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On the systematic placement of *Pyreneplax* Ossó, Domínguez & Artal, 2014 (Decapoda, Brachyura, Vultocinidae)

Taksonomska uvrstitev rodu *Pyreneplax* Ossó, Domínguez & Artal, 2014 (Decapoda, Brachyura, Vultocinidae)

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Ključne besede: Goneplacoidea, Martinocarcinidae, sistematika, eocen, priabonij, Evropa

Abstract

Examination of the thoracic sternum and pleonal elements of a new male specimen of *Pyreneplax basaensis* Ossó, Domínguez & Artal, 2014 from the upper Eocene of northern Spain confirms its assignment to the family Vultocinidae Ng & Manuel-Santos, 2007 and reveals the presence of an old lineage (*Pyreneplax* and possible allies) that appeared during the Eocene, persisting to the present day.

Izvleček

V prispevku opisujemo nove fosilne ostanke primerka samca vrste *Pyreneplax basaensis* Ossó, Domínguez & Artal, 2014 iz zgornjega eocena na severu Španije. Ohranjene podrobnosti delov oprsja in repa potrjujejo njegovo uvrstitev v družino Vultocinidae Ng & Manuel-Santos, 2007 in razkrivajo prisotnost stare linije (*Pyreneplax* in sorodni taksoni), ki se je pojavila v eocenu in je prisotna še danes.

Introduction

A new specimen of *Pyreneplax basaensis* with complete sternal and pleonal features and remains of ambulatory legs reveals additional features that were not seen in the type series. It has allowed observation of additional similarities to the extant species *Vultocinus anfractus* Ng & Manuel-Santos, 2007 and a more detailed comparison between both taxa (see Domínguez & Ossó, 2019).

The genus *Pyreneplax* Ossó, Domínguez & Artal, 2014 was erected to accommodate *P. basaensis* from the Priabonian of the south Pyrenean basins of Spain. Subsequently, other, closely similar species have been recorded from the Eocene of the Atlantic Coast of North America and from northern Italy. On the basis of dorsal carapace morphology, fossil crab species such as *Lobonotus saundersi* (Blow & Manning, 1997) from South Carolina (USA) and *L. granosus* (Beschin, Busulini, De Angeli & Tessier, 2002) and *L. sommarugai* Beschin, Busulini & Tessier, 2009 from northern Italy, have lately been transferred to the genus *Pyreneplax* (see Ossó, Domínguez & Artal, 2014; De Angeli, 2014).

Dorsal and ventral (thoracic sternum, pleon) features of *Pyreneplax basaensis* confirm its family relationship with *Vultocinus anfractus*, in spite of the time span that separates both species, placing the origins of the family Vultocinidae in the late Eocene. Furthermore, new DNA molecular studies of *Vultocinus anfractus* have revealed that, "it comes out as a long branch inside the Heterotremata, far away from the rest of the Goneplacoidea" (Ng & Tsang, pers. comm., June/2019).

The studied material is housed at Museo de Ciencias Naturales de la Universidad de Zaragoza (Spain), under acronym MPZ.

Systematic palaeontology

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
Genus *Pyreneplax* Ossó, Domínguez & Artal, 2014 , emend.

Type species: *Pyreneplax basaensis* Ossó, Domínguez & Artal, 2014.

Other species included: *Pyreneplax granosa* (Beschin, Busulini, De Angeli & Tessier, 2002), *Pyreneplax saundersi* (Blow & Manning, 1997) and *Pyreneplax sommarugai* (Beschin, Busulini & Tessier, 2009).

Diagnosis (emended): Small- to medium-sized carapace, suboctagonal, from wider than long to slightly wider than long, slightly convex in anterior third, widest at level of third anterolateral tooth. 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 deep fold; supraorbital margin with three teeth separated by two notches, inner orbital tooth 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; protogastric lobes, swollen, oval, U-shaped, anterior portion medially depressed; mesogastric lobe broad posteriorly; anterior portion slender, low, long, reaching basal portion of epigastric lobes; metagastric lobe indistinct; urogastric region swollen, well delimited from meso-metagastric 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 into 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. Male thoracic sternum flattened, covered by coarse granules; sternopleonal cavity narrow, deep; sternite 3 with a shallow longitudinal median groove connecting with sternopleonal cavity, reaching end of sternite 4; sternites 1 and 2 fused, subtriangular; sternite 3 subtriangular; sternite 4 subtrapezoidal, with prominent lateral edges, with marked grooves paralleling edges; sternites 5, 6 and 7 subtrapezoidal, elongate; sternite 7 shorter than sternite 6; suture 1/2 absent; suture 2/3 complete; suture 3/4 distinct, defined by groove, suture visible only laterally; sutures 4/5, 5/6 medially interrupted; episternites not laterally extended, episternite 7 strongly produced, spur shaped, reaching coxa of P5. Male pleon narrow, with free somites, axially vaulted; somites 1, 2 not folded ventrally, visible dorsally; somites 1 to 5 subrectangular, transversely narrow, somite 6 almost as long as broad; somite 3 largest, reaching coxa of P5; somites 4, 5, 6, with slightly concave upper and lateral margins covered by uniformly distributed granules; telson subtriangular, rounded tip. Ischium of third maxilliped subrectangular with median sulcus, inner margin convex, outer margin concave, covered by scarce granules; exognath slender; merus subquadrate. Ambulatory legs keeled, spiny.

Remarks: At the time, the dorso-ventral similarities highlighted by Ossó et al. (2014, pp. 36-38) were considered sufficient to place the Late Eocene *Pyreneplax* within the extant family Vultocinidae (Fig. 1); the additional sternal and pleonal features observed in the new specimen (Fig. 2) confirm this course of action (Domínguez & Ossó, 2019, pp. 70-72). Indeed, in the new specimen, a male, the sternopleonal cavity is deep and relatively narrow, almost reaching the end of sternite 4, as in *Vultocinus* (Ng & Manuel-Santos, 2007, p. 43, figs. 12A, 9A). The position of the press-button in *Vultocinus,* considered important by Ng & Manuel-Santos (2007, p. 42), cannot be observed in the new specimen due to preservation; however, in view of the position of the pleon,

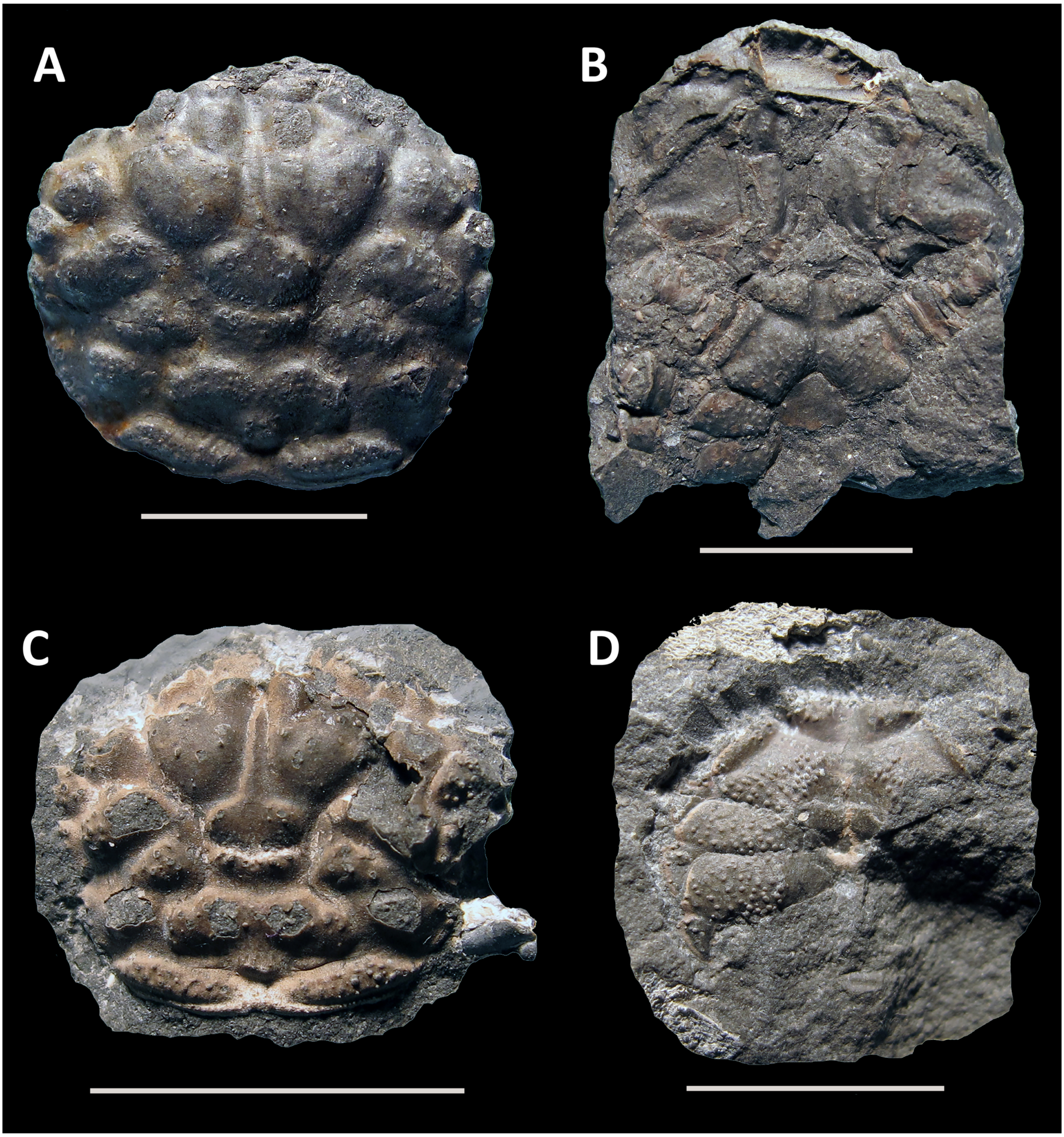

Fig. 1.: *Pyreneplax basaensis* Ossó, Domínguez & Artal, 2014 from the Priabonian (Upper Eocene) of the central Pyrenees of Huesca (Aragón, Spain). A: holotype MPZ 2013/80, dorsal view; B: ventral view of holotype. C: paratype MPZ 2013/82, dorsal view. D: paratype MPZ 2013/83, ventral view. Scale bars equal 10 mm.

slightly shifted down, it is believed that it is on the posterior part of sternite 5, close to sternite 6, as in *Vultocinus* (Figs. 2B, C).

It should be noted that the male pleonal somites 1 and 2 of the new specimen do not appear to be folded ventrally and are therefore located in dorsal position, as in *Vultocinus anfractus* (Figs. 2A, D; compare Ng & Manuel-Santos, 2007, figs. 1B-C, 2). Likewise, it presents a pleonal pattern similar to that of *Vultocinus anfractus*, namely free pleonal somites, axially vaulted, pleonal somites 4 to 6 showing slightly concave upper and lateral margins and pleonal somite 6 almost as long as broad (Figs. 2C, D; Ng & Manuel-Santos, 2007, figs. 5B, 9A, 10A, 11A; Ng & Richer de Forges, 2009, fig. 1B).

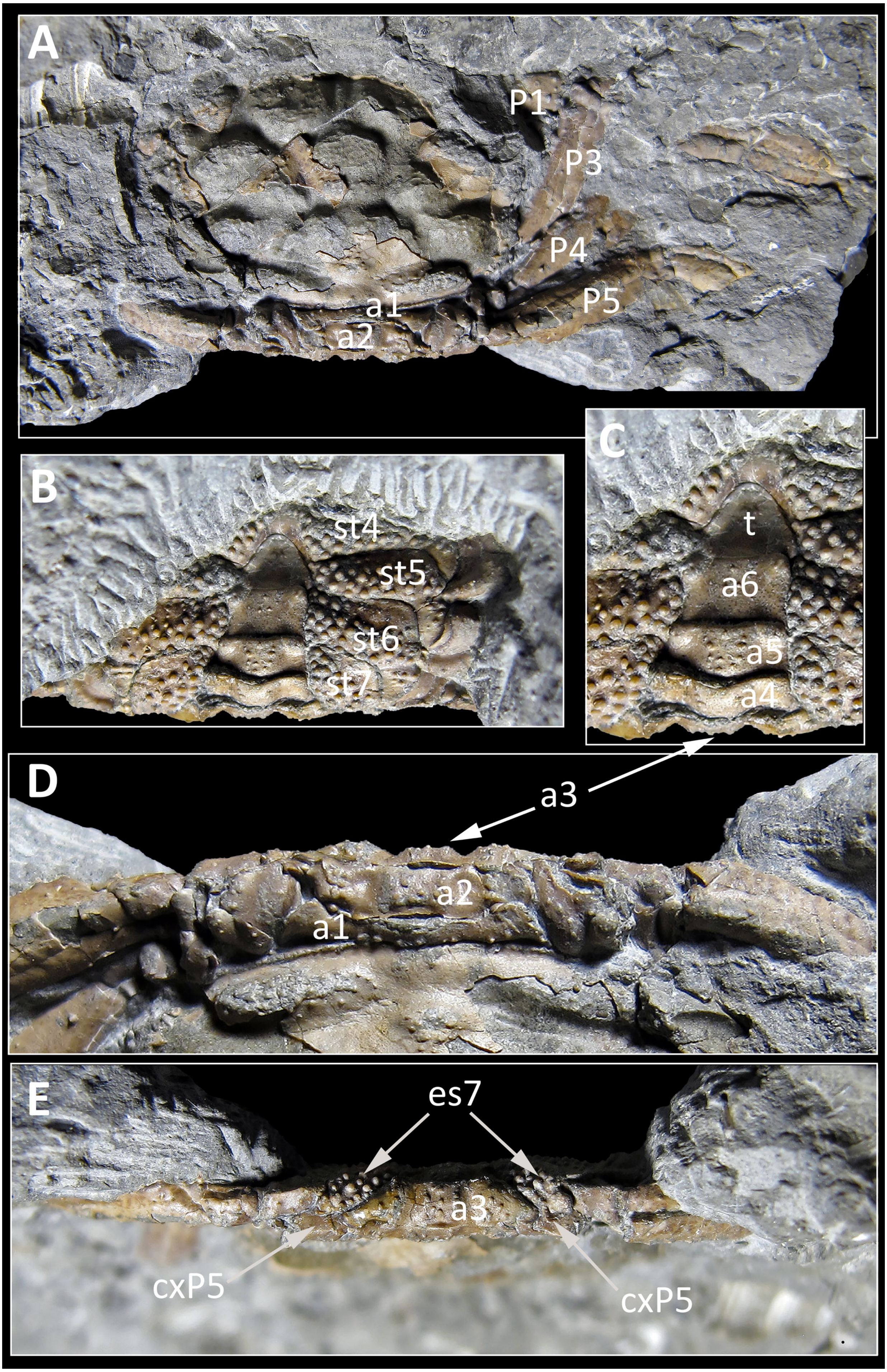
A
P1
P3
P4
P5
a1
a2
B
st4
st5
st6
st7
C
t
a6
a5
a4
D
a3
a2
a1
E
es7
a3
cxP5
cxP5

Fig. 2.

In addition, the posterior edge of episternite 7 in *Pyreneplax basaensis* is, similar to *Vultocinus anfractus*, "strongly produced posteriorly to form a spur which reaches coxa of P5" (Ng & Manuel-Santos, 2007, p. 44). This character, considered "unusual" by Ng & Manuel-Santos (2007), which together the lateral expansion of pleonal somite 3 covers the penis completely, differentiates the Vultocinidae from other goneplacoid families (Ng & Manuel-Santos, 2007, pp. 44, 49, figs. 13A-B; Castro et al., 2010). It is also seen in *Pyreneplax* (Fig. 2E).

Discussion: Penis protection is present, in a range of expressions, among the Heterotremata (Guinot et al., 2013, pp. 84-90). In most goneplacoid families, to which the vultocinids were initially compared, it is usually present as an extension of sternite 7. For example, Davie et al. (2015) noted this condition in the families Acidopsidae Števčić, 2005, Chasmocarcinidae Serène, 1964, Conleyidae Števčić, 2005, Euryplacidae Stimpson, 1871, Goneplacidae MacLeay, 1838, Litocheiridae Števčić, 2005, Progeryonidae Števčić, 2005 (just touching coxa P5) and Scalopidiidae Števčić, 2005. This sternal protection is not present in the Mathildellidae Karasawa & Kato, 2003, Progeryonidae Števčić, 2005 and Sotoplacidae Castro, Guinot & Ng, 2010. However, none of the families that have penis protection possess the spur-shaped prolongation that is seen in *Vultocinus anfractus* and *Pyreneplax basaensis*. This unique character, shared by both genera, in addition to the set of the above-mentioned characters, shows their clear family relationship.

In this respect, the Eocene *Martinocarcinus ickeae* Böhm, 1922 (family Martinocarcinidae Schweitzer, Feldmann & Bonadio, 2009 within the Goneplacoidea) also deserves attention. Indeed, Schweitzer et al. (2009, p. 4) already pointed out the striking similarities in sternal and pleonal features of *Martinocarcinus* and *Vultocinus* (Schweitzer et al., 2009, pl. 1, fig. 4; pl. 2, figs. 1-5), but in view of the substantial differences in dorsal carapace and chelae, they did not conclude that there was a close relationship between them. Ossó et al. (2014, p. 38) also noted the sternal and pleonal similarities between *Martinocarcinus* and *Pyreneplax* but argued against a family relationship, based on differences of dorsal carapace morphology. However, in view of the new pieces of evidence provided by the new specimen of *Pyreneplax*, regarding penis protection, a re-examination of the holotype of *Martinocarcinus ickeae* would appear to be interesting, in particular to see whether or not it has the same pattern of penis protection as in *Vultocinus anfractus* and *P. basaensis*; this cannot be seen in the illustrations of Schweitzer et al. (2009). This character may well connect these three taxa phylogenetically.

Another Eocene taxon, *Agostella terrersensis* Ossó-Morales, 2011 (Goneplacoidea, *incertae sedis*), reveals an extension of sternite 7, as a plate that reaches the coxa of P5, with the lateral margin of pleonal somite 3 completely covering the penis (Ossó, 2011, fig. 4.3). This pattern of penis protection is similar to that seen in some goneplacoid families (Ng & Manuel-Santos, 2007, fig. 10), which supports its original placement within this superfamily and consequently rejects inclusion in the Tumidocarcinidae Schweitzer, 2005 (see Schweitzer et al., 2018, pp. 10-12, fig. 8/1a, b).

The nomenclature of *Pyreneplax saundersi* (Blow & Manning, 1997) (formerly *Eohalimede saundersi*) must be retained as it was originally spelled by Blow & Manning (1997), instead of the correct *sandersi* (see Blow & Manning, 1998). This change of spelling is not allowed under the current Code (ICZN, 1999), in accordance with articles 32.5.1 and 32.5.1.1 (Ng, pers. comm., November/2019).

Conclusions

Molecular studies carried out recently, using several mitochondrial and nuclear genes, have demonstrated that *Vultocinus* sits in its own deep lineage within the Heterotremata and is not related to any of the known goneplacoids, including those without living relatives (Ng & Tsang, pers. comm., October/2019). These results are consistent with what had already been stated in the original paper by Ng & Manuel-Santos (2007, p. 40) that, "*Vultocinus*, new genus, possesses a suite of unusual characters that make its precise affinities difficult to ascertain".

The fossil evidence suggests that we are dealing with a case of an extinct family with an ex-

Fig. 2. *Pyreneplax basaensis* Ossó, Domínguez & Artal, 2014, MPZ 2019/265, from the Priabonian of the central Pyrenees of Huesca (Aragón, Spain). A: dorsal view; B: ventral view; C: closeup view of pleon; D: closeup view of posterior margin of carapace; E: closeup view of the spur-shaped prolongation of sternite 7 (episternite). Abbreviations: a - pleonal somites; cxP5 - coxa of fifth pereiopod; es - episternite; P - pereiopods; st - thoracic sternites; t - telson. Scale bar equals 10 mm.

tant representative rather than an extant family with fossil representatives. The dorsal morphology of *Pyreneplax* is relatively common in numerous Eocene genera, but only preserved sternal and pleonal features can establish the relationship among these (Ossó et al., 2014, p. 41; Jagt et al., 2015, p. 883). The persistence of this dorsal carapace pattern is interpreted either as evolutionary success or an example of convergence. In the case of the Vultocinidae and in view of the preserved ventral features now observed in *Pyreneplax basaensis*, this indicates that the unusual penis protection structures are a successful adaptation and hence persisted over time. Future works and new discoveries will be expected to shed light on the suprafamily relationships of this family and their possible allies.

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