

***Pyrenicola* (Crustacea: Decapoda: Brachyura), new genus for *Litoricola macrodactyla* (Van Straelen, 1924) and *Litoricola macrodactyla pyrenaica* (Artal and Vía, 1989), and remarks on *Coeloma* (Milne-Edwards, 1865).**

***Pyrenicola* (Crustacea: Decapoda: Brachyura), género nuevo para *Litoricola macrodactyla* (Van Straelen, 1924) y *Litoricola macrodactyla pyrenaica* (Artal y Vía, 1989), y comentarios acerca de *Coeloma* (Milne-Edwards, 1865)**

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Abstract

A new genus, *Pyrenicola*, is proposed to accommodate *Xanthilites macrodactylus* Van Straelen, 1924 from the Thanetian of Haute Garonne (France), and *X. macrodactylus pyrenaicus* Artal and Vía, 1989 from the Ypresian of Aragon (Spain), as well as clarify their relationships with the morphologically close *Litoricola* Woodward, 1873, where both are currently placed, and with *Coeloma* A. Milne-Edwards, 1865. As a result, *Litoricola* is herein revalidated as an available genus, different from *Coeloma*, of which it has frequently been considered either a subgenus or a synonym. Also, the subspecies *Xanthilites macrodactylus pyrenaicus* is elevated to full species rank as *Pyrenicola pyrenaica* n. comb. The familial placement of *Pyrenicola* n. gen., *Litoricola* and particularly of *Coeloma*, currently placed within Polybiinae Paulson, 1875 (Portunoidea Rafinesque, 1815) is revised. Consequently, a new placement of the three genera within Geryonidae Colosi, 1923, the most basal portunoid crabs, is herein proposed.

Keywords: Paleogene, Pyrenees, Eubrachyura, Portunoidea, Geryonidae, non-swimming crabs.

Resumen

En el presente trabajo se propone un nuevo género, *Pyrenicola*, para ubicar a *Xanthilites macrodactylus* Van Straelen, 1924 del Thanetiano de la Haute Garonne (Francia) y *X. macrodactylus pyrenaicus* Artal y Vía, 1989 del Ypresiano de Aragón (España), así como clarificar sus relaciones con géneros morfológicamente cercanos como *Litoricola* Woodward, 1873 y *Coeloma* A. Milne-Edwards, 1865. Como resultado, *Litoricola* se revalida aquí como un género singular y diferente de *Coeloma*, del cual frecuentemente se le ha considerado un subgénero o un sinónimo. La subespecie *Xanthilites macrodactylus pyrenaicus*, se eleva al rango de especie como *Pyrenicola pyrenaica* n. comb. Asimismo, se revisa la ubicación familiar de *Pyrenicola* n. gén., *Litoricola* y en particular la de *Coeloma*, actualmente ubicado en Polybiinae Paulson, 1875 (Portunoidea Rafinesque, 1815). En consecuencia, se propone una nueva ubicación para los tres géneros dentro de Geryonidae Colosi, 1923, considerados los portunoideos más basales.

Palabras clave: Paleoceno, Pirineos, Eubrachyura, Portunoidea, Geryonidae, cangrejos no nadadores.

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1. Introduction

Fossil decapods from the Thanetian/Ypresian outcrops of both slopes of the Pyrenees have been recorded since the beginning of the twentieth Century until present times, this last decade has been the most important in terms of number of reports (van Straelen, 1924; Vía Boada, 1973; Artal and Vía, 1989; Artal and Castillo, 2005a, b; Artal *et al.*, 2006; Artal *et al.*, 2013a, b; Artal and van Bakel, 2018a, b; Ferratges *et al.*, 2019; Artal and van Bakel, 2020; Artal *et al.*, 2021; Ferratges *et al.*, 2021a, b; Artal *et al.*, 2022; Ferratges *et al.*, 2022a, b, c; van Bakel *et al.*, 2023).

Among the mentioned articles, three of them have been specifically dealing with two very morphologically similar taxa that were originally assigned to the genus *Xanthilites* Bell, 1858: *Xanthilites macrodactylus* van Straelen, 1924, and *X. macrodactylus pyrenaicus* Artal and Vía, 1989. Since then, the generic placement of both taxa has been controversial, and has been moved to different genera such as *Litoricola* Woodward, 1873 or *Coeloma* Milne-Edwards, 1865 (Table 1). For instance, *Xanthilites macrodactylus* and *X. macrodactylus pyrenaicus* were considered “unknown” and *Coeloma?* respectively (see Schweitzer, 2005, p. 287, t. 3), *X. macrodactylus pyrenaicus* as *Litoricola macrodactylus pyrenaicus* (Jagt *et al.*, 2010, p. 247), *X. macrodactylus* as *L. macrodactylus* (Ossó, 2016, p. 239; 2021, p.

151), or *Litoricola* spp. as *Coeloma* spp. (e.g. Schweitzer *et al.*, 2010, p. 137; 2021, p. 7–9).

When Artal and Vía (1989) erected *Xanthilites macrodactylus pyrenaicus*, from the Ypresian of La Pobla de Roda (Aragon, Spain), considered it as a subspecies of *X. macrodactylus* of the Thanetian of Boussens (Haute Garonne, France), in despite of existing differences reported in their work. However, the review of a range of well-prepared specimens and old material located in museums, preserving both dorsal and ventral features, leads us to consider that the aforementioned taxa belong to a different species rather than a single species with subspecies. They can be also considered different species of a new genus, clearly separated from *Litoricola* or *Coeloma*. Moreover, we think that *Litoricola* should be considered a valid genus, rather than a subgenus of *Coeloma*, in agreement with Jagt *et al.* (2010, p. 247). The familial placement of the proposed new genus, *Litoricola* and *Coeloma*, is revised, given that the current placement of this group of taxa within Polybiinae (Paulson, 1875) (see Schweitzer *et al.*, 2021) cannot be sustained from a morphological point of view (*cf.* Spiridonov *et al.*, 2014; Evans, 2018; Spiridonov, 2020).

Thus, in order to disentangle the relationships among these taxa, the aims of the present work are: i) to reevaluate the taxonomic position of *Litoricola* as a valid genus; ii) to propose a new genus to accommodate *L. macrodactyla* and *L. macrodactyla pyrenaica*; iii) to reevaluate the subspecies status of

Tabla 1. Different generic placements through time of *Xanthilites macrodactylus* and *X. macrodactylus pyrenaicus*.

<i>Xanthilites macrodactylus</i> Van Straelen, 1924.	<i>Xanthilites macrodactylus pyrenaicus</i> Artal and Vía, 1989.	Unknown (<i>Xanthilites macrodactylus</i>) Schweitzer, 2005.	<i>Coeloma?</i> (<i>Xanthilites macrodactylus pyrenaicus</i>) Schweitzer, 2005.	<i>Coeloma macrodactylus</i> (subspecies included) Schweitzer <i>et al.</i> , 2010; 2021.	<i>Litoricola macrodactylus pyrenaicus</i> Jagt <i>et al.</i> , 2010; Ferratges, 2017; Ferratges <i>et al.</i> , 2021, 2022b.	<i>Litoricola macrodactyla</i> Ossó, 2016, 2021; Van Bakel <i>et al.</i> , 2023.
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L. macrodactyla pyrenaica and consider elevating it to full species rank within the new genus; iv) to discuss the familial placement of all the aforementioned taxa.

2. Repository

Museu de Geologia del Seminari de Barcelona (Barcelona, Catalonia), acronym: MGSB. Museu de Geologia de Barcelona (Barcelona, Catalonia), acronym MGB. Sedgwick Museum of Earth Sciences (Cambridge, United Kingdom), acronym: SGC.

3. Systematic paleontology

Order Decapoda Latreille, 1802

Infraorder Brachyura Latreille, 1802

Section Eubrachyura de Saint Laurent, 1980

Subsection Heterotremata Guinot, 1977

Superfamily Portunoidea Rafinesque, 1815

Family Geryonidae Colosi, 1923

Litoricola Woodward, 1873

Fig. 1A-F

Type species. *Litoricola dentata* Woodward, 1873, by subsequent designation of Glaessner (1929, p. 237)

Species included. *Litoricola dentata* Woodward, 1873 (= *L. glabra* Woodward, 1873 [see Collins *et al.*, 2020, p. 45, as *Coeloma*]).

Stratigraphical range. Lower Eocene.

3.1. Emended diagnosis

Medium-sized carapace, inverted subtrapezoidal in shape, broader than long, L/W ratio about 0.73, nearly flat in both directions; maximum width at the anterior third of carapace. Front bilobed, protruding beyond the orbits, slightly downturned. Lobes bifid, resulting in a tetra-lobed appearance, with outer spines markedly divergent. Orbits broad, with two distinct open fissures; width of the supraorbital margin twice the width of the front. Anterolateral margins short, near vertical with three unequal spines, blunt anterior corner

(excluding the extra-orbital tooth). Posterolateral margins straight, markedly longer than the anterolateral ones. Dorsal regions barely defined. Thoracic sternum relatively broad, slightly longer than broad, and ovate in shape. Sternite 3 is inverted subtrapezoidal and fused; sternite 4 broad, three times as tall as the sternite 3; sternites 5 to 7 subtrapezoidal, horizontally elongated, sternite 5 the wider. Suture 2/3 complete; suture 3/4 only visible laterally and defined by a marked oblique groove nearly reaches the axis; sutures 4/5 and 5/6 interrupted axially; sutures 6/7 and 7/8 complete. Sterno-pleonal cavity shallow, slightly surpassing coxa of P1 and reaching half of sternite 4. Male pleon subrectangular elongated; pleonal somites completely free; third male somite the wider. Chelipeds long, slender, present notable heterochely; dactylus of major claw with an eccentric proximal molariform tooth, followed by serial conical teeth. Major cheliped twice as long as the minor cheliped. Left handedness of chelipeds being frequent. Ambulatory legs long, slender, and compressed.

3.1.1. Remarks

Litoricola was erected by Woodward (1873, p. 28-30, pl. 2, figs. 1-5) based on several specimens coming from the early Eocene of Hampshire and he described two species: *L. dentata* and *L. glabra*. Subsequently, Glaessner (1929, p. 237) designated *L. dentata* as the type species and continued referring to them as feminine gender. Collins *et al.* (2020, p. 45 [as *Coeloma*]) considered '*C. glabrum*' as junior synonym of '*C. dentatum*'. *Litoricola* has been recurrently considered as subgenus of *Coeloma* or synonymized with *Coeloma* by different authors (e.g. Lörenthey in Lörenthey and Beurlen, 1929, p. 241; Glaessner, 1969, p. R524; Schweitzer *et al.*, 2010, p. 137; Quayle and Collins, 2012, p. 39; Collins *et al.*, 2020, p. 45; Schweitzer *et al.*, 2021, p. 7-9). However, Jagt *et al.* (2010, p. 247), considered *Litoricola* as valid genus, opinion followed by other authors, for instance Ossó (2016, 2021), Ferratges (2017), Ferratges *et al.* (2021c) and van Bakel *et al.* (2023).

In any case, *Litoricola* have enough morphological differences to be separated from *Coeloma* and from the new genus herein proposed. *Coeloma* is characterized by a more subhexagonal outline of the carapace (vs. subtrapezoidal in *Litoricola*); the fronto-orbital margins are wider than those in *Litoricola*; the

dorsal surface is generally granulated, slightly vaulted in both directions and the regions are fairly defined (vs. flattened and smooth carapace in *Litoricola*); the frontal margin, similarly bilobed and four-lobed-like, is wider and more downturned than in *Litoricola*; the outer orbital teeth is subtriangular, remarkably

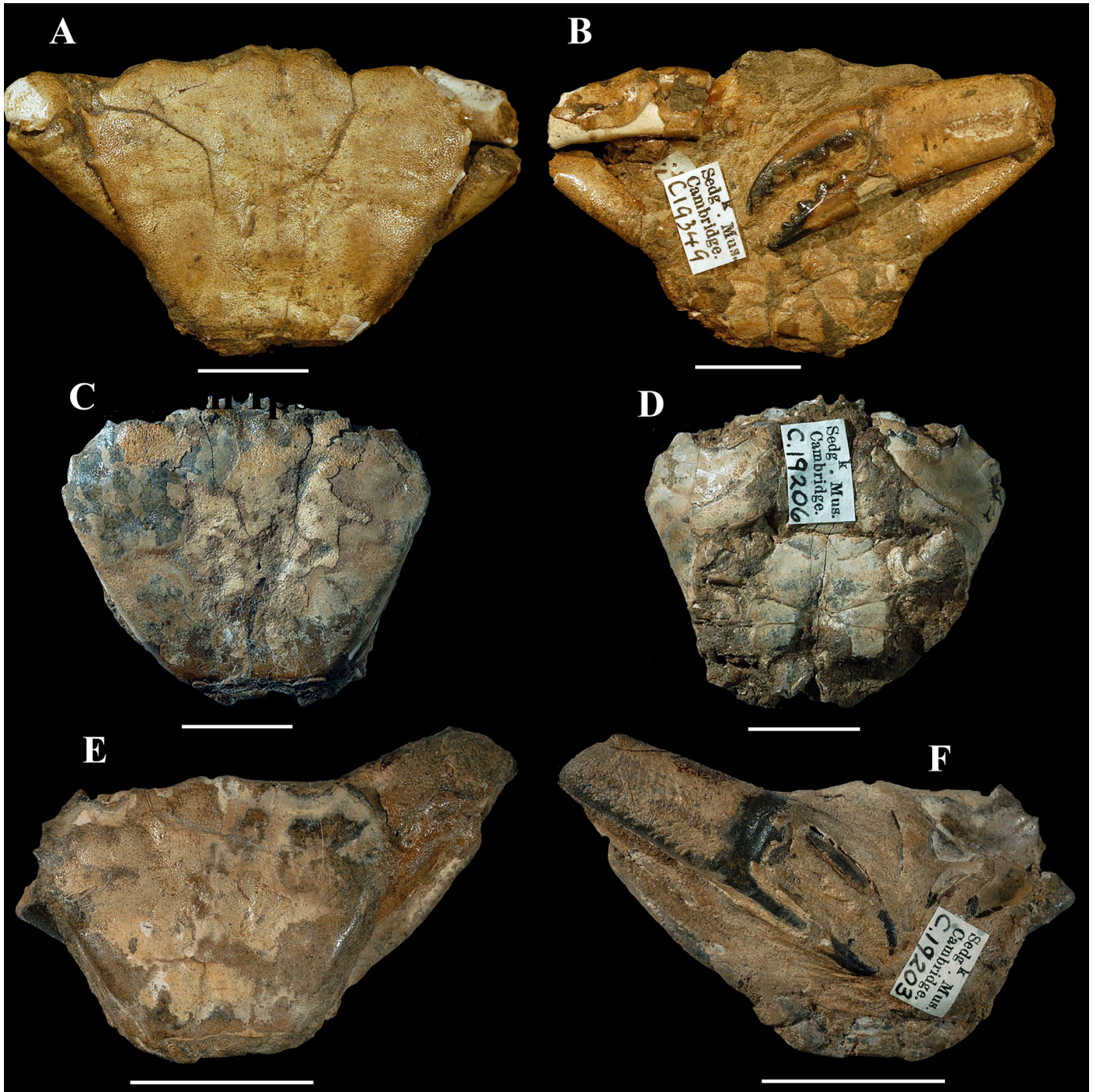


Figure 1. A-F, *Litoricola dentata* (Woodward, 1873) from the Ypresian of Hampshire, United Kingdom. A, B, SGC C19349, A: dorsal view; B: ventral view. C, D, SGC C19206, C: dorsal view, D: ventral view. E, F, SGC C19203, E: dorsal view, F: ventral view. Scale bar equal to 10 mm. (Pictures courtesy of Barry van Bakel).

stout, larger than any other in the outline (*vs.* blunt in *Litoricola*); the anterolateral margins are weakly arched, nearly-vertical, with three smaller teeth, and notably longer than in *Litoricola*; posterolateral margins are fairly longer than the anterolateral, posterior portion is broadly arched (*vs.* much longer and straight in *Litoricola*); the branchial regions are subdivided, in particular the epibranchial ridges are fairly marked (*vs.* poorly defined by swellings in *Litoricola*); dorsal grooves are shallow but well defined (*vs.* barely defined in *Litoricola*). The thoracic sternum is fairly subcircular, broad (*vs.* ovate, narrower in *Litoricola*). Chelipeds are shorter than *Litoricola* and do not present the strong heterochely that *Litoricola* shows (e.g. Milne-Edwards, 1865, p. 324, pl. 12, figs. 1-3; Lörenthey in Lörenthey and Beurlen, 1929, pl. 12, figs. 15, 16; Sorgenfrei, 1940, t. 7, figs. 1-5, t. 8, figs. 1-5; Bachmayer and Mundlos, 1968, pls. 10-15; Glaessner, 1969, fig. 332, 2a, b; Allasinaz, 1975, fig. 12, pls. 6, 7; Jagt *et al.*, 2010, p.247-248, t. 1, pl. 1; Hyžný and Zagorsek, 2012, text-fig. 3A-C; Hyžný and Zorn, 2016, pl. 4, figs. 2a-e; Schweitzer *et al.*, 2021, p. 7-8; <http://www.mbfossilcrabs.com/Portunoidea.html> accessed March, 8, 2024).

The entire set of differences listed above warrant *Litoricola* as different genus, separated from *Coeloma* and their subgenera. See below the differences with the proposed new genus.

Genus *Pyrenicola* new genus

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Type species. *Xanthilites macrodactylus* Van Straelen, 1924.

Etymology. From *Pyrene*, related to the origin of Pyrenees in Greek mythology, and joining the suffix *-cola*, from *Litoricola*, the most related genus. Gender feminine.

Species included. *Pyrenicola macrodactyla* (Van Straelen, 1924) [as *Xanthilites macrodactylus*]; *Pyrenicola martinezensis* (Rathbun, 1926) [as *Coeloma martinezensis*]; *Pyrenicola pyrenaica* (Artal and Vía, 1989) [as *Xanthilites macrodactylus pyrenaicus*].

Stratigraphical range. From upper Paleocene to lower Eocene.

3.2. Diagnosis

Carapace medium-sized, subhexagonal in outline, fairly broader than long, maximum width at the level of the epibranchial region, slightly vaulted in both directions. Front bilobed, with bifid lobes giving tetra-lobed appearance, slightly downturned, protruding beyond the orbits. Orbits broad, subquadrate; supraorbital margin with vestiges of closed fissure medially, along with an open fissure or notch distally at the base of the outer-orbital tooth; outer orbital tooth subtriangular forwardly directed. Anterolateral margins slightly arched, with three to four subtriangular teeth (excluding outer-orbital tooth). Posterolateral margins straight. Posterior margin straight. Dorsal regions well defined by swellings; branchial areas few differentiated. Thoracic sternum narrow, ovate, longer than broad; maximum width at 5 sternite level; sternite 4 elongate; suture 3/4 visible laterally. sutures 4/5 and 5/6 interrupted axially. Sterno-pleonal cavity shallow, surpassing coxa of P1 and reaching half of sternite 4. Male pleon subtriangular, pleonal somites completely free; third male somite the wider. Chelipeds show notable heterochely; dactylus of major claw bearing an eccentric proximal molariform tooth, followed by serial conical teeth. Left handedness relatively common. Ambulatory legs long, slender, compressed.

3.2.1. Remarks

Pyrenicola n. gen. is compared with the morphological closest genera, such as *Litoricola* and *Coeloma*. Major differences distinguishing *Litoricola* from *Pyrenicola* n. gen. are a different outline of carapace, inverted subtrapezoidal in *Litoricola* (*vs.* subhexagonal in *Pyrenicola* n. gen.); the carapace reaches its maximum width towards the anterior (*vs.* more posteriorly in *Pyrenicola* n. gen.); an almost flattened carapace (*vs.* more vaulted in *Pyrenicola* n. gen.); slightly narrower front, clearly notched medially with divergent spines (*vs.* more notched

front in *Pyrenicola* n. gen.); the orbits are much wider, being the length twice the length of the front, and the supraorbital notches clearly open (*vs.* supraorbital fissures closed or fused in *Pyrenicola* n. gen.); the anterolateral margin is clearly shorter, with only three unequal teeth (*vs.* longer anterolateral margin with four teeth in *Pyrenicola* n. gen.); the groove defining the sternal suture 3/4 nearly reaches the axial portion of sternites (*vs.* only defined laterally in *Pyrenicola* n. gen.) (*e.g.* Woodward, 1873, p. 28-30, p. 2, figs. 1-5; Glaessner, 1969, p. R524, figs. 1a, b [as *Coeloma*]; Ossó, 2016, figs. 6F-I; Collins *et al.*, 2020, p. 45; Schweitzer *et al.*, 2021, p. 7, Fig 3.5 [as *Coeloma*]).

Coeloma differs from *Pyrenicola* n. gen. in having a different outline of the carapace, nearly subquadrate, and more flattened dorsal surface (*vs.* vaulted in *Pyrenicola* n. gen.); wider fronto-orbital margin, with orbits being extremely large, sinuous, and clearly divided in two portions, with two opened, deep, fissures (*vs.* shorter orbits and closed fissures in *Pyrenicola* n. gen.); much shorter anterolateral and nearly vertical margins (*vs.* longer and slightly arched in *Pyrenicola*); and noticeable epibranchial ridges, not well-defined in *Pyrenicola* n. gen. Moreover, the thoracic sternum is broader and the chelipeds are not so stout and do not show the extreme heterochelely as in *Pyrenicola* n. gen. (*e.g.* Milne-Edwards, 1865, p. 324, pl. 12, figs. 1-3; Glaessner, 1969, p. R524, fig. 332a, b; Allasinaz, 1975, fig. 12, pls. 6, 7; Jagt *et al.*, 2010, p. 247-249, t. 1, pl. 1; Hyžný and Zorn, 2016, pl. 4, figs. 2a-e; Schweitzer *et al.*, 2021, p. 7-9, fig. 5 [*Litoricola*]).

The set of characters listed above clearly distinguishes *Litoricola* and *Coeloma* from *Pyrenicola* n. gen., and justifies the erection of a new genus for the two reported species of crabs. Jagt *et al.* (2010, p. 247), included *Coeloma martinezensis* in *Litoricola* from the early Eocene of California (USA), unfortunately a detailed examination of the type material is not possible, given that the sole specimen (the holotype) USNM MO 353370 was marked as 'Missing back' in 2017 by the National Museum of Natural History (Nicolas Drew, Smithsonian

Institution, pers. comm.). However, based on its front protruding beyond the orbits, and the subquadrate orbits depicted in Rathbun (1926, pl. 11, figs. 1-3), we place *L. martinezensis* within *Pyrenicola* n. gen. rather than in *Litoricola*. Also, *Coeloma vareolata* Lörenthey, 1898, is left as it is, although based on the examination of images of the holotype, kindly provided by M. Hyžný, indicate that perhaps it could be placed in a new genus. Future works will determine its generic position.

Pyrenicola pyrenaica (Artal and Vía, 1989) n. comb.
Fig. 2A-F

Stratigraphic range. Middle Ypresian.

- 1973 *Xanthilites cf. interpunctus* (Schafhäütl, 1863); Vía Boada; p. 56, pl. 1.
1988 *Xanthilites interpunctus*; Vía, p. 351, fig. 343J.
1989* *Xanthilites macrodactylus pyrenaicus* Artal and Vía; p. 58 pl. 1.
1989 *Xanthilites macrodactylus pyrenaicus* Artal and Vía, 1988 [*sic*]; Solé and Vía, p. 32.
1995 *Xanthilites macrodactylus pyrenaicus* Artal and Vía, 1989; Fraaye p. 65.
2005 *Xanthilites macrodactylus pyrenaicus* Artal and Vía, 1988 [*sic*]; Schweitzer, p.287, t. 3.
2010 *Litoricola macrodactylus pyrenaicus* Artal and Vía, 1989; Jagt *et al.*, p. 249.
2017 *Litoricola macrodactylus pyrenaicus* (Artal and Vía, 1988) [*sic*]; Ferratges, fig. 41A, pl. 27, figs. A, B.
2021c *Litoricola macrodactylus pyrenaicus* (Artal and Vía, 1988) [*sic*]; Ferratges *et al.*, t1, fig. 7T.
2022b *Litoricola macrodactylus pyrenaicus* (Artal and Vía, 1988) [*sic*]; Ferratges *et al.* in Zamora *et al.*, figs. 10M, N.

3.3. Emended diagnosis

Medium-sized carapace, subhexagonal outline, slightly vaulted in both directions, L/W ratio about 0.76. Front bilobed, lobes bifid resulting in a tetra-lobed appearance, just protruding beyond the orbits, the frontal spines are directed forward, but in a slightly lower plane. Orbits of similar size to the front; supraorbital margin nearly straight, with an open fissure close to the outer-orbital tooth, and a vestige of a medial closed fissure. Anterolateral margin somewhat arched, with four subtriangular

teeth (excluding outer-orbital tooth) similar in size, the first one blunt, almost obsolete. Posterolateral margins straight, longer than anterolateral. Posterior margin nearly straight somewhat broader than frontal margin. Dorsal regions well defined by gentle, rounded, swellings; dorsal surface densely and uniformly covered by small granules. Thoracic sternum ovate, notably longer than broad; sternites 1–2

subtriangular, fused; sternite 3 inverted subtrapezoidal and fused with sternite 4; sternite 4 elongate; sternites 5 to 7 subtrapezoidal horizontally elongated, sternite 5 the wider. Suture 2/3 complete; suture 3/4 only visible laterally and defined internally by a shallow oblique depression; sutures 4/5 and 5/6 interrupted axially; sutures 6/7 and 7/8 complete. Episternites 4 to 6 posteriorly directed, suture barely

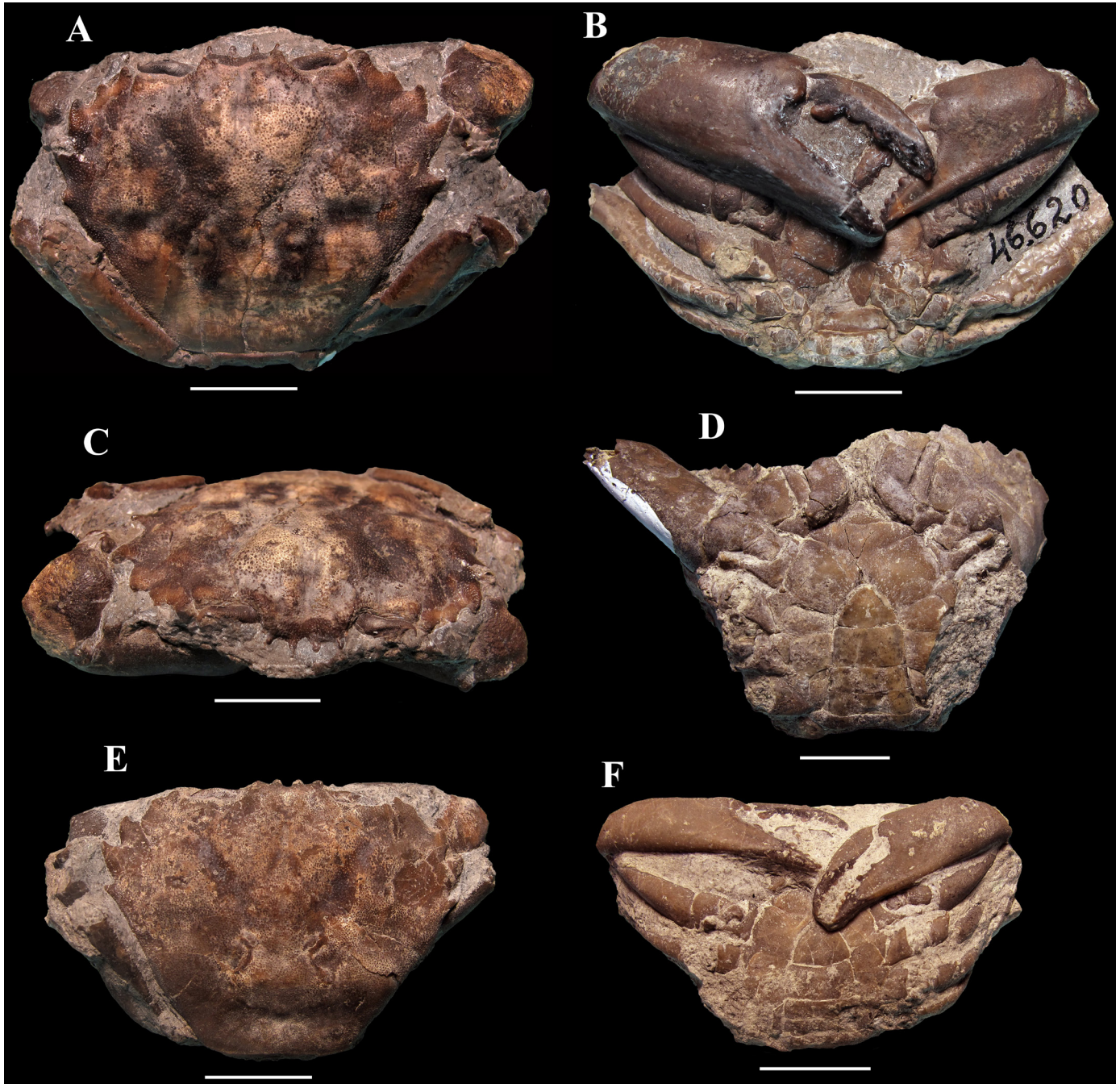


Figure 2. A-F, *Pyrenicola pyrenaica* (Artal and Vía, 1989) n. comb., from the Ypresian of La Pobla de Roda (Aragon, Spain). A-C, holotype MGSB 46620, A: dorsal view; B: ventral view; C: frontal view. D, MGSB 75445b, ventral view. E, F, MGSB 75445a, E: dorsal view, F: ventral view. Scale bar equal to 10 mm.

visible. Sterno-pleonal cavity shallow, surpassing coxa of P1 and reaching half of sternite 4. Male pleon subtriangular, pleonal somites completely free; third male somite the wider. Ambulatory legs long, slender, compressed. Male pleon subtriangular elongated, pleonal somites completely free; third male somite the wider. Female pleon subtriangular, somewhat wider than male pleon. Chelipeds show notable heterochely; major claw elongated, dactylus bearing an eccentric proximal molariform tooth, followed by serial conical teeth. Minor claw slender, dactyli with serial conical teeth. Ambulatory legs long, slender, compressed.

3.3.1. Remarks

Pyrenicola pyrenaica n. comb. was erected by Artal and Vía (1989) as *Xanthilites macrodactylus pyrenaicus* and considered as a subspecies of *Xanthilites macrodactylus* (Figs. 3A-F), based on the strong morphological similarities with the French Thanetian species. Also, its placement within the genus *Xanthilites* seemed appropriated at that time because their striking similarity with the imaginative drawing of *X. interpunctus* in Förster (1970, text-fig. 4) (see also Vía, 1988, fig. 343J, 344; Schweitzer, 2005, p.287). Schweitzer (2005, p. 287) reported it as *Coeloma?*, and Jagt *et al.* (2010, p. 247) moved it to *Litoricola*, albeit Schweitzer *et al.* (2021, p. 7-9) retained it as synonymous of *Coeloma*. To entangle even more the generic placement of this species, it has been synonymized with *Harpactocarcinus macrodactylus* (H. Milne-Edwards in d'Archiac, 1850) in Sasaki (2023, p. 11031).

To summarize, herein we elevate the Ypresian *Pyrenicola pyrenaica* n. comb. to full species rank, thus separating it from the Thanetian *P. macrodactyla*. We compare both species as follows.

Pyrenicola macrodactyla differs from *P. pyrenaica* n. comb. in having a major L/W ratio, of about 0.8 (vs. 0.76 in *P. pyrenaica* n. comb.); the front is slightly smaller and more protruded beyond orbits compared to

P. pyrenaica n. comb.; the medial fissure of the supraorbital margin is slightly open (vs. completely closed or fused in *P. pyrenaica* n. comb.); the anterolateral teeth of similar size are more developed, in particular the first one (vs. blunt or obsolete in *P. pyrenaica* n. comb.); the dorsal regions are defined by more salient, nearly conical swellings; the dorsal surface is covered by less dense small granules compared to *P. pyrenaica* n. comb.; the thoracic sternum and pleon, in both males and females, are narrower than those in *P. pyrenaica* n. comb.; the notable heterochely and heteromorphy of the chelipeds are more extremely marked compared to *P. pyrenaica* n. comb. (cf. Figs. 2, 3; Van Straelen, 1924, fig. 2, pl. 1, figs. 2, 2a, b; Artal and Vía, 1989, fig. 2, pl. 1; Goret *et al.*, 2013, pl. E, figs. 4, 7-9; Ossó, 2016, fig. 6D, E; van Bakel *et al.*, 2023, fig. 1I-J; <http://www.mb-fossilcrabs.com/Portunoidea.html> accessed March 8, 2024).

Hence, there are enough distinct features to justify elevating the subspecies *pyrenaica* to full species rank.

4. Remarks on the familial placement of *Litoricola*, *Pyrenicola* n. gen., and *Coeloma*

The familial placement of *Litoricola*, and by extension *Pyrenicola* n. gen., within Geryonidae, the most basal non-regularly swimming portunoids, was widely argued by Ossó (2016, p. 239, 240). The same applies for *Coeloma* (Ossó, 2021, p. 151), currently placed within Polybiinae (Schweitzer *et al.*, 2021). Indeed, *Coeloma* has been treated through time as geryonid, mathildellid, among others, ending up within Polybiinae, along with a series of heterogeneous fossil genera previously placed within Macropipidae Stephenson and Campbell, 1960 (see Feldmann *et al.*, 2018, p. 580). In parallel, the constantly changing classification of extant Portunoidea, based mainly in molecular studies, subsumed Macropipidae (*sensu* Karasawa *et al.*, 2008) within Polybiinae (Schubart and Reuschel, 2009; Spiridonov *et al.*, 2014; Evans, 2018; Spiridonov, 2020; Schweitzer *et al.*, 2021), about which Spiridonov (2020,

p. 158) warned: “In this case, extinct genera return to an uncertain status, which is not a desirable situation”. According to the current diagnosis of Polybiinae (Spiridonov *et al.*, 2014: 422; Davie *et al.*, 2015, p. 1102; Feldmann *et al.*, 2018, p. 580; Schweitzer *et al.*, 2021, p. 6, 7), *Coeloma* cannot be kept there.

Alternatively, placing together *Coeloma*, *Litoricola* and *Pyrenicola* n. gen. within Geryonidae, seems more appropriate. For instance, the maximum width of carapace is placed posteriorly in Polybiinae than in Geryonidae, *Coeloma*, *Litoricola*, or *Pyrenicola* n. gen. The orbito-frontal margin in Polybiinae is shorter,

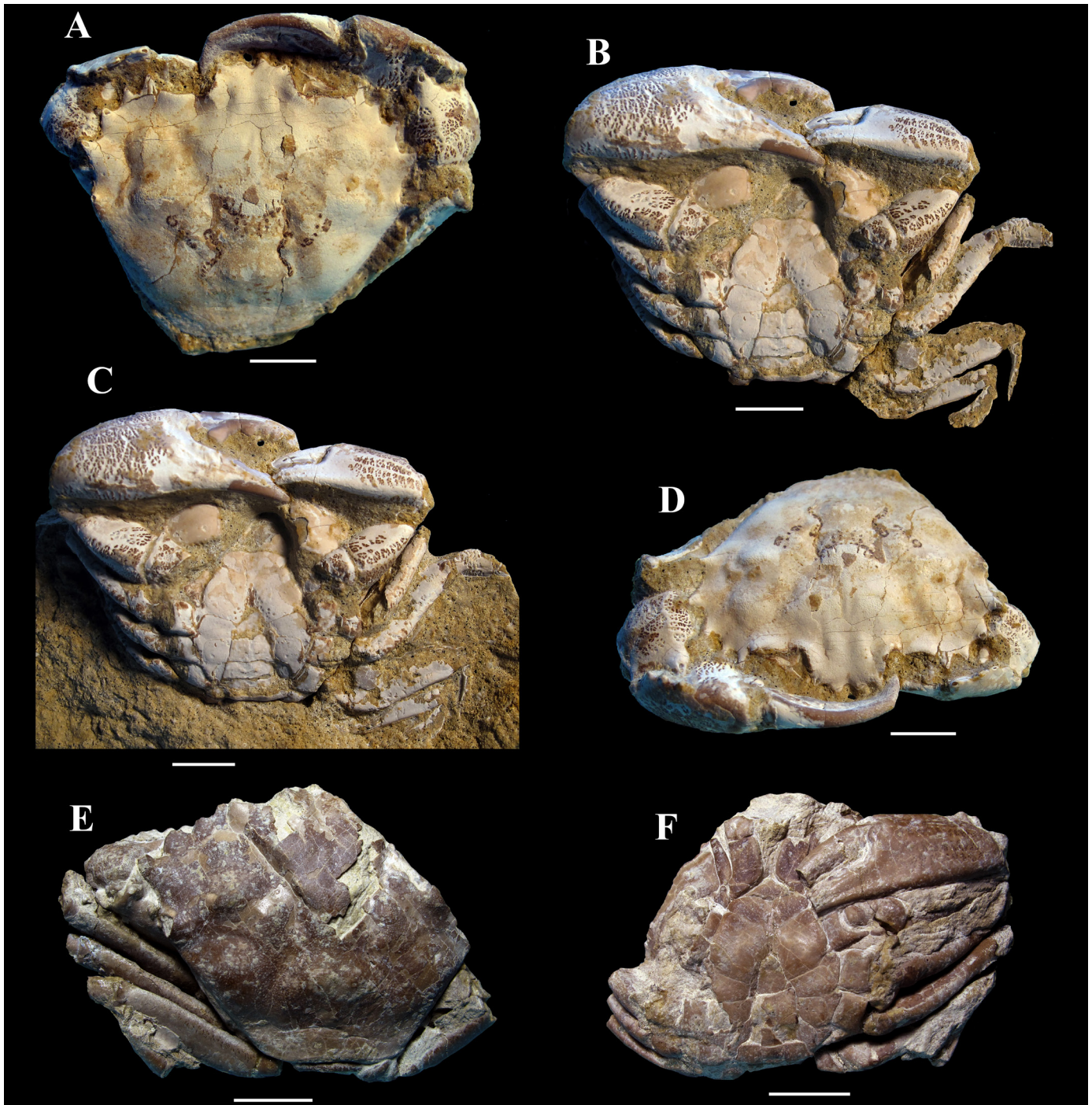


Figure 3. A-F, *Pyrenicola macrodactyla* (Van Straelen, 1924), from the Thanetian of Boussens (Haute Garonne, France). A-D, MGB 69154, A: dorsal view; B: ventral view digitally cropped from matrix; C: ventral view attached to the matrix; D: frontal view. E, F, MGSB 88577, E: dorsal view; F: ventral view. Scale bar equal to 10 mm.

the orbits are smaller, and the front is generally uneven (Spiridonov *et al.*, 2014, p. 422), whereas in Geryonidae and the three aforementioned genera, the orbits are broader, and the front four-toothed or bilobed with a tetra-lobed aspect (Figs. 1C, 2A, C, E, 3A, D; Manning and Holthuis, 1989). The presence of a well-developed posterolateral re-entrant for insertion of last pereopods typical in Polybiinae, is not seen neither in Geryonidae, nor in *Coeloma*, *Litoricola*, or *Pyrenicola* n. gen. (Figs. 1A-C, E, 2A, E, 3A, E; Allasinaz, 1975, fig. 12, pls. 6, 7; Manning and Holthuis, 1989). In Polybiinae, a portion of male sternite 8 is visible, and pleonal somites 3-5 are fused (*vs.* somites 3-5 in male separated by sutures but immovable in Geryonidae, and free in *Coeloma*, *Litoricola* and *Pyrenicola* n. gen.; Davie *et al.*, 2015, p. 1100). Most of the extant representatives of Polybiinae possess a wide thoracic sternum with a maximum width at the level of sternite 6 (Spiridonov, 2020, p. 139), whereas usually in Geryonidae, and the three aforementioned genera the maximum width of the sternum is at the level of sternite 5 (Figs. 1D, 2D, 3B, C, F; *e.g.* Allasinaz, 1975, fig. 12, pl. 6, fig. 4b, pl. 7, fig. 3; Davie *et al.*, 2007, figs. 6A, B). Thoracic sternal sutures 4/5 and 5/6 are usually well defined, and the sutures 6/7 and 7/8 are incomplete (Davie *et al.*, 2015, p. 1102), instead, in Geryonidae and in *Litoricola*, *Pyrenicola* and *Coeloma*, the sutures 4/5 and 5/6 are often incomplete, and the sutures 6/7 and 7/8 nearly complete (Figs. Davie *et al.*, 2015, p. 1099; Mychko, 2018, pl. 5, 1b, 3b). The P5 in representatives of Polybiinae the propodus is broadened and the dactylus is usually modified (*vs.* long and slender and not particularly modified in Geryonidae, neither in *Coeloma*, *Litoricola* and *Pyrenicola* n. gen.). The heterochely of chelipeds is very attenuated in Polybiinae (*vs.* strongly heterochely present in Geryonidae, *Coeloma*, and particularly in *Litoricola* and *Pyrenicola* n. gen.).

The above-listed array of differences between Polybiinae and Geryonidae, is enough to remove *Coeloma* from their current placement in Polybiinae, as shown by the set of

characters that justify its placement within Geryonidae, along to *Litoricola* and *Pyrenicola* n. gen., where it was previously placed on various occasions by different authors (see Ossó, 2016, p. 239, 240, and references therein).

5. Conclusions

The access to numerous well-preserved specimens of the various studied species, has permitted a detailed study of their morphology; as a result, it is observed that *Litoricola* possesses a sufficient number of distinctive characters *vs.* *Coeloma* and *Pyrenicola* n. gen., to be revalidated and retained as an available genus. As well as *Pyrenicola* n. gen., serves to accommodate the French Thanetian *P. macrodactyla*, and the Spanish Ypresian *P. pyrenaica*, the latter elevated herein to full species rank. Also, the familial placement of *Coeloma* has been revisited concluding that its placement within Geryonidae is better supported than in Polybiinae. In addition, the general dorsal morphology of these genera, particularly the fronto-orbital construction, strongly recall of Cretaceous non-swimming portunoids (see Ossó, 2023, p. 91), suggesting a possible phylogenetic relationship between these old taxa and the more derived Cenozoic and extant taxa, without discarding a possible convergence process. Future phylogenetic works, which are not within the reach of the authors, will confirm or not these assumptions and the systematic placements proposed herein.

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