

***Pyreneplax basaensis* new genus, new species (Decapoda, Brachyura, Vultocinidae) from the Priabonian (Late Eocene) of the Pyrenees of Huesca (Aragón, Spain), and remarks on the genus *Lobonotus* A. Milne-Edwards, 1863**

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Resum

OSSÓ, A., DOMÍNGUEZ, J.L. i ARTAL, P. *Pyreneplax basaensis* nou gènere, nova espècie (Decapoda, Brachyura, Vultocinidae) del Priabonià (Eocè Superior) del Pirineu d'Osca (Aragó, Espanya), i observacions sobre el gènere *Lobonotus* A. Milne-Edwards, 1863. Els nous braquiüers fòssils trobats a la Formació Margas de Arguís (Priabonià, Eocè superior) dels Pirineus Centrals (Aragó), permeten la descripció d'un nou gènere y una nova espècie (*Pyreneplax basaensis*), així com la revisió d'alguns tàxons previament assignats al gènere *Lobonotus* A. Milne-Edwards, 1863 (Carpilioidea: Tumidocarcinidae). Tenint en compte la gran similitud existent entre *Pyreneplax* n. gen. i les espècies *Lobonotus sandersi* (Blow i Manning, 1997), *L. granosus* (Beschin, Busulini, De Angeli i Tessier, 2002) i *L. sommarugai* Beschin, Busulini i Tessier, 2009, aquestes són també assignades al nou gènere.

A més, un conjunt de caràcters tant dorsals com ventrals, compartits amb la espècie actual *Vultocinus anfractus* Ng i Manuel-Santos, 2007, suggereixen la inclusió del nou gènere dins la família Vultocinidae Ng i Manuel-Santos, 2007 (Goneplacoidea). Al mateix temps es discuteixen alguns aspectes de la posició sistemàtica del gènere *Lobonotus* A. Milne-Edwards, 1863.

Paraules clau: Decapoda, Goneplacoidea, Vultocinidae, *Pyreneplax*, *Lobonotus*, *Titanocarcinus*, Priabonià.

Resumen

OSSÓ, A., DOMÍNGUEZ, J.L. y ARTAL, P. *Pyreneplax basaensis* nuevo género, nueva especie (Decapoda, Brachyura, Vultocinidae) del Priaboniense (Eoceno Superior) del Pirineo de Huesca (Aragón, España), y observaciones sobre el género *Lobonotus* A. Milne-Edwards, 1863. Nuevos braquiuros fósiles encontrados en la Formación Margas de Arguís (Priaboniense, Eoceno superior), en los Pirineos Centrales (Aragón), permiten la descripción de un nuevo género y una nueva especie (*Pyreneplax basaensis*), así como la revisión de algunos taxones previamente asignados al género *Lobonotus* A. Milne-Edwards, 1863 (Carpilioidea: Tumidocarcinidae). De acuerdo con la notable similitud entre *Pyreneplax* n. gen., y las especies *Lobonotus sandersi* (Blow y Manning, 1997), *L. granosus* (Beschin, Busulini, De Angeli y Tessier, 2002) y *L. sommarugai* Beschin, Busulini y Tessier, 2009, éstas se asignan al nuevo género.

Asimismo, un destacado conjunto de caracteres dorsales y ventrales compartidos con la especie actual *Vultocinus anfractus* Ng y Manuel-Santos, 2007, sugiere la inclusión del nuevo género en la familia Vultocinidae Ng y Manuel-Santos, 2007 (Goneplacoidea). También se efectúan algunas observaciones sobre el género *Lobonotus* A. Milne-Edwards, 1863.

Palabras clave: Decapoda, Goneplacoidea, Vultocinidae, *Pyreneplax*, *Lobonotus*, *Titanocarcinus*, Priaboniense.

Abstract

New fossil brachyuran finds in the Margas de Arguís Formation (Priabonian, Late Eocene) in the Central Pyrenees of Aragon (Spain), allow the description of a new genus and a new species (*Pyreneplax basaensis*), and the revision of some taxa previously assigned to the genus *Lobonotus* A. Milne-Edwards, 1863 (Carpilioidea: Tumidocarcinidae). According to the close similarity between *Pyreneplax* n. gen. and *Lobonotus sandersi* (Blow and Manning, 1997), *L. granosus* (Beschin, Busulini, De Angeli and Tessier, 2002) and *L. sommarugai* Beschin, Busulini and Tessier, 2009, these species are here assigned to the new genus.

In addition, an important set of dorsal and ventral characters shared with the extant species *Vultocinus anfractus* Ng and Manuel-Santos, 2007, suggests the inclusion of the new genus in the family Vultocinidae Ng and Manuel-Santos, 2007 (Goneplacoidea). Remarks on the genus *Lobonotus* are also discussed herein.

Key words: Decapoda, Goneplacoidea, Vultocinidae, *Pyreneplax*, *Lobonotus*, *Titanocarcinus*, Priabonian.

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INTRODUCTION

The recent discovery of fossil decapods in the uppermost levels the Margas de Arguís Fm. (Priabonian) enhances the knowledge of the Iberian Priabonian crustacean faunas. Usually scarce, few Priabonian taxa have been reported or described from the Iberian Peninsula (see: Artal *et al.*, 2013; Ossó & Domínguez, 2013), in contrast with the fossil crustacean richness of the Ypresian, Lutetian and Bartonian levels of the Ebro Foreland Basin and nearby basins cropping out in Aragón and Catalonia.

The co-occurrence of other brachyuran taxa in the same outcrop such as *Retrocypoda almelai* Vía, 1959 (Retroplumidae), *Portunus catalaunicus* Vía, 1959 (Portunidae), *Chasmocarcinus cf. guerini* (Vía, 1959) (Chasmocarcinidae) and *Stenodromia calasanctii* Vía, 1959 (Calappidae), all of them known from the Bartonian of the above mentioned basins, indicates the persistence of such taxa during the progressive infilling of the basins that shift to non-marine conditions by the end of the Eocene.

The good condition of preservation of specimens of *Pyreneplax basaensis* n. gen. and n. sp., with well-preserved partial ventral structures such as thoracic sternum, sterno-abdominal cavity and abdominal somites, allows an almost complete description of the characters of the new taxa, and its comparison with the extant *Vultocinus anfractus* Ng and Manuel-Santos, 2007. With regards to the genus *Lobonotus* A. Milne-Edwards, 1863, and its type species *L. sculptus* A. Milne-Edwards, 1863, the taxonomy has been a bit confused as many works frequently used *L. mexicanus* Rathbun, 1930 in their comparisons, instead of the type species (see discussion). Comparisons between the figures of the holotype of *L. sculptus* and the illustrations of several samples of *Archaeopilumnus caelatus* (a junior synonym of *L. sculptus*, according to Rathbun, 1920: 384) in Rathbun (1919) demonstrates that *L. sculptus* and *L. mexicanus* are not congeneric. Consequently, we remove *L. mexicanus* from *Lobonotus* and revise the composition of this genus.

Material. Type specimens of *Pyreneplax basaensis* n. gen., n. sp. are housed at Museo Paleontológico de la Universidad de Zaragoza (Spain) under the acronym MPZ. Other comparative specimens figured: A. Ossó collection (acronym AO); Crustacean Collection of the Philippine National Museum, Manila (Philippines) (acronym NMCR); and Muséum national d'Histoire Naturelle (Paris, France) (acronym MNHN).

Locality. The area object of this study is located in the central part of the southern Pyrenees, around the small village of Yebra de Basa, northwest of the province of Huesca (Aragón, N Spain). The locality is situated over the northern bank of the Basa River, a small contributor in the affluents network of the Ebro river basin (Fig. 1).

Geological setting. The area is located in the Basa anticline, in the so-called Jaca Basin. This basin, having an E-W orientation, developed in time along the continued S-N compression of the Pyrenees. The basin infilling started around Lutetian times, and the general depositional sequence, named Secuencia de Jaca (Remacha & Picart, 1991) comprises several different formations (see also Puigdefábregas, 1975).

The layers bearing the decapod crustaceans object of this study correspond to the Margas de Arguís Formation (Puigdefábregas, 1975), which in this area basically consist of a sequence about 700 meters thick of blue-grey marls interbedded with sandstone intervals. The base is defined by large scale sandstone deposits of offshore shelf facies, marked by several episodes of shallowing-deepening culminating in a relatively long transgressive episode that filled the basin. The general marine condition of the Margas de Arguís Fm. corresponds in fact to a tectonic transgressive-regressive cycle (Toledo, 1992). It is also worth noting that these layers began to be affected by deltaic contributions, with important terrigenous inputs, that become totally dominant in the upper levels. The distribution of fauna in the stratigraphic column with bryozoans, nummulites and bivalves in the lower levels, and corals, algae and gastropods in the upper ones, indicates a decrease of the bathymetry. These faunal associations suggest deep sediments corresponding to the aphotic zone of a platform that gradually became shallower. All the material studied here was recovered from the uppermost levels.

The sedimentological and biostratigraphic aspects of the Margas de Arguís Formation have been studied by several authors, including its planktonic foraminifers (Canudo & Molina, 1988; Canudo *et al.*, 1988), and magnetostratigraphy (Hogan, 1991). According to these authors, the material of the Margas de Arguís Formation corresponds to a Bartonian-Middle Priabonian age. This formation displays in its lower levels marly deposits corresponding to a distal offshore, grading to mouth bars sandstones with abundant vegetal remains in the upper levels. Leaves, stems and mangrove palm fruits as *Nypa* (Arecaceae) and other indeterminate ones, suggest the area was under such tidal and/or storm influences (Oms & Remacha, 1992).



Fig. 1. Location map of the Huesca province (Aragón) in northern Spain and the fossil locality (star).

Fig. 1. Mapa de la provincia d'Osca (Aragó) al Nord d'Espanya i del jaciment (estel).

As indicated in the stratigraphic column (Fig. 2), the crab remains were recovered from the uppermost levels of the section. The sediments where such decapods occur are included in the depositional sequence SD6 of Canudo *et al.* (1991). This sequence, according to the confirmed planktonic foraminifera corresponds to a Priabonian age. The upper part of the formation consists of marly layers locally interbedded with thin levels of sandstones. Both marls and sandstones locally present pockets with high accumulations of fauna, represented by corals, bryozoans, gastropods, bivalves, nummulites and vegetal remains or, conversely, levels with a low

accumulation of remains. In the latter, almost all the fossils are well preserved, with the brachyurans *Serrablopluma diminuta* Artal, Van Bakel, Fraaije and Jagt, 2013 (Retroplumidae) and *Chasmocarcinus cf. guerini* (Via, 1959) (Chasmocarcinidae) predominant. Most of the brachyurans are well-articulated, suggesting a low energy environment and scarce transportation. In contrast with that, in high accumulation layers most of the occurring fossils are fragmented and brachyurans consist of disarticulated carapaces or only small remains. The new taxon has been always recovered from such latter layers, interpreted as corresponding to a high energy environment involving transportation.

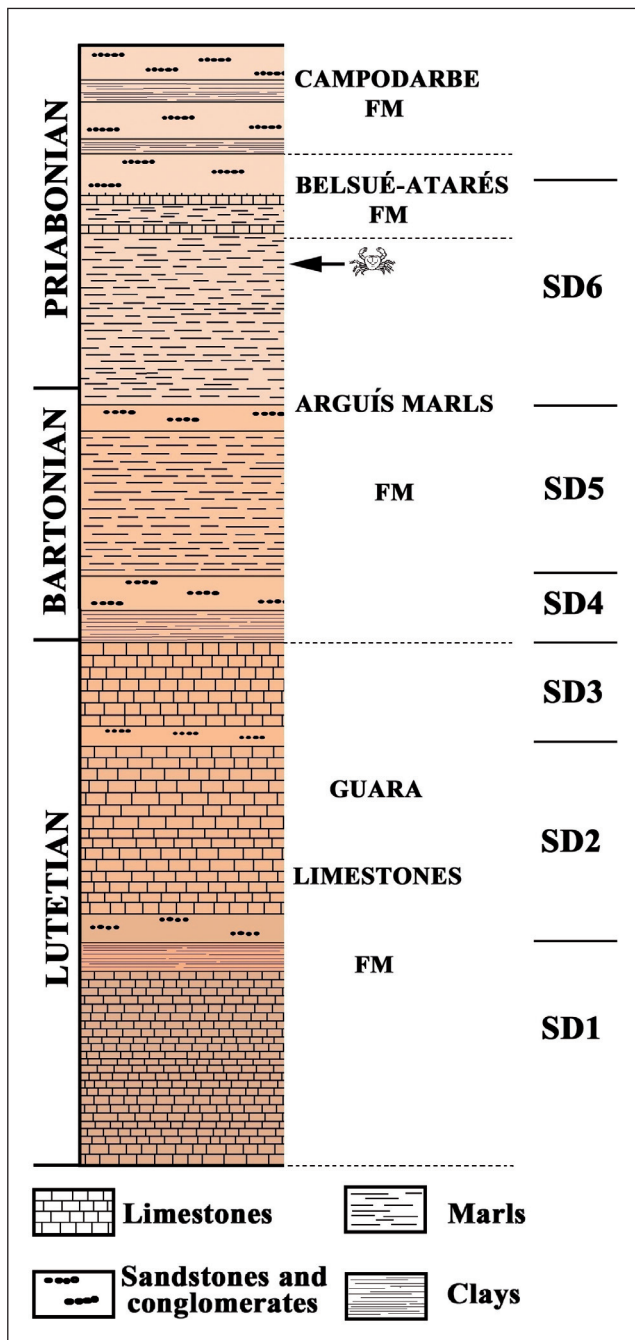


Fig. 2. Stratigraphic column of the outcrop area (modified from Canudo *et al.*, 1991).

Fig. 2. Columna estratigràfica de la zona de l'aflorament (modificada de Canudo *et al.*, 1991).

SYSTEMATIC PALAEOLOGY

Order DECAPODA Latreille, 1802
 Infraorder BRACHYURA Latreille, 1802
 Section EUBRACHYURA de Saint-Laurent, 1980
 Subsection HETEROTREMATA Guinot, 1977
 Superfamily GONEPLACOIDEA MacLeay, 1838
 Family VULTOCINIDAE Ng & Manuel-Santos, 2007

Pyreneplax n. gen.

Type species. *Pyreneplax basaensis* n. sp.
Species included. *Pyreneplax basaensis* n. sp.; *Pyreneplax granosa* (Beschlin, Busulini, De Angeli and Tessier, 2002) new combination; *Pyreneplax sandersi* (Blow and Manning, 1997) new combination (originally misspelled *Eohalimede sandersi*, Blow and Manning, 1997; emended by Blow and Manning, 1998); *Pyreneplax sommarugai* (Beschlin, Busulini and Tessier, 2009) new combination.

Etymology. From *Pyrene*, related to the origin of Pyrenees in Greek mythology, and joining the suffix *-plax* (meaning "flat" in Greek), usual within Goneplacoidea. Gender feminine.

Diagnosis. Small to medium sized carapace, suboctagonal, from wider than long to slightly wider than long, somewhat convex in anterior third, widest at third anterolateral tooth level. Dorsal regions well defined, elevated, ornamented with granules; delimited by large and smooth grooves. Frontal margin bilobed, slightly advanced, edge granulated. Orbits oval, oblique, separated from frontal margin by a deep fold; supraorbital margin with three teeth separated by two notches, inner orbital, subtriangular, prominent. Anterolateral margins with four rounded and granulated teeth (outer orbital spine excluded); first one smallest, at lower level. Posterolateral margins slightly convex, ornamented with granules. Posterior margin slightly convex, medially depressed, rimmed. Cervical and hepato-gastric grooves well-marked, broad, smooth. Gastric process well-marked; epigastric lobes swollen; proto-gastric lobes, swollen, oval, U-shaped, anterior portion medially depressed; mesogastric lobe broad posteriorly, anterior portion slender, low, long, reaching basal portion of epigastric lobes; metogastric lobe indistinct; urogastric region swollen, well delimited from meso- metogastric

lobe by narrow groove with gastric pits. Cardiac region swollen, broadly T-shaped. Intestinal region transversely elongate, inflated, narrow, subparallel along posterior margin medially divided by small smooth depression. Hepatic region inflated. Branchial regions well defined by swollen lobes, separated by broad, shallow, smooth grooves; epibranchial lobe subdivided in two, supra-epibranchial lobe transversely elongate, from horizontal to oblique, directed to fourth anterolateral tooth, sub-epibranchial lobe from rounded to triangular, both delimited by shallow smooth groove; mesobranchial lobe inflated. Thoracic sternum flattened, covered by coarse granules; sternite 3 with a shallow longitudinal median groove that connects with sterno-abdominal cavity reaching end of sternite 4; sternites 1 and 2 fused subtriangular; sternite 3 inverted subtriangular; sternite 4 subtrapezoidal, with prominent lateral edges with parallel grooves; sternites 5 and 6 subtrapezoidal elongate; suture 1/2 absent; suture 2/3 complete; suture 3/4 distinct, separated by groove, suture visible only laterally; sutures 4/5, 5/6 medially interrupted; episternites not laterally extended. Male abdomen apparently narrow; telson subtriangular, rounded tip; somites 1-3 subrectangular, transversely narrow, medially inflated, covered by uniformly distributed granules. Ischium of third maxilliped subrectangular with median sulcus, inner margin convex, outer margin concave, covered by scarce granules; exognath slender; merus subquadrate.

Discussion. *Pyreneplax basaensis* n. gen., n. sp. closely resembles some coeval taxa currently assigned to the genus *Lobonotus*: *L. sandersi* from the Eocene of South Carolina and *L. granosus* from the Lutetian (middle Eocene) of Northern Italy, both previously assigned to the genus *Eohalimede* Blow and Manning, 1996, and *L. sommarugai* from the Late Eocene of Northern Italy. On the basis of similarities described below, we propose the transfer of these four species into *Pyreneplax* n. gen. (see Blow & Manning, 1997; Beschin *et al.*, 2002, 2009).

A set of dorsal features, such as possessing a suboc-tagonal carapace which is slightly wider than long, a uniform pattern of regions with elevated lobes and covered by granules, regions which are well delimited by large smooth grooves, the anterolateral margins armed with four rounded and granulated teeth or lobes, the slightly convex posterolateral margin ornamented with granules, the posterior margin convex with a median concave depression, characteristic inflated and elongated intestinal lobes separated by a narrow depression, and an identical fronto-orbital structure, are shared by the species here included in *Pyreneplax* n. gen.

Pyreneplax n. gen., differs from *Lobonotus* (type species *L. sculptus* A. Milne-Edwards, 1863 = *Archaeopilumnus caelatus* Rathbun, 1919) *sensu stricto* in: 1) possessing a different carapace outline which is distinctly longer than broad compared to *Lobonotus*; 2) having relatively smaller orbits, and a greater fronto-orbital ratio as in *Lobonotus*; 3) with medially depressed proto-gastric lobes (distinctly inflated in *Lobonotus*); 4) the absence of the characteristic small urogastric lobe present

in *Lobonotus*; 5) the absence of a continuous intestinal ridge flanking the posterior carapace margin as in *Lobonotus*; 6) the anterolateral margin has granulated lobes instead of spines in *Lobonotus*; 7) the posterior carapace margin is proportionately shorter and medially depressed compared to *Lobonotus* which is more convex and continuous; and 8) the more prominent grooves delimiting the regions which are not so extended as in *Lobonotus*.

Regarding the ventral features, the differences are even more evident. *Pyreneplax* has a proportionately narrower, more flattened and granulated thoracic sternum instead of the wider, concave and smooth one of *Lobonotus*; thoracic sternite 3 has a shallow median longitudinal groove that connects with the sterno-abdominal cavity, reaching the end of sternite 4 in *Pyreneplax*, whereas sternite 3 is entire, with the sterno-abdominal cavity endings at sternite 4 in *Lobonotus*; sternites 3 and 4 in *Pyreneplax* n. gen. are divided by a complete groove while in *Lobonotus*, this groove is absent and the suture is only visible laterally; the telson in *Pyreneplax* has a rounded tip instead of the more acute one of *Lobonotus* (cf. A. Milne-Edwards, 1863, pl. 10, figs. 1, 1a, 1b, and 4, 4a, 4b; Rathbun, 1919, pl. 6, figs. 6, 7, pl. 7, figs. 10-13, and pl. 8, figs. 4 to 7; Natural History Museum London web, Picture library: <http://piclib.nhm.ac.uk/>).

The partially well preserved ventral structures of some samples of *Pyreneplax* n. gen., allow comparisons with members of fossil and extant brachyuran families, and as a result, we are relatively confident in its familial assignment.

On the basis of the dorsal and ventral features, the extant family Vultocinidae Ng and Manuel-Santos, 2007 (Goneplacoidea), represented by the sole species *Vultocinus anfractus* Ng and Manuel-Santos, 2007, appears to be clearly related to *Pyreneplax* n. gen.

Both genera share a set of characters and ratios, including: similar carapace outline, similar fronto-orbital pattern, similar shape of swollen regions covered by granules and divided by large and smooth grooves, bilobed frontal margin with granulated edges, supraorbital margin with two fissures, four anterolateral granulated teeth or lobes, posterolateral margin ornamented with granules, posterior margin slightly convex and medially depressed, and the characteristic transversally elongate and inflate intestinal lobes (Fig. 3.1, 2; Ng & Manuel-Santos, 2007, pl. 50, figs. 1, 2, 3a).

There are also many similarities in the ventral features. Both genera have a similar flattened and granulated thoracic sternum with sternites 3 and 4 divided by an axial shallow groove, sternites 1 and 2 fused, suture 2/3 complete, suture 3/4 possessing a shallow transversal groove, sternite 4 with prominent lateral edges, sutures 4/5 and 5/6 medially interrupted, suture 6/7 appearing complete, episternites 4-6 fused, similarly narrow, granulated and medially inflated abdominal somites 1-3, and a triangular telson with a rounded tip reaching half of sternite 4 (Fig. 3.3, 4). See also Ng & Manuel-Santos (2007, figs. 3c, 3d, 5, 8a, 9a, 10a, 11a, 12a) and Ng & Richer de Forges (2009, fig. 1).

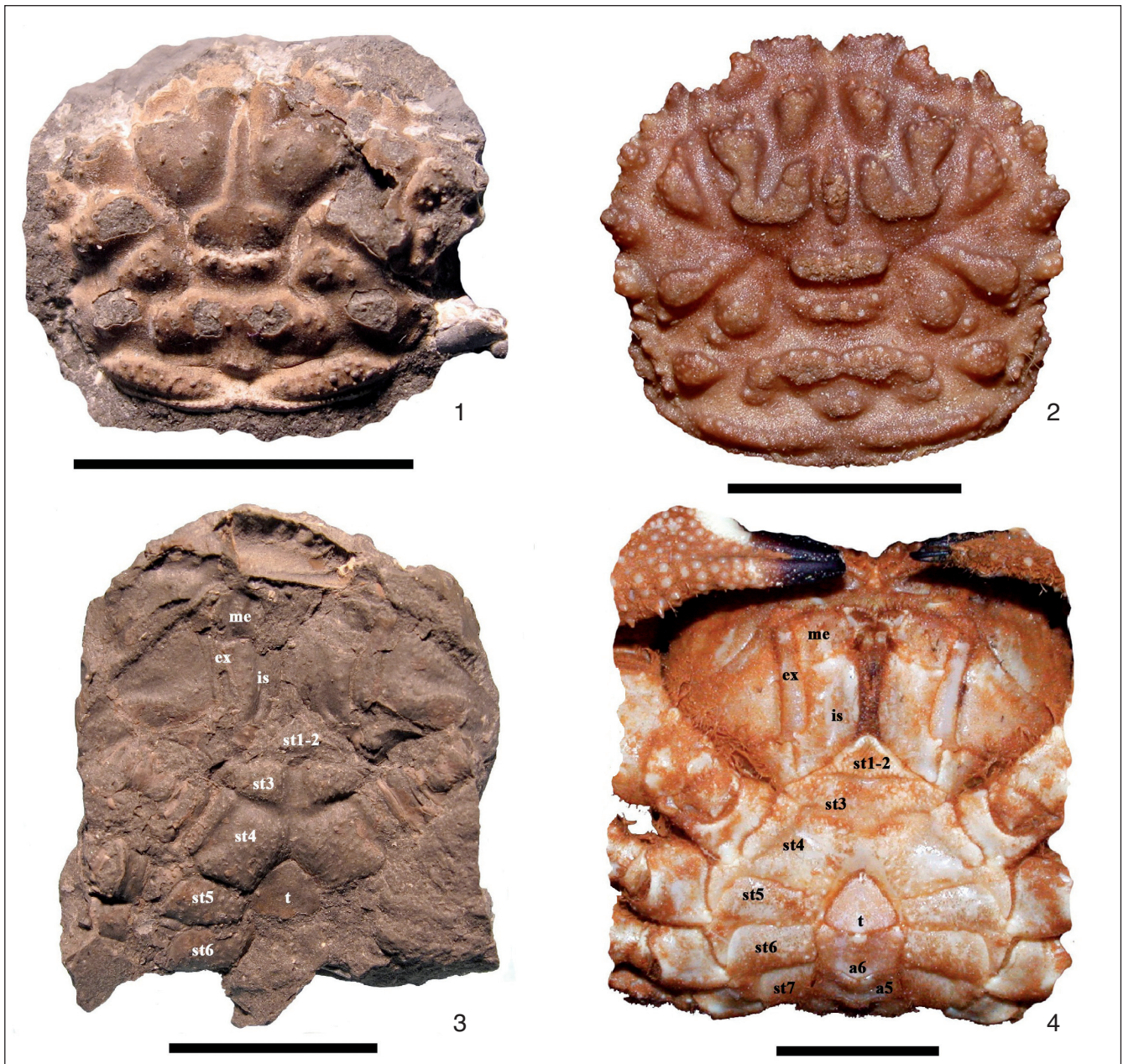


Fig. 3. 1, 3, *Pyreneplax basaensis* n. gen., n. sp. Priabonian, Yebra de Basa (Huesca, Aragón, N Spain). 1: paratype MPZ 2013/82, dorsal view; 3: holotype MPZ 2013/80, ventral view. 2, 4, *Vultocinus anfractus* Ng and Manuel-Santos, 2007. 2: holotype NMCR 19114, male, Santiago, Maribojoc Bay, Panglao, Bohol, Philippines, 9°0.043'N 123°0.051'E, dorsal view; 4: MNHN unnumbered, male, east coast of New Caledonia, collector B. Richer de Forges, 8 August 1986, 21°48.20'S 166°33.80'E, ventral view. Abbreviations: is = ischium of third maxilliped; me = merus of third maxilliped; ex = exognath of third maxilliped; st = thoracic sternites; a = abdominal somites; t = telson. Scale bar = 1 cm.

Fig. 3. 1, 3, *Pyreneplax basaensis* n. gen., n. sp. Priabonià, Yebra de Basa (Osca, Aragó, N d'Espanya). 1: paratip MPZ 2013/82, vista dorsal. 3: holotip MPZ 2013/80, vista ventral. 2, 4, *Vultocinus anfractus* Ng i Manuel-Santos, 2007. 2: holotip NMCR 19114, mascle, Santiago, Badia de Maribojoc, Panglao, Bohol, Filipines, 9°0.043'N 123°0.051'E, vista dorsal; 4: MNHN sense número, mascle, costa est de Nova Caledònia, recol·lector B. Richer de Forges, 8 d'agost 1986, 21°48.20'S 166°33.80'E, vista ventral. Abreviacions: is = isqui del tercer maxil·lípede; me = meros del tercer maxil·lípede; ex = exopodi del tercer maxil·lípede; st = esternites toràciques; a = somites abdominals; t = tèlson. Escala = 1 cm.

Moreover, both genera present a similar ornamentation that consists of small rounded tip granules scattered on the top of the dorsal region swellings, margins, thoracic sternum, abdomen and maxillipeds, and placed in identical areas.

Nevertheless, it would be important to compare the unusual narrow abdomen of *Vultocinus* females, with that of *Pyreneplax* females, once they are found to further cement this suggested relationship (see Ng & Richer de Forges, 2009, fig. 1).

The two genera can essentially be differentiated by the shape of some dorsal regions, more sculptured in *Vultocinus*, and the size and depth of carapace grooves, larger and deeper in *Vultocinus*; the median depression in the posterior margin which is more evident in *Pyreneplax* n. gen. than in *Vultocinus*, and the thoracic sternum is slightly broader in the new genus.

Therefore, in view of the above discussed similarities in the carapace sculpture and ornamentation and despite the age difference, a close relationship between the two

genera seems to be clear. In our opinion, *Pyreneplax* n. gen. should be classified in the family Vultocinidae.

Pyreneplax is also compared here with the Eocene genus *Martinocarcinus* Böhm, 1922 (type species, *Martinocarcinus ickenae* Böhm, 1922) the only genus and species of the family Martinocarinidae Schweitzer, Feldmann and Bonadio, 2009 (Goneplacoidea). *Pyreneplax* n. gen. shares with *Martinocarcinus* a very similar ventral pattern as described before: similar flattened and granulated thoracic sternum with sternites 3 and 4 divided by an axial shallow groove, sternites 1-2 fused, suture 2/3 complete, suture 3/4 with a shallow transverse groove, and sternite 4 with prominent lateral edges. They only differ in the depth of the sternoabdominal cavity and the width of grooves in sternites 3 and 4, being apparently deeper and wider in *Martinocarcinus*, and the thoracic sternum also appears to be relatively broader in the latter genus.

However significant differences are evident in dorsal view: *Pyreneplax* has the regions strongly swollen while, in *Martinocarcinus*, the regions even if discernible and with ornamentation covering the same areas, are practically flat. Other substantial differences are: a more ovate carapace outline and an anterolateral margin armed with five spines in *Martinocarcinus* versus a suboctagonal outline and an anterolateral margin with only four granulated lobes in *Pyreneplax* n. gen.; and a much broader fronto-orbital ratio in the new genus than in *Martinocarcinus*. These differences are sufficient to exclude the inclusion of the new genus in Martinocarinidae (see Schweitzer *et al.*, 2009).

Pyreneplax basaensis is also compared to several other Eocene brachyuran taxa with similar carapace features.

Lobonotus natchitochensis Stenzel, 1935 is close to *P. basaensis* n. gen., n. sp., especially because of its very similar outline and regions pattern; however it differs in its ornamentation, formed by coarse pustules, and by the lack of a deep groove between the mesogastric lobe and the urogastric lobe.

The genus *Pakicarcinus* Schweitzer, Feldmann and Gingerich, 2004 (Xanthoidea: Panopeidae) has superficial dorsal similarities with *Pyreneplax* n. gen., but differs by its more convex carapace as well as by the large and inflated protogastric lobes instead of the medially subdivided ones of the latter. While *Pyreneplax* displays four lobes in the anterolateral margin, *Pakicarcinus* has four spines and does not show the characteristic granulation covering the top of the dorsal regions in the new genus. Moreover, the much broader thoracic sternum and the clear suture 3/4 of *Pakicarcinus*, distinct in *Pyreneplax*, discard a possible relationship between both genera (see Collins & Morris, 1978; Schweitzer *et al.*, 2004).

Some species ascribed to *Titanocarcinus* A. Milne-Edwards, 1864 (Carpilioidea: Tumidocarinidae) exhibit several dorsal and ventral features similar to *Pyreneplax*: well-marked and granulated dorsal regions, dorsal surface moderately convex longitudinally, frontal margin bilobed, supra-orbital margin with two notches, developed lateral cardiac lobes, thoracic sternum with sternites 1 and 2 fused, sternites 2 and 3 divided by a clear suture, and sternites 3 and 4 divided by a clear groove (*sensu*

Schweitzer *et al.*, 2007b). It is noteworthy that only one species of this genus, *T. decor* Schweitzer, Artal, Van Bakel, Jagt and Karasawa, 2007, has preserved thoracic and abdominal structures and thus, the comparison based on ventral characters is limited to this taxon.

However, there are clear differences between the two genera. The carapace outline of *Titanocarcinus* is subtrapezoidal whereas it is suboctagonal in *Pyreneplax*; its anterolateral margins are proportionately longer, the posterolateral margins are more convergent and the posterior carapace margin relatively shorter than the new genus; the maximum width is placed more posteriorly than in *Pyreneplax*; *Titanocarcinus* also lacks the well extended intestinal lobes that *Pyreneplax* has. Ventral differences are also apparent. In particular, the strong transversally vaulted shape of thoracic sternites 3 and 4 (see Schweitzer *et al.*, 2007b, figs. 3b, 3c, 4) of *Titanocarcinus*, contrasts with the flattened ones that the new genus has (as usual in Goneplacoidea, see Ng *et al.*, 2007). In addition, the well-marked axial groove in the thoracic sternite 3 of *Pyreneplax* is barely distinguishable in *Titanocarcinus* (see Schweitzer *et al.*, 2007b, same figures). These differences argue against a close relationship between the two genera.

Pyreneplax basaensis n. sp.

Fig. 3.1, 3; Fig. 4.1-4, 6

Materials and dimensions (in mm). Six specimens partially preserved. Holotype MPZ 2013/80: carapace length = 17.5; width = 20.5; orbito-frontal width = 12.9. Paratype MPZ 2013/79: carapace length = 14.5; width = 16.4*; orbito-frontal width = 10.9. Paratype MPZ 2013/81: carapace length = 13; carapace width = 18. Paratype MPZ 2013/82: carapace length = 10.2; carapace width = 12.6; orbito-frontal width = 8.1. Paratype MPZ 2013/83: incomplete. Paratype MPZ 2013/84: incomplete. * Right margin incomplete.

Etymology: referring to the locality where the material was collected.

Type locality: Yebra de Basa, Huesca province, Aragón region, Northern Spain.

Geological age: Priabonian (Late Eocene).

Diagnosis: as for the genus.

Description. Carapace suboctagonal, slightly wider than long, flattened, somewhat convex anteriorly, widest at third anterolateral tooth level. Dorsal regions well defined, elevated, ornamented with granules dorsally, well delimited by large and smooth grooves. Frontal margin bilobed, straight, divided by U-shaped notch, faintly advanced, edge ornamented with pointed granules. Orbits oblique, relatively broad, slightly raised, separated from frontal margin by deep V-shaped fold; supraorbital margin semi-circular, ornamented with pointed granules; two shallow notches near outer margin separates outer-

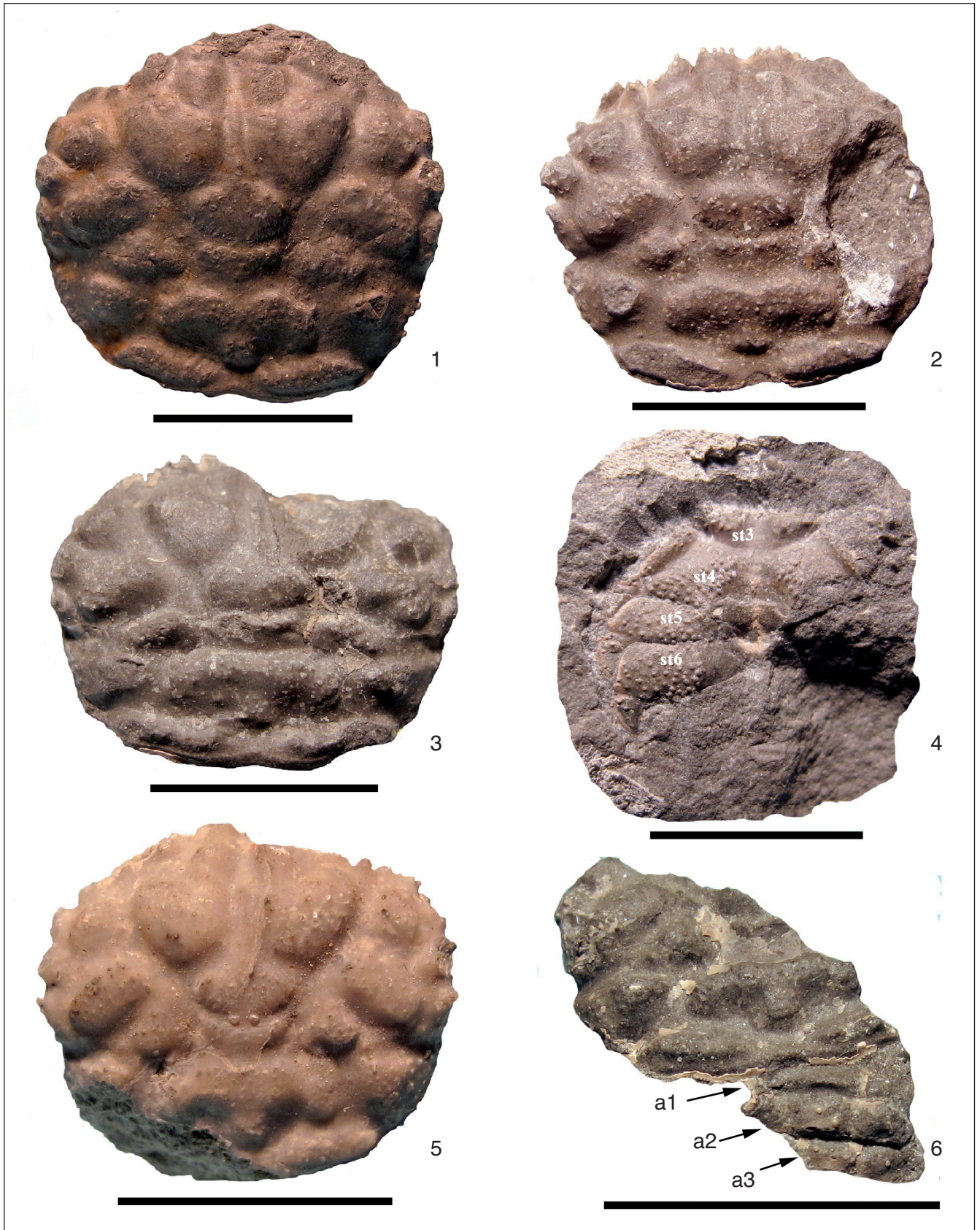


Fig. 4. 1-4, 6, *Pyreneplax basaensis* n. gen., n. sp. Priabonian, Yebra de Basa (Huesca, Aragón, N Spain). 1: holotype MPZ 2013/80, dorsal view; 2: paratype MPZ 2013/79, dorsal view; 3: paratype MPZ 2013/81, dorsal view; 4: paratype MPZ 2013/83, ventral view; 6: paratype MPZ 2013/84, dorsal view. 5, *Pyreneplax granosa* (Beschin, Busulini, De Angeli and Tessier, 2002) n. comb. AO C-456.1, Vicenza region (Italy), dorsal view. Abbreviations: st = thoracic sternites; a = abdominal somites. Scale bar = 1 cm.

Fig. 4. 1-4, 6, *Pyreneplax basaensis* n. gen., n. sp. Priabonià, Yebra de Basa (Osca, Aragó, N d'Espanya). 1: holotip MPZ 2013/80, vista dorsal; 2: paratip MPZ 2013/79, vista dorsal; 3: paratip MPZ 2013/81, vista dorsal; 4: paratip MPZ 2013/83, vista ventral; 6: paratip MPZ 2013/84, vista dorsal. 5, *Pyreneplax granosa* (Beschin, Busulini, De Angeli i Tessier, 2002) n. comb. AO C-456.1, regió de Vicenza (Itàlia), vista dorsal. Abreviacions: st = esternites toràciques; a = somites abdominals. Escala = 1 cm.

and intra-orbital teeth; inner-orbital tooth, large subtriangular. Anterolateral margins convex, with four rounded and granulated teeth (outer orbital spine excluded); first one smallest, at lower level. Posterolateral margins slightly convex, ornamented with rows of granules. Posterior carapace margin slightly convex, medially concave, rimmed, finely ornamented with a row of granules. Cervical and hepato-gastric grooves well marked, broad, smooth. Gastric process well marked; epigastric lobes swollen, slightly connected with protogastric lobe; protogastric lobes large, swollen, oval, with granulated edges, anterior portion medially depressed, U-shaped, smooth; mesogastric lobe posteriorly broad, granulated, anterior portion slender, low, long, reaching basal portion of epigastric lobes; metagastric lobe indistinct; urogastric region swollen, granulated, well delimited from meso- and metagastric lobe by a narrow groove with gastric pits. Cardiac region broad, swollen, laterally expanded, T-shaped, granulated. Both intestinal lobes transversely elongate, inflated, narrow, subparallel along posterior carapace margin, medially separated by small smooth depression. Hepatic region inflated, covered by granules. Branchial regions well defined by swollen and granulated lobes, separated by broad, shallow, smooth grooves; epibranchial lobe subdivided in two; supra-epibranchial lobe transversely elongate, slightly oblique, directed to fourth anterolateral tooth; sub-epibranchial lobe from rounded to triangular, both delimited by shallow and smooth grooves; mesobranchial lobe inflated, covered by granules. Pterygostomial regions subtrapezoidal, finely rimmed. Thoracic sternum relatively broad, flattened, covered by coarse granules. Sternite 3 with shallow axial groove reaching sterno-abdominal cavity that reaches end of sternite 4. Sternites 1 and 2 fused, subtriangular; sternite 3 inverted subtriangular; sternite 4 subtrapezoidal, prominent lateral edges with parallel groove; sternites 5 and 6 subtrapezoidal, elongate, narrowing towards sterno-abdominal cavity. Suture 1/2 absent; suture 2/3 complete; suture 3/4 distinct, marked by a groove, suture visible only laterally; sutures 4/5, 5/6 medially interrupted; suture 6/7 appears to be complete. Episternites not extended laterally, sutures distinct. Male abdomen apparently narrow; telson subtriangular, rounded tip, reaching halfway sternite 4; somites 1-3 subrectangular, transversely narrow, medially inflated, covered by dispersed coarse granules. Ischium of third maxilliped subrectangular with median sulcus; inner margin convex, outer margin concave, covered by scattered granules; exognath slender; merus subquadrate.

Discussion. Differences between the new species and the three ones assigned to the genus are not very evident. In the case of *Pyreneplax sandersi*, despite being poorly figured in Blow & Manning (1997, fig. 2), a thorough examination of the high resolution pictures of holotype ChM PI 15210 and paratype ChM PI 15200, kindly provided by the Charleston Museum (South Carolina, USA), allowed us a comparison with the new species.

Pyreneplax basaensis n. sp., can be differentiated from *P. sandersi*, mainly by the grooves separating the regions

being relatively narrower than in *P. sandersi*; the epigastric lobes are closer to the protogastric lobes in *P. basaensis* than in *P. sandersi*; the urogastric region is proportionately large in *P. basaensis* whereas is narrow and acute in *P. sandersi*; the supra-epibranchial lobe is slightly oblique in *P. basaensis* but is almost horizontal in *P. sandersi*, visible in particular in the paratype ChM PI 15200 (see Blow & Manning, 1997, 1998).

With regard to the two Italian species, the differences with *P. basaensis* are small. *Pyreneplax granosa* (Beschlin, Busulini, De Angeli and Tessier, 2002) n. comb. (Fig. 4. 5) differs from *P. basaensis* in having relatively less ornamented regions with the granules coarser, the supra-epibranchial lobe is more oblique than in *P. basaensis* and the sub-epibranchial lobe is rounded and less extended than in *P. basaensis*, also the fronto- and supra-orbital margin seems to be more swollen (see Beschlin *et al.*, 2002: 19-20, fig. 14, pl. 4, figs. 1, 2).

The carapace of *P. sommarugai* (Beschlin, Busulini and Tessier, 2009) n. comb. appears to be more lengthened than in *P. basaensis*, the grooves delimiting regions are narrower and the ornamentation of the regions is more uniform with granules completely covering all the lobes (see Beschlin *et al.*, 2009: 12, 14-15, pl. 3, figs. 1, 2).

Material found in the Bartonian (Eocene) of Catalonia, must be assigned to the new genus (see Maza & Moreno, 2012: 87-88, figs. 4, 5).

REMARKS ON *LOBONOTUS*

Lobonotus sculptus, the type species of the genus (Carpilioidea: Tumidocarcinidae), was erected by A. Milne-Edwards (1863) based on specimens from the Miocene of the Caribbean (see A. Milne-Edwards, 1863: pl. 10, figs. 1, 1a, 1b, 4, 4a, 4b).

Rathbun (1919: 177-179, pl. 6, figs. 6-7; pl. 7, figs. 10-13; pl. 8, figs. 4-7), erected *Archaeopilumnus caelatus* also with Miocene material from the same area, but one year later (Rathbun, 1920: 384), synonymised it with *L. sculptus*, stating: "It is the same as my *Archaeopilumnus caelatus*".

Subsequently, Rathbun (1930: 2-3, pl. 1, figs. 1-3) erected the new species *Lobonotus mexicanus* relating it with *L. sculptus*, marking anyway differences between the two species.

Lobonotus sculptus and *L. mexicanus* are clearly distinguishable between them. Examination of the good figures of dorsal and ventral features in Rathbun (1919) as *Archaeopilumnus caelatus* or even the pictures of the holotype, accessible online at the web of the Natural History Museum of London, regarding *L. sculptus*, and the figures of the holotype that illustrate Rathbun's (1930) work, regarding *L. mexicanus*, allow to make a comparison.

Lobonotus mexicanus differs from the type species because it is clearly lengthened, grooves separating regions are wider than in *L. sculptus* which has more tumid and lobulated regions; it lacks the well-marked urogastric lobe and the continuous intestinal inflation, parallel to the posterior margin; hepatic and epibranchial lobes are not separated from the anterolateral margin as in *L. sculptus*;

anterolateral margin is toothed whereas it is spiny in *L. sculptus*; posterior margin shorter than in *L. sculptus*; thoracic sternum narrower, sternites 3-4, vaulted, large groove parallel to lateral margin of sternite 4, whereas in *L. sculptus*, sternites 3 and 4 appear flattened and the groove parallel to lateral margin of sternite 4 appears narrow. These differences show clearly that the two species are not congeneric.

Some of the above mentioned differences were pointed out by Stenzel (1935: 384).

Several subsequent authors studying the genus *Lobonotus*, used in part *L. mexicanus* for comparisons instead of the type species *L. sculptus*. For instance, Schweitzer *et al.* (2004: 106) compared the thoracic sternal sutures of *Pakicarcinus orientalis* (Collins and Morris, 1978) (= *Lobonotus orientalis* Collins and Morris, 1978) with *L. mexicanus*. Schweitzer *et al.* (2007a: 8; 2007b: 279), emended the diagnosis of the genus and discussed on *Lobonotus* based on ventral features of *L. mexicanus*. De Angeli & Cecchi (2012: 39) also compared the ventral features of *L. beschini* with *L. mexicanus* in their systematic discussions.

Hence, numerous Eocene species were either assigned or moved to *Lobonotus*: *L. australis* Fritsch, 1878, *L. bakeri* (Rathbun, 1935), *L. beschini* De Angeli and Cecchi, 2012, *L. brazosensis* Stenzel, 1935, *L. granosus*, *L. natchitochensis* Stenzel, 1935, *L. purdyi* (Blow and Manning, 1996), *L. sandersi* (Blow and Manning, 1997), *L. sommarugai* Beschin, Busulini and Tessier, 2009, *L. sturgeonii* (Feldmann, Bice, Schweitzer, Salva and Pickford, 1998), and *L. vulgatus* Quayle and Collins, 1981 (although some of them were removed from the genus).

Despite the literature discussing on *Lobonotus* (Collins & Morris, 1978; Schweitzer *et al.*, 2002, 2004, 2007a, 2007b; and the particularly complete compilation in Beschin *et al.*, 2009), we are convinced that only *Lobonotus sculptus*, the type species, should be considered as *Lobonotus sensu stricto*. In any case, even if the revision of the species assigned to *Lobonotus* is beyond the aim of this paper, we recommend the need for a complete and thorough revision of the generic and familial placement of all the taxa associated to this genus.

Moreover, the familial placement of *Lobonotus* must be revised as well. We remove herein the genus *Lobonotus* from the Tumidocarcinidae Schweitzer, 2005 (Carpilioidea Ortmann, 1893) and according with its general shape, carapace transversely ovate, convex, spiny anterolateral margin, and free male somites, we retain the genus, with reservations, in Pilumnidae (Pilumnoidea) as already suggested by Rathbun (1920: 384) (see also Karasawa & Schweitzer, 2006).

CONCLUSIONS

Thanks to the discovery of *Pyreneplax basaensis* n. gen., n. sp., it has been possible to erect a new genus and, based in its dorsal features, to relate it to three species previously referred to *Lobonotus*, distributed along the Late Eocene across the western Tethys, from Italy and the Iberian Peninsula to the eastern coast of

North America in the western Atlantic Ocean. Also, on the basis of the ventral features preserved in some samples of *Pyreneplax basaensis*, the genus is clearly related to the extant genus *Vultocinus* (Vultocinidae, Goneplacidea) which occurs in the western Pacific Ocean.

As a result of the comparisons between *Pyreneplax* and the species formerly attributed to *Lobonotus*, we conclude that only the type species of the latter (*L. sculptus* A. Milne-Edwards, 1863) belongs to this genus and suggest a revision of all the species formerly attributed to it considering, as far as possible, the ventral characters. Furthermore, both the familial and suprafamilial assignment of these species should be revised. Currently placed into family Tumidocarcinidae, *Lobonotus* typically does not possess the general dorsal shape of this family members nor that of the Carpilioidea, being their ventral affinity based on features present in many brachyuran taxa. The same is true for the genus *Titanocarcinus*, also placed in Tumidocarcinidae. Even if the diagnosis for this family is expanded substantially (see Schweitzer *et al.*, 2007b: 279 and Schweitzer & Feldmann, 2012: 24), we still find difficult to keep both *Lobonotus* and *Titanocarcinus* in the Tumidocarcinidae. A revision is clearly necessary.

Several Eocene genera present a similar dorsal aspect resembling to *Pyreneplax* n. gen., however, no close relationships can be concluded between them as explained above. Dorsal features and, in particular, the characters present in the two anterior thirds of the carapace shown by the new genus, are relatively common in numerous fossil and extant brachyuran genera, representing different families of the Xanthoidea or Pilumnoidea. In the case of fossil taxa, many of them are only known by more or less well preserved fragments of their carapace, but lacking remains of thoracic and abdominal parts. Since such parts are important for a correct systematic diagnosis, their precise familial placement becomes very difficult to deal with (see Guinot, 1979). In their absence, no definitive statements can be made. The persistence of the dorsal carapace pattern through time, would suggest either an evolutionary success or an example of convergence. This convergence is well known (see Ng *et al.*, 2008; Lai *et al.*, 2011). It is clear that new discoveries of fossil taxa with well-preserved ventral parts would help to better interpret the fossil record of these groups.

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