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New spider crabs (Brachyura, Majoidea) from the early Eocene of Spain with a reassignment of the species "*Periacanthus*" *tetracornis*

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ABSTRACT

Spider crabs (superfamily Majoidea Samouelle, 1819) represent a highly diverse group within Eubrachyura de Saint Laurent, 1980. This study re-examines the species "*Periacanthus*" *tetracornis* Ferratges, Ortega, Fernández, Moreno and Maza, 2014 (Roda Formation, lower Eocene of Spain) which was previously considered as a member of Epialtidae MacLeay, 1838 and it is included as a new genus of majoid crabs, *Eoactinotocarcinus* n. gen. Additionally, *Tumulosternum ortegai* n. sp. is described from the same geological unit expanding the distribution of this genus to the southern Pyrenees. These taxa were found in siliciclastic facies co-occurring with a diverse assemblage of decapod crustaceans and other invertebrates. These facies are interpreted as deposited in a prodelta environment supporting the idea of such environments as highly diversified areas of decapods during the Eocene. These new taxa represent the earliest known record of the Subfamily Actinotocarcininae Jenkins, 1974 and the genus *Tumulosternum* respectively.

KEYWORDS **Malacostraca. Decapoda. Benthonic. Taxonomy. Ypresian.**

INTRODUCTION

Spider crabs displayed a notable diversity and widespread distribution during the middle–late Eocene (*e.g.* Schweitzer *et al.*, 2010, 2020), with a concentration of maximum diversity in Europe. This period is considered pivotal in their evolutionary history because the great diversity of taxa was adapted to different environments and also contain some forerunners of modern groups (Ferratges *et al.*, 2023, and references therein). Nevertheless, despite the rich fossil decapod assemblage found in the early Eocene of the south-central Pyrenees in northeastern Spain (Ferratges, 2022), spider crabs remain uncommon.

Spider crabs are typically characterized by elongated pyriform carapaces and bifid fronts, a distinctive feature known as a pseudorostrum (Davie *et al.*, 2015; Griffin, 1966a; Poore and Ahyong, 2023; Schweitzer *et al.*, 2020), but variations on this standard morphology exists in modern and extinct assemblages (Guinot and van Bakel, 2020; Jenkins, 1974; Poore and Ahyong, 2023). Some fossil genera, such as *Periacanthus* Bittner, 1875, and *Actinotocarcinus* Jenkins, 1974, exhibit extremely large lateral expansions (branchial spines). This feature is not found in any modern spider crab, with the exception of less developed spines in genus *Pteromaja* Ng and Anker, 2014, *Huenia* de Haan, 1839, and some species of the genus *Neophrys* Lee, Richer de Forges and Ng, 2019.

The species *Periacanthus tetracornis* was initially described by Ferratges *et al.* (2014) based on incomplete specimens (two carapaces and one external mold). However, due to inadequate preservation, these specimens were erroneously attributed to the genus *Periacanthus* based on superficial resemblance. This study aims to rectify the systematic position of this taxon and presents the description of a new majoid crab discovered from the same strata. These discoveries, found within prodelta marls of the Roda Formation expand the spatial and temporal distribution of Actinotocarcininae JENKINS, 1974, and the genus *Tumulosternum* MCCULLOCH, 1913, to the lower Eocene of western Pyrenees. The species *Tumulosternum ortegai* n. sp. constitutes the first fossil record of the genus in Spain. This research contributes significantly to enhancing our understanding of spider crab diversity during the Eocene, shedding light on potential paleobiogeographic connections between Iberia and other regions.

GEOLOGICAL SETTING

The southern Pyrenean basins harbor exceptionally comprehensive Eocene marine sedimentary successions, showcasing a rich paleocarcinological content previously documented across multiple outcrops (Ferratges, 2022 and references therein). Situated in the south-central Pyrenean zone (Fig. 1), these basins were geographically located in tropical latitudes during the Paleocene–Eocene (*e.g.* Hay *et al.*, 1999; Silva-Casal *et al.*, 2017). They corresponded to an elongated gulf connected to the west by the Bay of Biscay and were bound to the north by the axial zone of the Pyrenees (Garcés *et al.*, 2020; Plaziat, 1981).

Previously studied material from this outcrop, collected near the village of Atiart (Fig. 1A), a few kilometers west of Campo (La Fueva municipality, Province of Huesca, Spain), at the junction between the Ainsa Basin and the Graus-Tremp Basin (Fig. 1), was erroneously assigned to the Campodarbe Formation (Ferratges *et al.*, 2014). However, a detailed study reveals that the studied material comes from bioclastic limestones and marly beds of the upper Ilerdian–lower Cuisian (Ypresian, lower Eocene), corresponding to the lateral equivalent of the Roda Formation (Robador and Zamorano, 2013).

The Roda Formation is a coarsening and shallowing upwards succession (Molenaar and Martinius, 1990) and shows a progradational pattern to the south and southwest (Leren *et al.*, 2010). This formation contains a great diversity and abundance of decapod crustaceans and has provided several important assemblages of decapods in different associations (Table I; Ferratges *et al.*, 2022b). The presence of the fossil crab *Zanthopsis dufourii* (H. MILNE EDWARDS, 1850) stands out, which appears associated with other benthic fauna, previously documented in different localities (*e.g.* Ferratges *et al.*, 2021a).

In the studied locality, a few kilometers west of the Esera river area (Fig. 1), the distal equivalent of the Roda Formation consists of a marly-dominated succession and calcareous sandstone for which the total thickness cannot be determined, as its base corresponds to a mechanical contact (Robador and Zamorano, 2013). These materials have been interpreted as turbiditic deposits (Robador and Zamorano, 2013) deposited in aphotic platform and slope facies with "slumps" at the base, and an olistolithic section at the top with detrital-bioclastic levels containing re-sedimented fauna typical of platform environments (Remacha and Zamorano, 1989; Serra-Kiel *et al.*, 1994).

This area contains, however, some highly fossiliferous intervals with diverse benthic fauna, especially in the upper part of the formation, almost in contact with the Morillo Formation (Fig. 1B). These intervals have yielded a diverse array of small benthic invertebrates, encompassing gastropods, bivalves, echinoderms, branching bryozoans, sponges, foraminifera, and other decapod crustaceans (many of them articulated) might suggest periods of stability probably associated with prodelta and open platform environments.

MATERIAL AND METHODS

The data presented in this study comes from the re-examination of fossil specimens gathered from an outcrop near the village of Atiart (Fig. 1). Among the studied materials, there are six specimens, all of which are isolated carapaces. These specimens are attributed to two distinct genera, encompassing two species. Among these species, one is newly identified, while the other has been reclassified under a new genus.

The studied specimens are housed in the paleontological collection of the Museo de Ciencias Naturales de la Universidad de Zaragoza (Spain) under the acronym of MPZ. A latex cast was made for the specimens MPZ 2013/86, MPZ 2024/03 and MPZ 2024/06 (preserved as natural external molds). The external molds were previously brushed to remove cuticle remains using a wet brush and a needle. The specimen MPZ 2024/04 of *Tumulosternum ortegai* was prepared for a more detailed study, using a Micro Jack 2 air scribe (Paleotools) and binocular magnifying. The specimens MPZ 2024/04 and MPZ 2024/05 was found by Gregorio Ortega and Manuel Fernandez respectively, who found the specimens and kindly donated them for study. All the specimens were photographed dry and

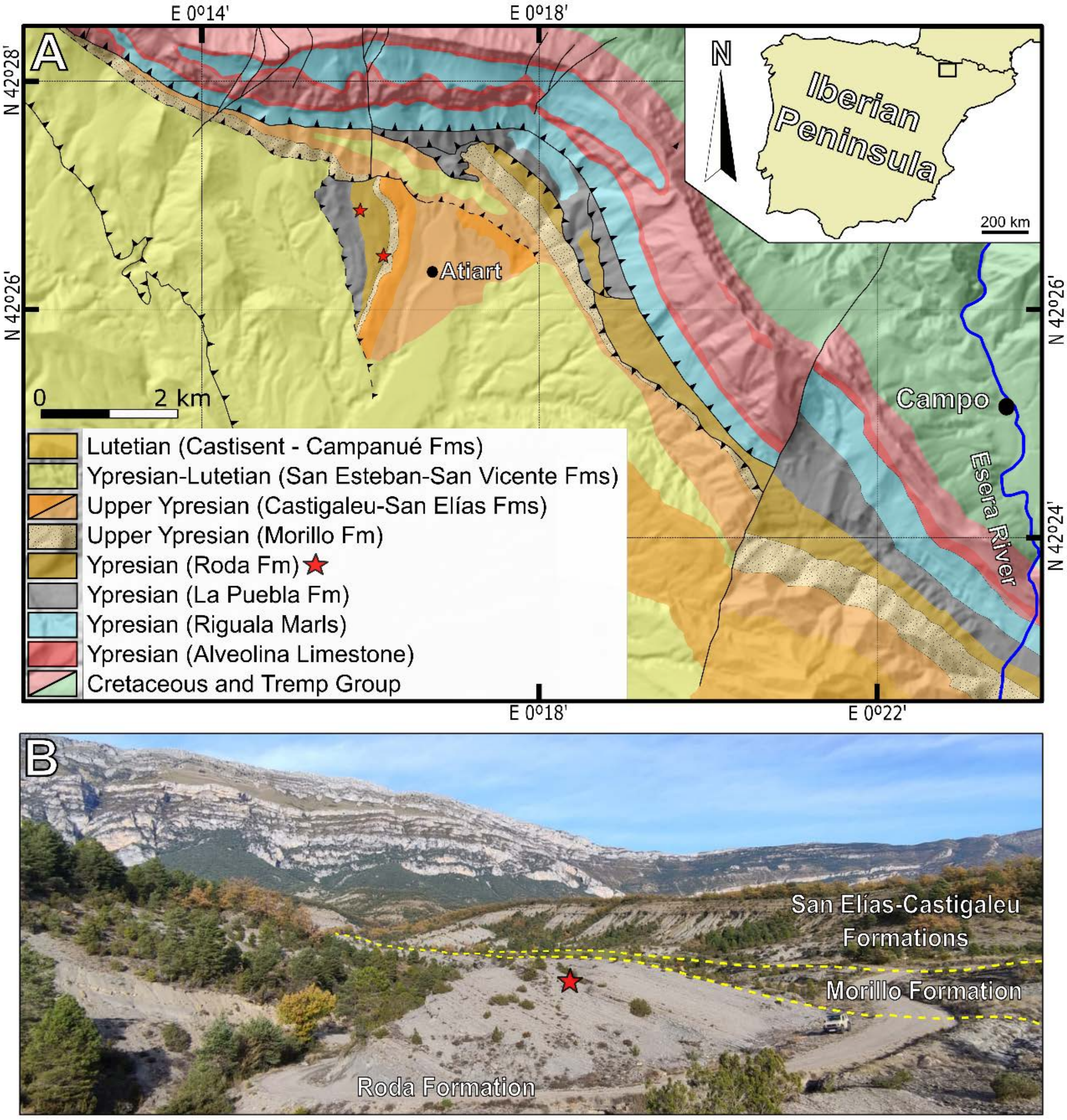

FIGURE 1. A) Simplified geological map with formations and location of the studied outcrop; B) Panoramic view of the studied outcrop with outlined formations. Red stars indicate the location where the material was recovered.

coated with ammonium chloride sublimated to enhance anatomical details and ornamentation of the cuticle. Detailed photography of the carapace surfaces was made using a Nikon d7100 camera (Nikon, Tokyo, Japan) with a 60 mm macro lens.

A count of the studied and associated taxa has been conducted based on the material housed in the Museo de Geología del Seminario Conciliar de Barcelona (MGSCB), and Museo de Ciencias Naturales de la Universidad de Zaragoza (MPZ) along with field observations by the author, to illustrate the relative abundance of each taxon. The data obtained, however, are only indicative, due the absence of an exhaustive and systematic sampling.

Morphological terminology used in the present work follows Griffin (1966a), Griffin and Tranter (1986) and Davie *et al.* (2015) (Fig. 2). Measurements of the carapace are presented as Carapace Width (CW), Carapace Length (CL) and Postrostral Carapace Length (PCL) in millimeters. Carapace width was taken at the widest point of the branchial region, carapace length was measured from the tips of the rostrum to the posterior margin of the carapace, and postrostral carapace length was measured from the base of the rostral spines to the posterior margin of the carapace (Fig. 2).

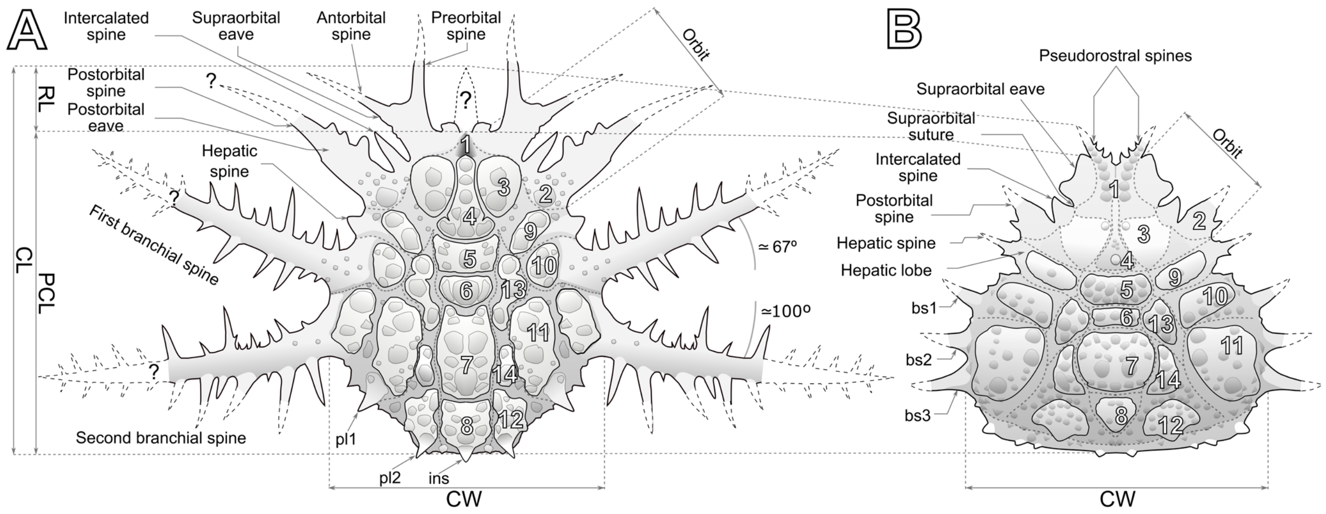

FIGURE 2. Carapace scheme of the two studied majiod (s. l.) crabs showing terminology used in the present work. A) *Eoactinotocarcinus* n. gen.; B) *Tumulosternum ortegai* n. sp.; 1: frontal region; 2: orbital region; 3: protogastric region; 4: mesogastric region; 5: metagastric region; 6: urogastric region; 7: cardiac region; 8: intestinal region; 9: hepatic region; 10: epibranchial region; 11: mesobranqual region; 12: metabranchial region; 13: branchial lobe; 14 lateral cardiac tubercle. CL: Carapace Length; CW: Carapace Width; RL: pseudorostral length; PCL: Postrostral Carapace Length; bs1–3: branchial spines; pl1–2: posterolateral spines; ins: intestinal spine.

SYSTEMATIC PALEONTOLOGY

The superfamily Majoidea SAMOUELLE, 1819 has been reviewed by some authors (Guinot and Van Bakel, 2020; Poore and Ahyong, 2023). Due to the incompleteness of the new material and the absence of critical characters (such as basal antennal articles, maxillipeds, sternum, etc.), no new systematic considerations are made in this contribution and higher systematic rank placements follow Schweitzer *et al.* (2020) and Poore and Ahyong (2023).

Superfamily: Majoidea SAMOUELLE, 1819
Family: Majidae SAMOUELLE, 1819
GENUS ***Tumulosternum*** MCCULLOCH, 1913
Figs. 2B; 3; 4

Type species. *Micippoides longimanus* HASWELL, 1880 accepted as *Tumulosternum longimanum* (Haswell, 1880) (type by original designation).

Fossil included species. *Tumulosternum ortegai* n. sp.

Remarks. The new material bears resemblance to some species of the genus *Mithracia* (*i.e. M. libinioides* BELL, 1858) in general outline of the carapace and the presence of branchial spines on the lateral margins. However, the genus *Mithracia* usually presents a rather rounded, globose carapace (*i.e. M. oppionii* LARGHI, 2002), not flattened as in the new material. Furthermore, *Mithracia* presents significant differences in the shape of the pseudorostral spines, in the posterior margin and the distribution and shape of dorsal regions. The genus *Micromaia*, contains some species that bear superficial resemblances to the new genus (*i.e. Micromaia batalleri* VÍA, 1959, p. 43, fig. 12). However, the genus *Micromaia* has a more elongated carapace, smaller orbits with less developed and less differentiated eaves, dorsal regions slightly different from the new material, hepatic margin without a single hepatic spine; lateral margins without large branchial spines, and posterior margin lacks spines.

The genus *Leptomithrax* MIERS, 1876, both modern and fossil representatives show similarities with the new material. Species of *Leptomithrax* are characterized by a pyriform outline of the carapace, presence of hepatic spine, relatively short pseudorostral spines, poorly developed supraorbital eave, short pre- and postorbital spines, and well-developed carapace regions. However, the genus *Leptomithrax* shows some differences with the new material: i) wider hepatic region, with more than one spine; ii) more elongated carapace; iii) rounded posterior margin, much more convex than the new material and iv) posterolateral margins rounded, in general without large spines. Furthermore, the fossil species assigned to this genus show great morphological variability, so a review seems to be necessary.

The studied material can be assigned to the genus *Tumulosternum* MCCULLOCH, 1913 based on the carapace general outline, not very elongate, the short pseudorostral spines, orbital position and shape of the orbits and eaves, the shape and position of the hepatic spine, the strong conical spines in branchial margins and the wide posterior margin, with two small spines (Griffin, 1963: p. 234–235;

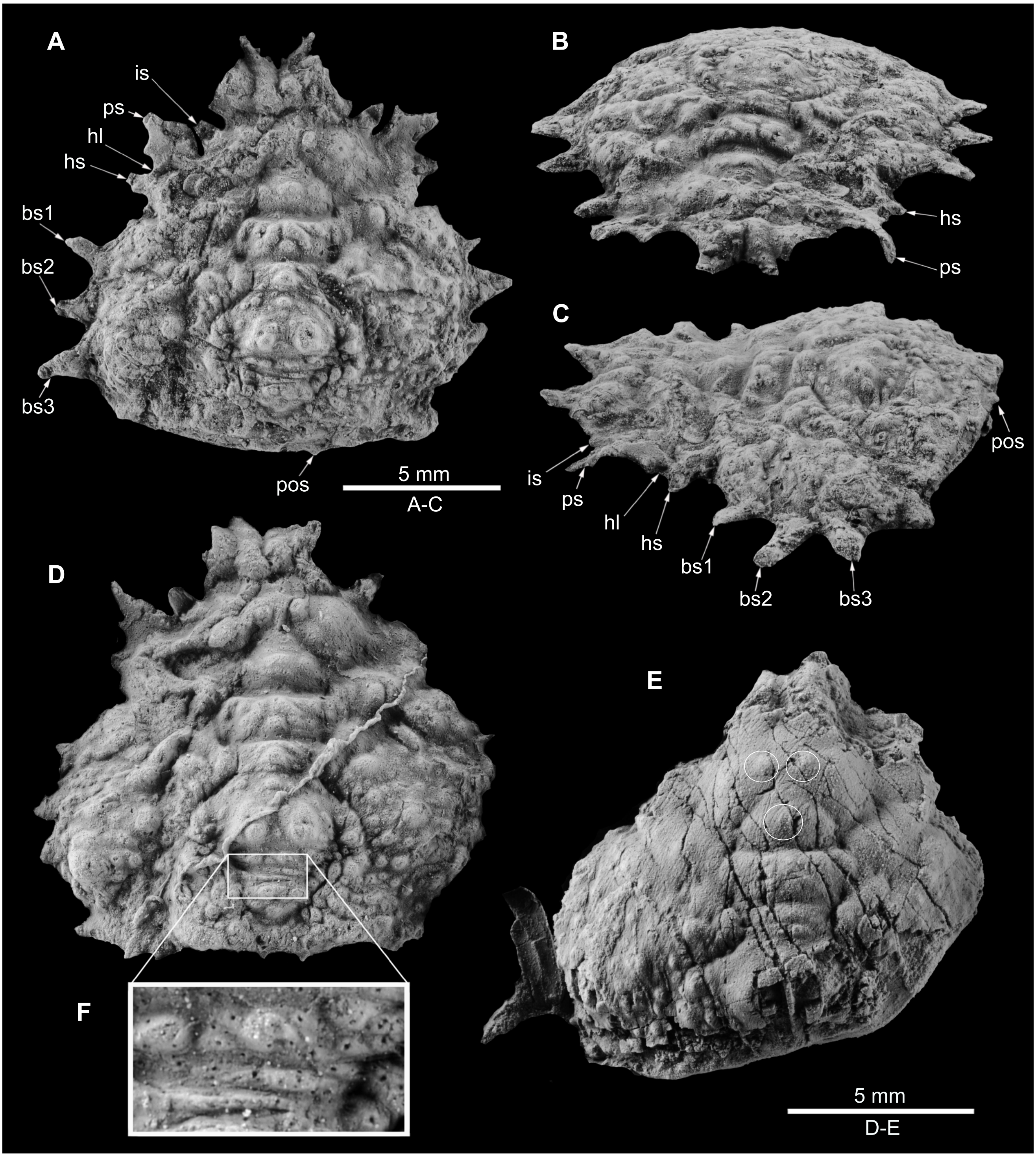

FIGURE 3. *Tumulosternum ortegai* n. sp. from the Roda Formation (lower Eocene, southern Pyrenees). A-C) Holotype MPZ 2024/04; A: dorsal view; B: oblique frontal view; C: left lateral view; D) latex cast whitened with ammonium chloride sublimate of the holotype, taken from de natural counterpart (MPZ 2024/06); E) paratype (MPZ 2024/05) showing the three tubercles of the gastric region with white circles; F) detail of the setal pits. Abbreviations: is= intercalated spine; ps= postorbital spine; hs= hepatic spine; hl= hepatic lobe; pos= posterior margin spine; bs1–3= lateral spines.

FIGURE 4. Idealized reconstruction of *Tumulosternum ortegai* n. sp. The parts not preserved in the fossil material have been tentatively inferred from closely related modern taxa.

1966b: 284; Griffin and Tranter, 1986: p. 257–264, figs. 94, 95; McCulloch, 1913, p. 334–335: fig. 45; Poore and Ahyong, 2023: p. 625–627, 633, fig. 14.86s; Ward, 1933: p. 392, pl. 23 fig. 4).

Tumulosternum ortegai n. sp.
Figs. 2B; 3; 4
Zoobank ID code: urn:lsid:zoobank.org:act:97442F2D-C7F2-43F8-84A6-20DA49A2E2DC

Type material. The holotype is a near-complete carapace, partially decorticated, (MPZ 2024/04). There is one paratype (MPZ 2024/05) and the natural counterpart of the holotype (MPZ 2024/06) (Fig. 3).

Etymology. In honor of Gregorio Ortega (Barcelona, Spain) who found and donated the specimen.

Diagnosis. Carapace pyriform, cordate, narrowing anteriorly, with few blunt tubercles; pseudorostrum short, bifid, diverging distally; supraorbital eave without antorbital spine; intercalated spine small; postorbital eave with postorbital spine; hepatic margin with strong hepatic spine; dorsal regions delimited by grooves; branchial margins with three large spines laterally oriented, a fourth spine oriented obliquely upwards; posterior margin with two small spines near the axis.

Description. Carapace pyriform in outline, as long as wide (PCL/CW ratio about 1). Frontal margin narrow, sulcate, with two short, divergent pseudorostral spines with tiny spines on inner margin, proximally situated; orbits anterolaterally directed, with small supraorbital eave, without antorbital spine; short and conical intercalated spine; postorbital eave with postorbital spine and small tooth in the posterior margin. Hepatic lobe with strong spine. Lateral margins arched, strongly convex; branchial margin with three large and conical spines, and a fourth, smaller one, oriented obliquely upwards; posterior margin broad, rimmed, with two small conical spines near to the axis; maximum width in mesobranchial region. Carapace regions well defined by grooves, covered by blunt tubercles. Hepatic region small, defined by shallow groves; proto- and mesogastric regions inflated, weakly defined, with three blunt tubercles forming a triangle, two in the anterior part of protogastric region (one in each side), and one in the widest part of mesogastric region (Fig. 3E); meta- and urogastric regions subrectangular, narrower than mesogastric and cardiac regions; branchial regions wide, delimited from axial regions by grooves; epibranchial region reduced, poorly differentiated by a shallow groove; mesobranchial region broadly inflated; metabranchial region small, weakly defined; cardiac region large, inflated, with two lateral subtriangular extensions defined by shallow grooves; intestinal region triangular, depressed.

Remarks. Only three modern species of the genus *Tumulosternum* MCCULLOCH, 1913 are known: *T. longimanum* (Haswell, 1880), *T. parvispinosum* (Ward, 1933), and *T. wardi* GRIFFIN AND TRANTER, 1986; all of them from Southeast Australia (Griffin and Tranter, 1986). The species of this genus are differentiated by the shape of basal antennal article and pleopods (not preserved in the fossil specimen), the number of spines of the branchial margin, length and size of the pseudorostral spines, shape of the orbits and eaves, and the shape of the hepatic spine (Griffin and Tranter, 1986). The modern species show strong similarities with *Tumulosternum ortegai* n. sp., but the new species differs in some aspects: i) markedly divergent pseudorostral spines, not subparallel or slightly divergent as in modern species, ii) shape of the postorbital eave, laterally oriented in the new species, iii) intercalated spine slightly larger in the new species, iv) less convex posterior margin in the new species, v) posterior margin spines greatly reduced compared to modern species (Figs. 3; 4, Griffin, 1963: p. 234–235; 1966b: p. 284; Griffin and Tranter, 1986: p. 257–264, figs. 94–95; McCulloch, 1913: p. 334–335, fig. 45; Ward, 1933: p. 392, pl. 23 fig. 4).

Subfamily Actinotocarcininae JENKINS, 1974

GENUS *Eoactinotocarcinus* n. gen.
Figures 2A–5; 6
Zoobank ID code: urn:lsid:zoobank.org:act:5C7DD011-8727-474C-8E04-1AB1FED11170

Type species. *Periacanthus tetracornis* FERRATGES, ORTEGA, FERNÁNDEZ, MORENO AND MAZA, 2014.

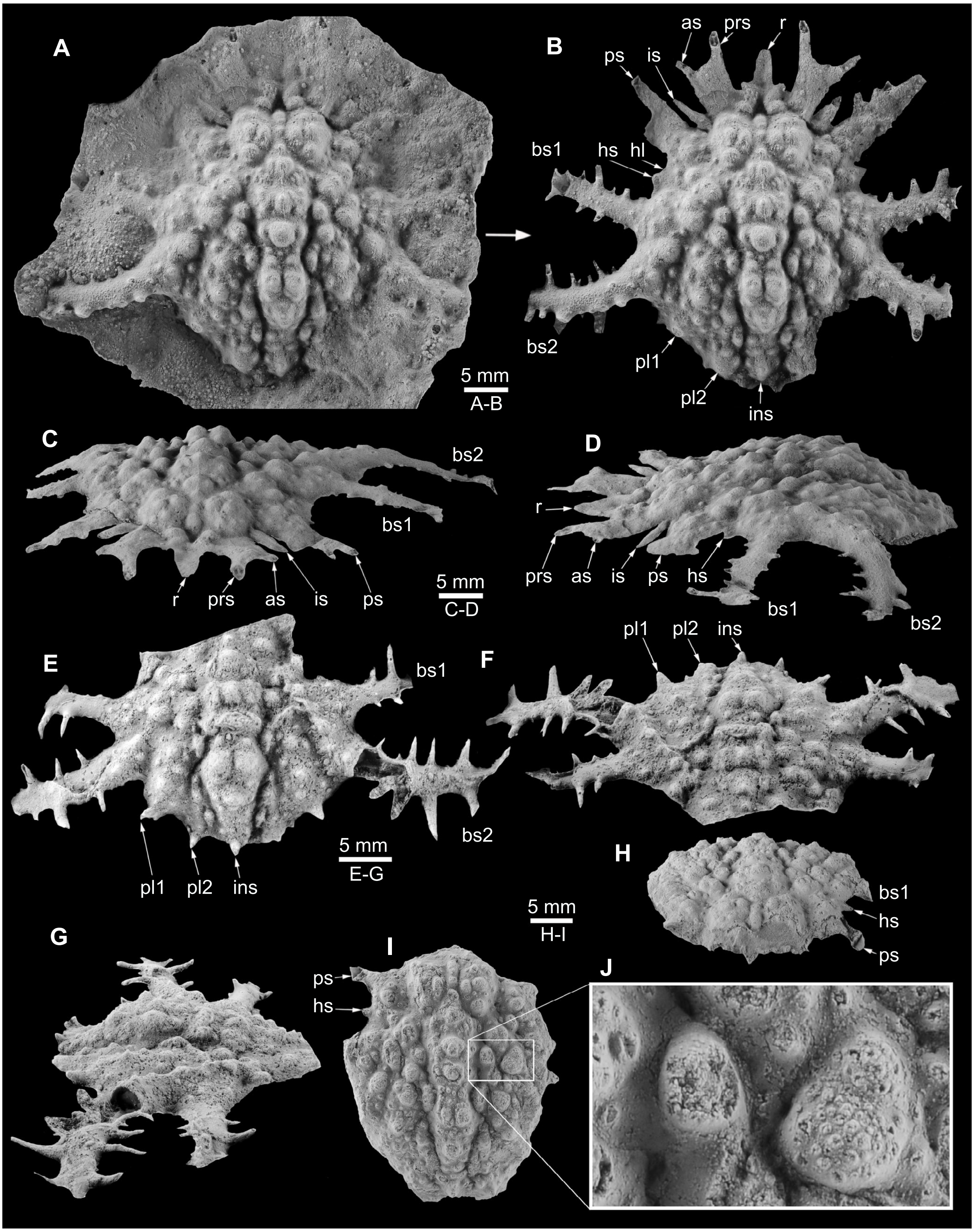

FIGURE 5. *Eoactinotocarcinus tetracornis* (Ferratges, Ortega, Fernández, Moreno and Maza, 2014) n. comb. from the Roda Formation (lower Eocene, southern Pyrenees). A-D) Latex cast whitened with ammonium chloride sublimate of the paratype MPZ2013/86. A: dorsal view; B: same specimen and view, cut out of matrix with interpretation of poorly preserved elements; C: oblique frontal view; D: left lateral view. E-G) Latex cast of the specimen MPZ 2024/03; E: dorsal view; F: oblique frontal view; G: right lateral view. H-I) Holotype MPZ2013/85; H: oblique frontal view; I: dorsal view; J: detail of the dorsal surface. Abbreviations: as= antorbital spines; prs= preorbital spine; is= intercalated spine; ps= postorbital spine; hs= hepatic spine; hl= hepatic lobe; bs1–2= branchial spines; r= interpreted rostrum; pl1–2= posterolateral spines; ins= intestinal spine.

FIGURE 6. Idealized reconstruction of *Eoactinotocarcinus tetracornis* (Ferratges, Ortega, Fernández, Moreno and Maza, 2014) n. comb. The parts not preserved in the fossil have been tentatively inferred from related taxa.

Diagnosis. Carapace subhexagonal, longer than wide; well-marked dorsal regions, with granulated tubercles; rostrum singular, elongated; orbits anterolaterally directed, formed above by supraorbital eave with long preorbital and antorbital spines, intercalated spine, and postorvital eave with postorbital spine. Short hepatic spine. Branchial margins with two extremely long spines, first in epibranchial margin, second in mesobranchial margin, both armed with small forward and backward spines. Long posterolateral margins.

Etymology. The generic name derives from the prefix *Eo-* (from ηως (gr.)= aurora), to generically indicate an ancestral form, in arbitrary combination with the generic name *Actinotocarcinus* Jenkins, 1974, to refer to its morphological affinities with the new genus.

Remarks. The subfamily Actinotocarcininae (within Majidae Samouelle, 1819) proposed by Jenkins (1974) found acceptance among certain authors (Feldmann, 1993; Števčić, 2005). However, Feldmann *et al.* (2006) omitted reference to this subfamily and retained the type genus (*Actinotocarcinus* Jenkins, 1974) within Majidae. Subsequently, the type genus was transferred to Epialtinae MacLeay, 1838 (family Epialtidae MacLeay, 1838) by De Grave *et al.* (2009), a position upheld by Schweitzer *et al.* (2010). Eventually, Schweitzer *et al.* (2020) transferred the genus back to Majidae and reinstated the subfamily Actinotocarcininae. In recent decades, several authors have adopted the consideration of the subfamilies of Majidae to family rank (Poore and Ahyong, 2023 and references therein). However, due to limited available material, this study tentatively considers the subfamily position within the family Majidae, following Schweitzer *et al.* (2020).

The type species of this new genus was originally assigned to the genus *Periacanthus* Bittner, 1875 (included in the family Epialtidae MacLeay, 1838) by Ferratges *et al.* (2014) due to its superficial resemblance, with pyriform shape of the carapace, the presence of branched lateral expansions, and due to an incorrect interpretation of the rostrum, in which the anterior part of the supraorbital eave was interpreted as the proximal part of the pseudorostral spines.

A re-examination of the preserved material in the specimens MPZ 2013/85 and MPZ 2013/86, and the examination of the new specimen MPZ 2024/03, important differences with the genus *Periacanthus* have been made. Firstly, the reinterpretation of the rostrum seems to suggest a single extension (Fig. 5B), unlike the genus *Periacanthus*, which has the two typical pseudorostral spines. The morphology of the orbits in the new genus, with a complex postorbital eave, carrying a postorbital spine and with small expansions forward directed is more similar with *Actinotocarcinus* than *Periacanthus*. The genus *Periacanthus* shows only a single hypertrophied lateral expansion in the mesobranchial margin, and a much less developed spine (compared to the later) on the epibranchial margin. The posterolateral margin of the new genus is more elongated and differentiated than in the genus *Periacanthus*, in which it is only slightly differentiated, partially fused with lateral expansions.

Eoactinotocarcinus n. gen. has strong similarities with the genus *Actinotocarcinus* Jenkins, 1974. The two known species included in this genus have similarities with the new genus like general elongated outline of the carapace,; same distribution of the dorsal regions; elongated and singular rostrum; similar shape of the orbits with supraorbital eave with antorbital spine, intercalated spine, and well-developed postorbital eave, with postorbital spine; branchial margins with two very long and characteristic spines, the anterior directed laterally forward, the second directed slightly posterolaterally (Feldmann, 1993; Jenkins, 1974; Schweitzer *et al.*, 2020, p. 13, fig. 8). The new genus possesses all these characteristics and is therefore referred to the subfamily Actinotocarcininae Jenkins, 1974.

However, the genus *Actinotocarcinus* have a more or less smooth carapace surface, with only slightly marked regions, unlike *Eoactinotocarcinus* n. gen. which presents dorsal regions clearly marked by grooves, with large tubercles on the upper part. The orbits of the new genus show a much more developed supraorbital eave, with well-developed pre- and antorbital spines, unlike in the genus *Actinotocarcinus* which presents a very small supraorbital eave, without preorbital spine. In addition, the genus *Actinotocarcinus* shows a simple, extremely long spines or lateral expansions in the branchial margin, without ramifications; in the new genus, lateral expansions are much thicker, armed with spines (ramifications). Furthermore *Eoactinotocarcinus* n. gen. exhibits a small spine in the hepatic margin which is not present in *Actinotocarcinus*. Due to all these differences with the genus *Actinotocarcinus*, a new genus has been erected.

Eoactinotocarcinus tetracornis (FERRATGES, ORTEGA, FERNÁNDEZ, MORENO AND MAZA, 2014) n. gen. n. comb.
Figures 5; 6

Type material. Holotype (MPZ 2013/85), a carapace without lateral expansions. Paratype (MPZ 2013/86) that correspond to natural counterpart of missing specimen.

Diagnosis. The original diagnosis provided by Ferratges *et al.* (2014) is considered outdated because it was based on ambiguous data. Consequently, a new diagnosis has been proposed (as for the genus, by monotypy).

Description. Carapace subhexagonal, pyriform in outline, longer than wide (PCL/CW ratio about 1.6); dorsal surface covered by granulated tubercles; maximum width in mesobranchial region; rostrum produced, formed by a single spine axially sulcate, straight, directed forwards (not preserved, but can be speculated by the countermold preserved in the specimen MPZ2013/86, Fig. 5B); orbital region wide, orbits anterolaterally directed, supraorbital eave very developed, with large preorbital and antorbital spines, conical in shape and slightly forward; long and conical intercalated spine, separated by supraorbital sutures; postorbital eave complex, very developed, with short triangular extensions near the base forward oriented, and postorbital spine (partially preserved), facing out. Lateral margins arched, with short hepatic spine and two massive cylindrical branchial spines (not totally preserved), ramified with sharp spines, the first, located in the epibranchial margin, with an angle about 67°; the second, in the mesobranchial margin, with an angle of approximately 100º (about 120º in the base) respect to the longitudinal line (Fig. 2A); hepatic region inflated, defined by groves; short and conical spine in the hepatic lobe. Frontal region with deep groove between preorbital eaves; elongated and globose gastric region; protogastric region inflated; mesogastric region weakly defined, anterior portion ridged; metagastric region large, rectangular; urogastric region u-shaped, bounded by shallow grooves; meta- and urogastric regions laterally flanked by branchial lobe; branchial regions delimited from axial regions by deep grooves; cardiac region large and elongated, accompanied laterally by lateral cardiac tubercle; epibranchial region inflated, oblique; mesobranchial region broadly inflated, the largest branchial region; metabranchial region small, delimited by shallow grooves; intestinal region subpentagonal, with a conic tubercle posteriorly directed; posterior margin narrow, slightly rimmed.

Remarks. The most similar species to *Eoactinotocarcinus tetracornis* (Ferratges, Ortega, Fernández, Moreno and Maza, 2014) n. gen. n. comb., are *Actinotocarcinus chidgeyorum* JENKINS, 1974 and *A. maclauchlani* FELDMANN, 1993, both from the Miocene of New Zealand. All of them show the same general structure, with a piriform and elongate carapace, similar distribution of the dorsal regions, orbits complex carrying long spines, and very long lateral expansions. However, both species assigned to *Actinotocarcinus* show important differences with *Eoactinotocarcinus tetracornis*: antorbital eave much more developed in *E. tetracornis*, carrying two spines (pre- and antorbital spines) instead one; hepatic margin with short spine in *E. tetracornis*, which is absent in the two species of *Actinotocarcinus*; much more complex and developed lateral expansions in *E. tetracornis*, straight and devoid of spines both in *A. chidgeyorum* and *A. maclauchlani*. Dorsal surface in *E. tetracornis* shows deep grooves between different regions, and covered by large, granulated tubercles, unlike *A. chidgeyorum*, which presents dorsal surface covered with small granulations and dorsal regions separated by superficial grooves (Jenkins, 1974, p. 872, pl. 117,1–4), and *A. maclauchlani*, presenting finely granulated dorsal surface and subtly differentiated dorsal regions (Feldmann, 1993, p. 209, pl. 16–18).

FINAL REMARKS AND CONCLUSIONS

The outcrop that provided *Eoactinotocarcinus tetracornis* n. gen. n. comb., and *Tumulosternum ortegai* n. sp. corresponds to the lateral equivalent of the Roda Formation, with sediments composed of fine calcareous sandstones and clays, with mollusks, sponges, bryozoans, abundant irregular echinoids, and other decapod crustaceans (Table 1). The observed differences between the decapod crustacean assemblages in the most proximal zones of the Roda Formation (Isábena/Bacamorta area) differ greatly in terms of composition from those observed in the distal studied area (Atiart area), with only a few coincidences (Table I). This could suggest different environments and a high tolerance for certain taxa.

The samplings conducted at the studied site revealed certain decapod species consistently found in a disarticulated state (including those under study, Tables 1 and I). This fact, coupled with the rarity of certain taxa, might indicate a blend of autochthonous and paraautochthonous associations, however it would be necessary to carry out more exhaustive analyses to confirm this hypothesis.

TABLE 1. Table displaying the different taxa observed in the studied outcrop along with their abundance. These data are approximate due to the absence of an exhaustive systematic sampling. Taxa marked with '*' were found articulated

GROUPS	TAXA	NUMBER	%
Raninoidea De Haan, 1839	?*Rogueus* sp.*	13	2.64
Carpilioidea Ortmann, 1893	Carpilioid indet.	1	0.20
	*Zanthopsis dufuorii**	460	93.31
Goneplacoidea MacLay, 1838	?*Pyreneplax* sp.	1	0.20
Majoidea Samouelle, 1819	*Eoactinotocarcinus tetracornis* n. gen. n. comb.	3	0.61
	Tumulosternum ortegai n. sp.	3	0.61
Portunoidea Rafinesque, 1815	*Litoricola macrodactyla**	8	1.63
	Portunoidea indet. *	2	0.41
	?*Archaeoportunus* sp.*	1	0.20
Xanthoidea MacLay, 1838	?*Collinscarcinus* sp.	1	0.20
Total		493	100.00

The morphological resemblance observed between Actinotocarcininae and the genus *Periacanthus*, characterized by significant lateral expansions in the branchial margin, suggests potential similarities in their lifestyles. Species within the genus *Periacanthus* are typically found in carbonate levels associated with muddy substrates showing some degree of terrigenous input, developed in the outer shelf zone (offshore) (Quayle and Collins, 1981; Vía, 1959), although certain discoveries correspond to nearer proximal zones (Artal and Castillo, 2004; Ferratges *et al.*, 2022a).

Fossil spider crabs generally appear associated with other crab species (Ferratges *et al.*, 2023 and references therein). Many findings of Periacanthus, like *Actinotocarcinus* and those of the new genus, were been unearthed in deposits showcasing a wide diversity of other organisms (Artal and Castillo, 2004; Beschin *et al.*, 2012, 2016; Feldmann, 1993, 1998; Feldmann *et al.*, 2006, for *Actinotocarcinus*; Ferratges *et al.*, 2022a-personal observation, for Periacanthus; Lőrenthey and Beurlen, 1929; McLay *et al.*, 1995; Quayle and Collins, 1981; Vía, 1959). Additionally, these outcrops harbor an abundance of bryozoans and sponges, suggesting potential camouflage habits akin to many modern spider crabs or decorator crabs (Poore and Ahyong, 2023).

An unrelated example lies in the modern parthenopoid *Aulacolambrus hoplonotus* (ADAMS AND WHITE, 1849), displaying extended lateral expansions and spiny ornamentation similar on their arms. At the same way, the fossil parthenopoid *Acantholambrus haumi* BLOW AND MANNING, 1996, shows very similar structures. These structures (both in the carapace and the extremely long and ramified arms) are utilized for camouflage (Davie *et al.*, 2015, and other modern examples in Crab Database). It is plausible that similar ornamentation was employed by *Eoactinotocarcinus* n. gen. to disrupt symmetry and conceal itself. The absence of modern representatives, or other modern taxa with similar characteristics, makes it difficult to understand the possible evolutionary implications and understand how these morphological structures could be related to adaptation to specific environments over time.

Previous fossil record of Actinotocarcininae were limited to *Actinotocarcinus maclauchlani* and *A. chidgeyorum* from the Miocene of New Zealand. While these taxa differ in certain aspects from the new genus herein described (see above), they exhibit significant similarities, warranting their assignment to the same subfamily. Moreover, the new genus represents the oldest record within this subfamily and marks its first appearance in the Eocene. On the other hand, the species *Tumulosternum ortegai* n. sp. represents the first fossil occurrence of the genus. This new discovery indicates it presence in temperate latitudes of the Northern Hemisphere, dispersing towards the Pacific. Both discoveries significantly expand the temporal and geographical distribution of both groups.

The faunal similarity analyses conducted by Ferratges *et al.* (2023), examining spider crab diversity across various basins, highlight substantial dissimilarities between the Mediterranean and New Zealand basins during the Eocene. However, these data, observed over an extended timeframe, hold promise in elucidating the origins of distinct groups and their temporal shifts.

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APPENDIX I

TABLE I. Diversity of decapod crustaceans at the Roda Formation in Isábena/Bacamorta vs. Atiart areas (proximal vs distal areas). Taxa marked with '*' were found articulated. Modified from Ferratges, 2022

Superfamily	Family	Subfamily	Isábena/Bacamorta area	Atiart area
	Callianassidae Dana, 1852		Callianassidae indet.	
	Ctenochelidae Manning and Felder, 1991		*Ctenocheles* sp.	
Paguroidea Latreille, 1802	Diogenidae Ortmann, 1892		*Parapetrochirus robustus* Ferratges, Artal and Zamora, 2021	
Dromioidea De Haan, 1833	Dromiidae De Haan, 1833	?Dromiinae De Haan, 1833	Dromidae indet.	
Homoloidea De Haan, 1839	Homolidae de Haan, 1839		*Paromola bretoni** Ferratges, Domínguez and Ossó, 2021	
Raninoidea De Haan, 1839	Raninidae De Haan, 1839	Symethinae Goeke, 1981	*Eosymethis aragonensis** Van Bakel, Guinot, Artal, Fraaije and Jagt, 2012	
		Rogueinae Karasawa, Schweitzer, Feldmann and Luque, 2014		?*Rogueus* sp.*
Carpilioidea Ortmann, 1893	Carpiliidae Ortmann, 1893		*Carpilius** sp.	*Carpilius* sp.
	Zanthopsidae Vía, 1959		*Zanthopsis dufourii** (H. Milne Edwards, 1850)	*Zanthopsis dufourii** (H. Milne Edwards, 1850)
	Tumidocarcinidae Schweitzer, 2005		*Titanocarcinus decor** Schweitzer, Artal, van Bakel, Jagt and Karasawa, 2007	
Goneplacoidea MacLay, 1838	Magyarcarcinidae Domínguez and Ossó, 2016		?*Magyarcarcinus** sp.	
	Vultocinidae			?*Pyreneplax* sp.

TABLE I. Continued

Superfamily	Family	Subfamily	Isábena/Bacamorta area	Atiart area
Majoidea Samouelle, 1819	Epialtidae MacLeay, 1838		*Periacanthus ramosus* Artal andCastillo, 2004	
	Majidae Samouelle, 1819	Actinotocarcininae Jenkins, 1974		***Eoactinotocarcinus tetracornis*** n. gen. n. comb. (Ferratges, Ortega, Fernández, Moreno and Maza 2014)
		Micromaiinae Beurlen, 1930	?*Micromaia* sp.	
				Tumulosternum ortegai n. sp.
	Inachidae MacLeay, 1838		Inachidae indet.	
Pilumnoidea Samouelle, 1819	Pilumnidae Samouelle, 1819		*Galenopsis* sp.	
Portunoidea Rafinesque, 1815	Geryonidae Colosi, 1923		*Litoricola macrodactyla** (Van Straelen, 1924) var. *pyrenaica* (Artal and Vía, 1988)	*Litoricola macrodactyla** (Van Straelen, 1924) var. *pyrenaica* (Artal and Vía, 1988)
	Portunidae Rafinesque, 1815			Portunoidea indet.*
				?*Archaeoportunus* sp.*
Retroplumoidea Gill, 1894	Retroplumidae Gill, 1894		*Gaudipluma bacamortensis** Artal, Van Bakel, Fraaije and Jagt, 2013	
			Retropluma gallica Artal, van Bakel and Castillo, 2006	
Xanthoidea MacLay, 1838	Xanthidae MacLeay, 1838		*Collinscarcinus obliquesulcatus* Artal and van Bakel, 2020	*Collinscarcinus* sp.
Grapsoidea MacLeay, 1838	Varunidae H. Milne Edwards, 1853	Asthenognathinae Stimpson, 1858	*Asthenognathus fernandezi** Ferratges, Zamora and Aurell, 2022	