Spider crabs (Decapoda: Brachyura: Majoidea) from the upper Eocene of south Pyrenees (Huesca, Spain)

Fernando A. Ferratges, Josep Lluis Domínguez, Àlex Ossó, and Samuel Zamora

ABSTRACT

Majoidea are one of the most plesiomorphic clades of Eubrachyura and display a huge diversity in modern ecosystems. We describe one new fossil genus and three new species including *Eoparanaxia eocenica* n. gen. n. sp., *Planobranchia elongata* n. sp., *Spinorstrimaia echinata* n. sp.; and one indeterminate species tentatively assigned to *Macrocheira* sp. from the Pamplona Marls Formation (upper Eocene, southern Pyrenees, Spain). All of them are new or first reported from the Iberian Peninsula. This shows a highly diversified fauna associated with prodelta clays that favoured preservation of decapods and other invertebrates. Cluster analyses based on Jaccard and Raup-Crick coefficients of Eocene Majidae suggest close affinities of Iberia with other European basins.

Keywords: benthic; biodiversity; crustaceans; new genus; new species; marine; taxonomy; palaeoecology.
INTRODUCTION

The superfamily Majoidea Samouelle, 1819, is considered as monophyletic according to molecular studies (i.e., Spears et al., 1992; Porter et al., 2005; Hultgren and Stachowicz, 2008; Tsang et al., 2014), larval development (i.e., Rice, 1980, 1983; Clark and Ng, 2004), and morphological studies (Brösing et al. 2007; Ng et al., 2008; Guinot and Wicksten, 2015). This group is generally represented by species with a characteristic morphology, including elongated and pyriform carapace and bifid front, and hooked setae (i.e., Davie et al., 2015). Majoidea comprises about 1000 species and more than 200 genera (i.e., Ng et al., 2008; De Grave et al., 2009). From a molecular point of view, this clade is considered one of the most plesiomorphic crabs within Eubrachyura de Saint Laurent, 1980 with an origin in the Jurassic (Porter et al., 2005, Crandall et al., 2009; Guinot, 2019 and references therein; Wolfe et al., 2019, 2022).

The fossil record does not match molecular estimates and the oldest considered fossil Majoidea correspond to species from the mid-Cretaceous of Europe (Breton, 2009; Klompmaker, 2013) and Mexico (Vega et al., 2019). There are more than 125 majoid species known in the fossil record (De Grave et al., 2009; Schweitzer et al., 2010), from which 47 have been found in the Eocene (see Table 1). Based on fossils some authors suggested that spider crabs diversified in the Miocene (Klompmaker et al., 2015). The aim of this paper is to describe a high diversified assemblage of spider crabs coming from a single formation in the late Eocene of the Pyrenees. This will serve as a basis to analyse the diversity of spider crabs in the Eocene and possible paleobiogeographic relationships of Iberia with other areas.

GEOLOGICAL SETTING

The studied material was collected from the Pamplona Marls Formation (Puigdefàbregas, 1975) in the Jaca-Pamplona Basin. This basin corresponds to an elongated basin from east to west in the south-central Pyrenean Zone (Figure 1) and was formed as a result of the southward propagation of the tectonic structures during the Paleogene (Millán et al., 1994; Muñoz et al., 1994; Castelltort et al., 2003; Huyghe et al., 2009).

The propagation fold and thrust belt of the southern Pyrenean resulted in the formation of a coeval relief, acting as a sediment source area for deltaic complexes (e.g., Dreyer et al., 1999). These deltaic complexes prograded progressively westwards, covering the turbiditic systems of the lower and middle Eocene of the Hecho Group (i.e., Mutti et al., 1985; Remacha et al., 2005). These middle and upper Eocene units form a c. 2 km thick succession, in which diverse environments were developed, including shallow-marine limestones of the Guara Formation, prodelta/outer ramp marls/clays of the Pamplona Marls Formation, deltaic Belsue-Atares Formation and the fluvial Campo-darbe Formation (Puigdefàbregas, 1975; Silva-Casal et al., 2019).

Decapod crustaceans studied in the present study come from lower Priabonian strata and were collected near the village of Fanlillo (Figure 1), in the municipality of Yebrá de Basa (province of Huesca, Spain). This outcrop shows a great abundance and diversity of small benthic invertebrates including gastropods, bivalves, bryozoans, foraminifera, and decapod crustaceans (Artal et al., 2013; Ossó et al., 2014; Domínguez and Ossó, 2016; Ossó and Domínguez, 2017; Ossó et al., 2020; Ferratges et al., 2023).

MATERIALS AND METHODS

The data presented here is based on the analysis of fossil specimens collected from the outcrop exposed in the road cut N-260 near the village of Fanlillo (42°28′30″N, 0°13′35″W, see Figure 1). Additionally, two specimens are included from a laterally equivalent outcrop (42°29′02″N, 0°15′13″W, see Figure 1), located west of Fanlillo (MPZ 2023/3 and MPZ 2023/4). The studied material comprises 22 specimens, represented by isolated carapaces and one specimen with one cheliped and partial thoracic sternum preserved. These specimens belong to four genera, represented by four species, from which three are new. Specimens are preserved in marls and are extremely delicate; this prevents the use of mechanical tools. For this reason, material was prepared manually with a needle, under a binocular magnifying microscope and, eventually with the help of a wet brush. During the process it was necessary to apply a 15 percent solution of Paraloid B-72 and acetone.

The specimens were then photographed dry and 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. Specimens were legally sampled under permit EXP: 032/2018 from the Servicio de Prevención, Protección e Investigación del Patrimonio Cultural...
TABLE 1. Diversity and distribution of described Majoids from the Eocene.

<table>
<thead>
<tr>
<th>Family</th>
<th>Sub-family</th>
<th>Genera</th>
<th>species</th>
<th>stage</th>
<th>country</th>
<th>Lithology</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Bolcapisa</strong></td>
<td>MacLeay, 1838</td>
<td><strong>B. giulianae</strong> Beschin, Busulini, Tessier and Zorzin, 2016</td>
<td><strong>B. giulianae</strong> Beschin, Busulini, Tessier and Zorzin, 2016</td>
<td>Ypresian</td>
<td>Italy</td>
<td>reef</td>
</tr>
<tr>
<td><strong>Eoinachoides</strong></td>
<td>Van Straelen, 1933</td>
<td><strong>E. senni</strong> Van Straelen, 1933</td>
<td><strong>E. senni</strong> Van Straelen, 1933</td>
<td>middle/late (Bartonian–Priabonian?)</td>
<td>Venezuela</td>
<td></td>
</tr>
<tr>
<td><strong>P. elongata</strong></td>
<td>Feldmann, Schweitzer, Bennett, Fransescu, Resar and Trudeau, 2011</td>
<td><strong>P. elongata</strong> n. sp.</td>
<td>Lutetian–Priabonian</td>
<td>Egypt</td>
<td>Siliciclastic</td>
<td></td>
</tr>
<tr>
<td><strong>P. laevis</strong></td>
<td>Feldmann, Schweitzer, Bennett, Fransescu, Resar and Trudeau, 2000</td>
<td><strong>P. laevis</strong></td>
<td>Lutetian–Priabonian</td>
<td>Egypt</td>
<td>Siliciclastic</td>
<td></td>
</tr>
<tr>
<td><strong>P. palmuelleri</strong></td>
<td>Artal, van Bakel and Onetti, 2014</td>
<td><strong>P. palmuelleri</strong></td>
<td>Lutetian</td>
<td>Spain</td>
<td>Siliciclastic</td>
<td></td>
</tr>
<tr>
<td><strong>P. simplex</strong></td>
<td>(Remy in Gorodiski and Remy, 1959)</td>
<td><strong>P. simplex</strong></td>
<td>Lutetian</td>
<td>Spain</td>
<td>Siliciclastic</td>
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<td>Beschin, De Angeli, Checchi and Zarantonello, 2005</td>
<td><strong>P. dallagoi</strong> Beschin, De Angeli, Checchi and Zarantonello, 2005</td>
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<td>Italy</td>
<td>Siliciclastic</td>
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<tr>
<td><strong>P. dalloni</strong></td>
<td>Via, 1959</td>
<td><strong>P. dalloni</strong></td>
<td>Lutetian</td>
<td>Spain</td>
<td>Siliciclastic/marls</td>
<td></td>
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<tr>
<td><strong>P. horridus</strong></td>
<td>Bittner, 1875</td>
<td><strong>P. horridus</strong></td>
<td>Lutetian–Priabonian</td>
<td>UK, Hungary, Spain, Italy</td>
<td>Siliciclastic</td>
<td></td>
</tr>
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<td><strong>P. ramosus</strong></td>
<td>Artal and Castillo, 2005</td>
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<td>Lutetian</td>
<td>Spain</td>
<td>Siliciclastic</td>
<td></td>
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<td><strong>P. tetracornis</strong></td>
<td>Ferratges, Ortega, Fernández, Moreno and Maza, 2014</td>
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<td>Spain</td>
<td>Siliciclastic</td>
<td></td>
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<tr>
<td><strong>Eoparanaxia</strong></td>
<td>n. gen.</td>
<td><strong>E. eocenica</strong> n. sp.</td>
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<td>Spain</td>
<td>Prodelta environment (siliciclastic)</td>
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<td>Cecon and De Angeli, 2018</td>
<td><strong>L. bolcense</strong> Cecon and De Angeli, 2018</td>
<td>Ypresian</td>
<td>Italy</td>
<td>reef</td>
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<td><strong>R. cf. hystrix</strong></td>
<td>Milne-Edwards, 1875</td>
<td><strong>R. cf. hystrix</strong></td>
<td>Lutetian</td>
<td>Argentina</td>
<td>Siliciclastic</td>
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<td><strong>H. antiquus</strong></td>
<td>White, 1847</td>
<td><strong>H. antiquus</strong> Beschin, Busulini and Tessier, 2018</td>
<td>Priabonian</td>
<td>Italy</td>
<td>reef</td>
<td></td>
</tr>
<tr>
<td><strong>G. vicariottoi</strong></td>
<td>Beschin, De Angeli, Checchi and Zarantonello, 2012</td>
<td><strong>G. vicariottoi</strong> Beschin, De Angeli, Checchi and Zarantonello, 2012</td>
<td>Lutetian</td>
<td>Italy</td>
<td>Siliciclastic (volcanic material)</td>
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<td><strong>Inachidae</strong></td>
<td>MacLeay, 1838</td>
<td><strong>Inachus</strong> Weber, 1795</td>
<td><strong>I. eocenicus</strong> Beschin, Busulini and Tessier, 2018</td>
<td>Priabonian</td>
<td>Italy</td>
<td>reef</td>
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<tr>
<td><strong>Pyromaja</strong></td>
<td>Stimpson, 1871</td>
<td><strong>P. inflata</strong> Collins and Morris, 1978</td>
<td>Ypresian</td>
<td>Pakistan</td>
<td>Siliciclastic</td>
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TABLE 1 (continued).

<table>
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<th>Family</th>
<th>Sub-family</th>
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<th>species</th>
<th>stage</th>
<th>country</th>
<th>Lithology</th>
</tr>
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<tbody>
<tr>
<td>Doubtfully placed within</td>
<td>Inachiodidae</td>
<td>Nachioides Beschin,</td>
<td><em>N. tuberculatus</em> Beschin, Busulini and Tessier, 2019</td>
<td>Priabonian</td>
<td>Italy</td>
<td>reef</td>
</tr>
<tr>
<td>Doubtfully placed within</td>
<td>Dana, 1851</td>
<td>Busulini and Tessier, 2019</td>
<td>P. scaber Beschin, Busulini and Tessier, 2019</td>
<td>Priabonian</td>
<td>Italy</td>
<td>reef</td>
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<tr>
<td>FAMILY</td>
<td>Macrocheiridae</td>
<td>Vicetiulita De Angeli and Ceccon, 2015</td>
<td><em>V. granulata</em> De Angeli and Cecon, 2015</td>
<td>Ypresian</td>
<td>Italy</td>
<td>reef</td>
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<tr>
<td>M. teglandi Rathbun, 1926</td>
<td>Macrhoëira de Haan, 1839</td>
<td><em>C. meneguzzoi</em> Beschin, Busulini, De Angeli and Tessier, 1985</td>
<td>Lutetian–Priabonian</td>
<td>Italy</td>
<td>Silicidastic</td>
<td></td>
</tr>
<tr>
<td>Micrornaia Bittner, 1875</td>
<td>Majinae Samouelle, 1819</td>
<td><em>C. elegans</em> (Beschin, Busulini, De Angeli and Tessier, 1985)</td>
<td>Lutetian–Bartonian</td>
<td>Italy</td>
<td>Silicidastic (vulcanodetritic)</td>
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<tr>
<td>Leptomithrax Miers, 1876</td>
<td>Majinae Samouelle, 1819</td>
<td><em>L. griffini</em> Feldmann and Maxwell, 1990</td>
<td>Priabonian?</td>
<td>New Zealand</td>
<td>Silicidastic</td>
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<td>Majinae Samouelle, 1819</td>
<td>M. batalleri Via, 1959</td>
<td>Lutetian–Priabonian</td>
<td>Spain, Hungary</td>
<td>Reef and silicidastic</td>
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<td>Majinae Samouelle, 1819</td>
<td>M. elegans Beschin, Busulini, De Angeli and Tessier, 1985</td>
<td>Lutetian–Bartonian</td>
<td>Italy</td>
<td>Silicidastic</td>
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<tr>
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<td>Majinae Samouelle, 1819</td>
<td>M. mainensis Beschin, Busulini, De Angeli and Tessier, 1985</td>
<td>Lutetian–Bartonian</td>
<td>Italy</td>
<td>Silicidastic</td>
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<tr>
<td>Micromaia Bittner, 1875</td>
<td>Majinae Samouelle, 1819</td>
<td>M. meneguzzoi Beschin Busulini, De Angeli and Tessier, 1985</td>
<td>Lutetian–Bartonian</td>
<td>Italy</td>
<td>silicidastic</td>
<td></td>
</tr>
<tr>
<td>Micromaia Bittner, 1875</td>
<td>Majinae Samouelle, 1819</td>
<td>M. tuberculata Bittner, 1875</td>
<td>Lutetian–Bartonian</td>
<td>Italy, UK and Spain</td>
<td>Silicidastic</td>
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<tr>
<td>Micromaia Bittner, 1875</td>
<td>Majinae Samouelle, 1819</td>
<td>M. soavensis Beschin, Busulini and Tessier, 2010</td>
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<td>Italy</td>
<td>Silicidastic</td>
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<td>Micrornaia Bittner, 1875</td>
<td>Majinae Samouelle, 1819</td>
<td>M. margantifera Beschin, Busulini, De Angeli and Tessier, 1994</td>
<td>Lutetian</td>
<td>Italy</td>
<td>Silicidastic</td>
<td></td>
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<td>Micrornaia Bittner, 1875</td>
<td>Majinae Samouelle, 1819</td>
<td>M. libinioides Bell, 1858</td>
<td>Lutetian</td>
<td>Italy</td>
<td>Silicidastic</td>
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<tr>
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<td>Majinae Samouelle, 1819</td>
<td>M. lovatoi Beschin, De Angeli, Checchi and Zarantonello, 2016</td>
<td>Lutetian</td>
<td>Italy</td>
<td>Silicidastic</td>
<td></td>
</tr>
<tr>
<td>Micrornaia Bittner, 1875</td>
<td>Majinae Samouelle, 1819</td>
<td>M. oppioni Larghi, 2002</td>
<td>Lutetian</td>
<td>Italy, Spain</td>
<td>Silicidastic</td>
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<tr>
<td>Micrornaia Bittner, 1875</td>
<td>Majinae Samouelle, 1819</td>
<td>M. hollandi Förster and Mundlos, 1982</td>
<td>Lutetian</td>
<td>Germany</td>
<td>Silicidastic</td>
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<tr>
<td>Micrornaia Bittner, 1875</td>
<td>Majinae Samouelle, 1819</td>
<td>M. simplex (Müller and Collins, 1991)</td>
<td>Priabonian</td>
<td>Hungary</td>
<td>reef</td>
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<tr>
<td>Ommaciria Beschin, De Angeli, Checchi and Zarantonello, 2012</td>
<td>O. mainensis Beschin, Busulini, De Angeli and Tessier, 1985</td>
<td>Lutetian</td>
<td>Italy</td>
<td>Silicidastic</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
(Gobierno de Aragón) and are deposited in the palaeontological collection of the Museo de Ciencias Naturales de la Universidad de Zaragoza under the acronym MPZ.

To analyse the degree of similarity between the different areas that have provided Eocene spider crabs (Majoidea), the Jaccard and Raup-Crick Coefficients have been analysed (following Cascales-Miñana, 2010). This probabilistic statistic shows the confidence level associated with a one-sided randomization test for each pair of time units (Maridet et al., 2007). For detailed absolute ages and information about the time units see Table 2 (absolute ages have been taken from Cohen et al., 2013). The presence/absence of each genus in each area/period is summarized in Table 3. The presence and absence of the different genera is summarized in Tables 4 and 5.

Similarity coefficients were clustered using the UPGMA algorithm, because this method shows the best cophenetic correlation values regardless of the similarity measures used (Table 6). The results are illustrated using dendrograms. The grouping was stratigraphically restricted (Ypresian-Lutetian and Bartonian-Priabonian). Although this might impose a default pattern on the output, bootstrapping reveals that a stratigraphically constrained cluster analysis provides a stronger reflection of the data structure than an unrestricted cluster. Analyses were performed using the PAST software package (Hammer et al., 2001).

**SYSTEMATIC PALAEONTOLOGY**

Relationships between families of Majoidea are strongly discussed in recent years (see Guinot and Van Bakel, 2020). Higher ranks systematic placement follows Guinot (2019), Guinot and Van Bakel (2020), and Guinot et al. (2022). Morphological terminology of Majidae follows Griffin (1966), Griffin and Tranter (1986), and Davie et al. (2015). Carapace measurements are given as carapace width (CW), carapace length (CL), and postrostral carapace length (PCL) in millimetres. The carapace width was measured in the widest part of the branchial region, carapace length was measured from the rostral apices to the posterior margin of the carapace, and postrostral carapace length was...
FIGURE 1. Simplified geological map of the Southern Central Pyrenees with location of the outcrops that provide the studied material (red stars near to Fanilillo). The star located to the east of Fanilillo corresponds to the main studied outcrop.

TABLE 2. Temporal range of the analysis of Eocene Majoids, time units and abbreviations. Absolute ages from Cohen et al. (2013).

<table>
<thead>
<tr>
<th>Time Units</th>
<th>Abbreviation</th>
<th>Ages (Myr)</th>
<th>Time interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ypresian</td>
<td>Y</td>
<td>56, 47.8</td>
<td>8.2</td>
</tr>
<tr>
<td>Lutetian</td>
<td>L</td>
<td>47.8, 41.2</td>
<td>6.6</td>
</tr>
<tr>
<td>Bartonian</td>
<td>B</td>
<td>41.2, 37.8</td>
<td>3.4</td>
</tr>
<tr>
<td>Priabonian</td>
<td>P</td>
<td>37.8, 33.9</td>
<td>3.9</td>
</tr>
</tbody>
</table>

measured from the base of the rostral spines to the posterior margin of the carapace (Figure 2).

Superfamily MAJOIDEA Samouelle, 1819
Family EPAIALTIDAE MacLeay, 1838
Subfamily PISINAES Dana, 1851
Genus EOPARANAXIA n. gen.
Figure 3
zoobank.org/07B9F785-4E4A-4018-9D7B-50B3576421F4
Type species. *Eoparanaxia eocenica* n. gen. n. sp. by monotypy and present designation. Gender feminine.

Diagnosis. Carapace pyriform, longer than wide; rostrum axially sulcate, with two fused, long pseudorostral spines, length 0.53 times CW. Hepatic region with small spine, directed anterolaterally. Intestinal tubercle strong, protruding beyond posterior carapace margin; carapace regions well defined with metagastric and urogastric regions narrower than mesogastric and cardiac regions; mesobranchial region with posteriorly directed large spine. Dorsal regions armed with long spines.

Etymology. The generic name derives from the prefix *Eo-* (from ηός (gr.)= aurora), to generically indicate an ancestral form, in arbitrary combination with the generic name *Paranaxia* Rathbun, 1924, to refer to its morphological affinities with the new genus.

Remarks. The material herein described is referred to the subfamily Pisinae Dana, 1851. Species of this subfamily possess elongated carapaces; elongated pseudorostral spines; orbits

### TABLE 3. Matrix showing the presence/absence of the different spider crabs genera recognized during the Eocene.

<table>
<thead>
<tr>
<th></th>
<th>Bolcapisa</th>
<th>Edmachioides</th>
<th>Planobranchia</th>
<th>Perviculoides</th>
<th>Eoparanaxia</th>
<th>Lessiniamathia</th>
<th>Periacanthus</th>
<th>Grimaldiana</th>
<th>Hapalinacea</th>
<th>Inachus</th>
<th>Pyromaja</th>
<th>Macchioides</th>
<th>Nacchioides</th>
<th>Paronachoides</th>
<th>Mammaliax</th>
<th>Crumenipeda</th>
<th>Micromegalax</th>
<th>Leptomithrax</th>
<th>Cryptomithrax</th>
<th>Notomithrax</th>
<th>Omachira</th>
<th>Omachiranida</th>
<th>Oxypodina</th>
<th>Pisimaja</th>
<th>Spinirostrimaja</th>
<th>Tumidomaja</th>
<th>Wilsonimaja</th>
<th>Micippida</th>
<th>Stenocirriga</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spain</td>
<td>1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0</td>
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always with postorbital spine or lobe, usually cupped, sometimes with antorbital spine; carapace triangular, sometimes with posterior spine (see Schweitzer et al., 2020). The new genus possesses all these characteristics and is therefore referred to this subfamily.

The new genus Eoparanaxia has similarities with Paranaxia, in the general outline of the carapace, showing a very elongated pseudorostral spines, parallel and distally bifid, slightly differentiated dorsal regions, with aligned spines in the dorsal part of the mesobranchial region, and well developed mesobranchial and intestinal spines (i.e., Windsor and Felder, 2014), sometimes beyond posterior carapace margin (see Rathbun, 1924, and Hosie and Hara, 2016, p. 128, figure 2; p. 129, figure 3).

However, Paranaxia presents the pseudorostral spines separated from their base, a supraorbital eave with a pronounced spine at the preorbital lobe, postorbital angle with a spine separated from the anterior lobe by a notch. In addition, Eoparanaxia n. gen. exhibits a postorbital spine between
the gastric region and the hepatic region, which is not present in *Paranaxia*.

The studied material has similar characteristics with the modern genus *Sphenocarcinus* A. Milne-Edwards, 1875, *Oxypleurodon* Miers, 1885, and *Rhinocarcinus* de Forges and Ng, 2009, including the shape of the rostrum with two long and coalescent cylindrical spines with slightly diverging sharp tips, and the shape and location of the orbits. However, *Eoparanaxia* n. gen. shows a different distribution of dorsal regions, with shallower dorsal grooves than in *Sphenocarcinus*, *Oxypleurodon*, and *Rhinocarciinus*: intestinal region with a prominent conical spine unlike in *Sphenocarcinus*, *Oxypleurodon*, and *Rhinocarcinus*, which lack such conical expansion; sinuous posterior margin; longitudinal antennal pits, parallel to the axis of the body unlike in the other three genera, which are oblique.

### TABLE 4. Presence absence of the different genera during the Ypresian-Lutetian.

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### TABLE 5. Presence absence of the different genera during the Bartonian-Priabonian.

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### TABLE 6. Cophenetic correlation values (r) of the several algorithms employed. Y-L and B-P refer to the abbreviations employed in Table 2.

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<tr>
<th>Algorithm</th>
<th>Jaccard</th>
<th>Raup-Crick</th>
<th>Euclidean distance</th>
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<td>Unweighted Pair-Group Mean Average (Y-L)</td>
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<td>Single Linkage Clustering Algorithm (Y-L)</td>
<td>0,8967</td>
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<tr>
<td>Ward’s Method (Y-L)</td>
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<td>Unweighted Pair-Group Mean Average (B-P)</td>
<td>0,9385</td>
<td>0,7489</td>
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<td>Single Linkage Clustering Algorithm (B-P)</td>
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<td>Ward’s Method (B-P)</td>
<td>0,7524</td>
<td>0,6468</td>
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the gastric region and the hepatic region, which is not present in *Paranaxia*.

The studied material has similar characteristics with the modern genus *Sphenocarcinus* A. Milne-Edwards, 1875, *Oxypleurodon* Miers, 1885, and *Rhinocarcinus* de Forges and Ng, 2009, including the shape of the rostrum with two long and coalescent cylindrical spines with slightly diverging sharp tips, and the shape and location of the orbits. However, *Eoparanaxia* n. gen. shows a different distribution of dorsal regions, with shallower dorsal grooves than in *Sphenocarcinus*, *Oxypleurodon*, and *Rhinocarcinus*; intestinal region with a prominent conical spine unlike in *Sphenocarci-

nus*, *Oxypleurodon*, and *Rhinocarcinus*, which lack such conical expansion; sinuous posterior margin; longitudinal antennal pits, parallel to the axis of the body unlike in the other three genera, which are oblique.
The modern genera *Pisa* Leach, 1815, *Leptopisa* Stimpson, 1871 (both included in Pisinae Dana, 1851), and *Oregonia* Dana, 1851 (Oregoniidae Garth, 1958) also show similarities with the new genus in the shape of the rostrum and orbits (i.e., Zariquiey-Álvarez, 1968; p.449, figure 151; Carmona-Suárez and Poupin, 2016, p. 369, figure 5). However, the shape and distribution of dorsal regions, posterior margin, dorsal surface with elevated regions, without spines, are clearly different in the modern genus. Furthermore, *Eoparanaxia* n. gen. presents the pseudorostrum fused throughout its length, only diverging at the tip, (while in the three mentioned taxa it separates from the base); presents a strong and long intestinal spine, a long branchial spines and spiny ridges on the dorsal surface (of which are absent in the three taxa). In addition, *Pisa* has anterolateral margins generally straight or slightly concave, with fewer or without spines and lacks the strong and prominent spine in the intestinal region that the new genus possesses.

Other modern genera, *Rochinia* A. Milne-Edwards, 1875, *Scyramathia* A. Milne-Edwards, 1880, *Minyorhyncha* Tavares and Santana, 2018, and *Anamathia* Smith, 1885 share with the new genus the general outline of the carapace, distribution of spines in the posterolateral and posterior margins, especially in juvenile stages (see Tavares and Santana, 2018; p. 206-214, figures 1-9). However, all these genera have clearly separated and divergent pseudorostral spines unlike in *Eoparanaxia* n. gen., which presents parallel and fused spines. Some species of *Doclea* Leach, 1815, show similarities with the new genus, for instance a fused bilobed pseudorostrum only diverging at the tip, a long and acute intestinal spine, a row of axial spines, oblique carinae, parallelling anterolateral margin, and also in the branchial regions. However, the modern genus *Doclea* differs from *Eoparanaxia* n. gen. in having a shorter pseudorostrum, a notch in the supraorbital eave, and mostly rounded or less elongated outline.

The material studied here also shows a certain resemblance to some representatives of Inachoididae Dana, 1851, in view of the general outline of the carapace (see Santana, 2008; Lima et al., 2022). However, Inachoididae have usually a shorter pseudorostral spine, strongly fused, and

---

generally ended in a single tip, concave posterior margin, and less spinose/tuberculate dorsal surface.

_Eoparanaxia eocenica_ n. sp.

Figures 3 and 4

zoobank.org/1AAD44D5-0D9C-4642-8FC2-85193465EFDF

**Type material.** Holotype (MPZ 2023/1), a near-complete carapace, partially decorticated. Paratypes (MPZ 2023/2 and MPZ 2023/3) that correspond to one rostrum and half of a posterior carapace.

**Diagnosis.** As for the genus, by monotypy.

**Description.** Carapace pyriform, longer than wide, with spines and conical tubercles; pseudorostral spines parallel and fused, distally bifid, 0.53 times CW, with a row of aligned granules on each spine; orbits not well preserved, small, rounded, obliquely directed. Regions well defined by shallow grooves and deep branchiocardiac groove, with spaced and large spines at the top of the dorsal regions. Gastric region prominent, slightly higher than other regions, with pointed tubercles distributed in anterior gastric region, becoming long gastric spines on the axis of the carapace; urogastric region more depressed. Hepatic region slightly swollen, with one acute stout spine directed anterolaterally. Branchial regions inflated; epibranchial region inflated; mesobranchial region crossed by oblique ridge with five tubercles/spines. Cardiac region elevated, with two tubercles in the anterior part and one in the posterior margin. Intestinal tubercle large, protruding beyond posterior margin of carapace, conical, apex pointed.

Anterolateral margin slightly sinuous. Posterolateral margin convex, with a long spine laterally directed obliquely. Posterolateral and posterior margin rimmed.

**Etymology.** The specific name refers to the Eocene.

**Remarks.** Some species of the genus _Paranaxia_ like _P. keessingi_ Hosie and Hara, 2016, and _P. serpullifera_ (Guérin, 1832, in Guérin-Méneville 1829-1837) show similarities with the material studied here. Nevertheless, these taxa have unfused pseudorostral spines, clearly divergent. The new taxon bears some similarities with _Macrocheira longirostra_ Schweitzer and Feldmann, 1999, with a similar outline of the carapace, bifid rostrum, very long pseudorostral spines fused at the base, and divergent at the tip. However, _M. longirostra_ show some differences: 1) lacks spines at the posterolateral margins; 2) has a posterior margin almost straight without intestinal spine; and 3) a dorsal surface much more tuberculated than the new taxon.

**Remarks.** The studied specimen can be assigned to _Planobranchia_ Schweitzer and Feldmann, 2010, because it shares the diagnostic characteristics of the genus (see Schweitzer and Feldmann, 2010) like: 1) the moderately vaulted transversely and longitudinally pyriform carapace; 2) weakly differentiated gastric regions, defined laterally by prominent V-shaped groove converging from anterior margin of orbits to urogastric region; 3) hexagonal to ovoid cardiac region, bearing two nodes on medial transverse ridge; 4) strongly inflated epi-branchial and mesobranchial regions, separated from one another by subtle arcuate attachment scar expressed on mold of the interior of the carapace; widest part of these regions converge as angular projections toward urogastric region. Metabranchial region extends from widest part of cardiac region posterolaterally around posterior margin of metabranchial region and clearly defined axially by posterior margin of cardiac region and intestinal region; depressed below other regions. Surface of carapace weakly ornamented by fine granules or pits; lacking strong tubercles, posterior margin convex, rimmed (new additions to the original diagnosis of Schweitzer and Feldmann, 2010).


**Fossil included species.** _Planobranchia egyptensis_ Feldmann, Schweitzer, Bennett, Franţescu, Resar, and Trudeau, 2011; _P. elongata_ n. sp. (herein); _P. laevis_ (Lörnethy, 1909); _P. pulchelli_ Artal, Van Bakel, and Onetti, 2014; _P. simplex_ (Remy in Gorodiski and Remy, 1959).

**Emended diagnosis.** Carapace pyriform, widest at midlength of branchial region; moderately vaulted transversely and longitudinally, front produced, singular, sulcate longitudinally. Orbits small, laterally situated, with strong and subtriangular orbital spines. Gastric regions only weakly differentiated; defined laterally by prominent V-shaped groove converging from anterior margin of orbits to urogastric region, the narrowest part of axial regions. Cardiac region nearly as wide as widest part of gastric regions, hexagonal to ovoid in outline; bearing two nodes on medial transverse ridge. Intestinal region well defined, long, approximately as wide as urogastric region. Epibranchial and mesobranchial regions strongly inflated, separated from one another by subtle arcuate attachment scar expressed on mold of the interior of the carapace; widest part of these regions converge as angular projections toward urogastric region. Meta-branchial region extends from widest part of cardiac region posterolaterally around posterior margin of metabranchial region and clearly defined axially by posterior margin of cardiac region and intestinal region; depressed below other regions. Surface of carapace weakly ornamented by fine granules or pits; lacking strong tubercles, posterior margin convex, rimmed (new additions to the original diagnosis of Schweitzer and Feldmann, 2010).
Some authors assigned Planobranchia to the subfamily Majinae (Schweitzer and Feldmann, 2010; Feldmann et al., 2011; and Schweitzer et al., 2020), and justify this inclusion by the supraorbital margin with an “eave orbital” and a postorbital spine. Subsequently, Artal et al. (2014) proposed to include the genus Planobranchia in Inachidae, justifying its inclusion by similarities in the frontal and orbital construction. Nevertheless, due to the bad preservation, specifically of the pseudorostrum and part of the supraorbital margin, Artal et al. (2014) have misinterpreted the fronto-orbital conforma-
FIGURE 4. Idealized reconstruction of *Eoparanaxia eocenica* n. gen. n. sp. carapace.
tion and the anterolateral spines. Due to the lack of
the anterior part of the pseudorostrum spines,
these authors have suggested that Planobranchia
could have a short pseudorostrum like many ina-
chids, placing the orbits laterally on the sides of the
pseudorostrum. Also, the antorbital spine has been
interpreted as the postorbital spine, and the two fol-
lowing spines (intercalated spine and postorbital
spine) as anterolateral spines. Instead, Planobran-
chia has a rather elongated rostrum and an orbital
construction consisting of three spines.

The characteristics of the new material and
the reanalysis of previously known taxa suggest
that this genus has more affinity with the subfamily
Pisinae, so its inclusion in this group is suggested
here. Placement in Pisinae is supported by the
morphology of the carapace outline, the distribution
and shape of the dorsal regions, supraorbital mar-
gin formed by a prominent antorbital spine, a small
intercalated spine, and a well-developed postor-
bital spine; axial regions separated from the periph-
ery by deep grooves; hepatic lobe marked by a
lump or spine; highly developed branchial regions;
thickened cardiac region; mesogastric region in
which a prominent lump stands out (see Griffin and
Tranter, 1986, Schweitzer et al., 2020).

Planobranchia elongata n. sp.

Figures 5 A-B and 6

zoobank.org/8FE98FE3-0E49-4C45-A30A-73324B9512B3

Type material. One partial specimen, partially

Diagnosis. Carapace pyriform, longer than wide,
maximum width in mesobranchial region; front sin-
gular, sulcate longitudinally, pseudorostral spines
short, fused; orbits small, laterally situated, with
strong and subtriangular orbital spines; dorsal
regions swollen, distinct, bounded by grooves;
mesogastric region inflated and smooth, narrow
and elongated anteriorly, bounded by two elong-
atoped ridges; metagastrian region narrow, U-
shaped; branchial regions differentiated; meso-
branchial region arched; posterior margin broad,
rimmed.

Description. Carapace pyriform in outline, longer
than wide; dorsal surface covered by small pits,
convex in both directions; maximum width in meso-
branchial region; front produced, straight, directed
forwards, with two fused spines, with longitudinal
ridges; orbits anterolaterally directed, supraorbital
margin with strong spines: antorbital spine is the
largest, triangular in shape and slightly forward;
intercalated spine shortest, conical, separated by
supraorbital sutures; postorbital spine triangular,
medium sized, facing out. Lateral margins smooth,
arched; hepatic region slightly inflated, defined by
shallow groves; notable subtriangular spine in the
postorbital lobe; mesogastric region inflated, u-
shaped, apparently smooth and anterior portion
ridged; protogastric region weakly defined; urogas-
tric region bounded by shallow grooves; branchial
regions delimited from axial regions by grooves;
cardiac region triangular; epibranchial region
inflated, oblique, arched posteriorly; mesobranchial
region broadly inflated; metabranchial region
depressed; intestinal region not preserved; poste-
rior margin not preserved, appears broad.

Etymology. The specific name refers to its elon-
gated morphology.

Remarks. The type species, Planobranchia laevis,
from the Lutetian of Egypt, shows clear affinity with
P. elongata n. sp., but has some differences: 1) dis-
tinct hepatic region, with smaller hepatic spine than
the new species; 2) gastric regions less pro-
nounced and more elongated and dorsal surface
ornated with very small granules, instead of the
smooth surface with setal pits that the new species
has. Planobranchia palmuelleri from the Lutetian of
Catalonia is clearly different from P. elongata n. sp.
in some aspects like: 1) its carapace outline, being
much wider and shorter than the new species; and
2) by its shorter rostrum. Planobranchia simplex
from the Lutetian of Senegal, shows clear affinity with
?P. egyptensis from the Lutetian of Egypt, in having
a slimmer outline and more inflated dorsal regions.

Family MACROCHEIRIDAE Dana, 1851
Genus ?Macrocheira de Haan, 1839

Type species. Maja kaempferi Temminck, 1836

Fossil included species. Macrocheira longirostra
Schweitzer and Feldmann 1999 (Eocene), M. tegliandi Rathbun, 1926 (Oligocene), M. ginzaensis
Imaizumi, 1965 (Miocene), and M. yabei (Imaizumi,
1957 as Paratomyalus yabei) (Miocene).

?Macrocheira sp.

Figure 5C

Material. One incomplete carapace with cuticle not
well preserved: MPZ 2023/5.

Description. Carapace pyriform, moderately con-
 vex, slightly more swollen in gastric and epibran-
chial portions. Frontal, posterior, and anterolateral
margins not preserved; lateral margins sinuous,
with strong incision between hepatic and branchial margins; mesobranchial margin strongly rounded. Dorsal surface densely granulated. Branchiocardiac grooves very close to each other; hepatic region inflated; Protogastric region inflated, with two large tubercles; mesogastric region narrow, moderately inflated; urogastric region extremely narrow, not well defined. Mesobranchial region large, inflated and rounded, separated from gastric regions by the cervical groove, with two tubercles separated from each other. Cardiac, intestinal, and metabranchial regions not preserved.

Remarks. Species of Macrocheira are characterized by a pyriform outline of the carapace, hepatic spine, bifurcate rostrum (two spines), poorly developed supraorbital eave, small ant- and postorbital spines, and well-developed carapace regions (see Miers, 1886; Rathbun, 1926; Sakai, 1976; Schweitzer and Feldmann, 1999). Moreover, Macrocheira usually have inflated protogastric and mesogastric regions; depressed metagastric region; a urogastric region poorly developed; epimand mesobranchial regions inflated, and depressed metabrancheal region; cardiac region oblong and bounded by wide grooves with parallel crenulations positioned oblique to the axis of the grooves.

The different fossil species of the genus Macrocheira are differentiated by the degree of inflation and shape of carapace regions, ornamentation on dorsal regions, length of the rostrum and size of the orbital and hepatic spines (see Schweitzer and Feldmann, 1999). The genus is only represented by one modern species, Macrocheira kaempferi, from Japan, reported from mud or sand bottoms at 50-300 m depth (Sakai, 1976).

Given the fragmentary condition of the specimen, the generic assignment is given tentatively and a proper specific assignation is not possible.

[Family MAJIDAE Samouelle, 1819
Subfamily ?MAJINAE Samouelle, 1819]
FIGURE 6. Reconstruction of Planobranchia elongata n. sp. carapace.
Genus **SPINIROSTRIMAIA** Beschin, De Angeli, Checchi, and Zarantonello, 2012

**Type species.** *Micromaia margaritata* Fabiani, 1910.

**Fossil included species.** *Spinirostrimaia margaritata* (Fabiani, 1910) (from Lutetian of Italy); *S. echinata* n. sp. (herein).

**Remarks.** The studied material can be assigned to *Spinirostrimaia* based on the carapace general outline elongation, distribution of dorsal regions, orbital position and shape of the orbits, and the long pseudorostral spines with three lateral spines on the outer margins (see diagnosis in Beschin et al., 2012).

*Spinirostrimaia echinata* n. sp.

Figures 7-9

zoobank.org/B169EC2C-D88A-465D-A140-14B3A9395D48

**Type material.** The holotype is a female specimen, near-complete carapace, partially decorticated, with one cheliped and thoracic sternum (MPZ 2023/6) (Figure 7). There are four paratypes (MPZ 2023/7-2023/10) (Figure 8).

**Additional material.** Thirteen additional specimens composed by near-complete carapaces (MPZ 2023/11-2023/23).

**Diagnosis.** Carapace pyriform, longer than wide, convex; regions separated by shallow grooves; dorsal surface covered by small spines. Frontal margin narrow, sulcate, with two long, subparallel pseudorostral spines with spiny outer margin proximally situated; dorsal surface covered by spines (pearl-shaped tubercles if partially decorticated); orbits with prominent supraorbital eaves, without orbital spines; anterolateral margins elongated, interrupted with hepatic and branchial grooves; hepatic lobe with three lateral spines; mesobranchial margin strongly convex, with numerous spines (10-13); posterior margin with small spines.

**Description.** Carapace pyriform, twice as long as wide, (not counting the pseudorostrum), ovate; pseudorostrum long, bifid, composed of two spines which have three tiny spines on outer margin; frontal region with two longitudinal crests, tuberculate. Almost complete orbits, with prominent supraorbital eave, without antorbital spine, but marked preorbital lobe; intercalated spine triangular; postorbital spine elongated, slightly curved forward; hepatic lobe with three pointed spines, slightly curved forward. Lateral margins convex, notched by the cervical groove. Dorsal regions ornamented with sharp spines, with pearl-shaped tubercles appearance if partially decorticated; carapace regions well defined by relatively shallow grooves; axial regions elevate above other regions. Proto- and mesogastric regions inflated; meta- and urogastric regions narrower than mesogastric and cardiac regions; hepatic region inflated; branchial regions wide; epi- and mesobranchial regions inflated, poorly differentiated by a shallow groove; metabranchial region slightly depressed; cardiac region inflated, with two lateral subtriangular extensions defined by shallow grooves; intestinal region small, slightly depressed; posterior margin broad, rimmed, with small spines. Branchiocardiac grooves deep.

Epistome wide, smooth, and rimmed. Female thoracic sternum strongly concave, with interrupted sutures (only preserved 1/2 to 5/6, see Figure 7B). Female chelipeds elongated and thin; merus elongated, with longitudinal depression on the ventral surface, surrounded by well-separated blunt spines; carpus slightly elongated, ornamented with small spines; palm slightly compressed, oval in cross section; fingers acute, relatively short, square in section, with longitudinal striae. Basal antennal article moderately wide, broader at the base than at its distal extremity.

**Etymology.** The specific epithet make reference to its spinose carapace.

**Remarks.** The new species shows similarities with the type species *Spinirostrimaia margaritata* in the general shape of the carapace, piriform and elongated, and long pseudorostral spines. However, the new species differs in some aspects: 1) subparallel pseudorostral spines, not convergent as in *S. margaritata*; 2) slightly smaller postorbital spine, without ornamentation; 3) the dorsal ornamentation, more spinose in the new species (instead of pearl-shaped tubercles of *S. margaritata*); 4) prominent spine in the margin of the hepatic region, that is absent in *S. margaritata*; 5) small, sharp spines covering the dorsal surface, lacking pearl-shaped tubercles as in *S. margaritata*; 6) wider posterior margin than *S. margaritata*, and less convex and rimmed; and 7) more spiny margins in the carapace of the new species than *S. margaritata* (see Beschin et al., 2012, figures 41, 80; t. 6, figures 3, 6a, b, 7a, b).

The fossil species *Cromimaia meneguzzoi* (Beschin, Busulini, De Angeli, and Tessier, 1985) bears some resemblance to the new species. However, *S. echinata* n. sp. differs in some aspects: 1) the urogastric region is narrower in the new species, with three tubercles forming a triangle, and not aligned as in *C. meneguzzoi*; 2) narrower cardiac region, better delimited by branchiocardiac grooves in the new species; 3) the pseudorostral spines are exceedingly shorter in *C. meneguzzoi*,
FIGURE 7. Female specimen of Spinostrimaia echinata n. sp. (Holotype MPZ 2023/6) from the Pamplona Marls Formation (upper Eocene, southern Pyrenees) in A: dorsal; B: ventral; C: frontal, and D: lateral views.
FIGURE 8. Paratypes of *Spinostrimaia echinata* n. sp. from the Pamplona Marls Formation (upper Eocene, southern Pyrenees). A: Large specimen MPZ 2023/7. B-C: Specimen MPZ 2023/8 in dorsal (B) and frontal (C) view; D: specimen MPZ 2023/9 in dorsal view; E: specimen MPZ 2023/10 in dorsal view. Abbreviations: hl: hepatic lobe; hs: hepatic spine; is: intercalated spine; pl: preorbital lobe; ps: postorbital spine; r1-3: spines of pseudorostral spines; se: supraorbital eave.
FIGURE 9. Idealized reconstruction of *Spinirostrimaia echinata* n. sp. carapace.
in contrast to the long spines of the new species (see Beschin et al., 2012, figure 40; t. 6, figures 4a-c). The new species also shows similarities with *Micromaiia tuberculata* Bittner, 1875, but has differences in the branchiocardiaco groove and both the urogastric region and the beginning of the cardiac region are narrower; the intestinal region is slightly more swollen; and chiefly in having two long and parallel pseudorostral spines, whereas in *M. tuberculata* they are much shorter and flattened subtriangular (see Beschin et al., 2012, figure 38; t. 6, figure 2).

**DISCUSSION**

Spider crabs are found both in siliciclastic and reef environments, but apparently they show preferences by siliciclastic meadows. Modern small-sized majoids are usually associated with specific substrates. Specially, they show a clear preference for life on hard substrates (like cavities of corals, stones, rubble, and sponges) or associated with aquatic vegetation, at depths between 1 and 60 m (see Carmona-Suárez and Poupin, 2016; Bearham et al., 2022), and only occasionally associated with sand or mud. However, almost all published Eocene occurrences are from siliciclastic areas (≈72.5%) and only a small percentage of this group has preference for coral or bryozoan meadows (≈21.5%, see Table 1).

During the middle-upper Eocene, spider crabs were relatively common and diversified. They are found all over the world, and the maximum diversity is concentrated in Europe (Table 1). Jaccard index descriptive binary similarity measure (Figure 10A and C) and Raup-Crick probabilistic similarity measure (Figure 10B and D), provide evidence for the similarity between different areas with spider crabs during the Eocene.

Based on the Jaccard Coefficients, similarity decreases non proportionally toward younger intervals (Figure 10A and C). The analyses carried out for the first interval (Ypresian-Lutetian) show that...
the Iberian basins have more affinity with Italy, and to a lesser extent with the UK and Hungary (<0.4), remaining very far (<0.05) from South America, Africa, and Middle East (Figure 10A). In the second interval (Bartonian-Priabonian) the results show that Iberia has higher differences with the rest of the areas, Hungary being the closest area (>0.4), followed by Italy (>0.3), and UK (>0.2), and there is a significant difference (<0.05) with America and New Zealand (Figure 10C).

Although in all cases the Raup-Crick Coefficient shows values higher than 0.05 (considered non-significant differences), the differences between the European basins and the rest of the basins can be observed. This coefficient provides better resolution, and UPGMA algorithm reveals major affinity between Spain, Hungary, UK (>0.9), Italy (>0.7), and Germany (0.535) during Ypresian-Lutetian interval, and only a value of 0.4 with more distant (not European) basins (Figure 10B). During Bartonian-Priabonian interval, the results show a slight increase in the difference between areas (Figure 10D). These results show the strongest affinity with Hungary (0.915), followed by UK (0.830) and Italy (0.585), and only of 0.345 with more distant areas.

According to the obtained results and even considering that the duration of the Ypresian-Lutetian interval (14.8 Ma) is twice as long than the Bartonian-Priabonian interval (7.3 Ma, see Table 2), differences are more significant in the late Eocene. This suggests more changes in distribution in the late Eocene that should be analysed including more crustacean groups.

CONCLUSIONS

The Eocene record of majoids includes 51 species described to date (Table 1), most records are from basins in the Mediterranean area (38 species). On the basis of sedimentological data, the Eocene majoid assemblage from Fanlillo corresponds to taxa associated with shallow-marine siliciclastic environments, probably developed in the euphotic zone, at depths that did not exceeded 20-30 m (see Ferratges et al., 2023).

The outcrop of Fanlillo includes a great abundance and diversity of small gastropods, and epiphytic bryozoans suggesting that some taxa were associated with a seagrass environment. This might support the coexistence of high diversities of crabs, especially of small sizes that found in such environment important areas for hiding against predators and enough food resources. The description of this assemblage increases our knowledge of majoids in the Eocene of Iberian Peninsula. They represent an interesting find in the prodelta marls of the Margas de Pamplona Formation and increase the spatial and temporal distribution of the genera *Planobranchia*, *Macrocheira*, and *Spiniostrimia* to the central Pyrenees. The great diversity of this single group of decapod crustaceans, associated with other small decapods in same outcrop, also suggest a complex soft bottom ecosystem, under favourable condition, probably related to seagrass meadows under euphotic conditions. Other European Eocene localities have similar spider crabs diversity (e.g., Beschin et al., 1985, 2012; De Angeli and Garassino, 2006; De Angeli et al., 2019).

The obtained results with the different coefficients employed, show great similarity of the Iberian basins with other relatively near areas (especially Italy, UK, and Hungary), but the degree of similarity varies over time. The data does not reveal a large difference with respect to the clustered groups in the different time intervals and assemblages from Iberian basins appear clustered with other European areas. The abundance and diversity of spider crabs in the upper Eocene, suggest this group was diversified and specialized for inhabiting this type of environment during the Eocene.

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REFERENCES


Leach, W.E. 1815. The zoological miscellany; being descriptions of new or interesting animals. Nodder and Son, London, UK.


MacLeay, W.S. 1838. On the brachyurous decapod Crustacea. Brought from the Cape by Dr. Smith. In Smith, A. (ed.), Illustrations of the Zoology of South Africa; consisting chiefly of Figures and Descriptions of the Objects of Natural History Collected During an Expedition into the Interior of South Africa, in the Years 1834, 1835, and 1836; Fitted Out by 'The Cape of Good Hope Association for Exploring Central Africa'. Published under the Authority of the Lords Commissioners of Her Majesty's Treasury, London, UK.


Samouelle, G. 1819. The entomologists’ useful compendium; or an introduction to the knowledge of British Insects, comprising the best means of obtaining and preserving them, and a description of the apparatus generally used; together with the genera of Linné, and modern methods of arranging the Classes Crustacea, Myriapoda, spiders, mites and insects, from...
their affinities and structure, according to the views of Dr. Leach. Also an explanation of the terms used in entomology; a calendar of the times of appearance and usual situations of near 3,000 species of British Insects; with instructions for collecting and fitting up objects for the microscope. Thomas Boys, London, UK.


