

New species of *Kromtitis* Müller, 1984 (Decapoda: Brachyura: Dynomenidae) from the Eocene of Iberian Peninsula

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ABSTRACT

A new species of a fossil brachyuran decapod crustacean, *Kromtitis lluisprietoi* sp. nov. (Dynomenidae, Paradynomeninae), from the Lutetian (middle Eocene) outcrops of Alicante province (Spain), is described. *Kromtitis* is a genus of dynomenid crabs, known only from the fossil record, characterized by a dorsal carapace with areolate morphology, with rounded tubercles ornate with granules, and irregular lateral teeth. In contrast to its congeners, *Kromtitis lluisprietoi* sp. nov. has less vaulted carapace with areolate regions bearing raised tubercles ornamented with granules. The genus *Kromtitis* is well-known from several species reported from the Eocene strata of northern Italy and Hungary. *Kromtitis lluisprietoi* sp. nov. represents the first record of the genus from the Iberian Peninsula.

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INTRODUCTION

The discovery of *Kromtitis* Müller, 1984, in Lutetian strata of La Vila Joiosa (Alicante) increases the number of decapod species previously reported from the Eocene of Alicante province (Via, 1991; Ossó, 2011). The presence of *Kromtitis* in the outcrops of Alicante province adds new evidence of the affinity between the decapod fauna of the eastern part of the Iberian Peninsula and the coeval faunas of the Central Pyrenees of

Aragon and Catalonia (north and north-eastern parts of the Iberian Peninsula, respectively), and the faunas of northern Italian Peninsula and Hungary. This further supports a relative faunal homogeneity among the westernmost Tethys decapod faunas during the Eocene (e.g., Domínguez and Ossó, 2016; Khodaverdi et al., 2016). *Kromtitis*, with its oldest representative reported from the Paleocene of Denmark (Collins, 2010), is relatively common in Eocene and Oligocene reefal outcrops

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of northern Italy (Beschinn et al., 2002, 2007, 2018) and Hungary (Müller and Collins, 1991). From the Miocene strata, *Kromtitis* has been reported from reefal settings of Austria, Hungary and Poland (Bachmayer and Tollmann, 1953; Müller, 1984, 1996), as well as from Jamaica (Portell and Collins, 2004).

GEOLOGICAL SETTINGS

The studied specimen was recovered in the municipality of La Vila Joiosa (Marina Baixa, Alicante province, Valencian Community, Spain), in the glades of a place called l'Arginent, in the northern flank of the Alt de l'Olivanet, midway between La Vila Joiosa and Finestrat (Figures 1.1, 2.1). Geologically, the area belongs to the Internal Prebetic System (sensu García-Hernández, 1978) of the Betic Ranges, eastern Iberian Peninsula. L'Arginent outcrop is well known since the nineteenth century as one of the localities within the Alicante province with rich record of Eocene echinoids (e.g., Cotteau, 1890; Vaello López, 2015). However, no specific geological or stratigraphic works have been published on this particular outcrop. The 1981 IGME Chart (847-

Villajoyosa) indicates the outcrop's area as undifferentiated Paleogene series of clayey marls, biocalcarenes and levels of fossiliferous limestones, ranging from Danian to Aquitanian (TA-Ba₁₁₋₁₂). Nevertheless, the abundant associate fauna of large foraminifera and echinoids found at l'Arginent, exemplified by *Assilina exponens* (Sowerby, 1840); *Nummulites millecaput* Boubée, 1832; *Ditremaster nux* Desor, 1853; *Linthia macphersoni* Cotteau, 1889; *Arachniopleurus reticulatus* Duncan and Sladen, 1882; *Salenia garciae* Cotteau, 1890; or even decapods as *Dromilites pastoris* Vía, 1959, *Lophoranina straeleni* Vía, 1959, and *Calappilia cf. scopuli* Quayle and Collins, 1981, is identical to that of other well-calibrated localities of the Alicante province, such as Orxeta, Busot, Villafranca or Agost, which indicates a Lutetian (middle Eocene) age for the l'Arginent outcrop (Jiménez de Cisneros, 1917; Sillero, 1992; Molina et al., 2000; Sillero, 2002; Ossó-Morales, 2011, 2013; Vaello López, 2015) (Figures 2.2–2.5).

SYSTEMATIC PALEONTOLOGY

Infraorder BRACHYURA Latreille, 1802
Section PODOTREMATA Guinot, 1977



FIGURE 1. Location map of the fossil locality (star) in Alicante Province (Spain).

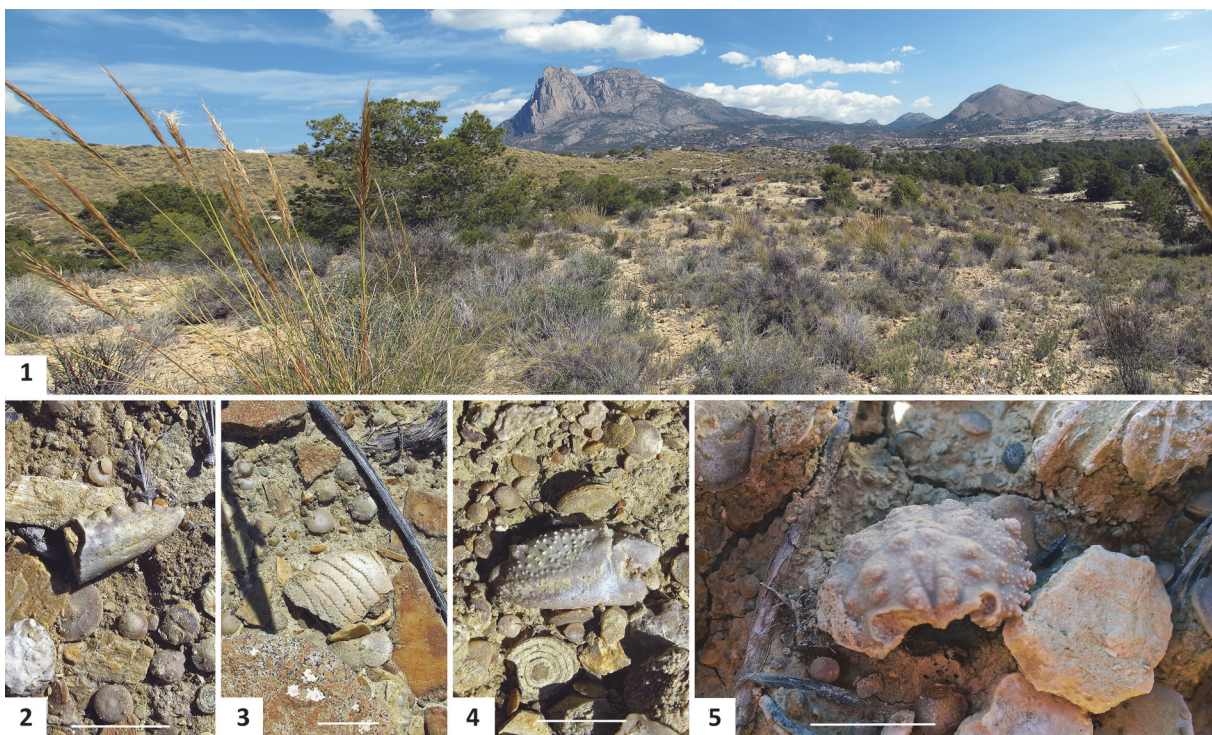


FIGURE 2. Study area. **1.** General view of l'Arginent outcrop, with the yellowish Lutetian fossiliferous levels in the foreground, and the Puig Campana (1 406 m) in the background (collectors in the center of the image for scale). **2-5.** Fossil decapod remains **2.** Left pollex of undetermined decapod. **3.** Carapace fragment of *Lophorantina* sp. **4.** Right propodus of undetermined decapod. **5.** *Kromtitis lluisprietoi* sp. nov., holotype. Scale bars equal 10 mm.

Subsection DYNOMENIFORMIA Guinot, Tavares and Castro, 2013

Superfamily DROMIOIDEA De Haan, 1833

Family DYNOMENIDAE Ortmann, 1892

Subfamily PARADYNOMENINAE Guinot, 2008

Genus KROMTITIS Müller, 1984

Type species. *Dromilites koberi* Bachmayer and Tollmann, 1953, by monotypy.

Included species. *K. bicuspidatus* Beschin et al., 2009; *K. daniensis* Collins, 2010; *K. koberi* (Bachmayer and Tollmann, 1953); *K. koberiformis* Beschin et al., 2007; *K. levigatus* Beschin et al., 2007; *K. lluisprietoi* sp. nov.; *K. pentagonalis* Müller and Collins, 1991; *K. spinulata* Portell and Collins, 2004; *K. subovatus* Beschin et al., 2007; *K. tergospinosus* Beschin et al., 2018; *K. tetratuberculatus* Beschin et al., 2002.

Kromtitis lluisprietoi sp. nov.

Figures 3.1–3.4

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Diagnosis. Carapace small, roundish subquadrate, as long as wide, markedly convex, surface areolate, sparsely granulate. Regions swollen, with rounded tubercles peaked with coarse granules and well-defined by grooves. Front with produced

and triangular rostrum. Orbits ovate, obliquely arranged, visible dorsally. Anterolateral margin with five irregular teeth (excluding the outer orbital tooth). Posterolateral margin with two teeth, the second being larger. Frontal groove deep. Epigastric lobes swollen with two tubercles. Mesogastric lobe subpentagonally elongate, acute anteriorly with one tubercle, larger posteriorly, with two contiguous tubercles. Metagastric region undifferentiated from mesogastric region. Protogastric lobes swollen, with three tubercles. Urogastric region wide, V-shaped, with two contiguous tubercles. Epibranchial region with two swollen lobes, each with one tubercle. Mesobranchial region with two swollen lobes bearing large tubercle. Metabran- chial region incomplete, bearing one tubercle. Cardiac region diamond shaped, swollen, with three tubercles. Hepatic region slightly swollen, with one tubercle. Sub-hepatic region with small tooth. Cervical, post-cervical, branchial and branchiocardiac grooves well-defined.

Kromtitis lluisprietoi sp. nov. is easily distinguishable from all the previously known *Kromtitis* species in having less globose dorsal carapace and by its particular dorsal aspect, with more areolate regions bearing raised tubercles ornamented

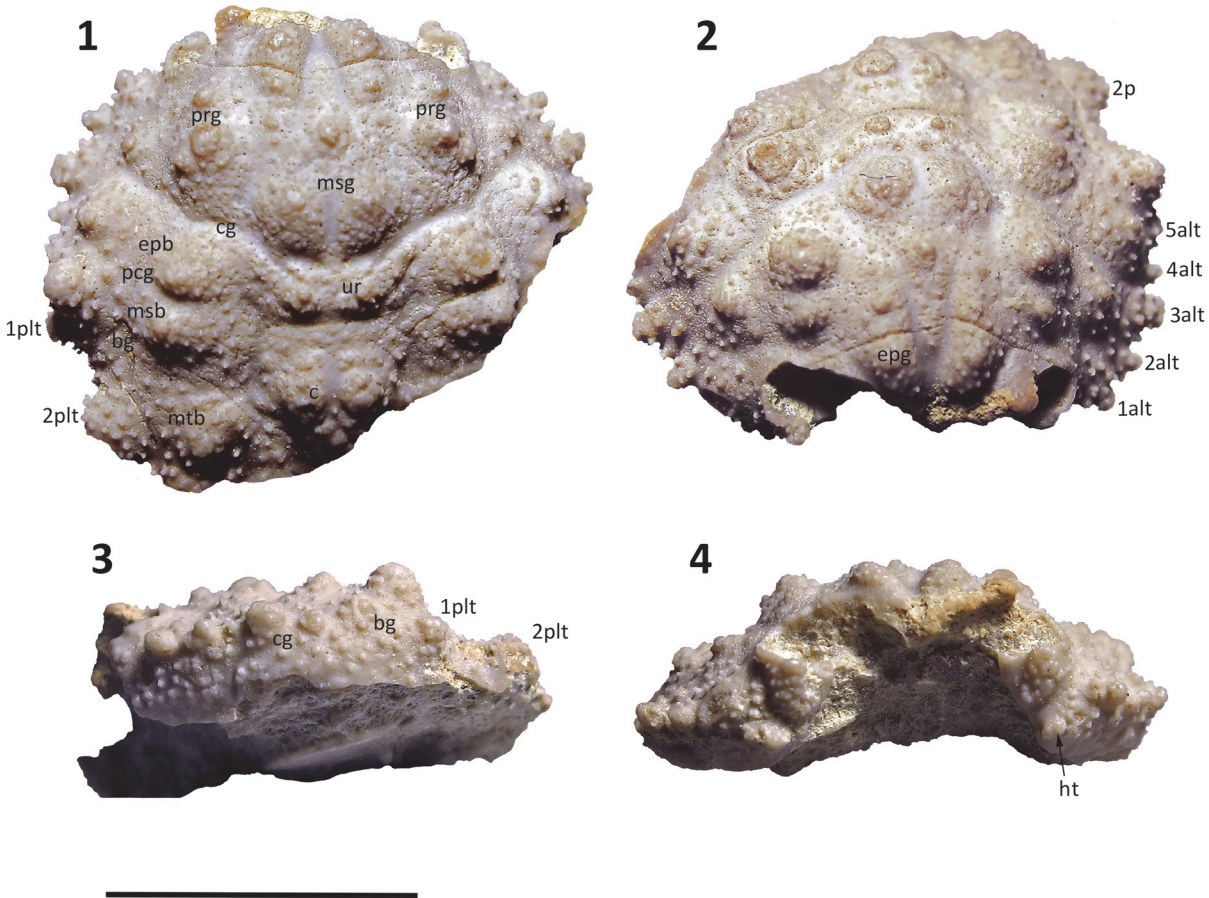


FIGURE 3. *Kromtitis lluisprietoi* sp. nov. holotype GCP-CI-4528, from the Eocene of l'Arginent, La Vila Joiosa (Alicante, Spain). **1.** Dorsal view. **2.** Frontodorsal view. **3.** Left lateral view. **4.** Frontal view. Abbreviations: alt = anterolateral tooth; bg = branchial groove; c = cardiac region; cg = cervical groove; epg = epigastric region; ht = subhepatic tooth; msb = mesobranchial region; msg = mesogastric region; mtb = metabranchial region; pcg = post-cervical groove; plt = posterolateral tooth; prg = protogastric region; ur = urogastric region. Scale bar equals 10 mm.

with granules. *Kromtitis bicuspidatus* from the upper Eocene of NE of Italy, differs from the new species in having a pair of semi-fused inner epi-branchial swellings, whereas in *K. lluisprietoi* sp. nov. there is only one swelling; moreover, the former presents more swollen region lobes and less individualized anterolateral teeth than the new species (Beschlin et al., 2009, p. 7–10, pl. 1, figs. 3–4). *Kromtitis daniensis* from the middle Danian of Denmark differs from the new species in having a pair of inner mesobranchial tubercles and fused metabranchial tubercles, whereas in *K. lluisprietoi* sp. nov., there is only one tubercle on each lobe, and its surface is more granulate (see Collins, 2010, p. 15, figs. 1.1, 2). *Kromtitis koberi* (the type species) from the middle Miocene of Central Europe and *K. koberiformis* from the lower Eocene of NE Italy dif-

fer from the new species by their coarser and tighter swellings and double or semi-fused inner epi- and mesobranchial tubercles (Müller, 1984, p. 63–64, pl. 31, figs. 1–4; Beschlin et al., 2007, p. 26–27, pl. 3, figs. 2–4; Schweitzer et al., 2012, p. 33, figs. 21.4a–21.4b; Collins, 2014, p. 36, pl. 2, figs. 7–8). *Kromtitis levigatus* from the lower Eocene of NE Italy differs from *K. lluisprietoi* sp. nov. by its smooth dorsal carapace (Beschlin et al., 2007, p. 26–27, pl. 3, fig. 5). *Kromtitis spinulata* from the lower Miocene of Jamaica differs from the new species by its subglobose carapace and more spiny lateral margin than in *K. lluisprietoi* sp. nov. (Portell and Collins, 2004, p. 11–113, fig. 1.1). *Kromtitis subovatus* from the lower Eocene of NE Italy differs from *K. lluisprietoi* sp. nov. in having a subglobose and subpentagonal carapace and more

acute lateral teeth (Beschin et al., 2007, p. 26–27, pl. 3, figs. 6–8). *Kromtitis tetratuberculatus* from the middle Eocene of NE Italy differs clearly from the new species by its coarser and swollen dorsal surface with a very dense granulation (Beschin et al., 2002, p. 12–13, text-fig. 7, pl. 2, figs. 2, 3a–3b). *Kromtitis tergospinosus* from the upper Eocene of NE Italy differs from *K. lluisprietoi* sp. nov. by its more flattened dorsal carapace, and regions and lateral margins more spiny than in the new species (Beschin et al., 2018, pl. 58, figs. 63–65). *Kromtitis pentagonalis* Müller and Collins, 1991 from the upper Eocene of Hungary was transferred to *Paradynomene* by Beschin et al. (2016a, p. 71), which indicates the strong similarities in respect with dorsal carapace morphology among both genera. However, the species was re-evaluated as a representative of *Kromtitis* by Beschin et al. (2018, p. 162). It differs from *K. lluisprietoi* sp. nov. by its more produced frontal margin and rostrum, general outline and more swollen regions (Beschin et al., 2018, p. 160–162, pl. 58, fig. 61). *Kromtitis pseudo-lothi* Beschin et al., 2016b, morphologically closely related to *Dromilites lothi* Förster and Mundlos, 1982 (ibid, p. 26), is not considered herein as *Kromtitis*, by the same reasons that *D. lothi* was excluded from *Kromtitis* (see discussion in Beschin et al., 2016a, p. 71, and references therein).

Etymology. The species is dedicated to the memory of late Lluís Prieto, an enthusiastic collector from Barcelona who discovered the holotype.

Holotype. GCP-CI-4528, near-complete carapace (without rostrum and posterior margin) with well-preserved cuticle, stored at Museo Paleontológico de Elche (Alicante, Spain), under acronym MUPE.

Measurements (in mm). Length=14.5; width=18.0; front-orbital width=9.5; height=7.0.

Description. Carapace small, roundish subquadrate, apparently as long as wide, markedly convex, surface areolate, sparsely granulate. Regions distinct, swollen, with well individualized rounded tubercles peaked with coarse granules, and well-defined by grooves. Front broken, probably with produced and downturned triangular rostrum. Orbits ovate, obliquely arranged, visible dorsally; supraorbital margin not well preserved, granulate; infraorbital margin with a prominent granulate tooth or projection. Anterolateral margin begins below level of postorbital tooth, armed with five irregular teeth (excluding outer orbital tooth), the third being larger, and the fifth broken; among them, irregular acute small projections ornate the margin. Posterolateral margin with two teeth, the first behind the branchial groove, the second being larger, near the

posterior corner. Posterior margin not preserved. Frontal groove deep. Epigastric lobes separated by the frontal groove, swollen, elongate, with two tubercles aligned longitudinally, the anterior larger. Mesogastric lobe subpentagonally elongate, anterior portion acute, bearing one tubercle, posterior portion larger, with two contiguous tubercles separated by short and smooth axial groove. Metagastric region undifferentiated from mesogastric region. Protogastric lobes swollen, with three tubercles, two aligned longitudinally on anterior and medial portion of the lobes, the second being larger; the third tubercle placed obliquely below between the second tubercle and the gastrohepatic groove. Urogastric region wide, swollen, V-shaped, separated from mesogastric and metagastric regions by the cervical groove; with two small contiguous tubercles separated by a weak axial depression; small anterior portion of lobe divided transversely, below two gastric pits; small lateral portions of lobe obliquely divided by a groove forming small secondary lobes at each side of the principal lobe. Epibranchial region laterally elongate, bounded anteriorly by the cervical groove and posteriorly by the post-cervical groove; with two separate swollen lobes, inner and outer, each bearing one tubercle, the inner one being larger. Mesobranchial region laterally elongate, bounded anteriorly by the post-cervical groove and posteriorly by the branchial groove; with two separate swollen lobes, each bearing large tubercle, larger than the epibranchial ones, the outer one being very large and prominent. Metabanchial region incomplete, bearing one tubercle. Cardiac region diamond shaped, separated from urogastric region by post-cervical groove and bounded laterally by deep branchiocardiac grooves; swollen, bearing three tightly positioned tubercles, two of them aligned transversely and separated by axial short groove; the third positioned posteriorly. Intestinal region not completely preserved. Hepatic region slightly swollen, with one tubercle surrounded by scattered granules. Sub-hepatic region bearing a tooth below the first anterolateral tooth and the infraorbital projection. Cervical, post-cervical, branchial and branchiocardiac grooves well-defined; cervical and branchial ones visible ventrally.

Remarks. In view of the dorsal and frontal features of the studied specimen, it can be assigned with confidence to the Dynomenidae, and more accurately within the Paradynomeninae. Indeed, regarding its carapace outline, densely ornamented with marked swellings crowned by tubercles, its antero- and posterolateral margins armed

with irregular salient teeth, and its produced ventral anterior area, it fits the diagnosis of *Paradynomeninae* (Guinot, 2008, p. 11–13). The assignment on the genus level is somewhat more complex because it lacks the posterior part of the carapace, obscuring the carapace outline and details of the intestinal region and the posterior margin. However, the roundish subquadrate carapace outline with anterolateral irregular teeth, the presence of posterolateral teeth, the swollen region lobes with rounded tubercles tipped with granules and its granulated surface with well-defined grooves correspond with the diagnosis of the genus *Kromtitis* (Müller, 1984, p. 64; Schweitzer et al., 2012, p. 33). Simultaneously, the new species also corroborates the diagnosis of *Paradynomene*, as far as the areolate dorsal carapace surface, densely covered with tubercles and granules, the anterolateral irregular salient teeth and the inflated sub-hepatic area, are concerned (McLay and Ng, 2004). Nevertheless, *Paradynomene* exhibits usually a more elongate and subquadrangular carapace outline, and anterolateral margins are more parallel to each other (Guinot, 2008, p. 11) than they are in the studied specimen and other species of *Kromtitis*, in which they are fairly convex. Additionally, the new species exhibits a wide transverse V-shaped urogastric region, which is wider than the cardiac region, a character typical for the genus *Kromtitis* (Müller 1984, pl. 31, figs. 1–4; Portell and Collins, 2004, fig. 1.1; Beschin et al., 2016a, pl. 8, figs. 4–6). Accordingly, based on the roundish subquadrate carapace and the particular shape of the urogastric region, the studied material is assigned herein to *Kromtitis*.

The systematic placement of *Kromtitis* changed through time. Originally it was considered a representative of Dromiidae De Haan, 1833 (Müller, 1984; De Grave et al., 2009). Guinot (2008) re-evaluated Dynomenidae Ortmann, 1892, and presented a key for extant subfamilies, chiefly based on sternal and abdominal characters, which are not preserved in the studied specimen. Therein, she proposed a new subfamily *Paradynomeninae* for the genus *Paradynomene* Sakai, 1963, as well as the fossil forms *Kieronopsis* Davidson, 1966, and *Kromtitis*, based on the strong similarities in dorsal carapace features in both fossil genera and the extant species of *Paradynomene* (Guinot, 2008, p. 21). Moreover, the specimen of La Vila Joiosa possesses an areolate dorsal ornamentation and irregularly toothed lateral margins, that strongly recall those of some extant species of *Paradynomene* (McLay and Ng, 2004),

which supports the current subfamilial placement of *Kromtitis* within *Paradynomeninae* (Guinot, 2008).

Occurrence. *Kromtitis lluisprietoi* sp. nov. is known only from the Lutetian (middle Eocene) strata of its type locality, i.e., La Vila Joiosa (Marina Baixa, Alicante province, Valencian Community, Spain).

DISCUSSION

Guinot (2008, p. 21), when including *Kromtitis* within *Paradynomeninae*, pointed out the scarce dorsal divergence between the fossil forms and the extant species of this subfamily. In fact, she considered that the modern *Paradynomeninae* clearly are “barely modified relicts” (Guinot, 2008), which is also evidenced with the discovery of *K. lluisprietoi* sp. nov., which shares characters and features with extinct genus *Kromtitis* and extant species of *Paradynomene* (McLay and Ng, 2004). In this respect, no significant morphological differences can be found among Eocene and Miocene species of *Kromtitis*, or even the only Paleocene representative, *K. daniensis*, although poorly preserved (cast). However, as mentioned above, dorsal regions with pronounced tubercles and the anterolateral outline with prominent irregular teeth of *Kromtitis lluisprietoi* sp. nov. differ slightly from the typical dorsal pattern of its congeners.

Extant *Paradynomeninae* are restricted to the Indo-West Pacific, and usually inhabit moderately deep to deep waters (McLay and Ng, 2004, p. 1). In contrast, most fossil representatives of *Paradynomeninae* lived in shallower reefal environments (e.g., Beschin et al., 2016a).

CONCLUSIONS

The genus *Kromtitis* is reported for the first time from the Iberian Peninsula. The presence of *Kromtitis lluisprietoi* sp. nov. in the Lutetian strata of the southeastern of the Peninsula, in addition to increasing the number of known decapod species from the respective area, further supports a suggested faunal homogeneity of the western Tethys during the Eocene. Dorsal morphology of *Kromtitis lluisprietoi* sp. nov. differentiates the species from its congeners; however, it simultaneously shows affinity to extant representatives of the subfamily *Paradynomeninae*.

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