

# The oldest dairoidid crab (Decapoda, Brachyura, Parthenopoidea) from the Eocene of Spain

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**Abstract:** Eubrachyurans, or ‘higher’ true crabs, are the most speciose group of decapod crustaceans and have a rich fossil record extending into the Early Cretaceous. However, most extant families are first found in the fossil record in the Palaeogene, and particularly in the Eocene. Unfortunately, fossils of many early eubrachyuran groups are often fragmentary, and only a few studies have combined extinct and extant taxa in a phylogenetic context using different optimality criteria. Here, we report the dairoidid crab *Phry-nolambrus sagittalis* sp. nov., an enigmatic eubrachyuran from the upper Eocene of Huesca (northern Spain), whose completeness and exquisite preservation permit examination of its anatomy in a phylogenetic context. Dairoidids have previously been considered among the oldest stone crabs (Eriphioidea) or elbow crabs (Parthenopoidea), two disparate and distantly related groups of true crabs living today. Mechanical preparation and computed tomography of the

fossil material revealed several diagnostic features that allow a detailed comparison with families across the crab tree of life, and test hypotheses about its phylogenetic affinities. *Phry-nolambrus sagittalis* is the first record of the genus in the Iberian Peninsula, and represents one of the oldest crown parthenopoidean crabs worldwide, expanding our knowledge of the biogeographical distribution of elbow crabs during the Palaeogene, as well as their early origins, anatomical diversity and systematic affinities. Understanding the disparity of Eocene eubrachyurans is pivotal to disentangling the systematic relationships among crown families, and interpreting the spatio-temporal patterns leading to the evolution of modern faunas.

**Key words:** eubrachyuran, fossil crab, phylogeny, Priabonian, Pyrenees, Iberian Peninsula.

THE origin of modern families of ‘higher’ true crabs (Eubrachyura) and how they relate to other extant and extinct clades is a matter of ongoing discussion (Luque *et al.* 2021). Phylogenetic analyses based on molecular and morphological data offer a good opportunity to quantitatively investigate the relationships among crab groups beyond alpha taxonomy-based inferences of relatedness (e.g. Ahyong *et al.* 2007; Tsang *et al.* 2008, 2014, 2022; Karasawa *et al.* 2011, 2014; Bracken-Grissom *et al.* 2013; Spiridonov *et al.* 2014; Schweitzer *et al.* 2016; Wolfe *et al.* 2019, 2022; Ma *et al.* 2019; Luque *et al.* 2019, 2021; among others). However, reliable well-preserved fossils of

early crown groups are crucial to accurately calibrate molecular trees, and to reduce the uncertainty of anatomical data recorded for morphological phylogenies. Moreover, to date, there are few works that combine morphological data of fossil and extant eubrachyuran taxa in a phylogenetic context using one or more optimality criteria (e.g. Karasawa *et al.* 2008; Luque *et al.* 2019, 2021).

Here, we describe *Phry-nolambrus sagittalis*, a new species of enigmatic parthenopid or elbow crabs found in the upper Eocene (Priabonian) Pamplona Formation of Huesca (southern Pyrenees), Northern Spain (Fig. 1),

and discuss: (1) its phylogenetic affinities with other eubrachiurans; and (2) its importance for understanding the early evolution of one of the most iconic groups of crabs. Mechanical preparation and computed tomography (CT) of the new fossil material revealed anatomical features well-preserved and in-volume, such as dorsal carapaces and its regions, the orbits and rostrum, the epistome and pterygostome, cuticular ornamentation, sternum, pleon, and the ventral carapace and the chelipeds. These and other characters are crucial for taxonomic and phylogenetic studies, especially given that most fossil elbow crabs are known only from isolated carapaces, and rarely from ventral carapaces or even legs and chelipeds associated to the body. In addition, based on a review of previous occurrences of *Phrynosolambus* and other parthenopoids in the fossil record, we discuss aspects of its palaeoecology as well, for extinct and extant relatives.

Modern representatives of the superfamily Parthenopoidea MacLeay, 1838, have received significant systematic attention in recent decades, and there is a good understanding of the morphology and ecology of the group (i.e. Tan 2004; Tan & Ng 2007a, 2007b). However, to date, there are no detailed studies exploring the phylogenetic relationships between the members of Parthenopoidea (Tan & Ng 2007a; Ferratges *et al.* 2019), especially considering extinct taxa, despite their anatomical character richness (Schweitzer *et al.* 2006). The oldest crown Parthenopoidea known to date are all Eocene in age (Ferratges *et al.* 2019 and references therein), and show that elbow crabs were relatively diverse early on (Ferratges *et al.* 2019; Schweitzer *et al.* 2020a). However, fossil material assigned to this group of odd-looking crabs usually consists of only carapaces (see exceptions in Ferratges *et al.* 2019 and references therein), hampering the interpretation of its origin and evolution.

The new species occurs in a diverse assemblage of decapod crustaceans (Table 1) recorded in siliciclastic sediments derived from a pro-delta environment. The outcrop providing the fossil material focus of this study has yielded specimens belonging to at least 18 superfamilies of decapods, some of the taxa of which have been previously studied by various authors (Artal *et al.* 2013; Ossó *et al.* 2014; Ossó & Domínguez 2017; Ossó *et al.* 2020). Although eubrachiurans have a rich fossil record extending back into the Early Cretaceous, it is during the Eocene that the oldest representatives of most extant families are first known (e.g. Luque *et al.* 2017). For this reason, understanding the anatomical diversity or disparity of Eocene brachiurans and how they relate to other extinct and extant groups is pivotal to the investigation of spatio-temporal patterns leading to the evolution of the modern groups seen today.

## GEOLOGICAL SETTING

The decapod specimens here studied come from the marly-dominated succession of the Pamplona Formation (Puigdefábregas 1975), which forms part of the sedimentary infill of the Jaca Basin, located in the central part of the South Pyrenean zone (Fig. 1). Specifically, this material was collected along the road N-260 located 400 m east-southeast of the village of Fanlillo, in the municipality of Yebra de Basa, Huesca province, Aragon, Spain. Data on the biostratigraphy (Canudo & Molina 1988; Canudo *et al.* 1988) and magnetostratigraphy (Hogan 1993) indicate a Bartonian–Priabonian age for the Pamplona Formation, and the calibration of Pueyo *et al.* (2002), established the lower and upper limits of this formation from 40.32 to 37.17 Ma, which corresponds to a Bartonian or early Priabonian age.

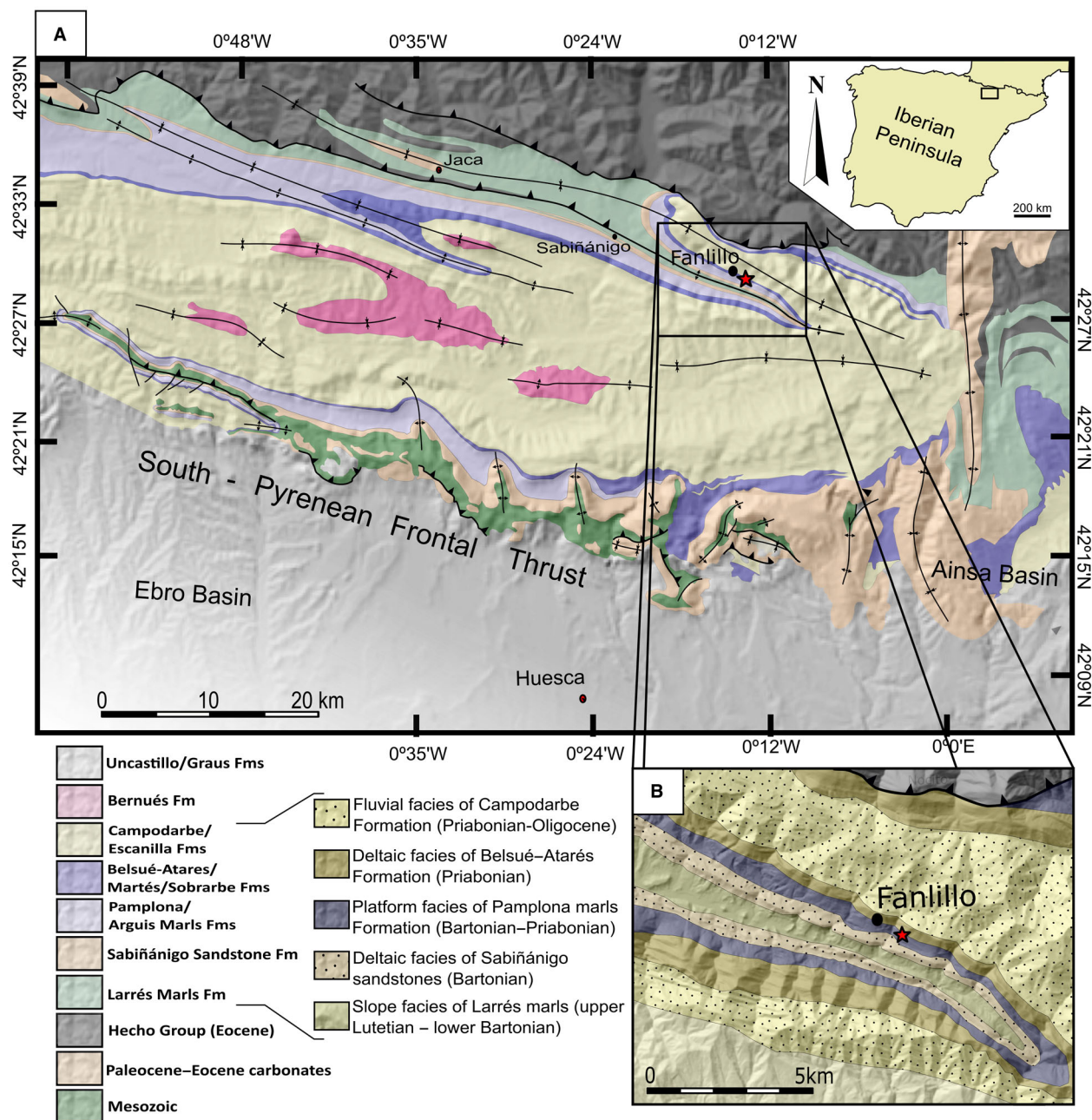
This formation consists of a thick grey and blue marl succession deposited in a distal offshore environment. The succession grades upwards into sandstone delta-mouth bars with abundant vegetal remains in the uppermost levels. According to Montes-Santiago (2009), the distribution of fauna in the stratigraphic log of the Pamplona Formation, with bryozoans, nummulitid foraminifera, bivalves, siliceous sponges and decapod crustacean remains in the lower levels, and corals, algae, gastropods and remains of decapod crustaceans and fishes in the upper ones (outcrop levels), indicates a progressive upwards decrease of the bathymetry, with sedimentation probably within the euphotic zone, above storm wave base.

## MATERIAL AND METHOD

### *Material and preparation*

Ten studied specimens were collected from the bioclastic interval found in the upper part of the Pamplona Formation exposed near the village of Fanlillo. Measurements of carapace length–carapace width are given in millimetres (mm). Specimens are deposited in the palaeontological collection of the Museo de Ciencias Naturales de la Universidad de Zaragoza under the acronym MPZ. The location of the outcrop is shown in Figure 1.

Specimens were prepared using a needle under  $\times 40$  binocular magnification, and in some cases (specimens MPZ2022/204, MPZ2022/763), chemically, using potassium hydroxide (KOH). The specimens were then photographed dry and coated with ammonium chloride sublimate. Detailed photography of the carapace surfaces was carried out using a Nikon d7100 camera with a macro 60 mm lens. One specimen (holotype, MPZ2022/761) preserving a complete carapace and chelipeds was selected to be scanned in the Micro-Computed



**FIG. 1.** A, simplified geological map of the Jaca Basin in the South Central Pyrenean zone (modified from Coll *et al.* 2022). B, detail of the studied area; the red star near Fanlillo shows the location of the studied outcrop.

Tomography Laboratory using a model V|Tome|X s 240 from GE Sensing & Inspections Technologies Phoenix X-Ray, at the Centro Nacional de Investigación sobre la Evolución Humana (CENIEH, Burgos, Spain). The specimen matrix was reduced in order to increase the contrast between rock and fossil and later scanned. As a result, we obtained 1680 sections of the fossil specimen. To process the data, we used the image reconstruction software SPIERSedit 3.1.0.

*Phylogenetic analysis*

The dataset, containing 46 taxa from 13 brachyuran families (5 taxa as outgroups, 41 taxa as ingroup), and 113 adult morphological characters, was constructed in Mesquite v2.75 (Maddison & Maddison 2009) (Appendix S1; Ferratges *et al.* 2023), and modified from the datasets in Luque *et al.* (2019, 2021). Although most of the characters used to distinguish modern parthenopoids are not

**TABLE 1.** Diversity of decapod crustaceans in the studied outcrop of the Pamplona Formation (Priabonian).

| Infraorder                      | Superfamily  | Family   | Subfamily  | Taxon   |
|---------------------------------|--|--|--|---|
| Axiidea<br>Achelata<br>Anomura  | Callinassoidea Dana, 1852  | Callinassidae Dana, 1852<br>Scyllaridae Latreille, 1825  | Scyllarinae Latreille, 1825  | ? <i>Verticillichirus</i> sp.<br>Scyllarinae indet.   |
|                                 | Paguroidea Latreille, 1802   | Calcinidae Fraaije, Van Bakel & Jagt, 2017<br>Annuntidiogenidae Fraaije, 2014  |  | <i>Eocalcinus</i> sp.<br>? <i>Paguristes</i> sp.<br>? <i>Tymolus</i> sp.<br>? <i>Xeinostoma</i> sp.<br><i>Basadromia longifrons</i> Artal et al., 2016<br><i>Dromia</i> sp.   |
|                                 | Cyclodorippoidea Ortmann, 1892   |  | Dromiinae De Haan, 1833  | <i>Dromiites</i> sp.<br><i>Dynomene collinsi</i> Ossó et al., 2020<br>? <i>Homola</i> sp.<br>? <i>Pseudorogatus</i> sp.<br><i>Raininoides</i> sp.   |
| Brachyura<br>Podotreme<br>crabs | Dromioidea De Haan, 1833   | Dromiidae De Haan, 1833  |  | <i>Hepatisca poverelli</i> Via, 1959<br>Aethridae indet.<br><i>Calappilia</i> cf. <i>scopuli</i><br><i>Calappilia dactia</i> Bittner, 1893<br><i>Taverodesia calasancii</i> (Via, 1959)<br>carpilid indet.<br><i>Chasmocarcinus</i> cf. <i>guerini</i> (Via, 1959)<br>Dorippid indet.<br><i>Ethusa</i> sp.<br>? <i>Goneplacoid</i> indet.<br><i>Magyarocarcinus yebraensis</i> Domínguez & Ossó, 2016<br><i>Pyreneplax basaeensis</i> Ossó, Domínguez & Artal, 2014<br>Hexapodid indet.<br>? <i>Paranaxia</i> sp.<br><i>Planobranchia</i> sp.<br>? <i>Macrocheira</i> sp.<br>? <i>Cromimaia</i> sp.<br><i>Micromia priabonensis</i> (Oppenheim, 1901)<br><i>Spiriostriima</i> cf. <i>margaritata</i> (Fabiani, 1910)<br><i>Montezumella</i> sp.<br><i>Eopidicus squamosus</i> Beschin et al., 1996<br><b><i>Phrynomalurus sagittalis</i></b> sp. nov.<br><i>Eopilumnus chechii</i> Beschin et al., 2002<br><i>Portunus catalaunicus</i> (Via, 1941)<br>Carcinidae indet.<br><i>Retrocyopa alméi</i> Via, 1959<br><i>Retropluma eocenica</i> Via, 1959<br><i>Serrablpluma diminuta</i> Artal et al., 2013<br><i>Scutoplax oscensis</i> (Ossó & Domínguez, 2017)<br><i>Baltacarcinus</i> sp.<br><i>Actaetes</i> sp.<br><i>Daragrapsus trispinosus</i> Müller & Collins, 1991<br>? <i>Pinnotheridae</i> indet. |
|                                 | Homoloidea De Haan, 1839<br>Raininoida De Haan, 1839   | Dynomenidae Ortmann, 1892<br>Homolidae De Haan, 1839<br>Raininidae De Haan, 1839   | Sphaerodromiinae Guinot & Tavares, 2003<br>Dynomeninae Ortmann, 1892<br>Rogueinae Karasawa, et al., 2014<br>Raininoidinae Lörenthey in Lörenthey & Beurlen, 1929                                     |   |
| Eubrachyura<br>Heterotremes     | Aethroidea Dana, 1851  | Carpilioidea Ortmann, 1893<br>Chasmocarcinidae Serène, 1964<br>Dorippoidea MacLeay, 1838<br>Goneplacoidea MacLeay, 1838  | Carpiliidae Ortmann, 1893<br>Dorippidae MacLeay, 1838<br>Ethusidae Guinot, 1977<br>? <i>Euryplocidae</i><br><i>Magyarocarcinidae</i> Domínguez & Ossó, 2016<br>Vultocinidae Ng & Manuel-Santos, 2007 |   |
|                                 | Calappoidea H. Milne Edwards, 1837   | Hexapodoidea Miers, 1886<br>Majoidea Samouelle, 1819   | Pisinae Dana, 1851   |   |
| Thoracotremes                   | Montezumelloidea Ossó & Domínguez, 2019<br>Palicoidea Bouvier, 1898<br>Parthenopoidea MacLeay, 1838<br>Pillunioidea Samouelle, 1819<br>Portunioidea Rafinesque, 1815<br>Retroplumioidea Gill, 1894 | Montezumellidae Ossó & Domínguez, 2013<br>Palicidae Bouvier, 1898<br>Parthenopidea MacLeay, 1838:<br>Pillunidae Samouelle, 1819<br>Portunidae Rafinesque, 1815<br>Carcinidae MacLeay, 1838<br>Retroplumidae Gill, 1894 | Dairoidinae Števíć, 2005<br>Portuninae Rafinesque, 1815<br>? <i>Polybinae</i> Paulson, 1875  |   |
|                                 | Xanthoidea MacLeay, 1838   | Xanthoidea MacLeay, 1838<br>Grapsoida MacLeay, 1838<br>? <i>Pinnotheroidea</i> De Haan, 1833   | Actaeinae Alcock, 1898   |   |

preserved in the fossil record (i.e. antennal articles, ambulatory legs), Tan & Ng (2007a, 2007b) listed useful morphological characters that can be recognized in fossil species, including in *Phrynosolambrus sagittalis* (e.g. carapace shape, carapace ornamentation, shape and distribution of the dorsal regions, shape of the rostrum and orbits, and cross-section shape and ornamentation of the chelipeds). Undetermined and not preserved characters were scored as '?' and inapplicable characters were scored as '-'. Multiple character states present in a given terminal were scored as polymorphisms.

The final dataset was analysed under Bayesian inference, as implemented in MrBayes v.3.2.6. The dataset was analysed under the traditional Mk model with an ascertainment bias correction to account for scoring only variable morphological characters. Each analysis was performed with two independent runs of  $3 \times 10^7$  generations each. We used the default settings of four chains (one cold and three heated) per each independent run. The relative burn-in fraction was set to 25% and the chains were sampled every 200 generations. We used Tracer v.1.6 to determine whether the runs reached stationary phase, and to ensure that the effective sample size for each parameter was greater than 200. Results of the Bayesian runs are summarized as a majority-rule consensus tree of the post-burn-in sample with a node support threshold of 75%.

## SYSTEMATIC PALAEOLOGY

Terminology used herein follows Tan & Ng (2007b) and is summarized in Figure 2.

Infraorder BRACHYURA Latreille, 1802

Section EUBRACHYURA de Saint Laurent, 1980

Superfamily PARTHENOPOIDEA MacLeay, 1838

Family PARTHENOPIDAE MacLeay, 1838

Subfamily DAIROIDINAE Števcíć, 2005

*Type genus.* *Dairoides* Stebbing, 1920.

*Included genera.* *Aragolambrus* Ferratges et al., 2019; *Dairoides*; *Phrynosolambrus* Bittner, 1893.

*Emended diagnosis.* Cephalothorax subhexagonal to triangular, anteriorly narrowing. Dorsal surface covered with mushroom-like perforate vesicular tubercles, with deep grooves not completely covered by mushroom-like tubercles. Front narrow, triangular, deflexed. Tridentate inter-antennular spine. Orbital regions domed, separated by deep interorbital depression. Orbits small, deep, rounded. Antennular and orbital cavities connected. Epistome covered with mushroom-like tubercles. Pterygostomial

region with deep grooves. Basal antennal segment mobile, short, not touching front, peduncle slender lying loosely in orbital hiatus. Junction between anterolateral and posterolateral margins produced and armed with epibranchial spine (lateral angle). Chelipeds markedly heterochelous, not pressed tightly against anterolateral margin. Endostomial ridge complete. Anterior margin of merus of third maxilliped straight. Sternal shield entering between third maxillipeds. Second gonopod very slender, longer than first, flagellum longer than basal segment, curved. Abdominal segments nearly freely articulated, segments 3–4 immovable, telson rounded in both sexes. (Modified after Števcíć 2005)

### Genus PHRYNOLAMBRUS Bittner, 1893

*Type species.* *Phrynosolambrus corallinus* Bittner, 1893, by original designation.

*Included species.* *Phrynosolambrus corallinus*; *P. italicus* De Angeli & Beschin, 2008; *P. sagittalis*.

*Emended diagnosis.* Carapace rhomboid (triangular?) anteriorly narrowing, rostrum short, projected; hepatic region convex laterally, remainder of anterolateral margin slightly convex, then extending into stout, triangular lateral spine; posterolateral margin convex; strong epibranchial spine, oriented obliquely posteriorly; posterior margin straight; carapace region broadly inflated and ornamented with mushroom-shaped tubercles. (Modified after Schweitzer et al. 2020a)

*Remarks.* The extinct genus *Phrynosolambrus*, previously included within the family Parthenopidae MacLeay, 1838, shares with species of the extant genus *Dairoides* (i.e. *D. kusei* (Sakai, 1938), *D. margaritatus* Stebbing, 1920 and *D. seafdeci* Takeda & Ananpongsuk, 1991) a similar general morphology, with a triangular frontal margin, a spinose lateral angle, a similar position of the spines and dorsal regions, the distribution of the grooves (dorsal and ventral), the morphology and structure of the cuticle, and the morphology of the chelipeds.

*Phrynosolambrus sagittalis* sp. nov.

Figures 3–5

*LSID.* <https://zoobank.org/NomenclaturalActs/62A52EB8-6BA7-4454-95EA-25B3FDC4255E>

*Derivation of name.* From the Latin *sagitta*, in reference to its arrowhead carapace shape.

*Type material.* The holotype, MPZ 2022/761, is a complete carapace (length and width, 15.1 mm and 12.2 mm, respectively) and chelipeds, with well-preserved cuticle. Additional specimens include the paratypes MPZ 2022/203, 2022/204, 2022/762, 2022/763, 2022/764, 2022/765, 2022/766, 2022/767 and 2022/768.

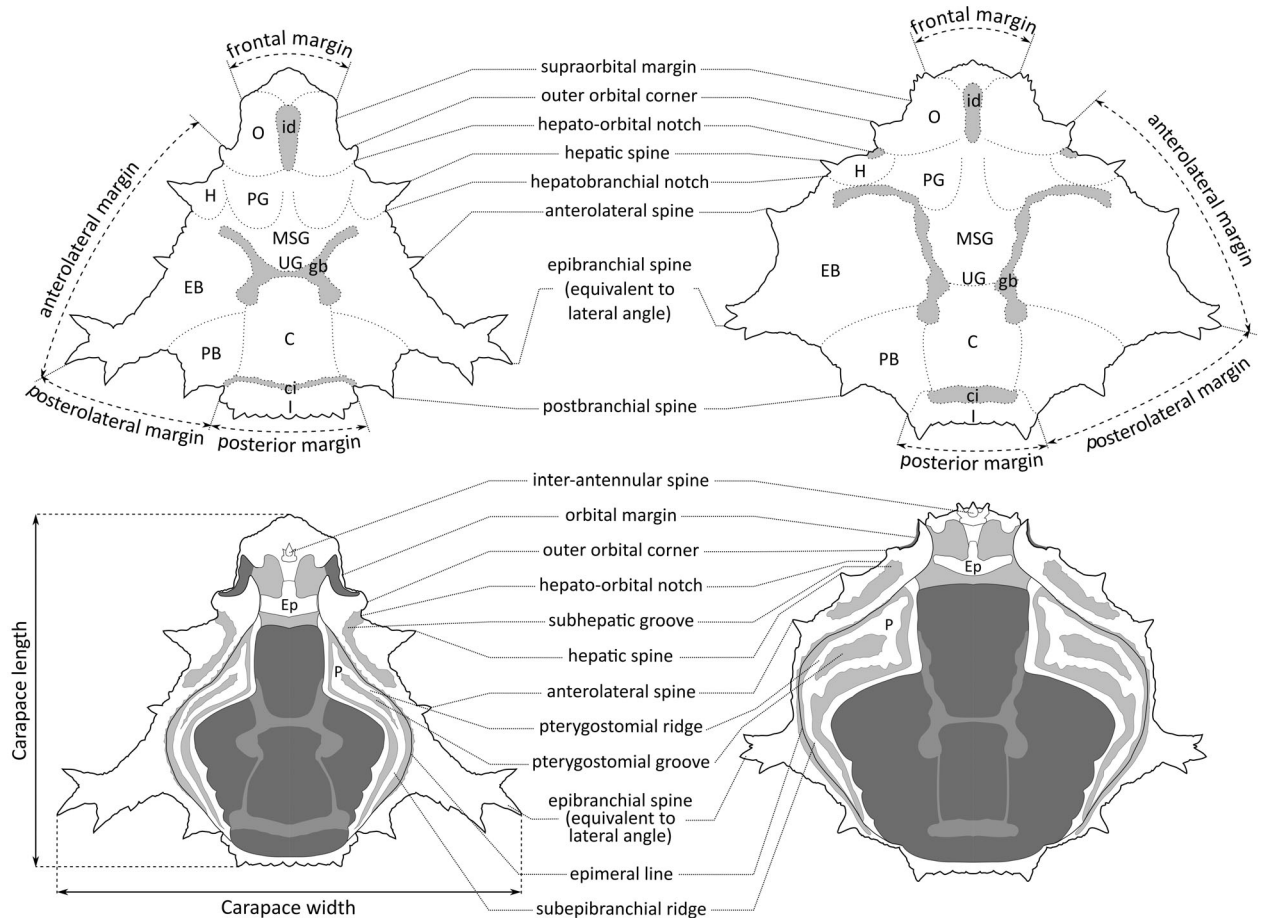
*Diagnosis.* Carapace triangular, wider than long; projected frontal margin; orbits inflated; anterolateral margins almost straight,

with small conical spine; posterolateral margin converging posteriorly, with strong spine and marked concavity behind epibranchial spine; armed epibranchial spine, oriented obliquely posteriorly; straight posterior margin; depressed postbranchial region; carapace surface densely tuberculated by mushroom-shaped tubercles.

**Description.** Cephalothorax triangular in outline, anteriorly narrowing (Fig. 3). The dorsal regions are well defined and strongly convex. Dorsal surface is almost completely covered with mushroom-shaped tubercles that abut around the edges leaving pores leading into subsurface canals (Fig. 3B), except in the interorbital depression, in which a 'window' is formed, and in the grooves that separate the gastric and cardiac regions from the branchial regions, and from the intestinal of the cardiac region. Front narrow, triangular. Below the frontal margin, between the antennular pits, there is a forward-facing oriented spine (inter-antennular spine). Orbits small, deep and rounded, laterally directed, bordered by a row of tubers. Ocular peduncle

short, ornate. Antennular and orbital cavities in communication. Hepatic margin distinct, not continuous with epibranchial region, with one prominent spine covered with mushroom-shaped tubercles. The anterolateral margins are strongly diverging and longer than the posterolateral ones, with hepato-orbital and hepatobranchial notches; on each lateral angle there is a large projecting epibranchial expansion (epibranchial spines), directed slightly backwards. In the distal part they present four spines: three oriented in a lateral plane and a fourth spine oriented upwards. The posterior margin is broad and concave; it occupies about half the carapace greatest width.

The regions are defined by wide grooves, but on the dorsal surface they are masked by the tubercles; they are much more evident seen from the interior view (Fig. 4). The small epigastric lobes are very apparent: they are inflated at the base of the front; the protogastric regions are large, vaulted. The mesogastric region is flattened. The urogastric region is short, arched, anterior portion undifferentiated, with the lateral and posterior margins bounded by deep grooves. The cardiac region is large,



**FIG. 2.** Anatomical comparison of the extinct genus *Phrynosoma* (left) and the extant genus *Dairoides* (right), and terminology used in the text. Shaded areas represent depressed areas not covered by mushroom-shaped tubercles. **Abbreviations:** C, cardiac region; ci, cardio-intestinal groove; EB, epibranchial region; Ep, epistome; gb, gastrobranchial groove; H, hepatic region; I, intestinal region; id, inter-orbital depression; MSG, mesogastric region; O, orbital region; P, pterygostomial region; PB, postbranchial region (meso- and metabranchial regions); PG, protogastric region; UG, urogastric region.

subrectangular, widening posteriorly, strongly convex, swollen, and prominent. The hepatic region is narrow, triangular, depressed, slightly lower than epibranchial and gastric regions. The epibranchial regions are very large; dorsally they have a conical central part. Laterally, approximately in the first third of the epibranchial region there is a pointed conical tubercle that stands out among the others (anterolateral spine). Towards the posterior part of the epibranchial region is the lateral expansion with four spines, equivalent to the lateral angle that has *Daldorfia* (see Tan & Ng 2007b). Postbranchial regions formed by meso- and metabranchial regions, undifferentiated, laterally surround the cardiac region, and are smaller than epibranchial region, depressed and have a subtriangular shape. Intestinal region subrectangular, wide and separated from cardiac region by a deep cardio-intestinal groove. Subhepatic region bordered by a subhepatic groove that separates the hepatic spine from the inferior border. Sub-epibranchial region narrow, covered with tubercles in shape of 'petaloid' mushrooms, with very marked epibranchial ridge. Epimeral line (or moult line) bordered by numerous small mushroom-shaped tubercles in the upper margin, and by a smooth groove in the pterygostomial region (Fig. 3D). Pterygostomial region ornamented with two rows of small mushroom-shaped tubercles that converge both anteriorly and posteriorly, forming the pterygostomial and subepibranchial ridges and the pterygostomial groove.

The chelipeds are markedly heterochelous (Figs 4, 5); major cheliped (right) robust. Carpus slightly higher than long; surface equipped with various complex long spines, with a narrowing at the base. Manus longer than high; outer margin with five spines (Fig. 4); lower margin slightly concave at base of fixed finger, with seven small aligned spines (Fig. 4); inner margin not well developed, with four tubercles (Fig. 4); upper, inner surface with spaced tubercles (Fig. 4); row of four long spines on outer side aligned in central part plus several spines irregularly distributed over surface (Fig. 4). Fixed finger short, slightly oblique downward, triangular, tip pointing slightly upward (Fig. 4). Dactylus strong, curved. Lateral surface with a small ridge; occlusal margin with molariform teeth, becoming smaller distally. Left cheliped slender (Fig. 4). Carpus slightly higher than long; surface armed with various long spines. Manus longer than high, slightly divergent distally; outer margin with four triangular spines, widely spaced; lower margin slightly concave at base of fixed finger, with eight small aligned spines; inner margin not well developed, with four tubercles; upper, inner surface with spaced conic tubercles. Fixed finger shorter than palm, threefold longer than high, oblique downward, with a longitudinal groove on the mesial part; dactylus curved, with longitudinal groove in upper mesial part; occlusal margin with small teeth, becoming smaller distally.

**Occurrence.** The genus *Phrynosolambrus* is known only from the upper Eocene of Italy, Hungary and Romania (Bittner 1893; Lörenthey & Beurlen 1929; Beschin *et al.* 2009) and the Oligocene of Italy (De Angeli & Beschin 2008). In this work we expand its distribution to the upper Eocene of the Iberian Peninsula.

**Remarks.** *Phrynosolambrus sagittalis* can be differentiated from congeners on the basis of: (1) its projected and triangular front, with a deep and narrow interorbital depression (Figs 2, 3A, C, F,

4A–C, 5A); (2) a large hepatic spine and one conical spine in the anterolateral margin (Figs 2, 3A, C, 4A–F, 5); (3), the robust epibranchial spines that are posteriorly oriented (Figs 2, 3A, C–F, 4A–F, P, 5); and (4) a well-developed postbranchial spine on the posterolateral margin oriented obliquely backwards (Figs 2, 3A, C, D, F, 4A, C, E, F, 5). *Phrynosolambrus sagittalis* is morphologically close to *P. corallinus*, the type species of the genus. Both have a triangular outline, a carapace surface covered with mushroom-shaped tubercles, and similarly distributed dorsal regions. However, the latter is distinguished by having a wider interorbital depression, more convex anterolateral margins, epibranchial spines oriented laterally instead of posteriorly, and apparently lacking anterolateral and postbranchial spines.

The species *Phrynosolambrus corallinus* was named by Bittner (1893) based on three specimens from the upper Eocene of Romania. However, the poor state of conservation of specimens of the type material resulted in both the original description and the reconstruction drawing not corresponding faithfully to the true morphology of *Phrynosolambrus*. Subsequently, other authors (Lörenthey 1898; Lörenthey & Beurlen 1929; De Angeli & Beschin 2008; Beschin *et al.* 2009) carefully analysed other carapaces from Italy and Hungary and corrected some of the inaccuracies of the original description. Almost all of the previous studies on the genus *Phrynosolambrus* are based on carapaces that have lost the external part of the cuticle (Beschin *et al.* 2007, 2009; De Angeli & Beschin 2008), and consequently do not preserve the structure of the tubercles and the actual external appearance. This is important to mention because the presence of cuticle is key for the appearance of crabs (Waugh 2013; Klompaker *et al.* 2015).

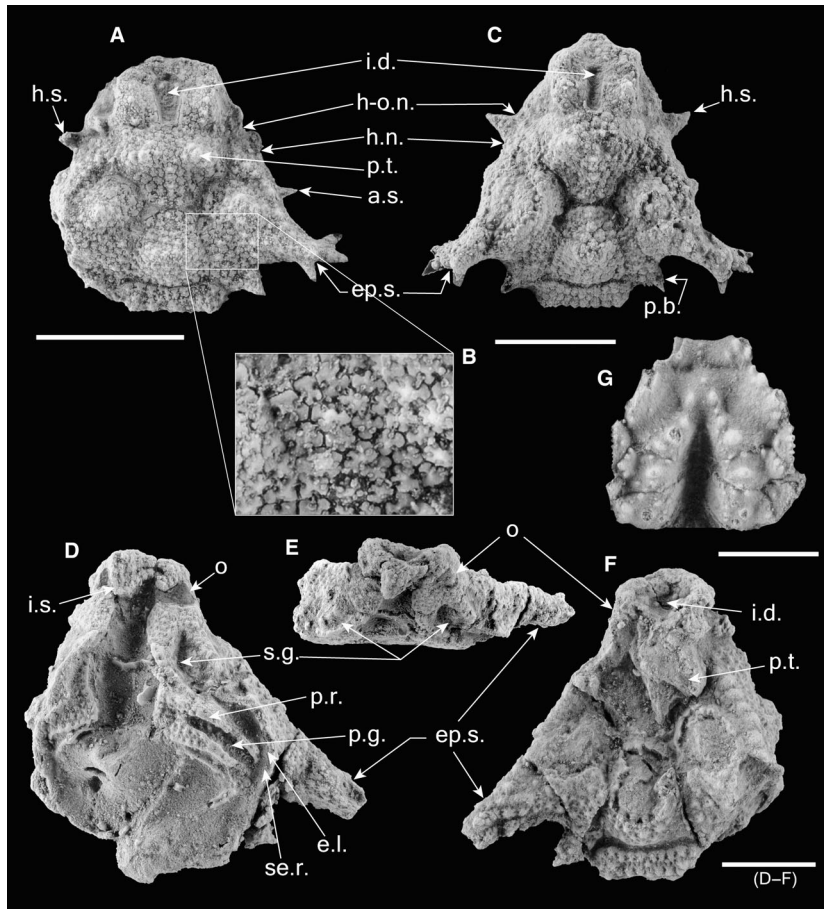
The new species is also close to *P. italicus*, but that species differs in having a wider and more prominent frontal margin and a wider interorbital depression. In addition, the gastrobranchial and cardio-intestinal grooves of *P. italicus* are wider than in the new species. The dorsal granulation in *P. italicus* is also dense, but with smaller tubercles (preserved only as an internal mould in *P. italicus*). The poor state of conservation of *P. italicus* does not enable further comparisons.

The species '*Parthenope*' (*Pseudolambrus*) *pentagonus* Quayle & Collins, 1981, is considered as a species of *Phrynosolambrus* in Schweitzer *et al.* (2010). However, it: (1) does not show the characteristic structures of this genus (i.e. very marked interorbital depressions and dorsal grooves); (2) has a much more circular outline of the carapace than other species of *Phrynosolambrus*; and (3) has a lateral angle barely marked. For all of these reasons we are excluding '*Parthenope*' (*Pseudolambrus*) *pentagonus* from the genus *Phrynosolambrus*, and hence from our phylogenetic analysis. The genus placement of this species is beyond the scope of this study.

## PHYLOGENETIC POSITION OF *PHRYNOSOLAMBRUS* AND ITS RELATIONSHIP WITH *DAIROIDES*

*The genus Dairoides: Eriphioidea or Parthenopoidea affinities?*

The systematic position of *Dairoides* (the sole extant genus of the subfamily Dairoidinae) has been a matter of



**FIG. 3.** Paratypes of *Phrynosoma sagittalis* sp. nov. from the upper Eocene (Pamplona Fm) of Huesca, Spain. A–B, paratype MPZ 2022/763 in dorsal view; B, detail of the cuticle with mushroom-shaped tubercles. C, MPZ 2022/203. D–F, paratype MPZ 2022/204 in: D, ventral; E, frontal; F, dorsal views. G, isolated sternum (MPZ 2022/767) assigned to the new species due to similarities with the modern *Dairoides* and other parthenopoids. *Abbreviations:* a.s., antero-lateral spine; e.l., epimeral line; ep.s., epibranchial spine (equivalent to lateral angle); h.n., hepatobranchial notch; h-o.n., hepato-orbital notch; h.s., hepatic spine; i.d., inter-orbital depression; i.s., inter-antennular spine; o, orbit; p.b., postbranchial spine; p.g., pterygostomial groove; p.r., pterygostomial ridge; p.t., protogastric tubercles; s.g., subhepatic groove; se.r., subepibranchial region. All scale bars represent 5 mm, except G (= 2 mm).

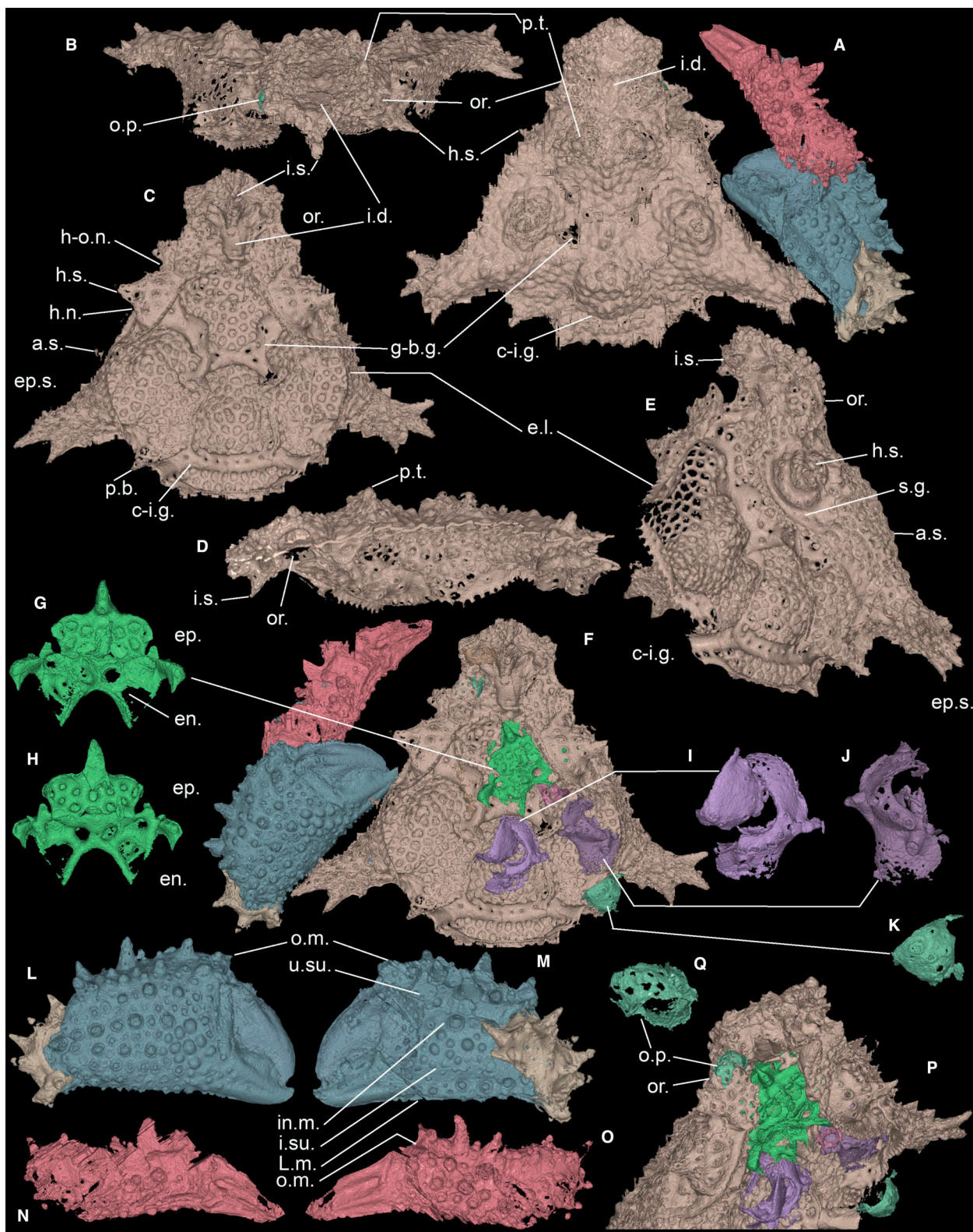
discussion in the past due to its peculiar claw and body form and its cuticular ornamentation, with some authors considering it closer to either the ‘stone crab’ superfamily Eriphioidea MacLeay, 1838, or to the ‘elbow crab’ superfamily Parthenopoidea (e.g. Sakai 1976; Ng *et al.* 2001, 2008; De Grave *et al.* 2009; Davie *et al.* 2015; Jagt *et al.* 2015; Schweitzer *et al.* 2020b). Moreover, a number of authors have previously discussed the potential relationships between *Dairoides* and other genera, mainly *Daira* and *Dacryopilumnus* (Guinot 1967; Sakai 1976; Ng & Tan 1984, 1985; Serène 1984; Dai & Yang 1991; Ng *et al.* 2001; Števcic 2005; Ng *et al.* 2008; Lai *et al.* 2014).

Guinot (1967, 1979) noted that *Dairoides* seemed to have more in common with parthenopids than with *Daira*, and suggested its possible inclusion in the family Parthenopidae. Subsequently, Ng & Rodríguez (1986) described the family Dairidae to accommodate *Daira* and *Dairoides*, and included it in the superfamily Parthenopoidea. Števcic (2005) established the family Dairoididae to accommodate *Dairoides*, and placed both families Dairidae and Dairoididae in the superfamily Dairoidea. Later, Ng *et al.* (2008) placed ‘Dairoididae’ (with only the genus *Dairoides*) within Eriphioidea, and

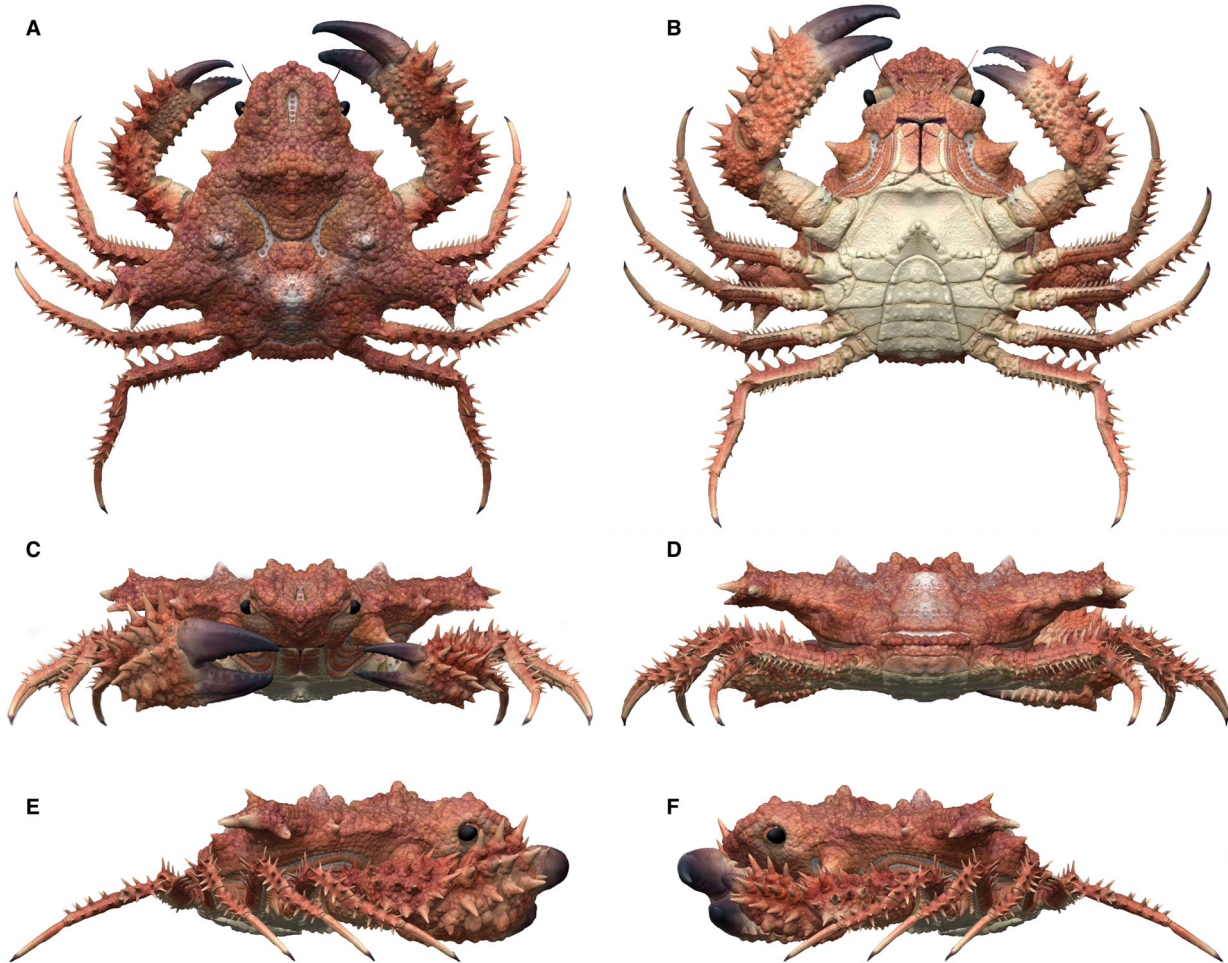
considered the similarities between *Dairoides* and many parthenopid genera as convergence. More recently, Lai *et al.* (2014) suggested that there may be a phylogenetic basis for the relationship between ‘Dairoididae’ and Parthenopidae, given that *Dairoides* is a moderately well-supported sister group of *Daldorfia*, while Wolfe *et al.* (2022) recovered *Dairoides kusei* as sister to Parthenopidae.

In our phylogenetic analysis, based on adult morphological characters, the three species of *Dairoides* (i.e. *D. kusei*, *D. seafdeci* and *D. margaritatus*) are recovered as forming a well-supported clade (crown Dairoidinae) that is sister to a clade formed by species of the genus *Daldorfia* (crown Daldorfiinae), and both Dairoidinae and Daldorfiinae as forming a well-supported clade that is sister to the remainder of the parthenopid genera (Fig. 6). Our results support the conclusion of Lai *et al.* (2014) that *Dairoides* is a sister group to *Daldorfia*. Taxa in the Dairoidinae + Daldorfiinae clade share the possession of a cervical or branchiocardiac groove that reaches the ventral carapace (char. 26-0), the presence of bulges on the protogastric region that are larger than those on the mesogastric region (char. 31-1), the presence of an inter-





**FIG. 4.** CT scan of the holotype of *Phrynombrus sagittalis* sp. nov. (MPZ 2022/761). A–E, carapace in: A, dorsal; B, frontal; C, ventral; D, oblique ventral; E, lateral view; anatomical parts that hinder the view of the cephalothorax have been digitally extracted. F, ventral view with ventral unremoved remains. G–H, epistome in outer and inner view, respectively. I–J, coxa–ischium, of both chelipeds. K, isolated ischium. L–M, right cheliped: L, outer; M, inner surface. N–O, left cheliped: N, inner; O, outer surface. P, oblique anteroventral view, showing the orbit (or.) and the position of the ocular peduncle (o.p.). Q, detail of the ocular peduncle. The holes of the carapace, coxa, ischium and ocular peduncle correspond to mushroom-shaped tubercles, with less contrast. *Abbreviations:* a.s., anterolateral spine; c-i.g., cardiointestineal groove; en., endostome; ep., epistome; ep.s., epibranchial spine (equivalent to lateral angle); g-b.g., gastrobranchial groove; h.n., hepatobranchial notch; h-o.n., hepato-orbital notch; h.s., hepatic spine; i.d., interorbital depression; in.m., inner margin; i.s., inter-antennular spine; i.su., inner surface; L.m., lower margin; o.m., outer margin; o.p., ocular peduncle; or., orbit; p.b., postbranchial spine; p.t., protogastric tubercles; s.g., subhepatic groove; u.su., upper surface. See Appendix S2 for a video of the full model.



**FIG. 5.** 3D artist's reconstruction of *Phrynombrus sagittalis* sp. nov. based on the type material and the CT scan in: A, dorsal; B, ventral; C, frontal; D, posterior; E–F, lateral view. The ambulatory legs and colour pattern are based on the modern genus *Dairoides*. Drawings by Hugo Salais (Metazoa Studio).

antennular spine (char. 41-1), and a cheliped palm that is rhomboidal in transversal section rather than triangular (char. 97-0). In our study, the pointed and triangular front (chars 2, 4), and the presence of an epibranchial region that is larger than the meso- and metabranchial regions (char. 28-1), unite a well-supported monophyletic family, Parthenopoidea.

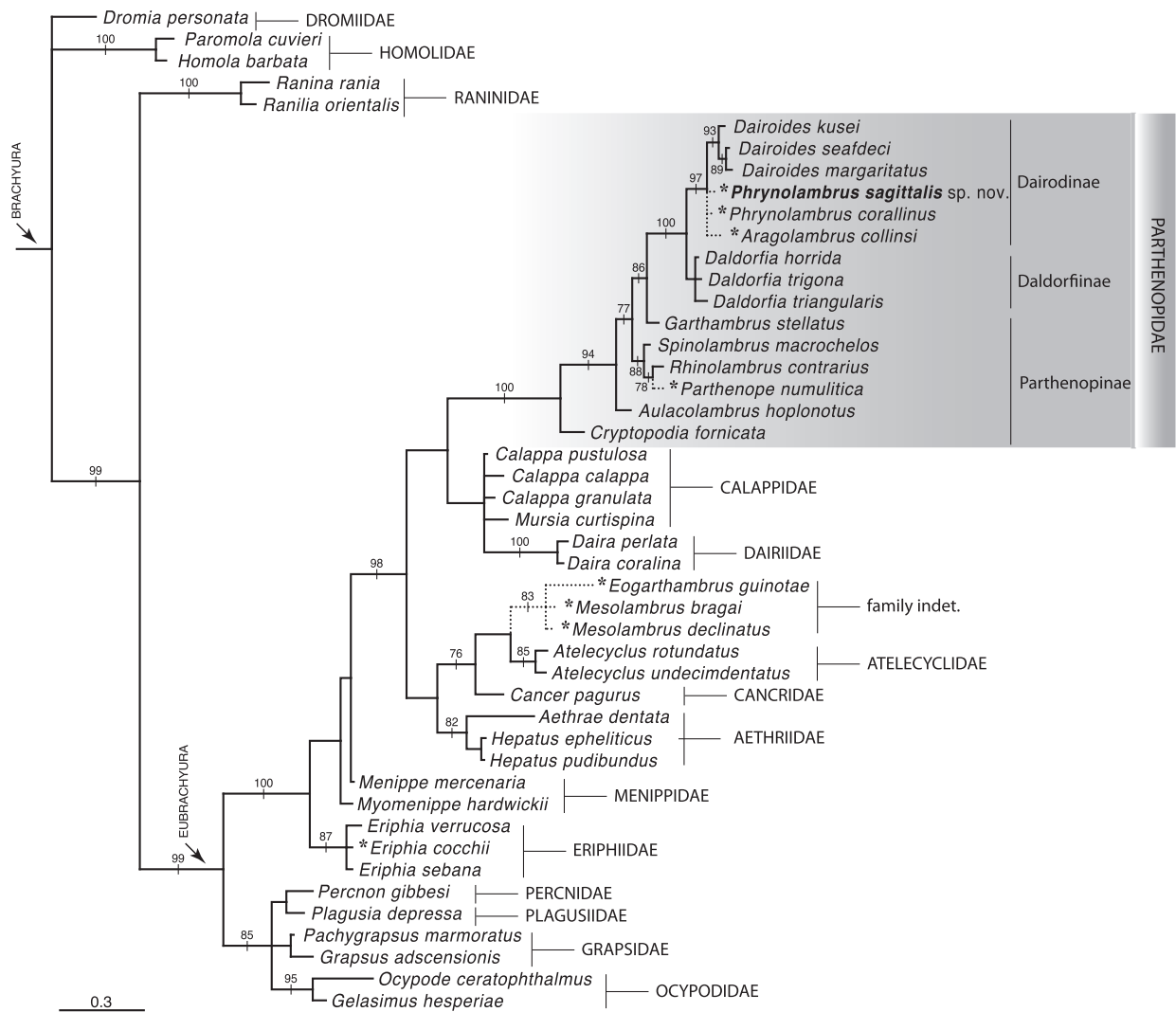
#### *Phrynombrus*, *Dairoidinae* and the origins of *Parthenopoidea*

Our re-evaluation of the anatomy and phylogenetic relationships the extinct genus *Phrynombrus* suggests a close relationship with the also extinct genus *Aragolambrus*, and together with the genus *Dairoides* they form the

monophyletic subfamily Dairoidinae (Fig. 6). *Phrynomalambros* shares with *Dairoides* some diagnostic features, such as: (1) a dorsal surface covered with fused mushroom-like perforate vesicular tubercles, with deep grooves (interorbital, gastrobranchial and cardiointestinal grooves, in dorsal view); (2) a narrow and deflexed front; (3) small, deep, and rounded orbits; (4) the antennular and orbital cavities in communication; (5) strong chelipeds that are not pressed tightly against the anterolateral margin; and (6) the junction between the anterolateral and posterolateral margins (lateral angle) armed with spines (Števcíć, 2001, 2005). The presence of two to three anterolateral spines (char. 14), an ornamented epistomia with one or more rows of tubercles (char. 46), and the pterygostome with grooves (char. 48-1) are synapomorphies

that unite *Phrynomalambros*, *Aragolambros* and *Dairoides* under the subfamily Dairoidinae (Fig. 6).

Not only does the new material from Spain show the morphology of the dorsal carapace but it also provides information on the ventral view of the carapace and the chelipeds. The ventral morphology provides critical information on: (1) the characteristic ornamentation and distribution of tubercles in the pterygostomial region that give rise to grooves and ridges (these characteristic grooves are not observable in any other brachyuran representative with the exception of *Dairoides* and *Aragolambros*); (2) the shape and delimitation of the hepatic spine in the lower margin with a groove; and (3) the cuticle with its mushroom-shaped petaloid tubercles. In addition, the presence of the semi-articulated chelipeds in one



**FIG. 6.** Bayesian majority-rule consensus topology of the post-burn-in sample of trees for selected fossil and extant brachyuran families, including the superfamily Parthenopoidea and *Phrynomalambros sagittalis* sp. nov. Posterior probability support values  $\geq 75\%$  indicated on branches. Terminal taxa indicated by an asterisk (\*); dotted branch lines are extinct.



**FIG. 7.** Reconstruction of *Phrynoslambrus sagittalis* in the lower Priabonian (upper Eocene) benthos of the Pamplona Formation (Huesca province, Spain), on a hypothesized muddy bottom and seagrass meadow. Parts not preserved in the fossil are interpreted by comparison with the closest modern representative. Reconstruction by Hugo Salais (Metazoa Studio).

specimen (MPZ 2022/761) permits observation of their relative size in comparison to the cephalothorax, the type of ornamentation, and the distribution and number of spines that comprise it. All of these conservative characters have not been mentioned in previous works.

*Phrynoslambrus* was originally included in the family Parthenopidae based on dorsal characters that resemble other parthenopids (Bittner 1893), and retained in the same family by subsequent authors (e.g. Lörenthey & Beurlen 1929; Roger 1954; Glaessner 1969; Via 1969; De Angeli & Beschin 2008; Beschin *et al.* 2009). Due to the peculiar cuticular ornamentation, Guinot (1967, 1978, 1979) proposed the possible relationship between *Phrynoslambrus* and the modern genera *Dairoides*, *Daira* De Haan, 1833 and *Actaea* De Haan, 1833. Our results support the phylogenetic proximity between *Phrynoslambrus* and *Dairoides*, but not between *Phrynoslambrus* and Eriphiidae or Dairidae (Fig. 6).

The recognition of *Phrynoslambrus* and *Aragolambrus* as extinct members of Dairoidinae pushes back the origins of the subfamily into the early Eocene, *c.* 48 Ma, and provides a reliable calibration point of the subfamily for molecular phylogenetic studies. This description of *Phrynoslambrus sagittalis* is also the second report of Eocene elbow crabs from the Iberian Peninsula, and it is one of the oldest parthenopid crabs discovered to date, increasing our understanding of the anatomical disparity seen among early parthenopoids during the Palaeogene.

## ECOLOGICAL IMPLICATIONS

Modern parthenopids are usually found at tropical or subtropical latitudes, in the intertidal to deep water zones, and are usually associated with siliciclastic substrates into

which they dig and remain motionless (Tan *et al.* 1999; Tan & Ng 2007a; Ferratges *et al.* 2019 and references therein). Eocene parthenopoids are supposedly represented by 20 species in 14 genera, although some of them need to be revised in the future, given that the phylogenetic results indicate that some are far from Parthenopidea (Fig. 7). In any case, these taxa are mainly known from basins located in the Mediterranean region, associated with different depositional settings. Based on sedimentological data, the Eocene parthenopoids occupied either siliciclastic or carbonate depositional settings, being more abundant in reef environments during the early Eocene (Ferratges *et al.* 2019 and references therein). However, based solely on the information available to date, during the middle and late Eocene this trend appears to have reversed, with higher diversities occurring in siliciclastic depositional settings over shallow platforms (see Ferratges *et al.* 2019).

In contrast, extant dairoidids represent a rare and controversial group (see above), represented by only three species reported from sandy and muddy soft bottoms, front reef and outer reef (at depths of up to 400 m). These taxa are distributed in tropical or subtropical latitudes (i.e. Clarke 1972; Takeda & Ananpongsuk 1991; Padate *et al.* 2020) and, to date, no other representatives are known in the fossil record.

The three species belonging to the extinct genus *Phrynoslambrus* are currently known from reef environments from the upper Eocene of Hungary (Bittner 1893) and Italy (Beschinn *et al.* 2007), and the lower Oligocene of Italy (De Angeli & Beschinn 2008). The palaeoenvironmental reconstruction of the locality herein studied indicates a relatively low energy sedimentary environment dominated by clay sedimentation, with eventual episodes of high energy. Based upon the sedimentological and

palaeoecological data, the studied outcrop can be related to a relatively shallow environment, which suggests that *P. sagittalis* inhabited soft bottoms in siliciclastic environments with bryozoans, small and isolated spherical coral colonies (*Stylocoenia* sp.), and seagrass meadows (Fig. 7). These probably developed in the euphotic zone, above the storm wave base level, at depths that did not exceeded 20–30 m as represented in Figure 7. All of the above seems to suggest a gradual transition from shallow environments inhabited by the oldest taxa, to deeper platform environments, as is seen today for the genus *Dairoides*.

## CONCLUSION

*Phrynombrus sagittalis*, from the upper Eocene of Spain, is the oldest record of fossil crabs of the enigmatic subfamily Dairoidinae. The completeness and exquisite preservation of the new fossil material enabled us to examine aspects of the anatomy of *Phrynombrus* and *Dairoides* (the type and only genus of Dairoidinae previously known) and to place them in a phylogenetic context. We conclude that *Dairoides* is indeed a type of elbow crab, or Parthenopoidea, rather than a type of stone crab, superfamily Eriphioidea, to which it is only superficially similar due to convergence.

The recognition of *Phrynombrus* as sister group to *Dairoides* pushes back the origins of the subfamily Dairoidinae more than 48 myr into at least the early Eocene and provides a reliable calibration point of the subfamily for molecular phylogenetic studies. This description of the new species is also the second report of Eocene elbow crabs from the Iberian Peninsula, and it is one of the oldest parthenopid crabs discovered to date.

Our results: (1) expand our understanding of the stratigraphic and palaeobiogeographic distribution of Palaeogene elbow crabs; (2) highlight the Eocene as a time of rapid evolution of higher eubrachyuran groups; and (3) shed light on the early origins, anatomical diversity and systematic affinities of ancient Parthenopoidea, one of the most emblematic and anatomically distinctive groups of true crabs. Understanding the anatomical diversity or disparity of Palaeogene eubrachyurans is pivotal to disentangle the systematic relationships of several of the main crown families, and to investigate spatio-temporal patterns leading to the evolution of modern faunas.

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**Author contributions.** SZ, FAF and JL designed the study. JLD helped to collect the fossil specimens. FAF prepared the specimens. FAF and SZ processed the CT scans. FAF and JL constructed the dataset and performed the phylogenetic analysis. All authors described and interpreted the specimens. FAF and JL prepared the figures. FAF, SZ and JL, wrote the manuscript with input from JLD, AO and MA.

## DATA ARCHIVING STATEMENT

This published work, and the nomenclatural act it contains, have been registered with ZooBank (<https://zoobank.org/References/2DE8DFF9-92E1-4AF6-88A7-3114EF46A5D2>). The phylogenetic data matrix is available in MorphoBank (<http://morphobank.org/permalink/?P4528>). CT scan data for the specimen are available in MorphoSource (see Appendix S2 for a list of DOIs).

**Editor.** Imran Rahman

## SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1002/spp2.1494>):

**Appendix S1.** List of characters for the phylogenetic analysis.

**Appendix S2.** List of DOIs for associated MorphoSource records.

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