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New records of portunoids (Decapoda, Brachyura) from the late Eocene of the South Pyrenean basins (NE, Spain) with description of a new genus and species

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New records of portunoids (Decapoda, Brachyura) from the late Eocene of the South Pyrenean basins (NE, Spain) with description of a new genus and species

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ABSTRACT
We describe a new portunoid crab, *Pyreneites fandielloensis* n. gen., n. sp., from the Margas de Pamplona Formation (late Eocene) of the western Pyrenees (Huesca, Aragon, Spain). This new taxon increases the known diversity of the family Polybiidae in the Eocene of the Iberian Peninsula, where representatives of this group are otherwise rare. Additionally, new specimens of the portunid *Portunus catalaunicus* (Vía, 1941) are reported from the lower Priabonian Pamplona Marls Formation at Fanlillo and from the upper Bartonian Arguis Marls Formation at Belsué (Huesca Province, Aragon, Spain). These occurrences confirm the presence of *P. catalaunicus* throughout the middle and late Eocene of the western Pyrenees. The palaeoecology of this species is also discussed.

KEY WORDS
Eubrachyura,
Portunoidea,
Polybiidae
Priabonian,
Pyrenees,
fossil crab,
new genus,
new species.

RÉSUMÉ
Nouveau signalement de crabe portunoïde (Decapoda, Brachyura) de l'Éocène supérieur des bassins du sud des Pyrénées (NE de l'Espagne) et description d'une espèce nouvelle d'un genre nouveau.
Nous décrivons un nouveau crabe portunoïde, *Pyreneites fandielloensis* n. gen., n. sp., provenant de la Formation des Margas de Pamplona (Éocène supérieur) des Pyrénées occidentales (Huesca, Aragon, Espagne). Ce nouveau taxon accroît la diversité connue de la famille des Polybiidae dans l'Éocène de la péninsule Ibérique, où les représentants de ce groupe sont par ailleurs rares. En outre, de nouveaux spécimens du portunidé *Portunus catalaunicus* (Vía, 1941) sont signalés dans la Formation des Marnes de Pamplona (Priabonien inférieur) à Fanlillo et dans la Formation des Marnes d'Arguis (Bartonien supérieur) à Belsué (province de Huesca, Aragon, Espagne). Ces occurrences confirment la présence de *P. catalaunicus* tout au long de l'Éocène moyen et supérieur des Pyrénées occidentales. La paléoécologie de cette espèce est également discutée.

MOTS CLÉS
Eubrachyura,
Portunoidea,
Polybiidae,
Priabonien,
Pyrénées,
crabe fossile,
genre nouveau,
espèce nouvelle.

INTRODUCTION

Portunoids are a group of brachyuran crabs that were highly diversified in past environments (see Schweitzer *et al.* 2021, and references therein), with fossil representatives ranging from the Cretaceous to the Holocene (e.g., Vega & Feldmann 1991; Schweitzer *et al.* 2007; Karasawa *et al.* 2008; Ossó 2016). In recent years, molecular studies (Schubart & Reuschel 2009; Spiridonov *et al.* 2014; Evans 2018), together with efforts to reconcile molecular phylogenies with the fossil record (Spiridonov 2020), have prompted a reevaluation of traditional classifications, particularly by subsuming Macropipidae Stephenson & Campbell, 1960, within Polybiinae Paulson, 1875. Feldmann *et al.* (2018) and Schweitzer *et al.* (2021) adopted a systematic framework aligned with these molecular studies and reassigned several fossil genera previously included in Macropipidae (sensu Karasawa *et al.* 2008) to Polybiinae (sensu Evans 2018). Nevertheless, the phylogenetic placement of many genera within this group remains controversial and warrants further revision (e.g., Spiridonov 2020; Ossó *et al.* 2022; Artal & Ossó 2024), especially considering that the most recent phylogenetic and taxonomic studies have treated Polybiinae as a full family, Polybiidae (e.g., García-Raso *et al.* 2024; Luque *et al.* 2024; Wolfe *et al.* 2024), an approach followed herein. In particular, in Poore & Ahyong (2023: 688), the array of subfamilies placed within Carcinidae MacLeay, 1838 by Schweitzer *et al.* (2021) – such as Carcininae MacLeay, 1838, Pirimelinae Alcock, 1899, Polybiinae Paulson, 1875, and Thiinae Dana, 1852 – are treated as full families or reassigned to other families, for example through the placement of Coelocarcininae Števčić, 2005 in a different family.

Despite the group's overall abundance in the fossil record, portunoids are relatively uncommon in the Eocene of Spain, with some representatives documented to date (see Table 1). These include *Archaeoportunus isabenensis* Artal, Ossó & Domínguez, 2021 – Archaeoportunidae; *Pyrenicola pyrenaica* (Artal & Vía, 1989) – Geryonidae; *Colneptunus hungaricus* (Lőrenthey, 1898), *Viaophthalmus zariquieyi* (Vía, 1959), and *Portunus catalaunicus* (Vía, 1941) – all within Portunidae; as well as three polybiids from the early Eocene (Ferratges *et al.* 2025), associated with shallow reefal facies.

Two distinct portunoid taxa are presented herein, one representing a new species and the other identified as *Portunus catalaunicus*, both from lower Priabonian prodelta deposits exposed near the Fanlillo and Arguís areas. These strata have yielded a rich decapod assemblage (Artal *et al.* 2013a; Ossó *et al.* 2014; Domínguez & Ossó 2016a, 2016b; Ossó & Domínguez 2017; Ossó *et al.* 2020; Ferratges *et al.* 2023, 2024), showing strong affinities with middle-late Eocene decapod assemblages from the westernmost Tethys (Italy and Hungary) and, to a lesser extent, with those from the northeastern Atlantic (British Isles; see Quayle & Collins 1981). The aim of the present study is to describe the new portunoid genus and species and to report and discuss the occurrence of the genus *Portunus* Weber, 1795 in different sectors of the Jaca-Pamplona Basin. These new records enhance our understanding of Eocene portunoid diversity and biogeographic connections within the western Tethys realm.

GEOLOGICAL SETTING

The studied material was recovered from the Pamplona Marls and Arguis Formations (Puigdefàbregas 1975), located within the Jaca-Pamplona Basin. This basin is an east-west elongated structure in the south-central Pyrenean Zone (Fig. 1), formed as a result of the southward propagation of tectonic structures during the Paleogene (Millán *et al.* 1994; Muñoz *et al.* 1994; Castelltort *et al.* 2003; Huyghe *et al.* 2009). The advancement of the southern Pyrenean fold-and-thrust belt led to the formation of a coeval relief that acted as a sediment source for deltaic complexes (e.g., Dreyer *et al.* 1999), which progressively prograded westward into the southern part of the Jaca-Pamplona Basin (Mutti *et al.* 1985; Remacha *et al.* 2003, 2005).

The middle and upper Eocene units (Lutetian-Priabonian) comprise a *c.* 2 km-thick succession of several formations, representing a range of depositional environments from shallow marine to deltaic and fluvial settings (see Puigdefàbregas 1975; Silva-Casal *et al.* 2019). Decapod crustaceans studied herein were collected from lower Priabonian deposits at two localities consisting of a thick grey and blue marl succession deposited in a distal offshore environment:

Locality 1

Marls and clays of the Pamplona Marls Formation, exposed near the village of Fanlillo, in the municipality of Yebra de Basa (Huesca province, Spain) (Fig. 1). These outcrops exhibit an exceptionally high abundance and diversity of small benthic invertebrates – especially molluscs, bryozoans, decapod crustaceans – and plant remains, suggesting a progressive upward shallowing of the depositional environment, with sedimentation likely occurring within the euphotic zone and above the storm wave base (see Montes-Santiago 2009).

Locality 2

Equivalent strata on the southern flank of the basin, belonging to the Arguis Marls Formation, near the village of Arguis (Huesca province, Spain, Fig. 1). These deposits are characterized by a higher siliciclastic and detrital content, and a comparatively lower diversity of invertebrates (see details in Ferratges *et al.* 2024).

MATERIAL AND METHODS

Two specimens of *Pyreneites fandielloensis* n. gen., n. sp. and three of *Portunus catalaunicus* with partially preserved cuticle have been studied from locality 1 (near Fanlillo). The specimens of *Pyreneites fandielloensis* n. gen., n. sp. do not preserve sternopleonal elements nor appendages. Additionally, six specimens of *Portunus catalaunicus* without cuticle and with a greater degree of disarticulation have been collected from the locality 2 (near to Arguis and Belsue). The material was prepared using a MicroJack 2 air scribe

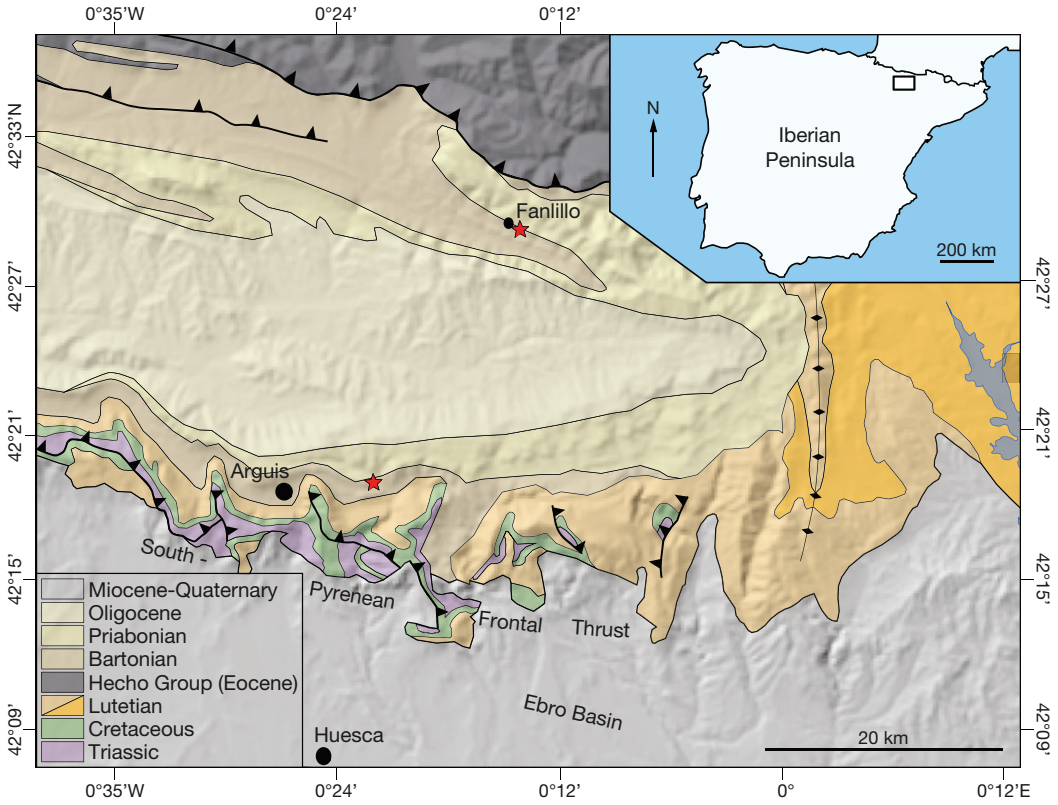


FIG. 1. — Simplified geological map of the Jaca Basin in the South-Central Pyrenean zone (modified from Coll *et al.* 2022). The **red stars** represent the sampling points (locality 1 in the north, coordinates: 42°28'29.4"N, 0°13'34.6"W, and locality 2 in the south, coordinates: 42°19'00.6"N, 0°22'44.8"W).

TABLE 1. — Representatives of the Portunoidea Rafinesque, 1815 in the Eocene from Iberian Peninsula. In **bold**, the taxa reported in the present work.

Family	Taxa	Formation	Region	Age	Environment
Archaeoportunidae Artal, Ossó & Domínguez, 2021	*Archaeoportunus isabenensis* Artal, Ossó & Domínguez, 2021	Morillo Fm	North of Huesca (Aragon)	Ypresian	Shallow carbonate platform
Geryonidae Colosi, 1923	*Pyrenicola pyrenaica* (Artal & Vía, 1989)	Serraduy Fm Roda Fm	North of Huesca (Aragon)	Ypresian	Outer-fore reef
Polybiidae Paulson, 1875	*Liocarcinus tridentatus* Ferratges, Artal, van Bakel & Zamora, 2025	Serraduy Fm	North of Huesca (Aragon)	Ypresian	Inner-fore reef
	Lovaroides sp. Ferratges, Artal, van Bakel & Zamora, 2025	Serraduy Fm	North of Huesca (Aragon)	Ypresian	Inner-fore reef
	Microboschettia elegans Ferratges, Artal, van Bakel & Zamora, 2025	Serraduy Fm	North of Huesca (Aragon)	Ypresian	Inner-fore reef
	***Pyreneites fandielloensis* n. gen., n. sp.**	Margas de Pamplona Fm	North of Huesca (Aragon)	**Priabonian**	Siliciclastic and mud bottom
Portunidae Rafinesque, 1815	*Colneptunus hungaricus* (Lörenthey, 1898) see Sole & Vía 1989)	Banyoles Fm	Central and north of Catalonia	Lutetian	Siliciclastic and mud bottom
	***Portunus catalaunicus* (Vía, 1941)**	Collbas Fm Arguis Marls Fm Margas de Pamplona Fm	Central and north of Catalonia and north of Huesca (Aragon)	**Bartonian-Priabonian**	Siliciclastic
	Viaophthalmus zariquieyi (Vía, 1959)	Banyoles Fm	Central Catalonia	Lutetian	Siliciclastic and mud bottom

(Paleotools; Brigham, Utah, USA). Next, specimens were photographed dry and coated with ammonium chloride sublimate. Detailed photographs of carapace surfaces were taken using a Nikon D7100 camera (Nikon, Tokyo, Japan) with a macro 60-mm-lens.

Specimens were collected legally under permit EXP: 032/2018 from the Servicio de Prevención, Protección e Investigación del Patrimonio Cultural (Gobierno de Aragón) and are deposited in the Museo de Ciencias Naturales de la Universidad de Zaragoza (Spain) (MPZ).

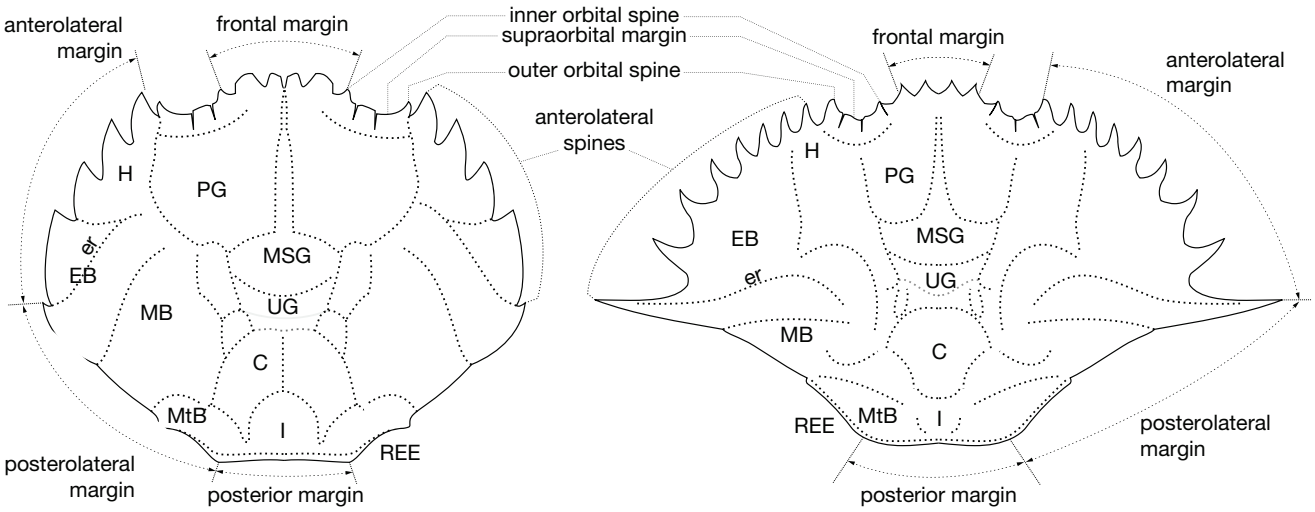


Fig. 2. — Carapace regions and terminology in a portunoid crab used in the text. Abbreviations: **PG**, protogastric region; **MSG**, mesogastric region; **UG**, urogastric region; **C**, cardiac region; **H**, hepatic region; **EB**, epibranchial region; **MB**, mesobranchial region; **MtB**, metabranchial region; **I**, intestinal region; **er**, epibranchial ridge; **REE**, re-entrant of the pereopod 5. Drawings: Fernando A. Ferratges.

SYSTEMATIC PALAEONTOLOGY

Terminology used herein follows Davie *et al.* (2015) and is summarized in Figure 2.

Order DECAPODA Latreille, 1802
Infraorder BRACHYURA Latreille, 1802
Section EUBRACHYURA de Saint Laurent, 1980
Subsection HETEROTREMATA Guinot, 1977
Superfamily PORTUNOIDEA Rafinesque, 1815
Family POLYBIIDAE Paulson, 1875

Genus *Pyreneites* n. gen.
(Fig. 3)

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ETYMOLOGY. — From *Pyrene*, related to the origin of Pyrenees mountains in Greek mythology and *ites*, suffix used in palaeontology.

TYPE SPECIES. — *Pyreneites fandielloensis* n. sp. by monotypy.

DIAGNOSIS. — Carapace subhexagonal, wider than long; length-to-width ratio approximately 0.70. Maximum width at the level of the last anterolateral spine, located about halfway along the carapace length. Dorsal regions moderately defined, delimited by distinct grooves; surface ornamented with small granules. Frontal margin slightly projected, bearing four subtriangular spines and a median V-shaped notch; frontal width about 30% of carapace width. Orbits wide; fronto-orbital width about 60% of carapace width; supraorbital margin with two notches. Anterolateral margins arched, armed with five subtriangular spines with long outer and short inner edges (including outer orbital spine); fourth nearhly twice the size of the third. Posterolateral and posterior margins straight. Posterolateral corners with deep re-entrant accommodating the fifth pereopod. Epibranchial ridge well developed and strongly arched. Longitudinal branchial carinae appears distinct.

REMARKS

The dorsal features preserved in *Pyreneites* n. gen. are sufficient to determine its familial placement, including: 1) a subhexagonal carapace, broader than long; 2) a frontal margin with four spines; 3) a supraorbital margin with two notches; 4) defined dorsal regions; 5) broad anterolateral margins with five forward-directed spines, characterized by a long outer edge and a much shorter inner edge; 6) a straight posterolateral margin; and 7) a well-developed re-entrant for the P5. These features are consistent with the diagnosis of Polybiidae as outlined by Spiridonov *et al.* (2014: 422-423), Davie *et al.* (2015: 1102), and Poore & Ahyong (2023: 697-700, fig. 14.121), and support the inclusion of the studied specimens within Polybiidae. The presence of a well-preserved re-entrant of P5, indicative of a swimming leg, excludes their assignment to Carcinidae (see Spiridonov *et al.* 2014: 421, 422).

To differentiate *Pyreneites* n. gen. from both fossil and extant genera formerly assigned to Polybiinae (currently Polybiidae, see above), we compare it with the diverse assemblage of genera listed by Schweitzer *et al.* (2021: 6-13 [following Feldmann *et al.* 2018: 2]), excluding several genera considered herein to not fit within Polybiidae. For instance, the morphology of *Ophthalmoplax* Rathbun, 1935, does not conform to that of Polybiidae (e.g. Vega *et al.* 2013: 118-119; Spiridonov 2020: 158). *Coeloma* A. Milne-Edwards, 1865, has recently been transferred to Geryonidae Colosi, 1924 (see Artal & Ossó 2024: 198-200). *Faksecarcinus* Schweitzer, Feldmann, Franțescu & Klompmaker, 2012 – whose species were previously assigned to *Xanthosia* Bell, 1863 (Etyidae Guinot & Tavares, 2001) – exhibits a dorsal morphology that does not correspond to that of Polybiidae and only doubtfully to Portunoidea, particularly due to the concave posterior margin, which is more characteristic of podotreme crabs than of eubrachyuran crabs (cf. Jakobsen & Collins 1997: pl. 2, figs 1-2; Klompmaker *et al.* 2011: text-fig. 3A-F). Finally,



Fig. 3. — *Pyreneites fandielloensis* n. gen., n. sp. from the Pamplona Marls Fm (lower Priabonian) of Fanlillo (Yebra de Basa, Huesca, Spain) coated with an ammonium chloride sublimate (**A**, **C**) and natural (**B**, **D**): **A**, **B**, holotype MPZ 2025/465; **C**, **D**, paratype MPZ 2025/466. Scale bars: 2 mm. Photographs: Isabel Pérez Urresti.

Pleolobites Rémy, 1960, and *Rhachiosoma* Woodward, 1871, were transferred to Portunoidea *incertae sedis* (see Ossó *et al.* 2022: 3, 5, 6).

The genera *Archaeogeryon* Colosi, 1924, *Falsiportunites* Collins & Jakobsen, 2003, *Megokkos* Schweitzer & Feldmann, 2000, and *Portunites* Bell, 1858, clearly differ from *Pyreneites* n. gen. in having a bilobed or blunt spiny front, broader orbits, and a much shorter anterolateral margin usually bearing four spines, the last of which is typically the longest (see Colosi 1924: fig. 1; Collins & Jakobsen 2003: 72-74, fig. 5, pl. 4, figs 1-6; Schweitzer & Feldmann 2000: 640-641, fig. 5; Bell 1858: 21-22, pl. 3, fig. 2; Quayle 1984: 174, pl. 1, figs 1, 4, 6). *Liocarcinus* Stimpson, 1871, *Macropipus* Prestandrea, 1833, and *Polybius* Leach, 1820, three genera with dorsal features and general outlines similar to *Pyreneites* n. gen., differ by having smaller orbits and an uneven number of frontal spines (see Stimpson 1871: 10-11; Prestandrea 1833: 3-4; Leach 1820 *in* 1815-1875: pl. 9-B). *Olicarcinus* Beschin & Cecchi, 2018, appears morphologically very close to *Pyreneites* n. gen.; however, it differs in having smaller orbits, longer posterolateral margins, and a laterally directed epibranchial ridge (see Beschin & Cecchi 2018). Species of *Bathynectes* Stimpson, 1871, typically present a longer, laterally directed last anterolateral spine and a complete transverse carina connecting both spines, which clearly differs from the dorsal morphology of *Pyreneites* n. gen. (see Stimpson 1871: 145-147). *Boschettia* Busulini, Tessier, Beschin & De Angeli, 2003, has a shorter frontal margin, broader orbits, a strongly granulated dorsal surface, and a very long fourth anterolateral spine, all of which preclude a congeneric relationship with *Pyreneites* n. gen. (see Busulini *et al.* 2003: pl. 4, fig. 2). *Bericocarcinus* De Angeli, 2018, differs from *Pyreneites* n. gen. by its nearly subquadrate outline, extremely broad orbits, absence of branchial ridges, and the presence of only four anterolateral spines, whereas the

new genus possesses five (see De Angeli 2018: 33-34, fig. 2. *Lovaroides* Beschin, De Angeli, Checchi & Zarantonello, 2016, originally placed within Goneplacoidea MacLeay, 1838, differs from *Pyreneites* n. gen. by its smoother dorsal carapace, bearing only four anterolateral lobes; by the absence of marked branchial and epibranchial ridges; and by the lack of the well-marked P5 re-entrant that characterizes *Pyreneites* n. gen. (see Beschin *et al.* 2016: 64-65, fig. 57; pl. 12, figs 1, 2A, B, 3). *Maeandricampus* Schweitzer & Feldmann, 2002, shows a wider carapace, a longer and laterally directed last anterolateral spine, and less defined regions than *Pyreneites* n. gen., which rules out a congeneric relationship (see Rathbun 1926: 68, pl. 17, figs 3-6; Schweitzer & Feldmann 2002: 955). *Minohellenus* Karasawa, 1990, presents a wider carapace, poorly defined regions, six frontal spines, an anterolateral margin shorter than the posterolateral margin, and a laterally directed, pointed last anterolateral spine, features that exclude a congeneric relationship with *Pyreneites* n. gen. (see Karasawa 1990: 21-23, pl. 6, figs 7-8; Kato & Karasawa 1994: 53; Schweitzer *et al.* 2021: 11, fig. 5.2a-b). The genus *Necora* Holthuis, 1987, shows a frontal margin with six spines, an anterolateral margin shorter than the posterolateral margin, and a larger last anterolateral spine, all features that rule out a congeneric relationship with *Pyreneites* n. gen. (see Holthuis 1987: 3, fig. 1). *Parathranites* Miers, 1886, presents a similar dorsal aspect and outline to *Pyreneites* n. gen., but its subcircular orbits, acute and laterally directed last anterolateral spine, and the characteristic spine in the inner corner of the re-entrant distinguish it from the new genus (see Crosnier 2002). *Pororaria* Glaessner, 1980, differs from *Pyreneites* n. gen. in having a carapace as long as it is wide, shorter anterolateral margins armed with blunt granulate spines instead of subtriangular ones, and lacking a marked re-entrant (see Glaessner 1980: 187-188, figs 15, 15a, 16). *Portufuria* Collins, Schultz & Jakobsen, 2005, has a sharp rostrum and a short anterolateral margin with only four anterolateral spines, which precludes a congeneric relationship with *Pyreneites* n. gen. (see Collins *et al.* 2005: 20-21, pl. 1, figs 3a-b). Therefore, in view of the preceding comparisons, the erection of a new genus for the studied specimens within Polybiidae seems warranted.

Pyreneites fandielloensis n. sp.
(Fig. 3)

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ETYMOLOGY. — From Fandiello, Aragonese name of Fanlillo, the locality that has yielded the specimens

TYPE MATERIAL. — **Holotype. Spain** • 1 specimen (near-complete dorsal carapace, well-preserved but partially decorticated); Fanlillo, Yebra de Basa, Huesca, Spain; Late Eocene, early Priabonian, Pamplona Marls Formation; MPZ 2025/465; Dimensions length = 8.1 mm, width = 10.2 mm.
Paratype. Spain • 1 specimen (dorsal carapace preserving partially the cuticle); Fanlillo, Yebra de Basa, Huesca, Spain; Late Eocene, early Priabonian, Pamplona Marls Formation; MPZ 2025/466; Dimensions: length = 5.7 mm, width = 7.8 mm.

TYPE LOCALITY. — Fanlillo, Yebra de Basa, Huesca Province, Spain.

TYPE AGE. — Late Eocene, early Priabonian (Pamplona Marls Formation).

DIAGNOSIS. — As for the genus

DESCRIPTION
Carapace small, subhexagonal, wider than long, moderately vaulted in both longitudinal and transverse directions. Maximum width at the level of the last anterolateral spine, located slightly anterior to mid-length; length-to-width ratio approximately 0.70. Regions moderately defined; axial regions distinctly marked and bounded by well-developed grooves. Cuticle partially preserved, covered with fine, regular granules. Frontal margin slightly projected, bearing four subtriangular spines including the inner orbital spine, with a median V-shaped notch; frontal width about 30% of carapace width. Orbits relatively broad; supraorbital margin gently sinuous, divided into three lobes by two deep notches. Inner orbital spine triangular, separated from the frontal margin by a notch; outer orbital spine acute, subtriangular. Fronto-orbital margin approximately 74% of carapace width. Anterolateral margins broadly arched, longer than posterolateral margins, armed with five forward-directed, subtriangular spines with long outer and short inner edges (outer orbital spine included). The first three spines are subequal in size, the fourth nearly twice the size of the third, and the fifth distinctly smaller. Posterolateral margins short, slightly concave, and posteriorly convergent. Posterior margin straight, approximately 35% of carapace width, rimmed, with slightly rounded corners. Posterolateral corners exhibit a strong re-entrant accommodating the fifth pereopod. Gastric process well defined. Epigastric lobes moderately marked; protogastric lobes large, swollen, and sharply delimited by deep grooves. Mesogastric region broadly subpentagonal posteriorly and narrowing anteriorly into a slender extension. Metagastric region not clearly differentiated from the posterior mesogastric lobe. Urogastric lobe narrow and transversely elongate, separated anteriorly from the meso- and metagastric regions by the cervical groove, which bears two medial gastric pits, and separated from the cardiac region by a depressed transverse groove. Cardiac region broad, inverted subpentagonal, divided into two lobes by an axial groove. Intestinal region flattened and poorly differentiated from the cardiac region. Hepatic regions flattened, clearly delimited from the branchial regions by the cervical groove and faintly from the gastric regions by the gastro-hepatic groove. Branchial regions defined by a well-developed, strongly arched, sigmoidal epibranchial ridge extending to the last anterolateral spine. Meso- and metabranchial regions with two reniform lobes adjacent to the meso- and urogastric lobes, separated from them by a deep branchiocardiac groove, and a long, longitudinal lobe forming a distinct branchial ridge. Sternopleonal features and appendages not preserved.

REMARKS
Domínguez & Ossó (2016a: fig. 21) reported a single specimen of *Pyreneites fandielloensis* n. gen., n. sp., examined herein, as "*Portunites* cf. *P. sylviae*/*P. eocaenica*", based on

superficial similarities in dorsal morphology with both taxa. Nevertheless, detailed morphological examination reveals dorsal differences among *Portunites eocaenica* Lőrenthey *in* Lőrenthey & Beurlen, 1929, *P. sylviae* Quayle & Collins, 1981, and *Pyreneites fandielloensis* n. gen., n. sp. For instance, the holotype of *Portunites eocaenica* illustrated in Lőrenthey & Beurlen (1929: pl. 15, fig. 2), as well as the specimens attributed to that species figured in De Angeli & Beschin (2014: fig. 2), display a different outline of the anterolateral carapace margin, characterized by more acute, forward-directed anterolateral spines of similar size. In contrast, in *Pyreneites fandielloensis* n. gen., n. sp., the fourth anterolateral spine is approximately twice the size of the third. The same condition is observed in *Portunites sylviae*, as illustrated by Quayle & Collins (1981: pl. 105, fig. 4). Moreover, the generic attribution of *Portunites eocaenica* and *P. sylviae* to *Portunites* Bell, 1858 warrants re-evaluation, given the markedly different morphology of the anterolateral margins, particularly the last anterolateral spine, which is reduced in size and not laterally directed. This condition contrasts with that observed in *Portunites stricto sensu*, in which the last anterolateral spine is the largest and longest and is directed laterally (cf. Bell 1858: pl. 3, fig. 2; Quayle 1984: pl. 1, figs 1, 4, 6).

Family Portunidae Rafinesque, 1815
Subfamily Portuninae Rafinesque, 1815

Genus *Portunus* Weber, 1795

Type species. — *Cancer pelagicus* Linnaeus 1758, by subsequent designation by Rathbun (1926).

Included species (fossil and extant). — See Sasaki (2023: 10561-10611).

Remarks

Spiridonov (2020: 158, 159) suggested that, with respect to the generic placement of several fossil species attributed to *Portunus*, some could be assigned to extant genera such as *Achelous* De Haan, 1833, or *Monomia* Gistel, 1848, rather than to *Portunus* sensu stricto. We concur. Some species may belong to different or even entirely new genera. However, such generic assignments must be approached with caution. For instance, Hyžný & Dulai (2021), following Spiridonov (2020), reassigned *P. monspeliensis* (A. Milne-Edwards, 1860) to *Achelous*, a move that was not accepted by subsequent authors, who considered the reassignment premature (Garassino *et al.* 2021: 71). Furthermore, the genus *Portunus*, as well as the subfamily Portuninae, are subject to ongoing rearrangements based on molecular studies, underscoring the difficulty of drawing definitive conclusions from the available fossil material (e.g., Koch *et al.* 2022). Therefore, although we agree that the generic position of *Portunus catalaunicus* could be reconsidered, we retain its current classification until further detailed work, beyond the scope of this paper, can provide definitive conclusions.

Portunus catalaunicus (Vía, 1941)
(Fig. 4.)

Neptunus catalaunicus Vía, 1941: 65-70 (11-16), fig. 1, pl. 1, figs 1-6, pl. 2, figs 27, 28 (as *Colneptunus catalaunicus*); 1948: 284, figs1-4; 1952: 74, figs 7, 8; 1959: 378, 379 (48, 49); 1969: 206-218, fig. 26, pl. 17, figs 1, 2, pl. 18, figs 1-3, pl. 19, figs 1, 2. — Colom *et al.* 1970: 66. — Vela 1985: 22, pl. 2, fig. 4.

Neptunus sp.? – Via 1932: 142.

Portunus catalaunicus – Vía 1988: 349, 351, figs 337, 341F. — Gómez-Alba 1988: 506, pl. 250, figs 1, 1. — Schweitzer *et al.* 2010: 111. — Ferratges 2017, fig. 42A, B, pl. 28., fig. A. — Sasaki 2023: 10566.

Portunus catalanicus [sic] – Karasawa *et al.* 2008: 127.

Examined material. — **Spain** • Huesca province, From the village of Fanlillo; late Eocene, early Priabonian; Pamplona Marls Formation; MPZ 2024/02, MPZ 2025/468, MPZ 2025/467 • Huesca province, from the village of Arguis; middle Eocene, late Bartonian; Arguis Marls Formation (cuticle preserved in all specimens); MPZ 2025/469.

Description

Carapace transversely subhexagonal, ratio L/W about 0.46 (from the tip of the last anterolateral spine); surface relatively smooth; maximum width just posterior to midlength of carapace. Axial and branchial regions well marked. Front with four lobes. Orbits relatively small, weakly protruded inner orbital spine, acute forward directed outer orbital spine; supraorbital margin with two closed fissures. Anterolateral margin gently convex, armed with nine spines (outer orbital spine included), the latest extremely long and laterally directed. Posterolateral margin concave, rimmed; re-entrant of fifth pereopod well marked. Posterior margin short, weakly convex, rimmed. Epigastric region with two faint inflations. Mesogastric region subpentagonal, very elongate and narrow anteriorly, bearing two conical tubercles at the posterior portion. Metagastric region not defined. Urogastric region swollen, narrow, reniform, transversely shorter than meso- metagastric posterior region, and separated from the cardiac region by a transverse depression. Cardiac region diamond shaped, bearing three conical prominent tubercles, two anteriorly and one posteriorly. Intestinal region flattened, narrow. Hepatic region flattened, not well defined. Epibranchial region defined by a long and acute sigmoidal ridge that starts in a tubercle along the cervical groove, and ends at the last anterolateral spine. Meso branchial regions swollen bearing two conical tubercles forming branchial ridges, a third tubercle at the inner portion of the region confluent with the branchiocardiac region. Metabranchial region, faintly swollen. Ischium of Mxp3 long, subrectangular, strongly convex posterior inner corner, slightly concave outer margin; medial deep longitudinal groove; exopod subrectangular. Male sternum ovate and flattened up to the anterior half of thoracic sternite 4, where it slopes downward toward sternite 1., maximum width at sternite 6 level; sternite 2 subtriangular; sternite 3 inverted subtriangular with rounded angles, medial longitudinal groove; sternite 4 formed by two rectangle trapezoids divided by

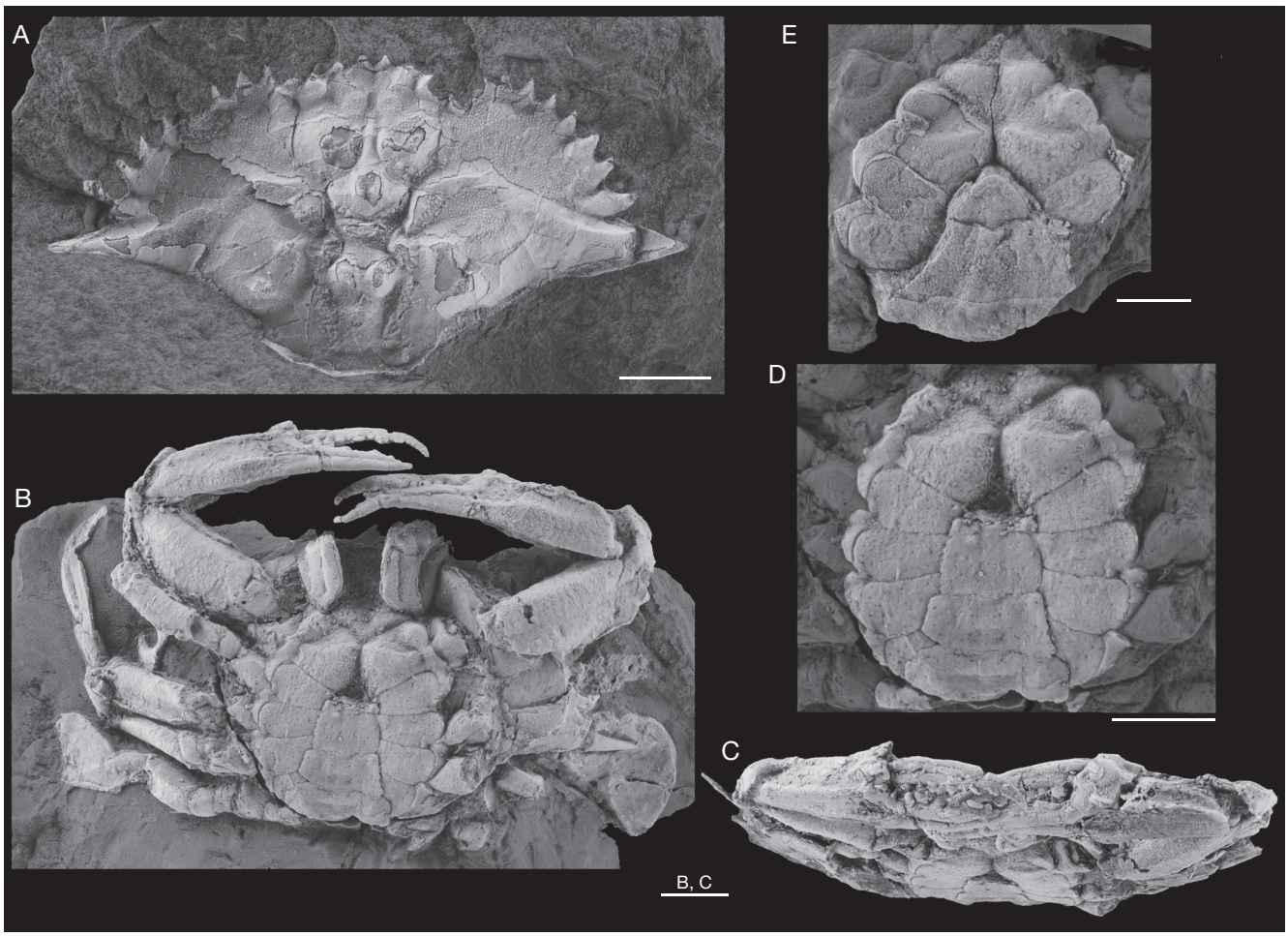


Fig. 4. — Studied specimens of *Portunus catalaunicus* (Vía, 1941): **A**-**D**, from Pamplona Marls Fm (lower Priabonian) of Fanlillo (Yebra de Basa, Huesca, Spain); **A**, carapace partially decorticated MPZ 2025/467; **B**-**D**, specimen MPZ 2024/02 in ventral (**B**) and frontal views (**C**), and detail of pleon and thoracic sternites (**D**); **E**, detail of the specimen MPZ 2025/469 figured in Ferratges *et al.* (2024) from Arguis/Belsué platform beds (Arguis Fm, upper Bartonian) of Belsué (Nueno, Huesca, Spain). Scale bars: 10 mm. Photographs: Isabel Pérez Urresti.

deep sternopleonal cavity, transverse medial keel separating anterior and posterior surfaces, sulcus paralleling the lateral margins, gynglyme receiving P1 coxa at midlength of the lateral margin; sternites 5-7 subtrapezoidal elongated; sternite 8 subtrapezoidal, clearly visible. Suture 2/3 complete; suture 3/4 well defined by a V-shaped groove; sternite 4/5 to 7/8 appear complete until disappearing under the pleon, suture 4/5 forms acute angle with axis, suture 5/6 making a right angle with axis, and sutures 6/7 and 7/8 a form progressively an obtuse angle with axis. Episternites 4-7 well developed, posteriorly directed, no suture visible. Male pleonal somites 4 and 5 subrectangular, fused, with remnant of suture; somite 6 subrectangular, longer than somite 5. Chelipeds long, slender, slightly heterochelous. Merus of cheliped long, smooth, subtriangular in section. Carpus of cheliped subtrapezoidal, upper surface ridged, spines forward directed at midlength of the outer margin and distal corner, blunt spine in the inner margin. Propodus long; palm about one half of propodus, smooth, heptagonal in section with seven longitudinal keels; two keels forming the outer and inner upper margin and ending each in a distal spine; two parallel keels in the outer surface of palm; two blunt forming the lower margin of the propodus; and a longitudinal one in the inner margin. Dactyli long, slender, about half of propodi, with longitudinal groove; dactylus bearing a proximal knobstick molariform tooth followed by tri-lobed and bi-lobed serial conical teeth; fixed finger bearing tri-lobed and bi-lobed serial conical teeth. Pereopods 2-4 long and flattened, smooth, dactyli styliform. Pereopods 5 much shorter than pereopods 2-4, dactyli paddle-like.

Remarks

The newly collected material from the lower Priabonian strata of Huesca Province (Aragon) is consistent in every aspect with the original material from the middle Eocene of Catalonia (cf. Vía 1941: 65-70, pl. 1, figs 1-6; 1969: 206-218, fig-text 26, pl. 17, figs 1-2, pl. 18, figs1-3, pl. 19, figs 1-2). The type material of *Portunus catalaunicus* was recovered from the middle Eocene of central Catalonia (Igualada, Spain) (Vía 1941), and it has subsequently been recorded from other middle Eocene outcrops in Catalonia (e.g., Vía 1969). Later, some authors (Artal *et al.* 2013a; Ossó *et al.* 2014; Domínguez & Ossó 2016a, b; Ossó & Domínguez 2017) reported its pres-

ence in the late Eocene of Huesca, although it was not illustrated and no further data were provided. The new material from the Fanlillo and Arguis sections (Huesca) confirms and extends the known stratigraphic range of the species into the middle and late Eocene of northern Iberian Peninsula. This taxon is among the most frequently recorded fossil species in sandy and muddy sediments spanning a broad bathymetric range during the middle Eocene. In the study area, it typically occurs in siliciclastic-dominated depositional environments characterized by shallow to moderately shallow depths (see Ferratges *et al.* 2024).

Due to its relatively large size and abundance, *Portunus catalaunicus* likely played a key role in structuring the benthic community, acting as a macrobenthic predator occupying a relatively high trophic position. It is striking that, despite the high dispersal capacity of portunoid crabs (e.g. Castejón & Guerao 2013; Gonzalez-Wangüemert & Pujol 2016) and their documented impact on benthic communities (e.g., Hamilton 1976; Choy 1986; Mori & Zunino 1987; Abelló *et al.* 1988; Hall *et al.* 1990; Careddu *et al.* 2017), this species appears to be restricted to the South Pyrenean basins (Catalonia and Aragon). A similar pattern is observed in several Eocene species of *Portunus*, listed by Artal *et al.* (2013b: 313), which are mainly from northern Italy and likewise appear to be confined to their regions of origin. The studied locality hosts a remarkably diverse invertebrate assemblage, including other decapods and molluscs. Large benthic predators such as this species can influence faunal composition, sediment dynamics, and even vegetation structure, among other key environmental variables (Hamilton 1976; Buck *et al.* 2003; Werry & Lee 2005; Kristensen 2008; Careddu *et al.* 2017). However, few specific studies have addressed the feeding habits of portunoid crabs, and their precise ecological role within marine ecosystems remains poorly understood (Abelló & Cartes 1987; Hall *et al.* 1990; Freire 1996).

DISCUSSION AND CONCLUSIONS

Portunoid crabs were well represented during the Eocene, however, to date fewer than ten taxa have been recorded so far in the Iberian Peninsula. The new discovery presented herein supports the affinity between the carcinofaunal assemblages of Italy and Hungary and those of the South-Pyrenean basins. This affinity is evidenced by the occurrence of the same species in both areas in several cases, or by the presence of closely related genera in others. These assemblages suggest that the South-Pyrenean basins may have acted as a migration corridor between the Tethys and the North Atlantic Ocean during the Eocene. Nevertheless, the progressive closure of marine connections between those basins during the late Eocene may have favoured allopatric speciation (see Vía 1959; Domínguez & Ossó 2016a).

Interestingly, despite the high dispersal capacity typically attributed to portunoid crabs (e.g., Castejón & Guerao 2013; Gonzalez-Wangüemert & Pujol 2016), the species *Portunus catalaunicus* seems to have been restricted to the South-Pyrenean basins, as observed for several Eocene portunoid taxa from northern Italy (Artal *et al.* 2013b). Such a pattern may reflect limited connectivity and progressive isolation of the western Tethyan basins during the late Eocene.

The generic assignment of *P. catalaunicus,* as well as other fossil species attributed to *Portunus*, remains open to revision (see Spiridonov 2020; Garassino *et al.* 2021; Koch *et al.* 2022). We therefore retain the species within *Portunus* sensu lato until further systematic work provides conclusive evidence.

The integration of paleontological and ecological evidence underscores the long-standing ecological success of portunoids and their importance in shaping both ancient and modern marine benthic ecosystems.

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