi) in MGSB85958a–s and one isolated dactylus at MPZ 2021/36.

Remarks.—The general morphology of chelae in the new taxon conforms with modern genus *Dardanus* Paul'son, 1875 because the chelipeds are globular, with rounded margins and sides, with inner and outer surface fairly convex (i.e., Collins and Donovan, 2010; Garassino et al., 2014) and because of the notable raised tubercles and lobes bearing numerous setal pits on the tips, and still more numerous setal pits in the anterior portion of each tubercle or elongated lobe. All of them appear obliquely situated, with the appearance of striations. This characteristic

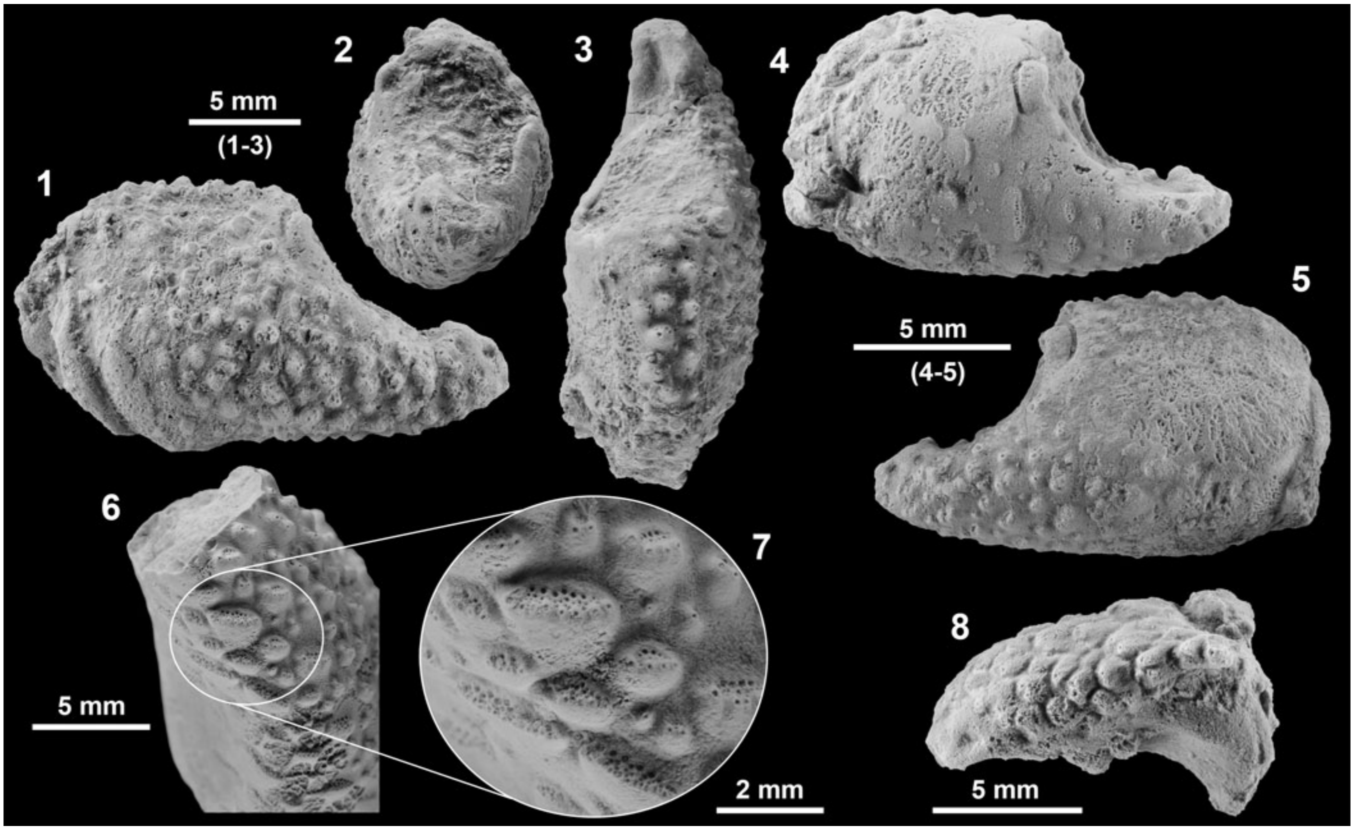

Figure 6. *Dardanus balaitus* n. sp. (**1–3**) Holotype MGSB77622, right chela: (**1**) lateral view of outer side; (**2**) frontal view; (**3**) upper view. (**4, 5**) Paratype MGSB77623, left chela: (**4**) lateral view of inner side; (**5**) lateral view of outer side. (**6**) Oblique interior view of the paratype MGSB77623. (**7**) Detail of the distribution of the setal pits. (**8**) Isolated dactylus (MPZ 2021/36).

can be observed in both extant (Sánchez and Campos, 1978; McLaughlin, 2003; McLaughlin et al., 2007, 2010) and fossil taxa (Collins and Donovan, 2010; Fraaije et al., 2011; Beschin et al., 2012; Garassino et al., 2014). In addition, the fossil species assigned to *Dardanus* usually present long oblique or vertical ridges (i.e., Garassino et al., 2014; Beschin et al., 2021), with some exceptions such as *D. colosseus* Fraaije and Polkowsky, 2016 and *D. vandeneeckhauti* Fraaije et al., 2011. Some of the distinctive characters of *D. balaitus* n. sp. are shared with the species *D. arrosor*, with robust chelae and oblique tuberculate ridges (McLaughlin et al., 2007, fig. 76). Nevertheless, the new species presents notable differences in the general shape of the chelipeds, being more rounded, and is distinct in having a peculiar distribution of tubercles and arched raised lobes, as it is the peculiar distribution of setal pits. The tubercles with one, two, three, or four setal pits on the tip; oblique arched lobes with up to eight setal pits on the tip: all tubercles and arched lobes with numerous and irregular setal pits in the anterior side (Fig. 6). The main difference with *D. substriatus* Garassino et al., 2014 from the Pleistocene of Italy is the complete vertical striae on the outer surface of the propodus, which is absent in the new species (Garassino et al., 2014).

Genus *Eocalcinus* Via, 1959

Type species.—*Eocalcinus eocenicus* Via, 1959, by original designation.

Fossil species included.—*Eocalcinus albus* Beschin, Busulini, and Tessier, 2010; *E. cavus* Beschin et al., 2002; *E. eocenicus* Via, 1959; *E. gerardbretoni* Ferratges, Artal, and Zamora, 2021 (Ferratges et al., 2021a); *E. veteris* n. sp.

Eocalcinus veteris new species
Figures 7, 8

Type material.—The holotype, MGSB77593, is a complete left propodus (length: 31.0 mm; palm length: 24.0 mm; palm height: 19.0 mm) with well-preserved cuticle. There are two paratypes, MPZ 2021/29 and MPZ 2022/13, complete left propodi.

Diagnosis.—Left propodus semicircular, stout. Palm longer than high; lower margin sinuous in both lateral and lower views. Fixed finger with occlusal edge sinuous, obliquely oriented.

Description.—The complete propodus of the holotype is 32.0 by 20.0 mm. Palm only somewhat longer than high. Lower margin slightly sinuous, nearly straight in proximal portion, fixed finger curving downward. Lower margin less ridged, more rounded. Dense tiny granulation on outer surface and fingers. Granules close together, pavement-like. Spaced bigger granules in upper portion. Clear setal pits, mainly on fingers. Inner portion of palm smooth, with scarce granules (Fig. 7).

Stout left propodus planoconvex and subcircular. Lower margin sinuous in lateral and lower inferior views; outer surface

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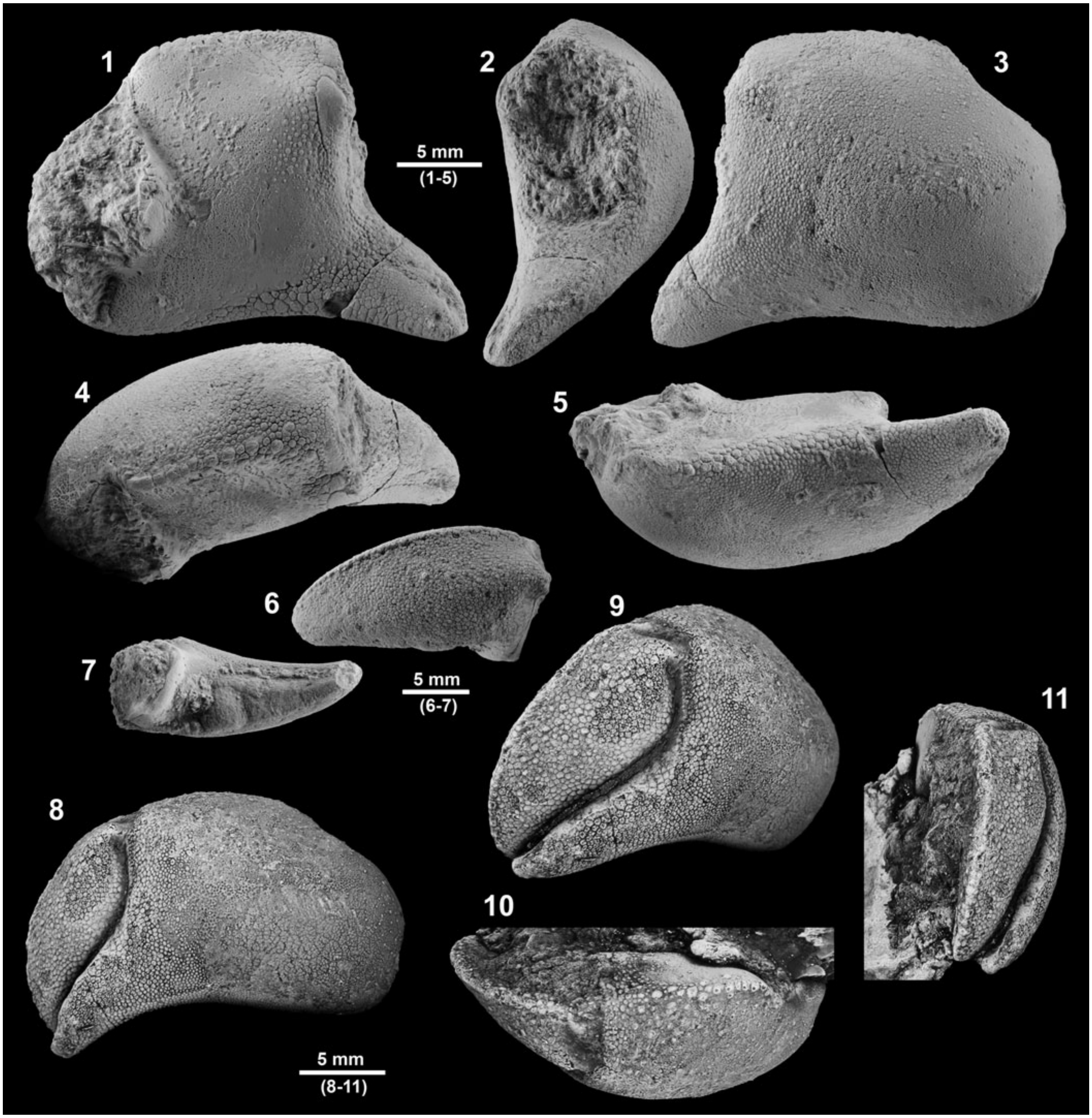

Figure 7. *Eocalcinus veteris* n. sp. (**1–5**) Paratype MPZ 2021/29), left chela: (**1**) lateral view of inner side; (**2**) frontal view; (**3**) lateral view of outer side; (**4**) upper view; (**5**) inferior view. (**6, 7**) Isolated dactylus (MPZ 2022/13) in lateral and occlusal margin (inferior view). (**8–11**) Holotype (MGSB77593), left chela: (**8**) oblique lateral view of outer side; (**9**) oblique frontal view; (**10**) upper view; (**11**) frontal view.

convex; inner surface weakly convex, nearly flat. Palm slightly longer than high. Fixed finger short, robust, arched (strongly convex). Dactylus very robust, triangular in cross section, with the occlusal edge concave, smooth. Ornamentation on the fixed finger and palm is densely covered with small granules, very close together (pavement-like), and very uniform.

Etymology.—The specific name *veteris* comes from Latin and means "old," "ancient," referring to the fact that it is the oldest member of the genus.

Other material examined.—Thirty-six additional specimens numbered MGSB77594a–z and MGSB85959a–j and 24 additional specimens numbered MPZ 2022/14–37.

Remarks.—The studied specimens can be assigned to *Eocalcinus* because of the general outline of the left chela, being hemicircular in shape; the lower margin of the propodus that is concave in the middle portion; the upper margin of the palm, which is broadly arched; the robust fixed finger, without

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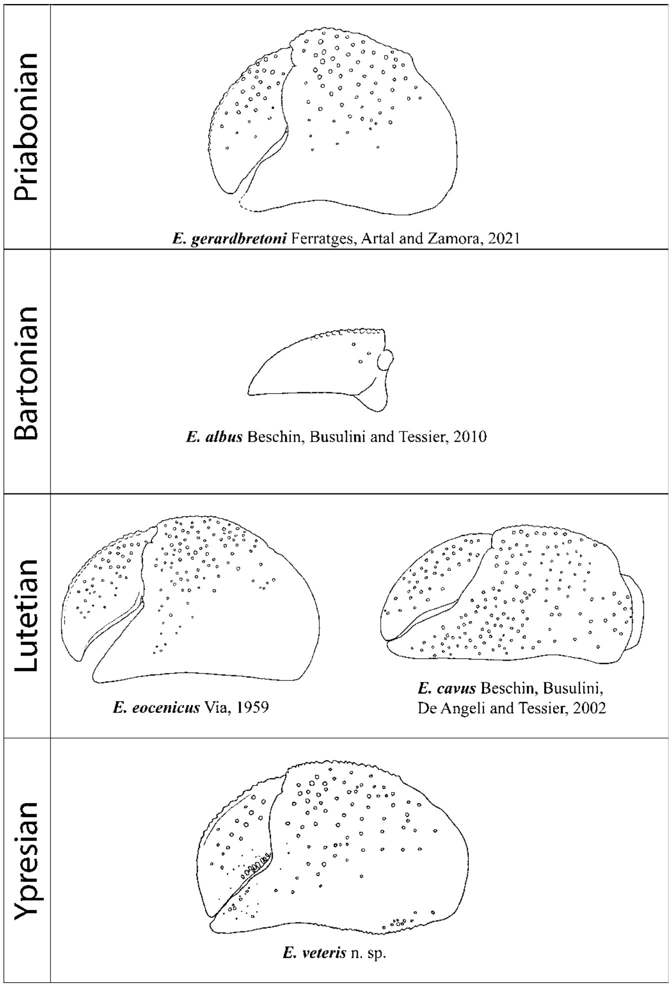

Figure 8. Shape change of the left chelas of *Eocalcinus* during the Eocene.

teeth on the occlusal edge, joining tightly the movable finger; the dactylus, which exhibits a broadly arched upper margin; and because the whole chela is densely ornamented with small granules. The new species, *E. veteris*, is clearly distinguishable from other species of the genus in having a less subcircular general outline; the distinction is also based on a palm somewhat longer than high and a lower margin convex in the proximal portion and concave in the middle portion.

The type species, *E. eocenicus*, shows some differences from *E. veteris* n. sp. In *E. eocenicus*, the major chela is more semielliptical; the propodus longer than high, the palm longer than high; the lower margin of the propodus is nearly straight, only slightly concave in the middle portion; the fixed finger has straight margins; the dactylus is nearly straight in the occlusal edge and exhibits notable small teeth in the upper margin. The lower margin is only slightly sinuous from lateral view (slightly concave in median portion), strongly sinuous when seen from the lower view. The lower margin is strongly ridged and raised in the proximal portion (adaptation for gastropod apertures). There are spaced large granules, mainly in the upper portion; the ornamentation in the lower portion of the palm consists of very small circular granules, very uniformly distributed (Via, 1959), while granules are smaller in the new species. Granules are larger in *E. eocenicus* than in *E. veteris* n. sp. Inner portion of palm smooth, with scarce granules in *E. veteris*.

Eocalcinus cavus has a more elongated left chela; the palm is longer than high; the lower margin of the propodus is nearly straight and only weakly concave; the fixed finger is much more elongated, and the occlusal margin is only somewhat arched; the lower portion of the palm bears larger granules (Beschin et al., 2002; De Angeli and Caporiondo, 2017). Comparison of the new species with *E. albus* is almost impossible because the latter was described on the basis of a single dactylus only. However, this dactylus has a totally straight occlusal margin, and the upper margin is gently denticulated (Beschin et al., 2010).

All other species of *Eocalcinus*, with the exception of the type species, are represented by the left chelae (or a single dactylus of the left chelae in the case of *E. albus*). Recent finds of the right chelae of *E. eocenicus* allowed the assignment of this genus to the family Calcinidae (Ossó, 2020).

Eocalcinus veteris n. sp. corresponds to the stratigraphically oldest species of the genus (see Fig. 8) and allows us to trace a general trend toward more rounded shapes (Fig. 8). This oldest species presents a more elongated outline, a straighter lower margin, and a less marked plano-convex section (O-shaped section) than in more recent species (D-shaped section). This trend toward more rounded shapes, with a sinuous lower margin and a more plano-convex section, could be related to the progressive adaptation of the major chela to perform an opercular function, adapting to the shape of the aperture of the host shell (as proposed by Ferratges et al., 2021a, p. 9, figs. 4, 5).

Family Paguridae Latreille, 1802
Genus *Pagurus* Fabricius, 1775

Type species.—*Cancer bernhardus* Linnaeus, 1758 by original designation.

Fossil species included.—*Pagurus alabamensis* Rathbun, 1935; *P. alatoides* Philippe and Secrétan, 1971*; P. albus* Müller, 1979 (=*P. tuberculosus* Harvey, 1998); *P. avellanedai* Via, 1951; *P. banderensis* Rathbun, 1935; *p.* aff. *P. bernhardus* (Linnaeus, 1758); *P. concavus* Müller, 1979; *P. convexus* Whetstone and Collins, 1982; *P. granosipalm* (Stimpson, 1859); *P. langei* Collins and Jakobsen, 2003; *P. latidactylus* Müller and Collins, 1991; *P. malloryi* Schweitzer and Feldmann, 2001; *P. manzonii* (Ristori, 1888); *P. marceti* Via, 1959; *P. marini* Via, 1959; *P. mezi* Lörenthey, 1909; *P. rakosensis* Müller, 1979; *P. squamosus* Ristori, 1886; *P. texensis* Franţescu, 2014; *P. travisensis* Stenzel, 1945; *P. turcus* Müller, 1984, and *P. valdagnensis* Beschin et al., 2012.

?*Pagurus* sp.
Figure 9

Description.—Right cheliped moderately stout, short (Fig. 9). Palm subquadrate in shape, densely covered by subconical granules on the outer surface; inner surface smooth; gently convex dorsal surface, with numerous closely spaced small conical tubercles; inner surface gently convex, with scattered small, low tubercles. Lower margin slightly concave. The preserved portion of dactylus robust, with the same ornamentation as the palm.

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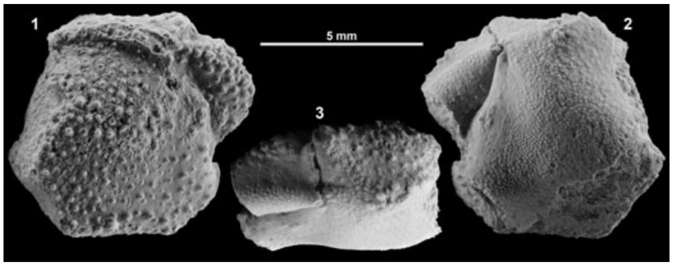

Figure 9. ?*Pagurus* sp. (**1–3**) Right cheliped (specimen MPZ 2021/32): (**1**) lateral view of outer side; (**2**) lateral view of inner side of right chela; (**3**) oblique upper view. Specimen whitened with ammonium chloride sublimate.

Material.—MPZ 2021/32 is a partial right chela (length 6.2 mm and width 6.5 mm) with well-preserved cuticle, and MPZ 2022/60 is a partial right propodus.

Remarks.—Numerous fossil taxa have been assigned to the genus *Pagurus* (see the preceding), and it is widely acknowledged to most likely be a cluster of different genera, so a revision is necessary (Schweitzer and Feldmann, 2001). This happens because most of the taxonomic and diagnostic features to differentiate between modern genera are not preserved in fossil material (i.e., Jagt et al., 2006; Fraaije, 2014; Fraaije et al., 2014).

The recovered material consists of a very incomplete single right chela, but it shares several features with extant members of *Pagurus*. According to the general shape of the chela (a well-developed palm that maintains its height along its entire length) and dense tuberculate ornamentation, appears to be most similar to the genus *Pagurus*. For this reason, we have taken the most conservative approach and placed the material within *Pagurus*.

The extant species of the genus present a robust right chela, globular, with outer and inner surface of the palm strongly convex, and the outer surface of propodus covered by dense granules (Sánchez and Campos, 1978; McLaughlin et al., 2010; Lima and Lemaitre, 2016). Fossil species are also characterized by globular, convex surfaces with the outer surface of the propodus densely granulated (Via, 1959; Schweitzer and Feldmann, 2001; De Angeli and Caporiondo, 2017). Some recent species (i.e., *P. spinossior* Komai, Reshmi, and Kumar, 2013) bear similarities with the scarce material recovered, so we tentatively assign the new material to this genus.

Genus *Anisopagurus* McLaughlin, 1981

Type species.—*Pylopagurus bartletti* Milne Edwards and Bouvier, 1893 by subsequent designation of McLaughlin, 1981.

Species included.—*Anisopagurus actinophorus* Lemaitre and McLaughlin, 1996; *A. asteriscus* Lemaitre, 2020; *A. bartletti* (Milne Edwards and Bouvier, 1893); *A. hopkinsi* Lemaitre and McLaughlin, 1996; *A. pygmaeus* (Bouvier, 1918); *A. vossi* Lemaitre and McLaughlin, 1996.

Remarks.—The genus *Paguritta* Melin, 1939 shows similarities with *Anisopagurus* due to the general shape of the chela and the row of spines on the upper and lower margins of the palm. *Anisopagurus* is distinguishable from *Paguritta* in having the outer surface of the palm densely covered by hemispherical, pearled granules closely spaced (while all species of *Paguritta* bear small conical spines); the fingers are characterized by strong longitudinal ridges, while in all species of *Paguritta* the fingers are flattened (see Komai and Nishi, 1996, p. 463–464, 472, figs. 4, 5; Komai and Okuno, 2001, p. 299, figs. 3, 4; McLaughlin and Lemaitre, 1993, p. 5, figs. 1, 3, 5, 7, 9, 11).

The modern genus *Rhodochirus* McLaughlin, 1981 also shows similarities with *Anisopagurus* in the general shape of the chela. However, *Rhodochirus* presents some differences, such as the more pointed fingers, coalescent granules on fixed finger, outer surface of the palm covered with large spiny tubercles with basal rosettes (see McLaughlin, 2003, p. 117, 127, fig. 6; Parente and Hendrickx, 2005, fig. 1; Komai, 2013, p. 29).

Anisopagurus primigenius new species
Figure 10

Type material.—The holotype, MPZ 2021/31, is a complete right propodus (propodus length: 9.9 mm; palm length: 5.2 mm; palm height: 5.6 mm) with well-preserved cuticle but without movable finger. There are two incomplete right propodi (paratypes), MPZ 2022/39 and MGSB77624.

Diagnosis.—Right cheliped suboperculate, D-shaped in cross section; posterior margin slightly offset toward the inner surface; outer surface of palm tuberculated, surrounded by spines directed vertically; inner surface with squamous tubercles.

Description.—Right cheliped suboperculate (Fig. 10), ovate, approximately twice as long as high, flattened dorsoventrally, D-shaped in cross section; angle of articulation propodus/carpus 15° from perpendicular; upper margin broadly arched, bearing small conical teeth directed forward; lower margin slightly arched. Palm semicircular, as long as high, with median region moderately elevated in the outer surface, surrounded by a more or less flat surface. Outer surface covered with numerous fungiform tubercles and surrounded by strong spines directed nearly vertically forming crown-like shape (Fig. 10). Inner surface convex, with small squamous tubercles. Fingers slender and elongated, dactylus and fixed finger with a longitudinal ridge. Fixed finger with blunt termination, about as long as the palm. Occlusal margin with two aligned molariform teeth. Left cheliped unknown.

Etymology.—From the Latin adjective *primigenius* (the oldest) to emphasize the geological seniority of this paguroid.

Other material examined.—Two partial right propodi (MPZ 2022/39 and MPZ 2022/61) and one isolated right dactylus (MPZ 2022/40).

Remarks.—Ferratges et al. (2021b) tentatively suggested that this taxon could be assigned to either *Paguritta* Melin, 1939 or *Rhodochirus* McLaughlin, 1981. However, a more detailed study of the material suggests that this species fits better in *Anisopagurus*. *Anisopagurus primigenius* n. sp. can be differentiated from other species of the genus on the basis of

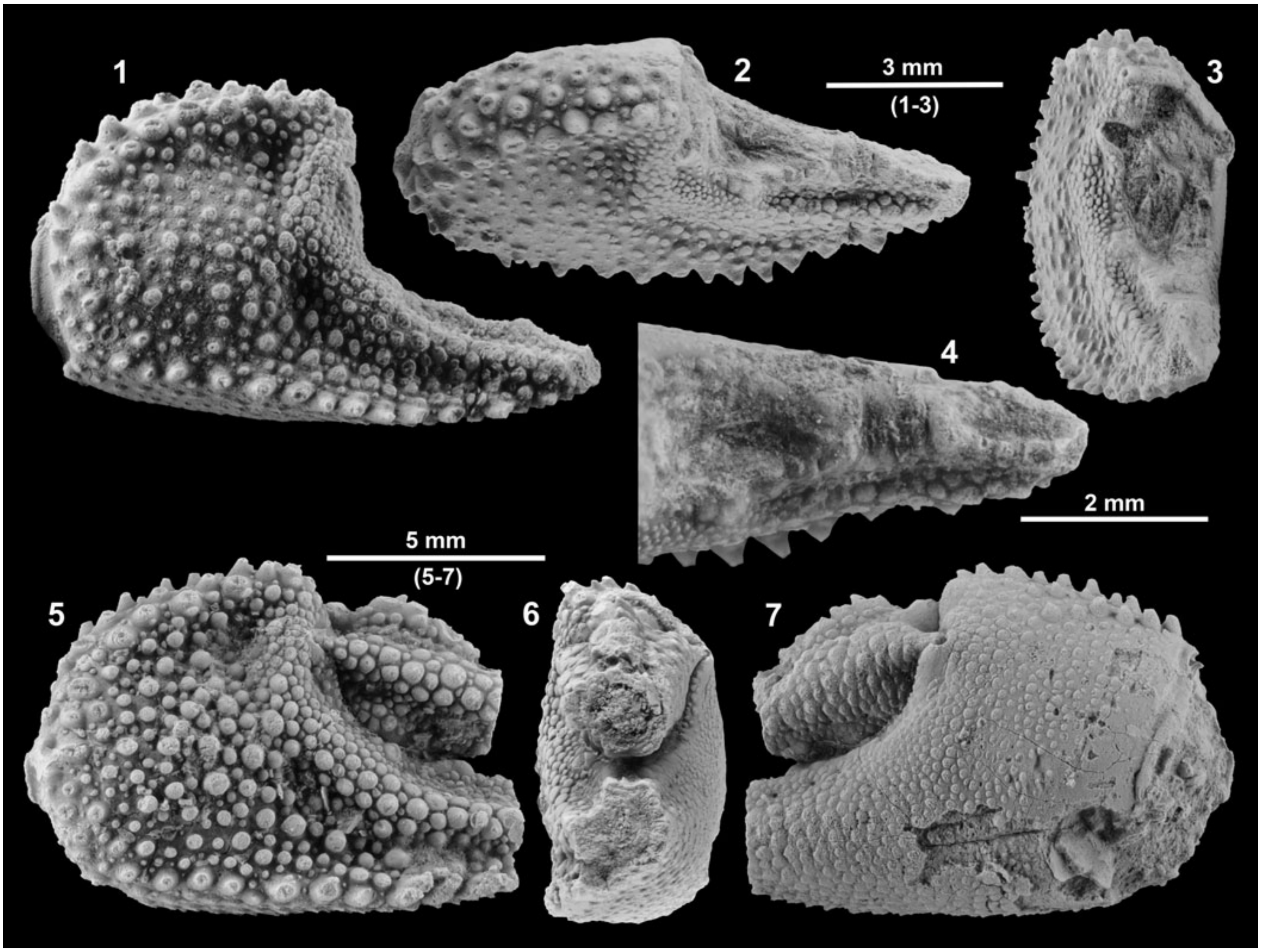

Figure 10. *Anisopagurus primigenius* n. sp. (**1–4**) Holotype (MPZ 2021/31), right chela: (**1**) lateral view of outer side; (**2**) oblique upper view; (**3**) frontal view. (**4**) Detail of the occlusal margin with two teeth. (**5–7**) Paratype (MGSB77624), right chela: (**5**) lateral view of outer side; (**6**) frontal view; (**7**) lateral view of inner side. Specimens whitened with ammonium chloride sublimate.

its density of ornamentation and shape of its fungiform tubercles, covering the entire outer surface, very tight on both fingers, almost coalescing, and the two rows of spines on the upper margin.

A. primigenius n. sp. is morphologically close to species of *Paguritta* due to the general shape of the chela and the row of spines in the upper and lower margins of the palm. Nevertheless, *A. primigenius* n. sp. is easily distinguishable from *Paguritta* sp. by having the outer surface of the palm densely covered by closely spaced hemispherical, pearled granules (while all species of *Paguritta* bear small conical spines); the fingers are characterized by strong longitudinal ridges in *A. primigenius* n. sp. while in all species of *Paguritta* the fingers are flattened (see Mclaughlin and Lemaitre, 1993, p. 5, figs. 1, 3, 5, 7, 9, 11; Komai and Nishi, 1996, p. 463–464, 472, figs. 4, 5; Komai and Okuno, 2001, p. 299, figs. 3, 4).

The modern species assigned to *Rhodochirus* also show similarities with *Anisopagurus primigenius* n. sp. in the general shape of the chela. However, differences include the more pointed fingers, coalescent granules on the fixed finger, and outer surface of the palm covered with large spiny tubercles with basal rosettes (see McLaughlin, 2003, p. 117, 127, fig. 6; Parente and Hendrickx, 2005, fig. 1; Komai, 2013, p. 29).

Regarding the fossil record, *Anisopagurus primigenius* n. sp. seems to share some characteristics with *Lessinipagurus granulatus* and *L. planus*, such as the general ornamentation and the fixed and movable fingers with elongated longitudinal ridges. Nevertheless, *A. primigenius* n. sp. presents differences in the general shape, with a more elongated propodus and fingers. In *Lessinipagurus*, the complete chela is subcircular, not elongated, and the upper margin is extremely salient, visor-shaped (see Beschin et al., 2012, p. 29, fig. 22; De Angeli and Caporiondo, 2017, p. 20–22, figs. 14, 15).

Final remarks and conclusions

The global record of Paleogene paguroids is poor and often fragmentary. Specifically, in the Iberian Peninsula, only six species have previously been described from the Eocene. Via (1959) first described *Pagurus marceti*, *Pagurus marini*, and *Eocalcinus eocenicus* on the basis of fragmentary material. Ferratges et al. (2020) described a nearly complete specimen of *Diogenes* *augustinus*, and Ferratges et al. (2021b) recently described two new species (*Parapetrochirus robustus* and *Eocalcinus gerardbretoni*) from the lower and upper Eocene, respectively.

This new contribution includes representatives of four families (Annuntidiogenidae, Diogenidae, Calcinidae, and Paguridae) and increases our knowledge of known taxa (six new species) of paguroids from the early Eocene associated with reef environments. Specifically, the studied assemblage of paguroids inhabited shallow reef complexes of the Serraduy Formation within the euphotic to mesophotic zone (see Ferratges et al., 2021b).

Some of the taxa studied in the present work show close relationships with several modern genera (*Anisopagurus*, *Clibanarius*, *Dardanus*, *Paguristes*, *Pagurus*, *Petrochirus*). In general, these modern hermit crabs are common in intertidal and shallow-water areas of tropical and temperate seas (i.e., Forest and Saint-Laurent, 1968; Hazlett, 1981; Leite et al., 1998; Melo, 1999; Rahayu, 2006; Rahayu and Forest, 2009; Mantelatto et al., 2010; McLaughlin et al., 2010; Trivedi and Vachhrajani, 2017).

This study contributes to the understanding of paguroid diversity during the Eocene in the southern Pyrenean basins. In addition, the data provided increase the knowledge of European fossil paguroids, providing several new taxa, some of which correspond to the oldest representatives of their respective genera. Our study also increases the temporal distribution of the genus *Eocalcinus* with the oldest record of the genus. In addition, the new materials assigned to this genus suggest an evolutionary trend toward more rounded shapes. The oldest species of *Eocalcinus* had a more elongated outline, a straighter lower margin, and a less marked plano-convex section of the palm. This trend toward more rounded shapes could be related to the progressive adaptation of the major chela to perform an opercular function (Ferratges et al., 2021a).

Gastropod shells are vital for most hermit crab species, being essential for their survival (see Tricarico and Gherardi, 2006 and references therein). The great abundance and diversity of gastropods observed in the studied outcrop (see Ferratges et al., 2021b) probably contributed to the diversity of hermit crabs. In modern ecosystems, the availability of gastropod shells plays an important role in limiting the abundance of hermit crabs (Vance, 1972; Bach et al., 1976; Kellogg, 1976), and their diversity reduces competition between different genera. In fact, some modern species show a marked preference for certain empty shells over others (i.e., Vance, 1972; Conover, 1978; Bertness, 1980). Thus, the mechanism allowing coexistence of several taxa in the same environment involves both resource and habitat partitioning (Vance, 1972).

The data provided here show a great diversity of paguriods at the beginning of the Eocene, which is richer than Paleocene records (see Jakobsen et al., 2020 and references therein), and show that the reefs of the lower Eocene were important hotspots of pagurid diversities comparable to modern ecosystems.

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