

A highly diverse dromioid crab assemblage (Decapoda, Brachyura) associated with pinnacle reefs in the lower Eocene of Spain

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Abstract.—A highly diverse fauna of dromioid brachyurans from the Serraduy Formation (lower Eocene) in the western Pyrenees (Huesca, Spain) is described and illustrated. Recorded taxa are *Mclaynotopus longispinosus* new genus new species, *Torodromia elongata* n. gen. n. sp., *Basidromilites glaessneri* n. gen. n. sp., *Basidromilites* sp., *Sierradromia gladiator* n. gen. n. sp., *Kromtitis isabenensis* n. sp., and *Basinotopus* sp. Other European outcrops have yielded dromioids in association with specific environments, likely coral and sponge reef and siliciclastic soft bottoms; but the present material constitutes the most diverse dromioid assemblage from the lower Eocene worldwide. These dromioids co-occurred with a rich invertebrate fauna and lived near coral–algal reef mounds. Sedimentological data suggest that most of the fauna accumulated in fore reef settings as a result of storm activity. The present material greatly increases the diversity of known dromioid crabs associated with Eocene reef environments.

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Introduction

The superfamily Dromioidea De Haan, 1833 comprises notable representatives in modern ecosystems from rocky shores to deep sea (McLay, 1993, 1999, 2001; McLay and Ng, 2005). The fossil record of dromioids extends back to the Jurassic (see Jagt et al., 2015 and Luque et al., 2019 and references therein), and the group attained maximum diversity during the lower Eocene (Ypresian; see Table 1) in reef environments of northern Italy (Beschin et al., 2002, 2005, 2007, 2012, 2016a, b, 2018) and Spain (herein). Detailed systematic reviews of dromioids during recent years have resulted in new classificatory schemes (Karasawa et al., 2011; Schweitzer et al., 2012; Guinot et al., 2013; Jagt et al., 2015; Guinot, 2019; Van Bakel et al., 2020) based mainly on new discoveries and considering their importance in decapod crustacean phylogeny.

The Eocene record of dromioid crabs is comparatively rich, but material is often fragmentary. To date, 53 extinct species of dromioids are known from the Eocene, with the highest diversities associated with reef environments in the Atlantic–Tethyan Realm (Desmarest, 1822; Bittner, 1893; Checchia-Rispoli, 1905; Via, 1959; Quayle and Collins, 1981; Solé and Via, 1989; Müller and Collins, 1991; Blow and Manning, 1996; Beschin et al., 2002, 2007, 2009b, 2012, 2015, 2016a, 2016b,

2017, 2018, 2019; Collins and Jakobsen, 2004; Jakobsen and Feldmann, 2004; Van Bakel et al., 2009; Franțescu et al., 2010; De Angeli and Cecon, 2014; Artal et al., 2016; Ossó, 2019; Ferratges et al., 2020) (see Table 1).

Here we describe new dromioid taxa from a decapod crustacean assemblage associated with reef facies of an early Eocene age in the Pyrenees (Huesca, Spain). This specific locality corresponds to a reef environment that has already yielded a wide range of decapod crustaceans (Artal and Via, 1989; Artal and Castillo, 2005a; Artal and Van Bakel, 2018a, b; Ferratges et al., 2019). Among the material recognized at this outcrop, dromioids represent only a small portion (3.1%) of the total assemblage (see Ferratges et al., 2021), yet surprisingly, they are unusually highly diverse compared with other Eocene assemblages. This new discovery has prompted a revision of all Eocene dromioid faunules to compare these in terms of diversity and environment with the present material.

Geological setting

The southern Pyrenean basins were located at tropical latitudes during the Paleogene (e.g., Hay et al., 1999; Silva-Casal et al., 2019) and, in the Eocene, formed part of an elongated gulf that connected in the west to the Bay of Biscay and was limited in the north to the axial zone of the Pyrenees (see Plaziat, 1981; Garcés et al., 2020). These basins rank among the most complete records of Eocene marine sedimentary successions in Europe,

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Table 1. Eocene representatives of genera placed in the superfamily Dromioidea De Haan 1833. New representatives of genera within the superfamily Dromioidea from the “Barranco de Ramals” outcrop and described herein indicated in bold.

Family	Subfamily	Genus	Species	Locality	Age	Lithology	Environment	
Dromiidae De Haan, 1833	Basinotopinae Karasawa, Schweitzer, and Feldmann, 2011	<i>Basinotopus</i> M’Coy, 1849	<i>lamarekii</i> (Desmarest, 1822)	UK, Italy	Lutetian	siliciclastic	shallow platform	
			<i>lothi</i> (Förster and Mundlos, 1982)	Germany	Priabonian/Oligocene	siliciclastic	shallow platform?	
			<i>tricornis</i> Collins and Jakobsen, 2004	Denmark	Ypresian–Lutetian	siliciclastic	shallow platform	
		<i>Mclaynotopus</i> n. gen.	<i>sp.</i>	<i>alpina</i> (Glaessner, 1929)	Spain	Ypresian	limestone	reef
			<i>longispinosus</i> n. sp.	<i>claudiopolitana</i> (Bittner, 1893)	Austria	Lutetian	siliciclastic	shallow platform?
			<i>Noetlingocarcinus</i> Karasawa, Schweitzer, and Feldmann, 2011	<i>messinai</i> Beschin et al., 2012	Spain	Ypresian	limestone	reef
				<i>veronensis</i> (Bittner, 1886)	Italy	Lutetian	siliciclastic	shallow platform
				<i>zannatoi</i> Beschin et al., 2016a	Italy	Bartonian	siliciclastic	shallow platform
				<i>hyneorum</i> Blow and Manning, 1996	Italy	Priabonian	siliciclastic	shallow platform
					Italy	Ypresian	limestone	reef
	Dromiinae De Haan, 1833	<i>Acanthodromia</i> Milne-Edwards, 1880	<i>Ameridromia</i> Blow and Manning, 1996	<i>longifrons</i> Artal et al., 2016	South Carolina (USA)	Lutetian–Bartonian	limestone	shallow platform?
				<i>fossata</i> (Müller and Collins, 1991)	Spain	Priabonian	siliciclastic	shallow platform
		<i>Basadromia</i> Artal et al., 2016	<i>Dromia</i> Weber, 1795	<i>subglobosa</i> (Müller and Collins, 1991)	Hungary	Priabonian	limestone	reef
				<i>bedetteae</i> Blow and Manning, 1996	Hungary	Priabonian	limestone	reef
		<i>Dromidia</i> Stimpson, 1858	<i>Pseudodromilites</i> Beurlen, 1928	<i>hilarionis</i> (Bittner, 1883)	South Carolina (USA)	Lutetian–Bartonian	siliciclastic-carbonate	shallow platform
				<i>holthuisi</i> Frantescu, Feldmann, and Schweitzer, 2010	South Carolina (USA)	Bartonian	limestone	shallow platform
		<i>Torodromia</i> n. gen.	<i>Biohermia</i> Beschin et al., 2016a	<i>elongata</i> n. sp.	Spain	Ypresian	limestone	reef
				<i>chalmasi</i> Beschin et al., 2016a	Italy	Ypresian	limestone	reef
				<i>denticulata</i> Beschin et al., 2016a	Italy	Ypresian	limestone	reef
				<i>piccolii</i> Beschin, Busulini, and Tessier, 2015	Italy	Ypresian	limestone	reef
<i>Trechmannius</i> Collins and Donovan, 2006	<i>Basidromilites</i> n. gen.	<i>glæssneri</i> n. sp.	Jamaica	Lutetian–Bartonian	siliciclastic	shallow platform		
		<i>pastoris</i> (Via, 1959)	Spain	Ypresian	limestone	reef		
Sphaerodromiinae Guinot and Tavares, 2003	<i>Dromilites</i> Milne Edwards, 1837	<i>sp.</i>	Spain, Italy	Lutetian	siliciclastic	shallow platform		
		<i>belli</i> Van Bakel et al., 2017	Spain	Ypresian	limestone	reef		
	<i>Cracchidynomene</i> Beschin et al., 2016a	<i>areolata</i> Beschin et al., 2016a	<i>bucklandii</i> Milne Edwards, 1837	UK	Ypresian	siliciclastic (phosphatic nodules)	shallow platform	
			<i>vicensis</i> Barnolas, 1973	Spain, Italy	Lutetian	siliciclastic	shallow platform	

Dynomenidae Ortmann, 1892	Dynomeninae Ortmann, 1892	<i>Dynomene</i> Desmarest, 1822	<i>vetusta</i> Beschin et al., 2016a	Italy	Ypresian	limestone	reef
			<i>lessinea</i> Beschin, De Angeli, and Checchi, 2001	Italy	?Priabonian– Oligocene	limestone	reef
		<i>Eotrachynotocarcinus</i> Beschin et al., 2007	<i>airaghii</i> Beschin et al., 2007	Italy	Ypresian	limestone	reef
	Graptocarcininae Van Bakel, Guinot, Corral and Artal, 2012	<i>Ovamene</i> Müller and Collins, 1991	<i>franciae</i> Müller and Collins, 1991	Hungary	Priabonian	limestone	reef
		<i>Graptocarcinus</i> Roemer, 1887	<i>eocenicus</i> Beschin et al., 2016b	Italy	Lutetian	siliciclastic	shallow platform
	Metady- nomeninae Guinot 2008	<i>Dromiopsis</i> Reuss, 1858	<i>ceratoi</i> Beschin et al., 2016a	Italy	Ypresian	limestone	reef
			<i>longitudovata</i> Beschin et al., 2016a	Italy	Ypresian	limestone	reef
			<i>marginospinosa</i> Beschin, Busulini, and Tessier in Beschin et al., 2019	Italy	Priabonian	limestone	reef
			<i>paleogenica</i> De Angeli and Cecon, 2014	Italy	Ypresian	siliciclastic	reef
			<i>parvula</i> Beschin et al., 2016a	Italy	Ypresian	limestone	reef
			<i>paucigranosa</i> Beschin et al., 2007	Italy	Ypresian	limestone	reef
			<i>rocchetti</i> Beschin, Busulini, and Tessier in Beschin et al., 2019	Italy	Priabonian	limestone	reef
			<i>vicetinus</i> Beschin et al., 2016a	Italy	Lutetian	siliciclastic	shallow platform
			<i>veronensis</i> Beschin, Busulini, and Tessier, 2015	Italy	Ypresian	limestone	reef
			<i>Metadynomene</i> McLay, 1999				
	Paradynomeninae Guinot, 2008	<i>Kromtitis</i> Müller, 1984	<i>bicuspidatus</i> Beschin, Busulini, and Tessier, 2009a	Italy	Priabonian	siliciclastic	shallow platform
			<i>isabensis</i> n. sp.	Spain	Ypresian	limestone	reef
			<i>koberiformis</i> Beschin et al., 2007	Italy	Ypresian	limestone	reef
			<i>levigatus</i> Beschin et al., 2007	Italy	Ypresian	limestone	reef
			<i>lluisprietoi</i> Ossó, 2019	Spain	Lutetian	?siliciclastic	shallow platform
			<i>pseudolothi</i> Beschin et al., 2016b	Italy	Lutetian	siliciclastic	shallow platform
			<i>subovatus</i> Beschin et al., 2007	Italy	Ypresian– Priabonian	limestone	reef
			<i>tergospinosus</i> Beschin, Busulini, and Tessier in Beschin et al., 2018	Italy	Priabonian	limestone	reef
			<i>tetratuberculatus</i> Beschin et al., 2002	Italy	Lutetian	siliciclastic	shallow platform
			<i>antiqua</i> Beschin et al., 2016a	Italy	Ypresian	limestone	reef
	<i>Paradynomene</i> Sakai, 1963	<i>pentagonalis</i> (Müller and Collins, 1991)	Hungary-Italy	Priabonian	limestone	reef	
		<i>Sierradromia</i> n. gen.	Spain	Ypresian	limestone	reef	
	Insertae sedis	<i>Cyamocarcinus</i> Bittner, 1883	<i>angustifrons</i> Bittner, 1883	Italy	Ypresian– Priabonian	limestone	reef
			<i>budensis</i> Oppenheim, 1899	Italy	Ypresian	limestone	reef
			<i>disalvoi</i> Beschin, Busulini, and Tessier in Beschin et al., 2018	Italy	Priabonian	limestone	reef
			<i>loerentheyi</i> Checchia-Rispoli, 1905	Italy	Lutetian– Priabonian	limestone	reef
			<i>riglosensis</i> Ferratges, Zamora, and Aurell, 2020	Spain	Priabonian	limestone	reef

with decapod crustacean taxa described from several outcrops (e.g., Via, 1969, 1973; Artal and Castillo, 2005b; Artal et al., 2006, 2013; Ossó et al., 2014; Dominguez and Ossó, 2016; López-Horgue and Bodego, 2017; Artal and Van Bakel, 2018a, b, 2020; Ferratges et al., 2019, 2020). These successions document a wide range of depositional settings, from proximal alluvial to shallow marine in the east to slope and deep-marine and abyssal plains in the west (e.g., Garcés et al., 2020).

The material described herein was collected from the lower Eocene (middle Ypresian) Serraduy Formation of the Tremp-Graus Basin, and more specifically from the classic outcrop of “Barranco de Ramals” near the villages of La Puebla de Roda and Serraduy in the northeast of the province of Huesca (Aragón, Spain; Fig. 1). This locality has yielded an important assemblage of decapod crustaceans in association with pinnacle coral reefs (Via, 1973; Artal and Via, 1989; Artal and Castillo, 2005a; Fraaije and Pennings, 2006; Artal and Van Bakel, 2018a, b; Ferratges et al., 2019, 2021) as well as diverse invertebrate faunas (see Zamora et al., 2018; Ferratges et al., 2021). However, dromioid crabs remained undescribed until now.

Low depositional rates and optimum climatic conditions favored the development of a set of pinnacle reefs on top of the *Alveolina* limestones, which suggests a setting of intermediate depth and wave action (Gaemers, 1978). The Riguala Marls Member, which overlies the reefal unit, has been dated as early to middle Ilerdian (Serra-Kiel et al., 1994), which corresponds to the global Ypresian Stage (Pujalte et al., 2009). This unit formed as a foreereef facies in which most of the material was derived from the reef as a result of storm activity, inclusive of the crab specimens described herein (see Ferratges et al., 2021 for more details). Thus, the dromioids, as well as other decapod crustaceans recovered from the same outcrop, lived near these reef pinnacles (Ferratges et al., 2021).

Materials and methods

Specimens were collected from the outcrop that exposes the transition between the reef limestones and the overlying Riguala Marls at a locality known as “Barranco de Ramals.” A total of 162 specimens of dromioids have been studied from this outcrop. Some of this material (18 carapaces and 17 isolated propodi; 3.1% of total assemblage) was recovered during a detailed paleoecological study of the area in years 2018–2019 (see Ferratges et al., 2021 for more details). The remaining specimens (95 carapaces and 33 isolated propodus) were taken from historical museum collections. All material was prepared using a Micro Jack 2 air scribe (Paleotools; Brigham, Utah, USA), and fine, marly matrix was removed chemically using potassium hydroxide (KOH). Next, specimens were photographed dry and coated with ammonium chloride sublimate. Detailed photographs of carapace surfaces were taken using a Nikon D7100 camera (Nikon, Tokyo, Japan) with a macro 60 mm lens.

Repositories and institutional abbreviations.—Part of the material was collected during the early 1980s (see Artal and Via, 1989); this is housed in the collections of the Geological Museum of the Barcelona Seminary (MGSB). More recent collections in the area were made to quantify the abundance and distribution of taxa (see Ferratges et al., 2021); this material was recovered under permit EXP: 032/2018 from the

“Servicio de Prevención, Protección e Investigación del Patrimonio Cultural (Gobierno de Aragón)” and is currently deposited in the paleontological collections of the Museo de Ciencias Naturales de la Universidad de Zaragoza (MPZ). The terminology used in the text is summarized in Figure 2.

Systematic paleontology

Classification and terminology used herein follow Guinot (2008, 2019), Guinot et al. (2013), and Jagt et al. (2015), but see alternative hypothesis of classification in Karasawa et al. (2011) and Luque et al. (2019).

Superfamily Dromioidea De Haan, 1833

Family Dromiidae De Haan, 1833

Subfamily Basinotopinae Karasawa,

Schweitzer, and Feldmann, 2011

Diagnosis.—“Carapace slightly longer than wide, broadly triangular; rostrum broadly triangular, axially sulcate, with well developed median rostral spine; orbits deep, oblique, directed anterolaterally, suborbital margin with large spine; short segment between outer-orbital angle and first anterolateral spine, placing them at same level; lateral margin with three spines anterior to intersection of cervical groove and one very long, posterolaterally directed spine posterior to intersection of cervical groove; cervical, postcervical, and branchiocardiac grooves deep, cervical and branchiocardiac grooves intersecting carapace margin and extending onto flank; carapace with large nodes on regions” (Karasawa et al., 2011, p. 539).

Genus *Mclaynotopus* new genus

Type species.—*Mclaynotopus longispinosus* n. sp. by present designation.

Other species.—*Mclaynotopus alpina* (Glaessner, 1929).

Diagnosis.—Carapace subpentagonal, about as long as wide. Frontal margin trilobed, all spines of nearly equal size. Maximum width in anterior portion, at level of epibranchial region. Orbits directed anterolaterally, with blunt spine on suborbital margin. Anterolateral margins with three long spines, excluding outer orbital spine; last hepatic and large epibranchial nearly fused at base. Posterolateral margins with small spine, followed by small tubercle. Dorsal regions well defined by swellings and grooves. Dorsal surface with small granules in anterior portion, pitted posteriorly.

Etymology.—Named in honor of Colin McLay (University of Canterbury, New Zealand), who has contributed greatly to our general knowledge of dynomeniform crabs, plus the suffix “notopus.”

Remarks.—The morphologically most closely similar genus, *Basinotopus* (see the following), is characterized by a broadly triangular carapace outline (see Karasawa et al., 2011, p. 539); the maximum width is in the posterior portion, at the level of the metabranchial region. The front is prominent, with a long

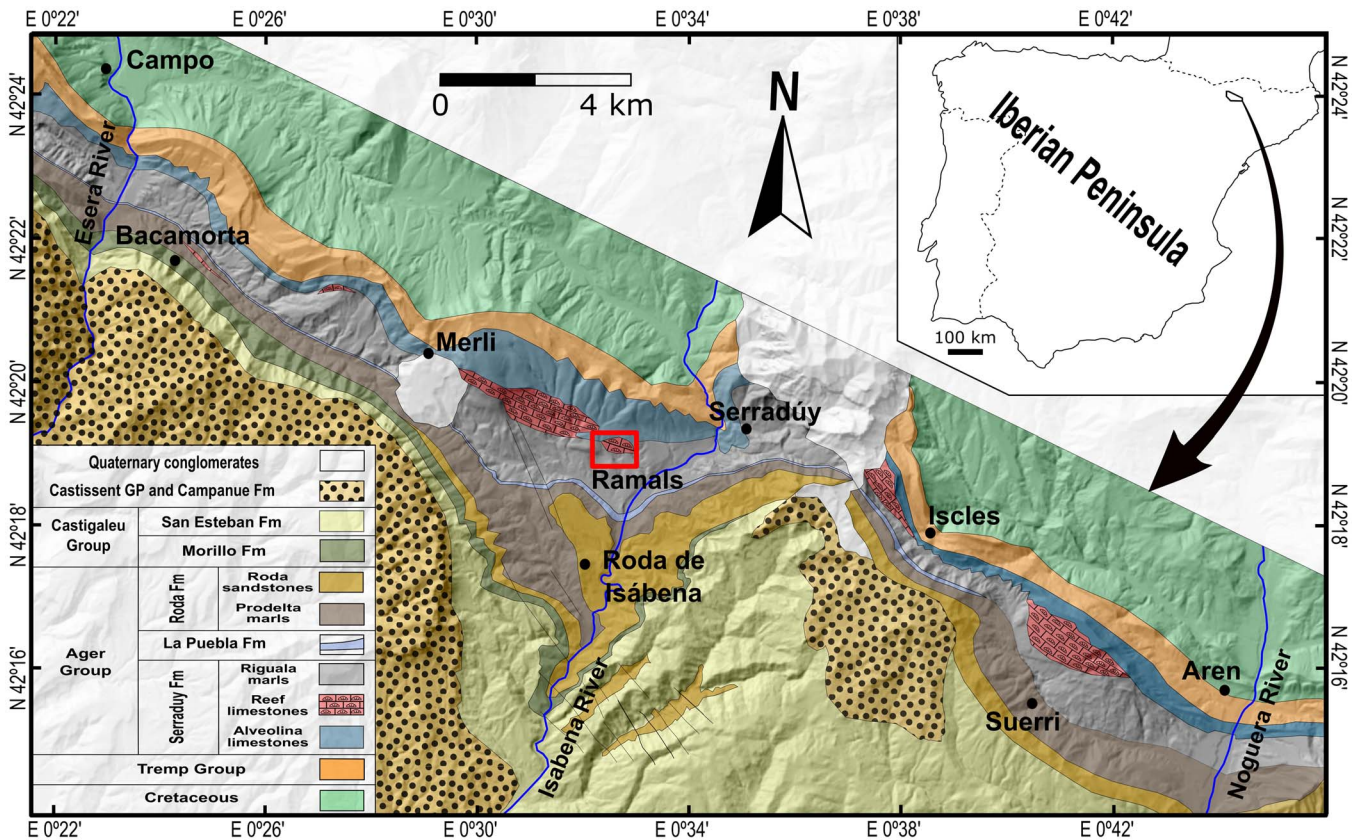


Figure 1. Geological map of the western sector of the Tremp-Graus Basin (modified after Serra-Kiel et al., 1994). The boxed area between Merli and Serraduy marks the location of the study area.

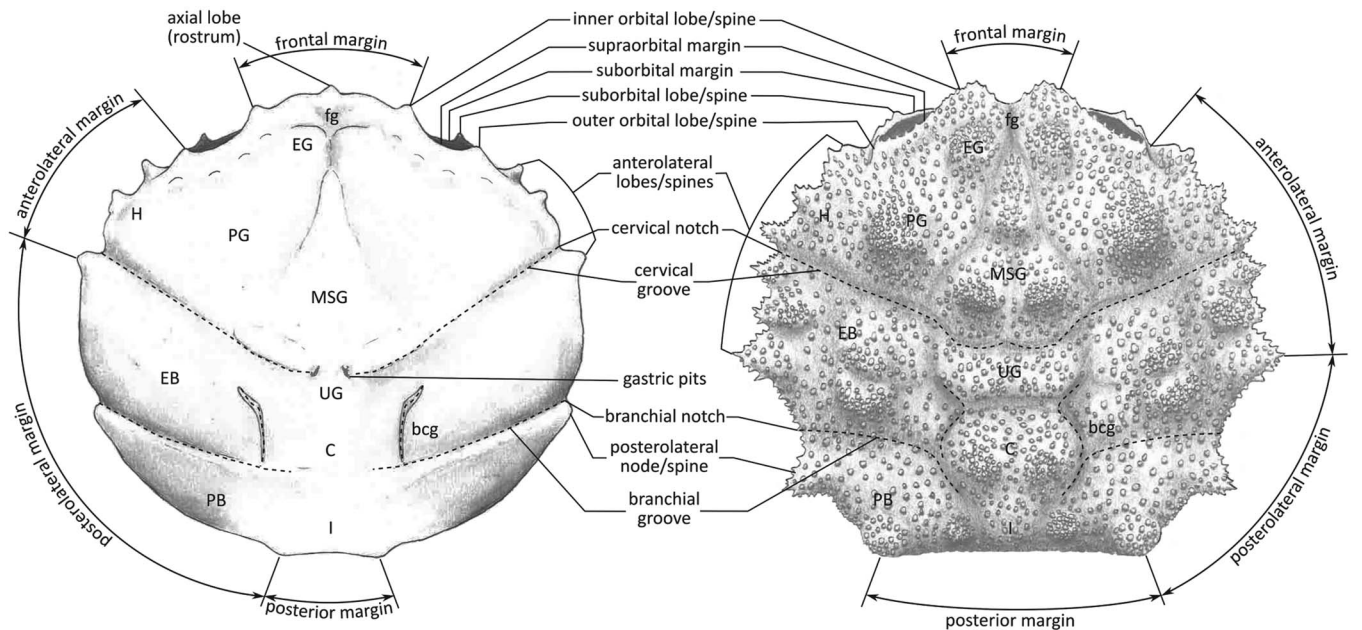


Figure 2. Carapace regions and terminology in a dromioid (s. lat.) crab used in the text (based on McLay, 1999). EG = epigastric region; PG = protogastric region; MSG = mesogastric region; H = hepatic region; UG = urogastric region; C = cardiac region; EB = epibranchial region; PB = postbranchial region (meso- and metabranchial regions); I = intestinal region; fg = frontal groove; bcg = branchiocardiac groove.

axial spine; the orbits are larger, with oblique supraorbital margin; the epibranchial spine is invariably weak, short, and thin; a more-projected lateral spine is situated posterior to the branchial notch, being posterolaterally directed. The lateral spines in *Basinotopus* are always weak, thin, and moderately long (see Busulini et al., 1983; Collins and Jakobsen, 2004; Beschin et al., 2005; Van Bakel et al., 2009).

The new genus shows a number of clearly distinct characters, such as a subpentagonal carapace, with the maximum width in the epibranchial region; the frontal margin is nearly straight, with a weakly projected axial spine, two longer and thin inner orbital spines; the outer portion of the supraorbital margin is nearly horizontal; the epibranchial spine is extremely large and long, with a very broad base; the second anterolateral spine is fairly strong, nearly fused to the epibranchial spine, both are in close approximation. On the basis of these features, we consider the erection of a new genus warranted. We transfer *Dromilites alpina* Glaessner, 1929 to the new genus because of similar outline of carapace and similar distribution of dorsal regions.

Mclaynotopus longispinosus new species
Figures 3, 4.

Type material.—The holotype is MGSB77597, a well-preserved carapace, with cuticle preserved; there are five paratypes: MGSB77598a–e.

Diagnosis.—Subpentagonal carapace. Trilobed front, lateral spines of similar size, axial spine somewhat smaller. Anterolateral margins with three long spines; second hepatic and the epibranchial nearly fused, close together. Epibranchial spine large, stout; base occupying entire epibranchial area. Tips of dorsal regions and dorsal granules blunt, clearly rounded.

Description.—Carapace subpentagonal, nearly as long as wide (length/width ratio about 0.95), broadly convex in both directions. Maximum width at level of epibranchial region, just posterior to extremely pronounced epibranchial spine. Dorsal surface strongly convex. Front broad, deflexed axially, broadly triangular or V-shaped in frontal view, with shallow axial depression, trilobed in dorsal view, with two robust inner orbital spines; the two inner orbital spines strong, stout, upwardly directed, not very projected, ventral side flattened, dorsal side rounded; axial spine situated in lower plane, short and robust subtriangular base, spinous tip, directed forward, visible in dorsal view. Orbits large, anterolaterally directed, slightly raised in lateral portion; outer orbital corner with deep incision, bounded by projected outer orbital and suborbital spines; subelliptical in frontal view, suborbital margin with strongly projected spine, with broadly triangular base and irregular lobe in distal portion.

Entire lateral margin with four spines, one small posterior tubercle, and two weak notches. Anterolateral margin nearly straight, only slightly convex, bearing two acute hepatic spines and one larger epibranchial spine, with broad triangular base; portion behind orbit, short, nearly vertical. Second hepatic spine larger than first spine, close to extremely projected epibranchial spine and almost fused to it. Epibranchial projection large,

projected, laterally and upwardly directed, with broadly triangular base occupying entire distal portion of epibranchial region. Anterolateral and posterolateral margins nearly equal in length, posterolateral nearly straight in first portion, broadly convex posteriorly, with thin, long postbranchial, conical spine, and small posterior tubercle. Lateral margins with two slight indentations, corresponding to intersection of cervical and branchial grooves. Posterior margin nearly straight, slightly concave axially, rimmed, slightly less wide than orbitofrontal margin.

Dorsal regions defined by swollen lobes, divided into portions by grooves. Cervical groove well defined, reaching ventral portion of carapace. Branchial groove straight, nearly horizontal, bounded posteriorly by strong rim, axially interrupted by broad cardiac swelling. Branchiocardiac grooves sinuous, deep, short. Mesogastric region subtriangular, with arched base, bounded by deep cervical groove; posterior portion divided into two gently swollen lobes, separated by shallow axial groove; anterior extension swollen, bearing notable scattered tubercles. Proto gastric region large; posterior portion defined by subelliptical swelling; anterior portion elongated, bearing tubercles. Hepatic region small, slightly inflated, with scarce tubercles. Suborbital region with small inflation. Urogastric region broad, arched, bounded by deep grooves, surface covered by large irregular pits and vertical depressions. Epibranchial region large, bearing two transverse swellings. Meso- and metabranchial regions undifferentiated, large, gently swollen, densely covered by small pits. Cardiac region large, subpentagonal, strongly swollen, bounded by numerous tubercles, bearing three notable tubercles; two anterior ones with large central pit and posterior one, situated apically, with some granules. Intestinal region small, depressed. Ventral portion of carapace with deep extensions of cervical and branchial grooves and with suborbital and subhepatic swellings. Chelipeds elongated; merus subtriangular in cross section, smooth; carpus slightly longer than tall; surface with some widely spaced smooth tubercles. Manus longer than tall, slightly divergent distally, elliptical in cross section; upper margin with three small, aligned tubercles; lower margin slightly concave at the base of the fixed finger, surface smooth (Fig. 3.6, 3.7).

Etymology.—The specific name refers to the elongated spines on the lateral carapace margins.

Other material examined.—Fifty-four incomplete carapaces (MGSB77630a–j; MGSB77632a–q; MGSB77634a–q; MPZ-2021/46; MPZ-2021/153–2021/161) and 15 isolated chelipeds (MGSB77620; MPZ-2021/148–2021/152).

Remarks.—*Dromilites alpina*, which was subsequently listed as *Basinotopus alpina* (see Collins and Jakobsen, 2004; Van Bakel et al., 2009), is a species that can be reassigned to *Mclaynotopus* n. gen. with confidence. Its carapace features match the generic diagnosis (see the preceding), e.g., the subpentagonal outline, the similarly distributed dorsal regions, and an extremely elongate epibranchial spine. However, the epibranchial projection in that species is much thinner, with the base not totally occupying the epibranchial margin. Moreover, the contiguous hepatic spine, which is nearly fused to it in the new species, is clearly separated in *M. alpina*. *Mclaynotopus alpina* also shows distinct dorsal

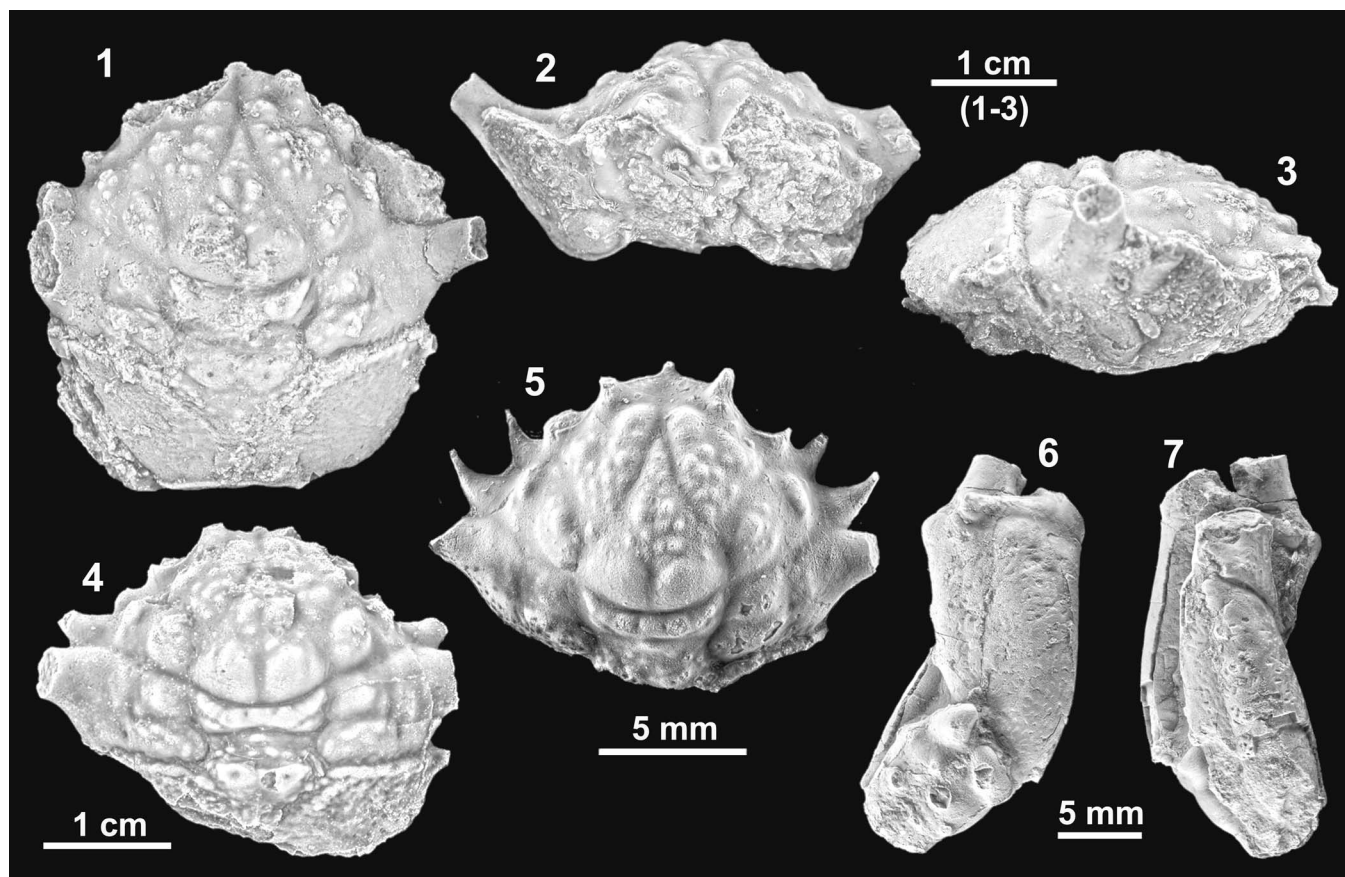


Figure 3. *Mclaynotopus longispinosus* n. gen. n. sp. from the Serraduy Formation (Huesca, North Spain). (1–3) Holotype MGSB77597 in dorsal, frontal, and right lateral views, respectively. (4) Paratype MGSB77598 in dorsal view. (5) Paratype MPZ-2021/153 in dorsal view. (6, 7) Isolated cheliped (MPZ-2021/148), presumably of *Mclaynotopus longispinosus*, in outer and inner views, respectively. Specimens whitened with ammonium chloride sublimate before photography.

regions: the protogastric and the anterior extension of the mesogastric are much more ridged. Regions in general have more acute conical tips, such as the mesogastric and epibranchial, and the urogastric has longer lateral portions (see Glaessner, 1929, pl. 8).

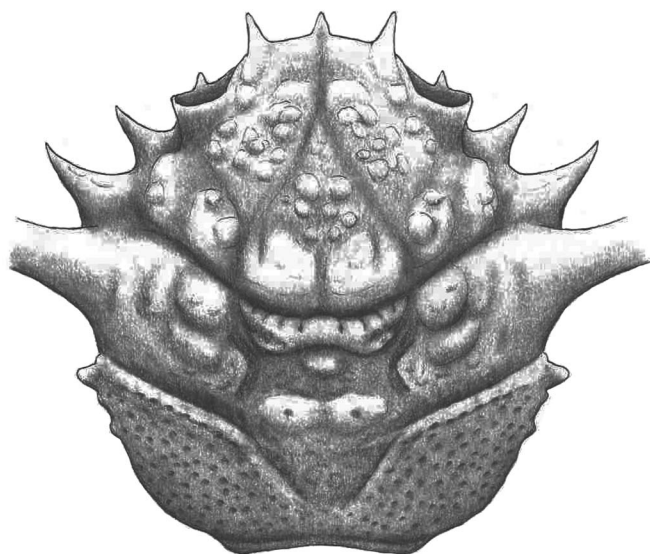


Figure 4. Reconstruction of *Mclaynotopus longispinosus* n. gen. n. sp.

Subfamily Dromiinae De Haan, 1833

Diagnosis.—“Carapace longer than wide to wider than long; rostrum typically bilobed; orbits without augenrest, deep, circular; orbital margin often with protuberance or rim, subuterorbital spine often visible in dorsal view; cervical groove weak; postcervical groove sometimes present; branchiocardiac groove present” (Karasawa et al., 2011, p. 541).

Genus *Torodromia* new genus

Type species.—*Torodromia elongata* n. sp. by present designation.

Diagnosis.—Carapace longitudinally elongate, slightly wider than long; frontal margin bilobed, with two thin, long inner orbital spines and barely visible axial spine; orbits large, concave, directed forward. Anterolateral margins with three conspicuously long spines; two posterior ones rather robust and with broad base. Posterolateral margin with single thin spine. Dorsal regions nearly smooth, with only gentle swellings and weak grooves. Small oblique depressions in gastric area.

Etymology.—The generic name combines *toro*, Spanish for bull, in reference to the horned rostrum, and *dromia*.

Remarks.—The main characters of *Torodromia* n. gen. allow placement in the Dromiinae. These include a carapace of equal length and width, a typically bilobed rostrum, a suborbital spine that is visible in dorsal view, weak cervical and branchial grooves, and marked branchiocardiac groove (Schweitzer et al., 2012; Feldmann and Schweitzer, 2019). Diagnostic features of the new genus include large and long spines on lateral carapace margins, barely defined dorsal regions, and a deep, short groove in the frontal margin. Fossil representatives of the Dromiinae can be easily distinguished from *Torodromia*, as indicated in the following.

Basadromia Artal et al., 2016, has a frontal margin with four spines, while lateral margins lack prominent spines, having merely small denticles. Dorsal regions in *Basadromia* are swollen; there are numerous grooves and a dense granulation. Artal et al. (2016) and Feldmann and Schweitzer (2019) placed this genus in the Dromiinae.

Pseudodromilites Beurlen, 1928 also possesses two strongly projected triangular spines on the frontal margin, and dorsal regions have pronounced grooves and are distinctly swollen. Lateral margins in *Pseudodromilites* have small lobes or small subtriangular spines while the dorsal surface is strongly granulated (De Angeli and Alberti, 2018, p. 158).

Quinquerugatus Frantescu, Feldmann, and Schweitzer, 2010 exhibits a nearly straight frontal margin when seen in dorsal view. It has larger supraorbital margins than in *Torodromia* and lateral margins bear small, short, and conical spines while the cervical groove is well defined, deep in the axial portion, bearing two small pits; the branchial groove is deep and well marked (Frantescu et al., 2010, p. 260).

The new genus can be differentiated from the extant *Cryptodromia* (Schweitzer et al., 2012) by possessing larger and longer spines on the lateral margins, a slightly developed axial spine in the frontal margin, a deep axial frontal groove, and deep branchiocardiac grooves.

Torodromia elongata new species
Figures 5.1–5.3, 6.

Type material.—The holotype is MGSB77595, a near-complete, well-preserved carapace, retaining cuticle. There is one paratype, MGSB77596, which lacks a portion of the posterior margin of the carapace.

Diagnosis.—As for genus (monotypy).

Description.—Carapace suboval, slightly wider than long (length/width ratio 0.93). Maximum width posterior to epibranchial spine. Dorsal surface convex in both directions. Front deflexed, relatively narrow, bilobed in dorsal view, strongly V-shaped in frontal view, margin slightly rimmed, with a short but deep axial groove; the two inner orbital spines strong, robust, directed forward, with broadly triangular base, the axial spine situated in lower plane, thin, short, inclined forward, poorly visible in dorsal view. Orbits large, arched in appearance in dorsal view, anterolaterally directed, slightly raised in lateral portion; large, subelliptical in frontal view, bearing small, thin suborbital spine. The whole lateral margins broadly arched, with four projected spines and two faint notches. Anterolateral margin arched, bearing two thin,

long hepatic projections (first one thinner, acute, second one larger) and strong epibranchial spine with broadly triangular base. Posterolateral margin equaling width of anterolateral, arched, bearing notable notch and posterior thin, projected, branchial spine. Lateral margins with two marked indentations corresponding to cervical and branchial grooves. Posterior margin nearly straight, slightly rimmed, slightly wider than frontal margin. Dorsal regions relatively well defined by gently swollen lobes and shallow grooves. Cervical groove weakly marked, more evident in central portion, interrupted by two small gastric pits. Branchial groove well defined, posteriorly bounded by a thin ridge. Branchiocardiac grooves deep, short, and axially concave. Epigastric regions small, well marked, swollen, separated by short but deep groove. Mesogastric and protogastric regions scarcely differentiated. Hepatic region large and gently swollen. Urogastric region subtrapezoidal and slightly inflated. Epibranchial and postbranchial regions large, gently swollen, separated by thin ridge. Cardiac region broad, swollen, subpentagonal. Intestinal region small, depressed. Anterior dorsal surface covered with diminutive pits.

Etymology.—From the Latin *elongatus*, in reference to its elongated carapace shape.

Other material examined.—Two additional specimens, MGSB77631a, b.

Remarks.—*Torodromia elongata* n. gen. n. sp. is morphologically close to the extant *Cryptodromia tuberculata* Stimpson 1858, which has an elongated carapace outline, the frontal margin characterized by a thin axial spine and two projected lateral spines, and the lateral margins arched, bearing thin and relatively elongated spines (McLay and Ng, 2005, p. 8). However, the new fossil species differs in having larger and longer spines on the lateral margins while the axial spine on the frontal margin is slightly developed, the axial frontal groove is deep, and branchiocardiac grooves are also deep.

Quinquerugatus holthuisi Frantescu, Feldmann, and Schweitzer, 2010, differs in several features (see the preceding); the familial level placement of this taxon should be revised. It would appear better accommodated in the subfamily Sphaerodromiinae (see the following).

Subfamily Sphaerodromiinae Guinot and Tavares, 2003

Diagnosis.—“Carapace longer than wide or about as long as wide; rostrum projecting beyond orbits; orbital area composed of two contiguous circular depressions, outer depression deeper, essentially continuous with orbit, poorly separated from orbit; lateral rim merging with or separated only by short distance from outerorbital angle; subhepatic region inflated; cervical groove weak, postcervical and branchiocardiac grooves well defined” (Schweitzer et al., 2012, p. 33).

Genus *Basidromilites* new genus

Type species.—*Basidromilites glaessneri* n. gen. n. sp. by the present designation.

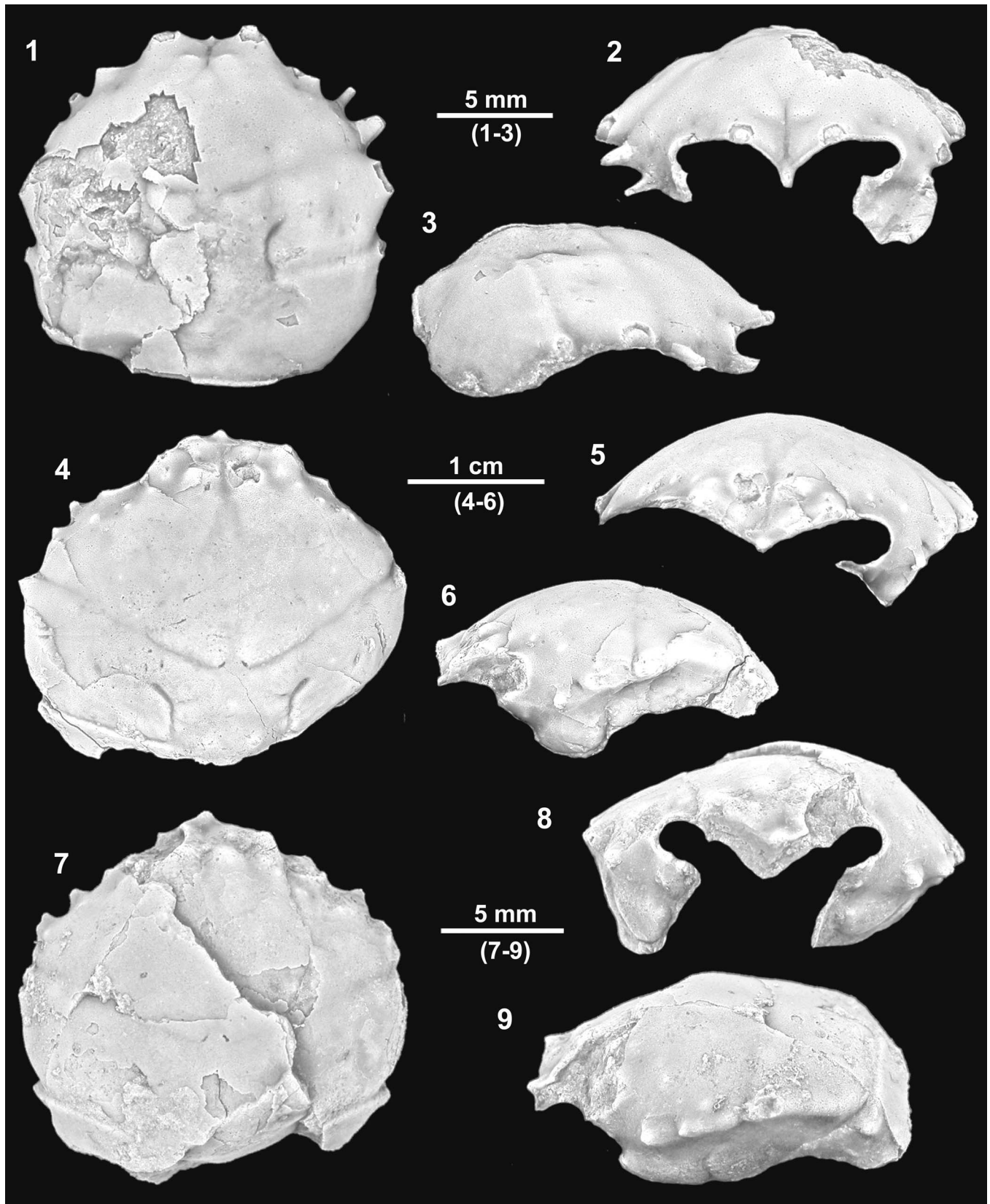


Figure 5. Dromioids from the Serraduy Formation (Huesca, North Spain). (1–3) *Torodromia elongata* n. gen. n. sp. holotype MGSB77595 in dorsal, frontal, and right lateral views, respectively. (4–9) *Basidromilites glaessneri* n. gen. n. sp.: (4–6) holotype MGSB77599 in dorsal, frontal, and left lateral views, respectively; (7–9) paratype MGSB77600 in dorsal, frontal, and left lateral views, respectively.

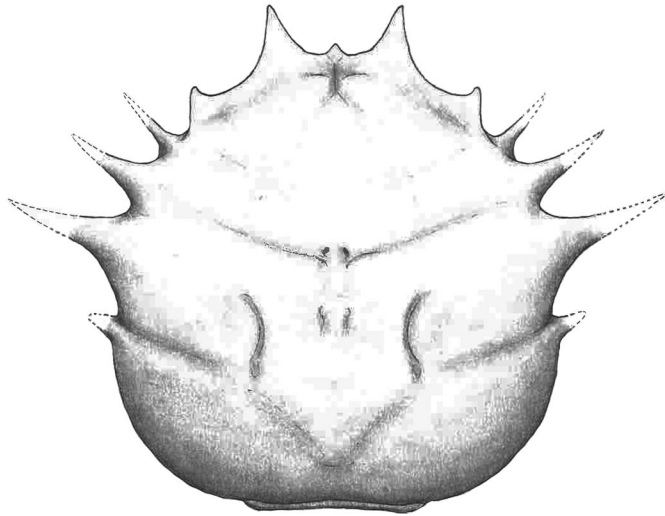


Figure 6. Reconstruction of *Torodromia elongata* n. gen. n. sp.

Other species.—*Basidromilites pastoris* (Via, 1959).

Diagnosis.—Carapace subcircular, length nearly equaling width. Maximum width at level of epibranchial region. Front subtriangular, trilobed in dorsal view, axial lobe slightly projected. Entire lateral margin convex, angular. Anterolateral margins broadly arched, bearing small spine and angular, crested, complex node. Small epibranchial spine behind cervical notch. Posterolateral margin broadly convex, bearing a small node behind branchial groove. Cervical groove slightly developed, branchial groove bounded by a ridge, branchiocardiac grooves short, arched, deep. Dorsal regions smooth except for small epibranchial swellings.

Etymology.—The generic name combines the root *Basi*, to match *Basinotopus*, and *dromilites*, a common generic name among dromioids.

Remarks.—The main characters of *Basidromilites* n. gen. match the diagnosis of the subfamily Sphaerodromiinae. These include a subglobose carapace of nearly equal width and length, the front projected beyond orbits, the dorsal surface with regions poorly defined, and weakly marked dorsal grooves (Guinot and Tavares, 2003; Schweitzer and Feldmann, 2010) as indicated in the preceding. *Basidromilites* n. gen. can be differentiated from *Dromidia bedetteae* Blow and Manning, 1996 in that the latter exhibits a narrow, U-shaped frontal margin with the lateral spines very projected, a suboval, transversely elongate carapace outline, and a marked suborbital spine that is clearly visible in dorsal view (Blow and Manning, 1996, pl. 1). *Quinquerugatus* shows peculiar characters, such as a near-straight front in dorsal view, a subpentagonal carapace outline, a very projected suborbital spine that is visible in dorsal view, and urogastric and cardiac regions that are swollen (Franțescu et al., 2010, p. 260, fig. 3).

Basidromilites glaessneri new species
Figures 5.4–5.9, 7.

Type material.—The holotype, an almost complete carapace, is MGSB77599. There is one paratype, MGSB77600, in comparable preservation.

Diagnosis.—Species of *Basidromilites* characterized by three clear lobes on frontal margin, with axial one more projected, dorsal surface rather smooth, dorsal grooves weak.

Description.—Carapace subcircular. Length nearly equaling the width (length/width ratio about 0.95). Maximum width at level of epibranchial region, about carapace mid-length. Dorsal surface strongly convex in both directions. Front broad, V-shaped in frontal view, short, shallow axial groove, strongly deflexed axially, broadly triangular, trilobed in dorsal view, with two robust lateral lobes; the two inner orbital lobes robust, not very projected; axial lobe situated in a lower plane, short and robust, subtriangular, directed forward, visible in dorsal view. Orbits large, anterolaterally directed, slightly raised in lateral portion, with suborbital spine visible dorsally; subelliptical in frontal view, bearing two small spines on suborbital margin.

Entire lateral margins markedly ridged, angular in cross section, bearing four projected nodes and two notable notches (Figs. 5, 7). Anterolateral margin broadly arched, bearing two strong lateral hepatic spines and strong epibranchial spine, with broadly triangular base; portion behind orbit short, arched. First lateral spine short yet robust, with blunt tip, not very projected, second node complex, composed of three ridged lobes, first two more pronounced. Posterolateral margins of equal size, broadly arched, bearing a strong branchial indentation and blunt yet robust branchial node. Entire lateral margin with two notable indentations, corresponding to cervical and branchial grooves. Posterior margin not well preserved.

Dorsal regions barely differentiated. Epibranchial regions well defined by two small subcircular swellings. Hepatic and suborbital regions bearing small tubercle. Mesogastric and urogastric regions undifferentiated, large, smooth. Epibranchial region large. Cardiac region defined only by branchiocardiac grooves. Ventral portions of carapace broadly swollen, suborbital region small, inflated; subhepatic region large, strongly swollen. Cervical groove shallow, V-shaped, weakly marked from side to side of carapace, interrupted by two oblique axial slits, present in ventral portion. Branchial groove well defined, oblique, relatively deep in outer portions, bounded by marked ridge, interrupted by broad cardiac area, deep in ventral portion. Branchiocardiac grooves arched, short.

Etymology.—The specific name honors Martin Fritz Glaessner (1906–1989) for his contributions to our knowledge of fossil dromiacean crabs.

Other material examined.—Five incomplete carapaces (MGSB77619a–d, MPZ-2021/162).

Remarks.—The new genus differs from species of *Dromilites* (e.g., *D. bucklandii* Milne Edwards, 1837; *D. belli* Van Bakel et al., 2017; *D. montenati* Robin et al., 2017; *D. vicensis*

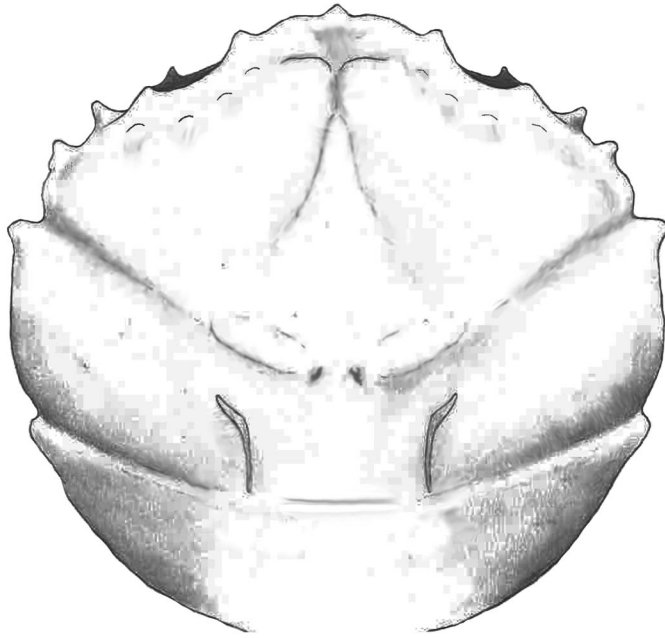


Figure 7. Reconstruction of *Basidromilites glaessneri* n. gen. n. sp.

Barnolas, 1973), which all have a frontal margin with two prominent lateral nodes, an axial node that is barely visible in dorsal view (see Milne Edwards, 1837; Via, 1959; Barnolas, 1973; Robin et al., 2017; Van Bakel et al., 2017) while usually the dorsal grooves are more clearly marked (see Barnolas, 1973), and a trend to have dorsal swellings (see Van Bakel et al., 2017).

However, the frontal margin in *Dromilites pastoris* Via, 1959 is similar to that of the present species, with a slightly projected axial lobe and similar cervical and branchial grooves. *Dromilites pastoris* does differ in having three small, lobe-like hepatic nodes anterior to the cervical groove and two small lateral nodes behind the cervical groove, two clear cardiac pits, and a prominent ridge behind the branchial groove. On this evidence, *D. pastoris* is reassigned to the new genus.

Basidromilites sp.
Figures 8.3, 8.4

Description.—Carapace suboval, longer than wide (length/width ratio about 1.14). Maximum width probably at level of epibranchial region, about carapace mid-length. Dorsal surface strongly convex in both directions. Front broad, conspicuously deflexed axially, broadly triangular, trilobed in dorsal view, with two robust lateral nodes; the two outer orbital lobes strong, robust, not very projected; axial lobe situated in lower plane, directed forward, barely visible in dorsal view. Front V-shaped in frontal view, shallow axial depression. Orbits large, anterolaterally directed, margins markedly raised; subelliptical in frontal view, with outer orbital corner pointed. The whole lateral margins not well preserved, appearing to have been angular in cross section. Anterolateral margin with one small hepatic node and larger posterior node anterior to cervical notch and one larger lobe posterior to cervical notch. Posterolateral margin somewhat longer, bearing angular lobe in front of

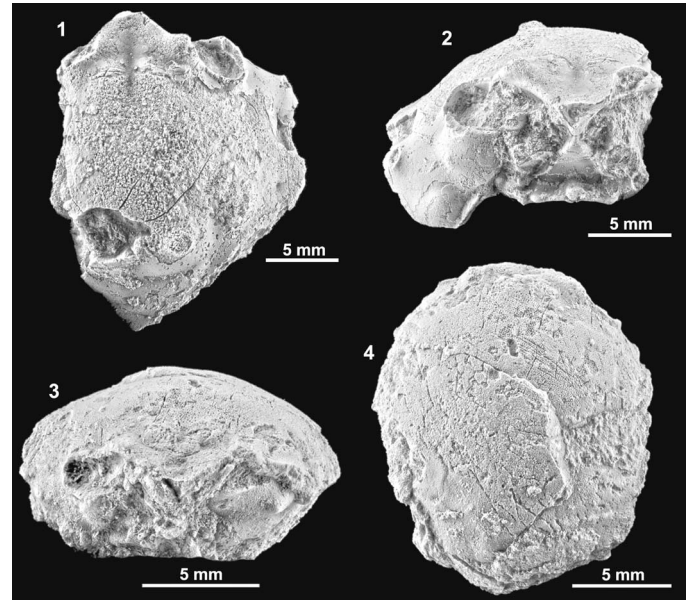


Figure 8. Specifically indeterminate dromiids from the Serraduy Formation (Huesca, North Spain). (1, 2) *?Basinotopus* sp. (MGSB77912) in dorsal and frontal views, respectively. (3, 4) *Basidromilites* sp. (MGSB77628) in frontal and dorsal views, respectively.

branchial notch. Posterior margin not preserved. Gastric regions undifferentiated except for two small epigastric inflations. Branchial regions large, broadly swollen, separated by weak branchial groove. Hepatic region small, barely differentiated. Cervical and branchial grooves weakly developed, more visible in distal portion. Branchiocardiac grooves not well preserved. Dorsal surface densely covered by diminutive pits.

Material.—A single, near-complete carapace, MGSB77628.

Remarks.—The slightly projected frontal margin, with three discrete nodes, and the lobes on the lateral margins (mainly the angular hepatic lobe) are similar to *Basidromilites* n. gen. The smooth carapace with weak cervical and branchial grooves also matches the diagnosis of that new genus. *Basidromilites* sp. bears a more elongated carapace outline and more weakly marked dorsal carapace grooves than *Basidromilites glaessneri*.

Family incertae sedis
Genus *Basinotopus* M'Coy, 1849

Type species.—*Dromilites lamarckii* Desmarest, 1822 by monotypy.

?Basinotopus sp.
Figure 8.1, 8.2

Material.—A single incomplete carapace, MGSB77912.

Description.—Carapace of probable elongate outline. Maximum width probably at level of epibranchial region, about carapace mid-length. Dorsal surface strongly convex in both directions. Front broad, deflexed axially, broadly

triangular, trilobed in dorsal view, with two robust lateral spines; the two inner orbital spines strong, robust, not very projected, with blunt tip, upwardly directed; axial spine situated in lower plane, very robust, broadly subtriangular, directed forward, entirely visible in dorsal view. Front V-shaped in frontal view, shallow axial depression. Orbits large, anterolaterally directed, margins markedly raised, with suborbital spine and suborbital margin, clearly visible dorsally; subelliptical in frontal view, bearing strong spine, with broadly triangular base on suborbital margin. Lateral margins not well preserved. Epigastric regions with small yet distinct swellings. Mesogastric regions well defined by large, projected, subcircular lobes. Hepatic region small, bearing small subcircular swelling. Suborbital and subhepatic regions large, broadly swollen. Cervical groove marked only in axial portion. Epistome robust, large, subtriangular.

Remarks.—This dromioid is of robust appearance, with thick cuticle and stout marginal nodes. The projected front, and particularly the robust axial spine, plus the two lateral spines recall *Basinotopus tricornis* Collins and Jakobsen, 2004. As seen in the genus *Basinotopus* are also the closed and obliquely directed orbit, with the suborbital margin and suborbital spine well visible in dorsal view. The main difference is the smooth or pitted carapace surface, which is also characteristic of *Lucanthonisia* Van Bakel et al., 2009. Features preserved in MGSB77912 match those of genera assigned to the Basinotopinae (Karasawa et al., 2011; Schweitzer et al., 2012).

Family Dynomenidae Ortmann, 1892
Subfamily Paradyomeninae Guinot, 2008

Diagnosis.—“Body thick, uniformly covered with tubercles, granules and/or spines. Carapace longer than wide or as long as wide, sometimes slightly wider than long, subquadrangular, may be suboval; dorsal surface convex, distinctly areolated, often with swellings or bosses, usually densely ornamented. Cervical groove entire, not reaching lateral carapace margin; frontal, cervical, branchial, branchiocardiac grooves pronounced. Anterolateral margins subparallel or slightly convex, distinctly joining corners of buccal cavity, armed with 4–6 irregular salient teeth or prominences. Posterolateral margin with produced and elongated subdistal tooth; a tooth present posteriorly, variously salient. Posterior region of carapace recessed; posterior margin strongly concave. Frontal margin usually distinctly projecting, tridentate, rarely bidentate; supraorbital margin with small tubercles, notch; infraorbital margin with granules, teeth, notches. Orbits oblique, clearly visible from dorsal view” (Guinot, 2008, p. 11–13).

Genus *Kromtitis* Müller, 1984

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

Other species included.—*K. bicuspidatus* Beschin, De Angeli, and Zorzin, 2009b; *K. daniensis* Collins, 2010; *K. koberiformis* Beschin et al., 2007; *K. levigatus* Beschin

et al., 2007; *K. lluisprietoi* Ossó, 2019; *K. pentagonalis* Müller and Collins, 1991; *K. pseudolothi* Beschin et al., 2016b; *K. spinulata* Portell and Collins, 2004; *K. subovatus* Beschin et al., 2007; *K. tergospinosus* Beschin, Busulini, and Tessier in Beschin et al., 2018; *K. tetratuberculatus* Beschin et al., 2002.

Kromtitis isabenensis new species

Figures 9, 10

Type material.—The holotype, MGSB75450, is a complete carapace (16 mm long and 15 mm wide) with well-preserved cuticle. There are two paratypes, MGSB75451a, b.

Diagnosis.—Carapace subquadrate, slightly wider than long, lateral margins arched; frontal margin projected, with two inner orbital nodes and deep axial notch; orbits inclined, with oblique supraorbital and suborbital margins; anterolateral margins broadly arched, bearing six robust, subtriangular spines; posterolateral margin converging posteriorly, bearing a strong spine and notable concavity behind epibranchial spine; posterior margin straight; dorsal regions well defined by numerous raised swellings with rounded sides; metabranchial region with horizontal row of four swellings; dorsal surface uniformly and densely granulate.

Description.—Carapace subquadrate, lateral margins arched, slightly wider than long (length/width ratio about 0.85). Maximum width at level of epibranchial region, about carapace mid-length. Dorsal surface convex in both directions. Front V-shaped in frontal view, narrow, granulated, strongly deflexed axially, broadly triangular, with deep axial groove; bilobed in dorsal view, with two robust lateral nodes and V-shaped axial incision; the two inner orbital nodes strong, robust, markedly projected. Orbits large, anterolaterally directed, granulated, slightly raised in lateral portion; margin strongly angular in outer corner, with two suborbital nodes visible dorsally; subelliptical in frontal view, bearing acute outer spine and stout inner lobe on suborbital margin. Entire lateral margins broadly arched, bearing numerous projected spines and small posterior concavity; postbranchial spine is the largest. Anterolateral margin broadly arched, bearing at least three projected irregular spines anterior to cervical notch, and two posterior ones; projected spines covered with numerous tubercles and intermediate space bearing acute granules; portion behind orbit short, arched. Posterolateral margins of similar length, slightly sinuous, bearing a very small epibranchial spine, slight concavity, relatively long and acute projection, and blunt posterior node. Posterior margin concave, equaling orbitofrontal margin in length. Dorsal regions defined by swollen lobes and shallow depressions. Dorsal grooves shallow, weakly marked. Cervical groove weakly defined, deeper in ventral portion of carapace. Branchial groove weakly marked in marginal portion, deeper in ventral portion of carapace. Branchiocardiac grooves arched. Mesogastric region subtriangular, with arched base, bounded by shallow cervical groove; posterior portion defined by two strong protuberances separated by shallow depression; narrow anterior extension bearing small swelling. Protogastric region large, posterior portion defined by strongly projected

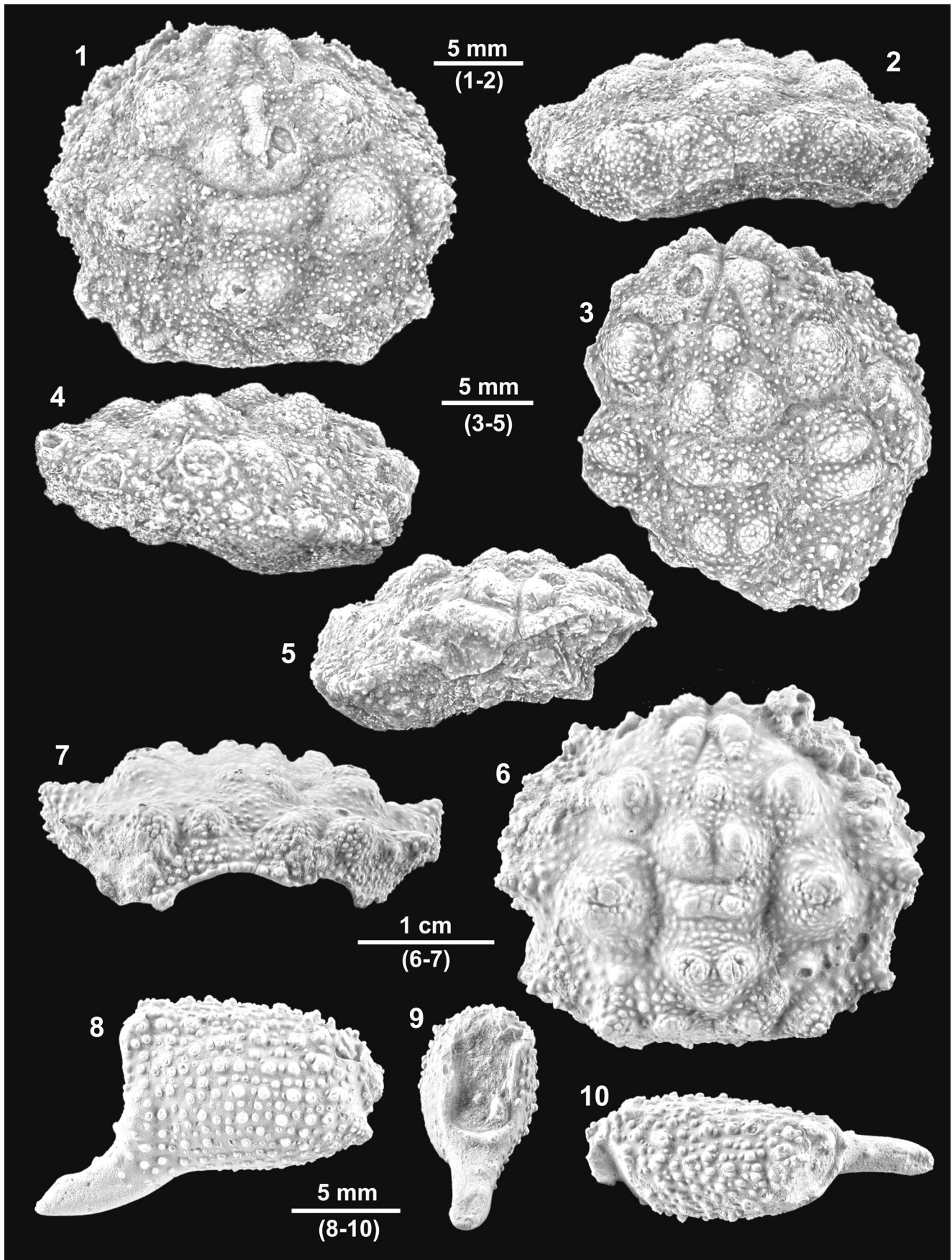


Figure 9. *Kromititis isabenensis* n. sp. from the Serraduy Formation (Huesca, Spain). (1, 2) Holotype (MGSB75450) in dorsal and posterior views, respectively. (3–5) Paratype (MGSB75451a) in dorsal, left lateral, and frontal views, respectively. (6, 7) MGSB77633 from Carrasquero, near Ramals, in dorsal and posterior views, respectively. (8–10) Isolated propodus, presumably of *Kromititis isabenensis* n. sp., in left lateral, frontal, and dorsal views, respectively (MPZ-2021/163).

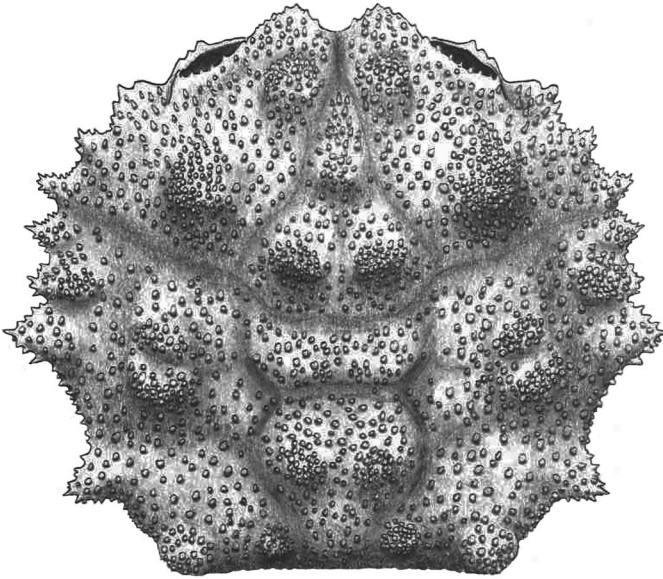


Figure 10. Reconstruction of *Kromtitis isabenensis* n. sp.

swelling, anterior portion elongated, joining epigastric swellings. Hepatic region small, bearing small tubercle. Urogastric region low, narrow, with two lateral tubercles. Epibranchial region large, inner portion defined by strong subcircular elevation, usually barely divided by a median sulcus; outer portion bearing two smaller elevations, anterior rounded, small, posterior stronger, with acute tip. Mesobranchial region depressed. Metabranchial regions large, with two strong protuberances, outer portion larger, reaching posterolateral carapace corner. Cardiac region large, raised, subpentagonal inverted in shape, anterior portion bearing strong elevations, apex barely marked. Intestinal region small, depressed. Dorsal surface densely covered by tiny granules.

Etymology.—The specific name refers to the municipality of Isabena, located a few kilometers to the south of the study area.

Other material examined.—MGSB77635a, b, two incomplete carapaces from Barranco de Ramals. Another well-preserved carapace, MGSB77633, originates from the neighboring locality of Carrasquero (Huesca). In addition, there are 30 isolated propodi (MGSB85952; MPZ-2021/163–2021/171).

Remarks.—*Kromtitis isabenensis* n. sp. can be differentiated from congeners on the basis of its projected front, with a deep V-shaped notch; oblique supraorbital margins, inclined at about 45°; a lateral margin with stout and subtriangular spines; a different distribution of dorsal regions, with broadly rounded tips; and a dorsal surface that is densely and uniformly covered by tiny granules.

The genus *Kromtitis* has previously been linked to certain extant dynomenids, such as *Paradynomene* Sakai, 1963 (see Beschin et al., 2007, p. 27; Guinot, 2008, p. 21). In *K. isabenensis*, as well as in its congeners, all features are those also seen in

modern representatives of the subfamily Paradynomeninae (see McLay and Ng, 2005). The four tubercles in the posterior carapace portion (metabranchial area) in *K. isabenensis* are a diagnostic feature of the genus *Paradynomene* (see McLay and Ng, 2005). This conservative character has often not been mentioned in previous papers. The concavities in the posterolateral margins are also remarkable. Finally, the orbitofrontal construction is similar, in dorsal view, in both *K. isabenensis* and *P. tuberculata* Sakai, 1963 (McLay and Ng, 2004, p. 5).

Kromtitis isabenensis is morphologically close to *K. lluispietroi* Ossó, 2019 (both have a subquadrangle outline, granular nodes on the lateral margins, and similarly distributed dorsal regions). However, the latter is easily distinguished in having clearly deeper cervical groove, an inner epibranchial swelling that is clearly separated into two differentiated portions, one below the other, and a dorsal surface that is covered by non-uniform and irregular granules (“surface sparsely granulate with coarse granules,” according to Ossó, 2019, p. 3). In addition, the dorsal regions are covered by numerous tubercles of different sizes, the spines on the lateral margins are composed of numerous tubercles of different sizes, and the concavity in the posterolateral margin is more clearly marked.

The new species is also close to *K. koberiformis*, but that species differs in having a straighter front with projected inner orbital spines. In addition, the posterior margin is straighter and broader and dorsal regions clearly differentiated, smaller, and more raised, like large tubercles. The dorsal granulation is also dense, but with larger and more irregular granules. *Kromtitis koberi*, type species of the genus, is easily distinguished by its more clearly ridged dorsal regions and irregular granules that are seen only on the highest portions of carapace regions. *Kromtitis tetratuberculatus* has an arched frontal margin, larger, more rounded swellings in dorsal regions, and larger dorsal granules, while *K. subovatus* exhibits a projected frontal margin with a less clearly developed median notch, and dorsal regions are more strongly tuberculated with less-evident dorsal granulation. *Kromtitis levigatus* differs even more, with a straight frontal margin, dorsal regions with fewer divisions, and a lack of small granules on the dorsal surface.

The sole American species, *K. spinulata*, is characterized by a nearly subelliptical outline, being wider than long, a projected axial portion of the frontal margin, long and acute spines on the lateral margins, and a lack of surface granulation. *Kromtitis pentagonalis* is clearly distinct in having larger, close-set dorsal swellings on dorsal regions, with limited space between them, and a smooth dorsal surface, without granules (Müller and Collins, 1991, pl. 3).

Genus *Sierradromia* new genus

Type species.—*Sierradromia gladiator* n. sp. by present designation.

Diagnosis.—Carapace transversely subelliptical, slightly wider than long; frontal margin projected, with two strong inner orbital spines and a deep axial notch; entire lateral margins broadly arched, bearing seven long, robust, and dorsoventrally flattened spines; posterior margin narrow, nearly straight; dorsal regions conspicuously subdivided, with numerous

strongly raised, conical swellings; two longitudinal axial grooves bounding mesogastric, urogastric, and cardiac regions; tips of dorsal regions with perforations.

Etymology.—The generic name derives from its resemblance to a mountain range, *sierra* in Spanish, and the suffix *dromia*.

Remarks.—The placement of extinct genera within the Dromiacea has always been controversial (Guinot, 2008, 2019; Guinot et al., 2013). Ventral characters are rarely preserved in fossil brachyurans, which explains why genera have been assigned to different families or subfamilies on the basis of few characters, in most cases only those of dorsal carapace (Schweitzer and Feldmann, 2010; Schweitzer et al., 2010, 2012; Karasawa et al., 2011). On the basis of particular dorsal carapace features, such as arched lateral margins, a projected frontal margin with two intraorbital nodes and a deep axial notch, inclined orbits with oblique supraorbital and suborbital margins, broadly arched anterolateral margins with some spines, a backward-converging posterolateral margin, well-defined dorsal regions by raised swellings, and a metabranchial region with a horizontal row of four swellings (in this case conical spines), we tentatively place *Sierradromia* n. gen. in the subfamily Paradynomeninae.

Sierradromia gladiator new species
 Figures 11, 12

Type material.—Holotype, a near-complete carapace, is MGSB75454. There are two paratypes, both of which are slightly compressed: MGSB75455a, b.

Diagnosis.—As for genus (monotypy).

Description.—Carapace subelliptical, slightly wider than long (length/width ratio about 0.91). Maximum width at level of epibranchial region, just posterior to second epibranchial spine. Dorsal surface strongly convex in both directions, flanks of carapace oblique. Front V-shaped in frontal view, narrow, deflexed axially, fairly bilobed in dorsal view, with two notable lateral spines and deep axial indentation, deep axial groove; the two inner orbital spines robust, short; axial node situated in lower plane, not visible in dorsal view.

Orbits large, anterolaterally directed, slightly raised in lateral portion, with strong suborbital spine visible dorsally; subelliptical in frontal view; bearing a strongly projected, robust subtriangular spine on ventral orbital region. The whole lateral margins with seven robust spines and three notably deep notches. Anterolateral margin broadly arched, with two strong hepatic spines and two projected epibranchial spines, portion posterior to outer orbital corner strongly concave. All projections robust, dorsoventrally flattened, laterally and upwardly directed; two epibranchial largest, with broad subtriangular base, separated by short yet deep indentation. Posterolateral margins of similar length, broadly arched, bearing two strong spines in meso- and metabranchial marginal sides, strongly projected, dorsoventrally flattened, and upwardly directed. Posterior

margin nearly straight, weakly concave, slightly narrower than orbitofrontal margin.

Dorsal regions well defined by shallow grooves and projected protuberances; axial swellings with rounded tip, upwardly directed, marginal swellings more conical, laterally directed. Mesobranchial region subtriangular with rounded sides; defined by two strong posterior protuberances and a smaller axial protuberance in anterior extension. Protogastric region defined by two protuberances of similar size, situated obliquely. Epigastric regions small, two transverse inflations separated by shallow groove. Hepatic region small, bearing weak conical swelling. Urogastric region inverted subtrapezoidal in shape, large, broad, and long, bearing two strong swellings with rounded tips. Cardiac region large, subpentagonal, transversely inflated, anterior portion with large pits. Epibranchial region large, bearing four conical protuberances. Meso- and metabranchial regions undifferentiated, bearing two transverse inflations. Intestinal region small, depressed. Ventral portion of carapace with conical suborbital spines and subhepatic and subbranchial inflations. Cervical groove shallow but well defined, well marked on ventral side and notching lateral margins. Branchial groove barely marked, bearing irregular small inflations and pits, reaching and notching lateral margins. Branchiocardiac groove sinuous, relatively deep. Dorsal surface densely covered by diminutive pits, bearing small perforations, mainly on highest part of the swollen regions.

Etymology.—The specific name “gladiator” refers to the fictitious Roman legionary, Maximus Decimus Meridius, in view of the resemblance of the carapace to the helmet that he wears in the film *The Gladiator*.

Other material examined.—MGSB77629a–q; MGSB77913a–e; MPZ-2021/50; MPZ-2021/172; MPZ-2021/173.

Remarks.—The new taxon is clearly distinct from *Kierionopsis nodosa* Davidson, 1966 (see also Armstrong et al., 2009, p. 749), which was assigned to the Dromiinae (Schweitzer et al., 2010) and subsequently transferred to the Dynomenidae (Schweitzer et al., 2012). The genus *Kierionopsis* Davidson, 1966 differs in having a much more elongated outline and in the number and shape of the spines on the lateral margins, the deeper cervical and branchial grooves, and the differently situated dorsal regions that are also distinct in shape and number, mainly the cardiac region, which is extremely raised and directed backward.

Sierradromia gladiator n. gen. n. sp. is superficially close to *Dromilites montenati*; however, the latter can be distinguished by the different number, shape, and length of the projections on the lateral margin. In addition, the dorsal regions exhibit important differences in shape, size, and distribution, being defined by small tubercles rather than raised conical swellings, and the dorsal grooves are clearly distinct in shape, course, and depths. The orbits are distinct, and the segment behind the outer corner is utterly different while the posterior margin is extremely concave (weakly concave or nearly straight in the new genus and species), and the carapace outline appears to be more subcircular.

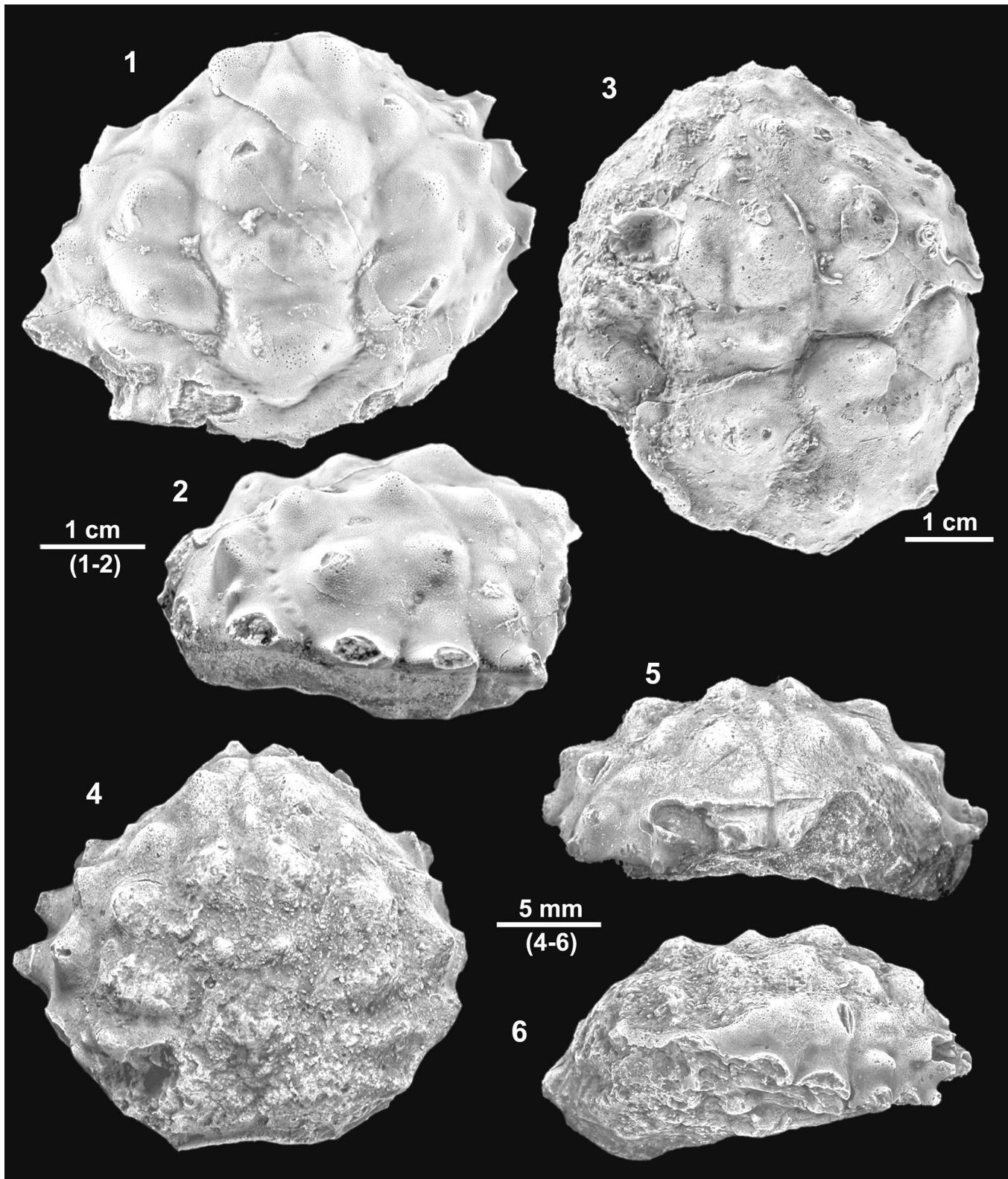


Figure 11. *Sierradromia gladiator* n. gen. n. sp. from the Serraduy Formation (Huesca, Spain). (1, 2) Holotype (MGSB75454) in dorsal and right lateral views, respectively. (3) Dorsal view of paratype (MGSB75455a) with some epibionts (serpulids and oysters). (4–6) Paratype (MGSB75455b) in dorsal, frontal, and right lateral views, respectively.

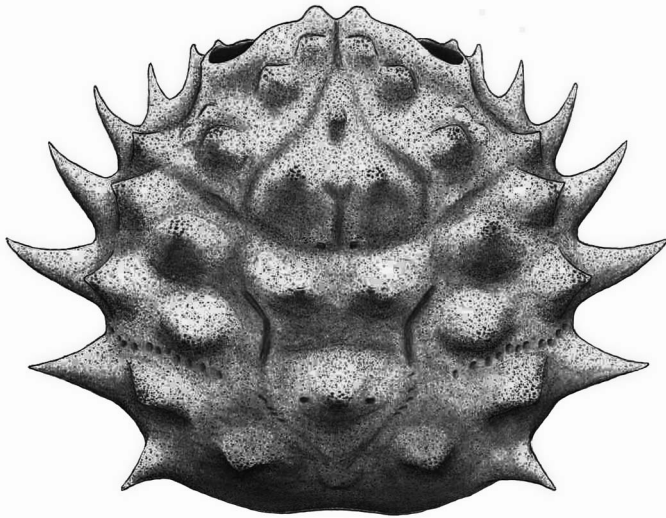


Figure 12. Reconstruction of *Sierradromia gladiator* n. gen. n. sp.

Eocene dromioid crabs in time and space

Modern dromioids are important constituents at tropical and subtropical latitudes and are represented by more than 140 species (e.g., Guinot and Tavares, 2003; De Grave et al., 2009). Usually, they are associated with coral- and sponge-rich environments and hard substrates (reefs, forereefs, or coral rubble) ranging from the intertidal to deep waters (1–450 m; e.g., McLay, 1993, 2001; Takeda and Manuel-Santos, 2006). Dromioids usually carry fragments of sponges or other objects with the help of P4–P5 (Dromiidae) or hide in crevices of coral and other hard substrates (Dynomenidae) (cf. McLay, 2001).

The Eocene dromioid assemblage from Ramals corresponds to taxa associated with reef environments. Other localities exposing Paleocene and Eocene rocks across Europe have similar dromioids and dynomenids (e.g., Beschin et al., 2007, 2015, 2016a, b, 2018, 2019; Tessier et al., 2011). However, all those assemblages are characterized by a low diversity. Decapod crustacean faunules from the middle Danian (lower Paleocene) at Fakse (eastern Denmark) comprise a wide array of dromioids in a coral-rich setting (e.g., Woodward, 1901; Wienberg Rasmussen, 1973; Collins and Jakobsen, 1994; Jakobsen and Collins, 1997; Collins, 2010). However, species and genera are different from those studied in the present work; dynomeniform crabs, in particular, are clearly distinct, with four species of *Dromiopsis* Reuss, 1859 (Jakobsen and Collins, 1997). The present faunule resembles the dromioid fauna from the Danian of the Paris Basin (France), with merely a single dynomenid and sphaerodromiid taxon each (Robin et al., 2017). The early Eocene faunas in northern Italy document an intermediate diversity, with at least four species of *Dromiopsis* and other paradynomenid forms. The only taxon in the Spanish assemblage in common with the Ypresian of Italy is the genus *Kromtitis*, with three recorded Italian species (Beschin et al., 2016a, b). Only three species of dromioids have been recorded from the Ypresian of the United Kingdom: two sphaerodromiids and one basinotopid (Collins, 2003; Van Bakel et al., 2017). Deposits of Ypresian/Lutetian age in Denmark share only a single basinotopid (Collins and Jakobsen, 2004) with the

Table 2. Summary of environmental distribution patterns, as listed in Table 1.

Eocene stage	Number of species in coral-rich settings	Number of species in setting lacking corals
Ypresian	26	3
Lutetian	1	15
Bartonian	0	4
Priabonian	12	4

Huesca assemblage. Thus, the Ramals faunule includes novel forms of dromioids that appear for the first time at such latitudes during the Eocene. Morphologically more modern dromioids are known mainly from Lutetian strata in Italy (Busulini et al., 1983; Beschin et al., 2005) and Catalonia (Via, 1969; Solé and Via, 1989).

The Eocene record of dromioids includes 58 species described to date (Table 1). Many of these are known from basins in the Mediterranean area and are related mainly to coral-rich settings (56%) (see Tables 1, 2). On the basis of sedimentological data, a preference for reef environments appears likely for the Ypresian (lower Eocene); almost all published occurrences stem from such depositional settings. This can be related to the development of “modern” reef complexes because of climatic and environmental conditions at the time (see Pomar et al., 2017), which enabled dromioids to inhabit such settings. However, during the middle Eocene, this trend appears to have reversed, and higher diversities then occur in siliciclastic or non-reef environments over shallow platforms. This could be related to a switch in environmental preferences of dromioids at that time and their expansion into siliciclastic environments, but it might also be linked to the poor record of reef facies in this time interval. Finally, during the late Eocene, a new increase in diversity is observed in reef settings.

The abundance and diversity of dromioids at Ramals suggest this group was diversified and specialized for inhabiting this type of coral-rich environment during the early Eocene. It was probably related earlier with the Cretaceous Crab Revolution (see Schweitzer and Feldmann, 2015; Luque et al., 2019), documenting several species that are closely similar to extant forms. Our present data support the widely accepted view that past reefs were biodiversity hotspots (e.g., Förster, 1985; Müller et al., 2000; Krobicki and Zatoń, 2008; Klomp maker, 2013; Klomp maker et al., 2013). The great diversity within a single group of decapod crustaceans (i.e., dromioids) is probably related to the location of the study area within reef mounds and associated coral rubble under mesophotic conditions, as well as to abundant crevices that this environment provided for refuge, feeding, and other interactions.

Although the present work discusses only a single reef mound environment of middle Ypresian (early Eocene) age, similar studies in other areas could potentially provide important ecological data on the distribution of dromioid crabs in ancient marine settings.

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References

- Armstrong, A., Nyborg, T., Bishop, G.A., Ossó-Morales, À., and Vega, F., 2009, Decapod crustaceans from the Paleocene of Central Texas, USA: *Revista Mexicana de Ciencias Geológicas*, v. 3, p. 745–763.
- Artal, P., and Castillo, J., 2005a, *Cyrtorhina ripacurtiae* n. sp. (Crustacea, Decapoda, Raninidae), primera cita del género en el Eoceno inferior español: *Batalleria*, v. 12, p. 33–38.
- Artal, P., and Castillo, J., 2005b, *Periacanthus ramosus* n. sp. (Crustacea, Decapoda), nueva especie del Eoceno inferior de Huesca: *Batalleria*, v. 12, p. 39–44.
- Artal, P., and Van Bakel, B.W.M., 2018a, Aethrids and panopeids (Crustacea, Decapoda) from the Ypresian of both slopes of the Pyrenees (France, Spain): *Scripta Musei Geologici Seminarii Barcelonensis*, v. 22, p. 3–19.
- Artal, P., and Van Bakel, B.W.M., 2018b, Carpilids (Crustacea, Decapoda) from the Ypresian (Eocene) of the Northeast of Spain: *Scripta Musei Geologici Seminarii Barcinonensis*, v. 22, p. 20–36.
- Artal, P., and Van Bakel, B.W.M., 2020, A new xanthid crab (Decapoda, Brachyura) from the lower Eocene (Ypresian) of Huesca (Aragón, Spain), in Jagt, J.W.M., Fraaije, R.H.B., van Bakel, B.W.M., Donovan, S.K., Mellish, C., and Schweigert, G., eds., *A lifetime amidst fossil crustaceans: a tribute to Joseph S.H. Collins (1927–2019): Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, v. 291, no. 1–2, p. 19–27.
- Artal, P., and Via, L., 1989, *Xanthilites macrodactylus pyrenaicus* (Crustacea, Decapoda) nueva subespecie del Ilerdiense medio del Pirineo de Huesca: *Batalleria*, v. 2, p. 57–61.
- Artal, P., Van Bakel, B.W.M., and Castillo, J., 2006, *Retropiuma* Gill, 1894 (Crustacea, Decapoda) from the Eocene of the eastern Pyrenees (Spain, France): *Cainozoic Research*, v. 5, no. 1–2, p. 65–71.
- Artal, P., Van Bakel, B.W.M., Fraaije, R.H.B., and Jagt, J.W.M., 2013, New retropiumid crabs (Crustacea, Brachyura, Retropiumidae Gill 1894) from the Eocene of Huesca (Aragón, Spain): *Zootaxa*, v. 3652, p. 343–352.
- Artal, P., Van Bakel, B.W.M., Domínguez, J.L., and Gómez, G., 2016, A new dromiid crab (Crustacea: Brachyura: Dromioidea) from the upper Eocene of Huesca (Aragón, northern Spain): *Zootaxa*, v. 4061, p. 438–446.
- Bachmayer, F., and Tollmann, A., 1953, Die Crustaceen-Fauna aus dem tortonischen Leithakalk (Steinbrüche der Firma Fenk) bei Groß-Höfleim im Burgenland: *Wien, Kober-Festschrift, Skizzen zum Anlitz der Erde*, v. 308, 314 p.
- Barnolas, A., 1973, *Dromilites vicensis* n. sp., nuevo Braquiuro del Eoceno marino de Cataluña: *Instituto de Investigaciones Geológicas*, v. 28, p. 5–13.
- Beschin, C., Busulini, A., De Angeli, A., and Tessier, G., 2002, Aggiornamento ai crostacei eocenici di cava “Main” di Arzignano (Vicenza-Italia settentrionale) (Crustacea, Decapoda): *Studi e Ricerche, Associazione Amici del Museo—Museo Civico “G. Zannato” (Montecchio Maggiore)*, v. 2002, p. 7–28.
- Beschin, C., De Angeli, A., Checchi, A., and Zarantonello, G., 2005, Crostacei eocenici di Grola presso Spagnago (Vicenza, Italia Settentrionale): *Studi e Ricerche - Associazione Amici del Museo, Museo Civico “G. Zannato,” Montecchio Maggiore (Vicenza)*, v. 12, p. 5–35.
- Beschin, C., Busulini, A., De Angeli, A., and Tessier, G., 2007, I decapodi dell’Eocene inferiore di Contrada Gecchelina (Vicenza – Italia settentrionale) (Anomura e Brachyura): *Museo di Archeologia e Scienze Naturali “G. Zannato,” Montecchio Maggiore (Vicenza)*, v. 2007, p. 5–76.
- Beschin, C., Busulini, A., and Tessier, G., 2009a, The decapod crustaceans from the upper Eocene of Parona (Veronese Lessini—NE Italy): *Studi e Ricerche—Associazione Amici del Museo—Museo Civico “G. Zannato,” Montecchio Maggiore (Vicenza)*, v. 16, p. 5–22.
- Beschin, C., De Angeli, A., and Zorzin, R., 2009b, Crostacei fossili del Veneto: una inedita fauna eocenica dei Lessini orientali (Monte Serea di San Giovanni Ilarione, Verona), con descrizione di tre nuove specie: *Bollettino del Museo civico di Storia naturale di Verona*, v. 33, p. 59–83.
- Beschin, C., De Angeli, A., Checchi, A., and Zarantonello, G., 2012, Crostacei del giacimento eocenico di Grola presso Spagnago di Cornedo Vicentino (Vicenza, Italia settentrionale) (Decapoda, Stomatopoda, Isopoda): *Museo di Archeologia e Scienze Naturali “G. Zannato,” Montecchio Maggiore (Vicenza)*, v. 2012, p. 5–99.
- Beschin, C., Busulini, A., and Tessier, G., 2015, Nuova segnalazione di crostacei associati a coralli nell’Eocene inferiore dei Lessini orientali (Vestenanova—Verona): *Lavori Società veneziana di Scienze naturali*, v. 40, p. 47–109.
- Beschin, C., Busulini, A., Tessier, G., and Zorzin, R., 2016a, I crostacei associati a coralli nell’Eocene inferiore dell’area di Bolca (Verona e Vicenza, Italia nordorientale): *Memorie del Museo Civico di Storia Naturale di Verona, series 2, Sezione Scienze della Terra*, v. 9, 189 p.
- Beschin, C., De Angeli, A., Checchi, A., and Zarantonello, G., 2016b, Crostacei Decapodi del “Tufo a *Lophoranina*” (Luteziano inferiore) della Valle del Chiampo (Vicenza—Italia Nordorientale): *Museo di Archeologia e Scienze Naturali “G. Zannato,” Montecchio Maggiore, (Vicenza)*, p. 1–92.
- Beschin, C., Busulini, A., Calvagno, M., Tessier, G., and Zorzin, R., 2017, Ypresian decapod crustacean faunas from the coral-algal environments in the eastern Lessini Mountains (Vicenza and Verona territory—NE Italy): a comparative analysis: *Bulletin de la Société géologique de France*, v. 188, no. 3, p. 1–17.
- Beschin, C., Busulini, A., Fornaciari E., Papazzoni C.A., and Tessier G., 2018, La fauna di crostacei associati a coralli dell’Eocene superiore di Campo-longo di Val Liona (Monti Berici, Vicenza, Italia nordorientale): *Bollettino del Museo di Storia Naturale di Venezia*, v. 69, p. 129–215.
- Beschin, C., Busulini, A., Tessier, G., and Zorzin, R., 2019, La fauna di crostacei dell’Eocene superiore di Parona di Verona (Italia nordorientale): nuovi ritrovamenti: *Bollettino del Museo di Storia Naturale di Venezia*, v. 70, p. 71–142.
- Beurlen, K., 1928, Die Decapoden de Schwäbischen Jura, mit Ausnahme der aus den oberjurassischen Plattenkalken stammenden: *Palaeontographica*, v. A70, p. 115–278.
- Beurlen, K., 1932, Brachyurenreste aus dem Lias von Bornholm mit Beiträgen zur Phylogenie und Systematik der Brachyuren Decapoden: *Paläontologische Zeitschrift*, v. 14, p. 52–66.
- Bittner, A., 1883, Neue Beiträge zur Kenntniss der Brachyuren-Fauna des Alttertiärs von Vicenza und Verona: *Denkschriften der kaiserlichen Akademie der Wissenschaften zu Wien*, v. 46, p. 299–316.
- Bittner, A., 1886, Neue Brachyuren des Eocäns von Verona: *Sitzungsberichte der kaiserlichen Akademie der Wissenschaften zu Wien*, v. 94, p. 44–55.
- Bittner, A., 1893, Decapoden des pannonischen Tertiärs: *Sitzungsberichte der kaiserlichen Akademie der Wissenschaften zu Wien*, v. 102, p. 10–37.
- Blow, W.C., and Manning, R.B., 1996, Preliminary descriptions of 25 new decapod crustaceans from the middle Eocene of the Carolinas, U.S.A.: *Tulane Studies in Geology and Paleontology*, v. 29, p. 1–26.
- Busulini, A., Tessier, G., Visentin, M., Beschin, C., De Angeli, A., and Rossi, A., 1983, Nuovo contributo alla conoscenza dei brachiuri eocenici di Cava Main (Arzignano)—Lessini orientali (Vicenza) (Crustacea, Decapoda): *Lavori—Società veneziana di Scienze Naturali*, v. 8, p. 55–73.
- Canudo, J.I., 2018, The collection of type fossils of the Natural Science Museum of the University of Zaragoza (Spain): *Geoheritage*, v. 10, p. 385–392.
- Cecchia-Rispoli, G., 1905, I crostacei dell’Eocene dei dintorni di Monreale in provincia di Palermo: *Giornale di Scienze Naturali ed Economiche di Palermo*, v. 25, p. 309–325.
- Collins, J.S.H., 2003, A taxonomic review of British decapod Crustacea: *Bulletin of the Mizunami Fossil Museum*, v. 29, p. 81–92.
- Collins, J.S.H., 2010, New species of crabs (Crustacea: Decapoda), one from the middle Danian of Denmark, and three new species from the Upper Cretaceous of Nigeria: *Bulletin of the Mizunami Fossil Museum*, v. 36, p. 13–19.
- Collins, J.S.H., and Donovan, S.K., 2006, New decapod crustaceans from the Palaeogene of Jamaica: *Bulletin of the Mizunami Fossil Museum*, v. 33, p. 59–65.
- Collins, J.S.H., and Jakobsen, S.L., 1994, A synopsis of the biostratigraphic distribution of the crab genera (Crustacea, Decapoda) of the Danian (Palaeocene) of Denmark and Sweden: *Bulletin of the Mizunami Fossil Museum*, v. 21, p. 35–46.
- Collins, J.S.H., and Jakobsen, S.L., 2004, New crabs (Crustacea, Decapoda) from the Eocene (Ypresian/Lutetian) Lillebælt Clay Formation of Jutland, Denmark: *Bulletin of the Mizunami Fossil Museum*, v. 30, p. 63–96.
- Davidson, E., 1966, A new Paleocene crab from Texas: *Journal of Paleontology*, v. 40, p. 211–213.
- De Angeli, A., and Alberti, R., 2018, Il genere *Pseudodromilites* Beurlen, 1928 (Crustacea, Brachyura, Dromiacea) nell’Eocene del Veneto, con la descrizione di una nuova specie: *Lavori Società veneziana di Scienze naturali*, v. 43, p. 155–163.
- De Angeli, A., and Ceccon, L., 2014, Nuovi Brachyura (Decapoda) dell’Eocene inferiore di Monte Magrè (Vicenza, Italia settentrionale): *Lavori Società veneziana di Scienze naturali*, v. 39, p. 77–92.

- De Grave, S. et al., 2009, A classification of living and fossil genera of Decapod Crustaceans: *Raffles Bulletin of Zoology*, v. 21, p. 1–109.
- De Haan, W., 1833–1850, *Crustacea. Fauna Japonica sive descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batava Imperium tenent, suscepto, annis 1823–1830, v. 1: Leiden, Lugduni-Batavorum*, 243 p.
- Desmarest, A.G., 1822, Malacostracés, Malacostraca. (Crust.): *Dictionnaire des sciences naturelles, dans lequel on traite méthodiquement des différents êtres de la nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connaissances, soit relativement à l'utilité qu'en peuvent retirer la médecine, l'agriculture, le commerce et les arts*, v. 28, p. 138–425.
- Dominguez, J.L., and Ossó, A., 2016, New decapod fauna at midway of the Tethys Sea and Atlantic Ocean; Central Pyrenees of Huesca (Aragon, Spain), in Charbonnier, S., ed., 6th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Villers-sur-Mer, Normandy, France. Abstract Volume, p. 23–24.
- Feldmann, R.M., and Schweitzer, C.E., 2019, Earliest known sponge crab (Brachyura: Dromiidae) from the Upper Cretaceous Wenonah Formation, New Jersey, USA: *Bulletin of the Mizunami Fossil Museum*, v. 45, p. 1–6.
- Ferratges, F.A., Zamora, S., and Aurell, M., 2019, A new genus and species of Parthenopidae MacLeay 1838 (Decapoda: Brachyura) from the lower Eocene of Spain: *Journal of Crustacean Biology*, v. 39, no. 3, p. 303–311.
- Ferratges, F.A., Zamora, S., and Aurell, M., 2020, Systematics and distribution of decapod crustaceans associated with late Eocene coral buildups from the southern Pyrenees (Spain), in Jagt, J.W.M., Fraaije, R.H.B., van Bakel, B.W.M., Donovan, S.K., Mellish, C., and Schweigert, G., eds., *A lifetime amidst fossil crustaceans: a tribute to Joseph S.H. Collins (1927–2019): Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, v. 296, no. 1–2, p. 79–100.
- Ferratges, F.A., Zamora, S., and Aurell, M., 2021, Unravelling the distribution of decapod crustaceans in the lower Eocene coral reef mounds of NE Spain (Trempe-Graus Basin, southern Pyrenees): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 575, 110439 <https://doi.org/10.1016/j.palaeo.2021.110439>
- Förster, R., 1985, Evolutionary trends and ecology of Mesozoic decapod crustaceans: *Transactions of the Royal Society of Edinburgh, Earth Sciences*, v. 76, p. 299–304.
- Förster, R., and Mundlos, R., 1982, *Krebse aus dem Alttertiär von Helmstedt and Handorf (Niedersachsen): Palaeontographica*, v. 179, p. 148–184.
- Fraaije, R.H.B., and Pennings, H.W., 2006, Crab carapaces preserved in nautiloid shells from the upper Paleocene of Huesca: Pyrenees, Spain: *Revista mexicana de ciencias geológicas*, v. 2, no. 3, p. 361–363.
- Frăntescu, A., Feldmann, R.M., and Schweitzer, C.E., 2010, A new genus and species of dromiid crab (Decapoda: Brachyura) from the middle Eocene of South Carolina, in Fransen, C.H.J.M., De Grave, S., and Ng, P.K.L., eds., *Studies on Malacostraca: Lipke Bijdeley Holthuis Memorial Volume: Crustaceana Monograph*, v. 14, p. 255–267.
- Gaemers, P.A.M., 1978, Biostratigraphy, paleoecology and paleogeography of the mainly marine Ager Formation (upper Paleocene lower Eocene) in the Treppe basin, Central South Pyrenees, Spain: *Leidse Geologische Mededelingen*, v. 51, p. 151–231.
- Garcés, M., López-Blanco, M., Valero, L., Beamud, E., Muñoz, J.A., Oliva-Urcia, B., Vinyoles, A., Arbués, P., Caballero, P., and Cabrera, L., 2020, Paleogeographic and sedimentary evolution of the south-Pyrenean foreland basin: *Marine and Petroleum Geology*, v. 113, 104105 <https://doi.org/10.1016/j.marpetgeo.2019.104105>
- Glaessner, M.F., 1929, Dekapodenstudien. IV. Die Dekapodenfauna des Alttertiärs der Nordalpen: *Neues Jahrbuch für Mineralogie und Paläontologie*, v. B63, p. 158–167.
- Guinot, D., 2008, A re-evaluation of the Dynomenidae Ortmann 1892 (Crustacea, Decapoda, Brachyura, Podotremata), with the recognition of four subfamilies: *Zootaxa*, v. 1850, no. 1, p. 1–26.
- Guinot, D., 2019, New hypotheses concerning the earliest brachyurans (Crustacea, Decapoda, Brachyura): *Geodiversitas*, v. 41, no. 22, p. 747–796.
- Guinot, D., and Tavares, M., 2003, A new subfamilial arrangement for the Dromiidae de Haan 1833, with diagnoses and descriptions of new genera and species (Crustacea, Decapoda, Brachyura): *Zoosystema*, v. 25, p. 43–130.
- Guinot, D., Tavares, M., and Castro, P., 2013, Significance of the sexual openings and supplementary structures on the phylogeny of brachyuran crabs (Crustacea, Decapoda, Brachyura), with new nomina for higher-ranked podotreme taxa: *Zootaxa*, v. 3665, no. 1, p. 1–414.
- Hay, W.W., et al., 1999, Alternative global Cretaceous paleogeography, in Barredera, E. and Johnson, C., eds., *The evolution of Cretaceous ocean/climate systems: Geological Society of America Special Papers*, v. 332, 47 p.
- Jagt, J.W.M., Van Bakel, B.W.M., Guinot, D., Fraaije, R.H.B., and Artal, P., 2015, Fossil Brachyura, in von Vaupel Klein, C., Charmantier-Daures, M., Schram, F., eds., *Treatise on Zoology—Anatomy, Taxonomy, Biology: The Crustacea*, v. 9: Leiden, Brill, p. 847–920.
- Jakobsen, S.L., and Collins, J.S.H., 1997, New middle Danian species of anomuran and brachyuran crabs from Fakse, Denmark: *Bulletin of the Geological Society of Denmark*, v. 44, no. 1, p. 89–100.
- Jakobsen, S.L., and Feldmann, R.M., 2004, Epibionts on *Dromiopsis rugosa* (Decapoda: Brachyura) from the late middle Danian limestones at Fakse Quarry, Denmark: novel preparation techniques yield amazing results: *Journal of Paleontology*, v. 78, p. 953–960.
- Karasawa, H., Schweitzer, C.E., and Feldmann, R.M., 2011, Phylogenetic analysis and revised classification of podotrematous Brachyura (Decapoda) including extinct and extant families: *Journal of Crustacean Biology*, v. 31, p. 523–565.
- Klompaker, A.A., 2013, Extreme diversity of decapod crustaceans from the mid-Cretaceous (late Albian) of Spain: implications for Cretaceous decapod paleoecology: *Cretaceous Research*, v. 41, p. 150–185.
- Klompaker, A.A., Schweitzer, C.E., Feldmann, R.M., and Kowalewski, M., 2013, The influence of reefs on the rise of Mesozoic marine crustaceans: *Geology*, v. 41, p. 1179–1182.
- Krobicki, M., and Zatoń, M., 2008, Middle and Late Jurassic roots of brachyuran crabs: palaeoenvironmental distribution during their early evolution: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 263, no. 1–2, p. 30–43.
- López-Horgue, M.A., and Bodego, A., 2017, Mesozoic and Cenozoic decapod crustaceans from the Basque-Cantabrian basin (Western Pyrenees): new occurrences and faunal turnovers in the context of basin evolution: *Bulletin de la Société géologique de France*, v. 188, no. 14, p. 1–28.
- Luque, J. et al., 2019, Exceptional preservation of mid-Cretaceous marine arthropods and the evolution of novel forms via heterochrony: *Science Advances*, v. 5, eaav3875 <http://doi.org/10.1126/sciadv.aav3875>
- M'Coy, F., 1849, On the classification of some British fossil Crustacea, with notices of new forms in the university collection at Cambridge: *Annals and Magazine of Natural History*, ser. 2, v. 4, p. 161–179, 330–335, 412–414.
- McLay, C.L., 1993, Crustacea Decapoda: the sponge crabs (Dromiidae) of New Caledonia and the Philippines with a review of the genera, in Crosnier, A., ed., *Résultats des Campagnes MUSORSTOM: Mémoires du Muséum National d'Histoire Naturelle*, v. 10, p. 111–251.
- McLay, C.L., 1999, Crustacea Decapoda: Revision of the family Dynomenidae, in Crosnier, A., ed., *Résultats des Campagnes MUSORSTOM: Mémoires du Muséum National d'Histoire Naturelle*, v. 180, p. 427–569.
- McLay, C.L., 2001, Dynomenidae and Dromiidae (Decapoda, Brachyura) from Guam, Philippine Islands, Tonga and Samoa: *Zoosystema*, v. 23, p. 807–856.
- McLay, C.L., and Ng, P.K.L., 2004, A taxonomic revision of the genus *Paradynomena* Sakai, 1963 (Crustacea: Decapoda: Brachyura: Dynomenidae): *Zootaxa*, v. 657, p. 1–24.
- McLay, C.L., and Ng, P.K.L., 2005, On a collection of Dromiidae and Dynomenidae from the Philippines, with description of a new species of *Hirsutodynomena* McLay 1999 (Crustacea: Decapoda: Brachyura): *Zootaxa*, v. 1029, p. 1–30.
- Milne-Edwards, A., 1880, Etudes préliminaires sur les Crustacés, 1ère Partie. Reports on the Results of Dredging under the Supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, '78, '79, by the U.S. Coast Survey Steamer "Blake", Lieut.-Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., Commanding, VIII: *Bulletin of the Museum of Comparative Zoology at Harvard College*, v. 8, p. 1–68.
- Milne Edwards, H., 1837, Description of *Dromilites*: *Journal Universel des Sciences et des Sociétés Savantes en France et à l'étranger 1ère section, Sciences, mathématiques, physiques, naturelles*, v. 5, p. 255.
- Müller, P., 1984, Decapod Crustacea from the Badenian: *Geologica Hungarica, Series Palaeontographica*, v. 42, 317 p.
- Müller, P., and Collins, J.S.H., 1991, Late Eocene coral-associated decapods (Crustacea) from Hungary: *Contributions to Tertiary and Quaternary Geology*, v. 28, p. 47–92.
- Müller, P., Krobicki, M., and Wehner, G., 2000, Jurassic and Cretaceous primitive crabs of the family Prosopidae (Decapoda: Brachyura)—their taxonomy, ecology and biogeography: *Annales Societatis Geologorum Poloniae*, v. 70, p. 49–79.
- Oppenheim, P., 1899, I supposti rapporti dei crostacei terziarii di Ofen descritti da Loerenthy con quelli veneti: *Rivista italiana di Paleontologia*, v. 5, p. 55–62.
- Ortmann, A., 1892, Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen, V. Theil. Die Abtheilungen Hippidea, Dromiidea und Oxystomata: *Zoologische Jahrbücher (Systematik)*, v. 6, p. 532–588.
- Ossó, À., 2019, New species of *Kromtitis* Müller 1984 (Decapoda: Brachyura: Dynomenidae) from the Eocene of Iberian Peninsula: *Palaeontologia Electronica*, v. 22.2, 47A, p. 1–9 <https://doi.org/10.26879/967>
- Ossó, À., Dominguez, J.L., and Artal, P., 2014, *Pyreneplax basaensis* new genus, new species (Decapoda, Brachyura, Vultocinidae) from the Priabonian (late Eocene) of the Pyrenees of Huesca (Aragon, Spain), and remarks on the genus *Lobonotus* A. Milne-Edwards 1863: *Treballs del Museu de Geologia de Barcelona*, v. 20, p. 33–43.

- Plaziat, J.C., 1981, Late Cretaceous to late Eocene palaeogeographic evolution of southwest Europe: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 36, p. 263–320.
- Pomar, L., Baceta, J.I., Hallock, P., Mateu-Vicens, G., and Basso, D., 2017, Reef building and carbonate production modes in the west central Tethys during the Cenozoic: Marine and Petroleum Geology, v. 83, p. 261–304.
- Portell, R.W., and Collins, J.S.H., 2004, Decapod crustaceans of the Lower Miocene Montpellier Formation, White Limestone Group of Jamaica, in Donovan, S.K., ed., The Mid-Cainozoic White Limestone Group of Jamaica: Cainozoic Research, v. 3, p. 109–126.
- Pujalte, V., Schmitz, B., Baceta, J.I., Orue-Echebarría, X., Bernaola, G., Dinarès-Turell, J., Payros, A., Apellaniz, E., and Caballero, F., 2009, Correlation of the Thanetian–Ilerdian turnover of larger foraminifera and the Paleocene–Eocene thermal maximum: confirming evidence from the Campo area (Pyrenees, Spain): Geologica Acta, v. 7, p. 161–175.
- Quayle, W.J., and Collins, J.S.H., 1981, New Eocene crabs from the Hampshire Basin: Palaeontology, v. 24, p. 733–758.
- Reuss, A.E., 1858, Über kurzschwänzige Krebse im Jurakalke Mährens: Stützungsberichte der Kaiserlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Classe, v. 31, p. 5–13.
- Reuss, A.E., 1859, Zur Kenntnis fossiler Krabben. I. Die Kurzschwänzer der Kreideformationen: Denkschriften der Kaiserlichen Akademie der Wissenschaften Wien, v. 7, p. 1–90.
- Robin, N., van Bakel, B.W.M., Pacaud, J.M., and Charbonnier, S., 2017, Decapod crustaceans from the Paleocene (Danian) of the Paris Basin (Vigny stratotype and allied localities) and a limpet palaeoassociation: Journal of Systematic Palaeontology, v. 15, p. 257–273.
- Roemer, F.A., 1887, *Graptocarcinus texanus*, ein Brachyure aus der Kreide von Texas: Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie, v. 1, p. 173–176.
- Sakai, T., 1963, Description of two new genera and 14 new species of Japanese crabs from the collection of His Majesty the Emperor of Japan: Crustaceana, v. 5, p. 213–233.
- Schweitzer, C.E., and Feldmann, R.M., 2010, Sphaerodromiidae (Brachyura: Dromiacea: Dromioiidea) in the fossil record: Journal of Crustacean Biology, v. 30, p. 417–429.
- Schweitzer, C.E., and Feldmann, R.M., 2015, Faunal turnover and niche stability in marine Decapoda in the Phanerozoic: Journal of Crustacean Biology, v. 35, p. 633–649.
- Schweitzer, C.E., Feldmann, R.M., Garassino, A., Karasawa, H., and Schweigert, G., 2010, Systematic list of fossil decapod crustacean species: Crustaceana Monographs, v. 10, 222 p.
- Schweitzer, C.E., Feldmann, R.M., and Karasawa, H., 2012, Part R, Revised, Volume 1, Chapter 8M: Systematic descriptions: Infraorder Brachyura, Section Dromiacea: Treatise Online, v. 51, p. 1–43.
- Serra-Kiel, J., Canudo, J.I., Dinares, J., Molina, E., Ortiz, N., Pascual, J.O., Samso, J.M., and Tosquella, J., 1994, Cronoestratigrafía de los sedimentos marinos del Terciario inferior de la Cuenca de Graus-Tremp (Zona Central Surpirenaica): Revista de la Sociedad Geológica de España, v. 7, p. 273–297.
- Silva-Casal, R., Aurell, M., Payros, A., Pueyo, E.L., and Serra-Kiel, J., 2019, Carbonate ramp drowning caused by flexural subsidence: the South Pyrenean middle Eocene foreland basin: Sedimentary Geology, v. 393, p. 1–23.
- Solé, J., and Via L., 1989, Crustacis Decápodes fòssils dels Països Catalans (Recopilació i actualització de dades des de 1855 a 1988: Batalleria, v. 2, p. 23–42.
- Stimpson, W., 1858, Prodrómus descriptionis animalium evertibratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers ducibus, observavit et descripsit W. Stimpson Pars VII. Crustacea Anomura: Proceedings of the Academy of Natural Science, Philadelphia 10, v. 4, p. 225–252.
- Takeda, M., and Manuel-Santos, M.R., 2006, Crabs from Balicasag Island, Bohol, the Philippines: Dromidae, Dynomenidae, Homolidae, Raninidae, Dorippidae, and Calappidae: Memoirs of the National Science Museum, Tokyo, v. 44, p. 84–104.
- Tessier, G., Beschin, C., and Busulini, A., 2011, New evidence of coral-associated crustaceans from the Eocene of the Vicenza Lessini (NE Italy): Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 260, no. 2, p. 211–220.
- Van Bakel, B.W.M., Artal, P., Fraaije, R.H.B., and Jagt, J.W.M., 2009, A new early Oligocene crab (Decapoda, Brachyura, Dromiacea) from northwest Belgium, with comments on its palaeobiology: Geologica Belgica, v. 12, p. 45–57.
- Van Bakel, B.W.M., Guinot, D., Corral, J.C., and Artal, P., 2012, Graptocarcininae n. subfam., an extinct subfamily of Dynomenidae Ortmann, 1892 (Crustacea, Brachyura, Podotremata): Zootaxa, v. 3534, p. 40–52.
- Van Bakel, B.W.M., Robin, N., Charbonnier, S., and Saward, J., 2017, Revision of *Dromilites bucklandii* (Crustacea, Decapoda, Brachyura): type material revealing its real identity, a junior synonym, and a new species: Palaeontologia Electronica, v. 20, p. 1–20 <https://doi.org/10.26879/813>
- Van Bakel, B.W.M., Mychko, E.V., Spiridonov, A., Jagt, J.W.M., and Fraaije, R.H.B., 2020, New Cretaceous crabs (Crustacea, Brachyura) from Moscow Oblast and Dagestan (Russia): patterns in phylogeny and morphospace of the oldest eubrachiurans (Dorippoidea): Cretaceous Research, v. 119, p. 1–21, 104675 <https://doi.org/10.1016/j.cretres.2020.104675>
- Via, L., 1959, Decápodos fósiles del Eoceno español: Boletín del Instituto geológico y minero española, v. 70, p. 331–402.
- Via, L., 1969, Crustáceos decápodos del Eoceno español: Pirineos, v. 91–94, 469 p.
- Via, L., 1973, Datos para el estudio de los crustáceos decápodos del Eoceno circumpirenaico: Pirineos, v. 107, p. 55–70.
- Weber, F., 1795, Nomenclator entomologicus secundum Entomologiam Systematicum ill. Fabricii adjectis speciebus recens detectis et varietatibus: Chilonii et Hamburg, C.E. Bohn, 171 p.
- Wienberg Rasmussen, H., 1973, En lyssky hulefauna fra Fakse som vidnesbyrd om koralkalkens dannelse i lyszonen: Dansk Geologisk Forening, Årsskrift 1972, p. 87–91.
- Woodward, H., 1901, On some Crustacea collected by Miss Caroline Birley and Miss L. Copland from the Upper Cretaceous of Faxé, Denmark: Geological Magazine, new ser. 4, v. 8, p. 486–501.
- Zamora, S., Aurell, M., Veitch, M., Saulsbury, J., López-Horgue, M.A., Ferratges, F.A., Arz, J.A., and Baumiller, T.K., 2018, Environmental distribution of post-Palaeozoic crinoids from the Iberian and south-Pyrenean basins (NE Spain): Acta Palaeontologica Polonica, v. 63, p. 779–794.

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