

# New genus and new species of portunoid crab: *Archeoportunus isabensis* from the Lower Eocene of Huesca (Aragon) and Lleida (Catalonia)

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Crabs recovered from marly strata of the upper Roda Formation (Ypresian) at Isàvena (Huesca, Aragón), and the Ypresian of Lleida (Catalonia), exhibit a clear set of characteristics, mainly in chelipeds and dorsal carapace that favour assignment to the superfamily Portunoidea, and confirm a close relationship with the family Portunidae. However, the presence of important and easily distinguished features, such as the strongly marked dorsal ridges or notably narrow sternum, leads us to erect a new genus and species, *Archeoportunus isabensis* gen. nov., sp. nov., and a new family, the *Archeoportunidae* fam. nov. The ventral features of the new taxon, in particular the fairly narrow sternum which notably becomes even narrower posteriorly, the strongly downturned sternites 1-4, bearing strong swellings, and the general adaptation of sternum, pleon and pereopods, substantiates the basal condition of the new taxon within the Portunoidea and also contributes to current knowledge of evolutionary issues within that group.

This publication principally serves to validate the nomenclatural acts in Artal et al. (2013), in order to fulfil the requirements outlined in ICZN (2012).

**Keywords.** *Crustacea, Decapoda, Portunoidea, Archeoportunus, Archeoportunidae, new family, Ypresian, Spain.*

## Nou gènere i nova espècie de cranc portunoid: *Archeoportunus isabensis*, de l'Eocè Inferior d'Osca (Aragó) i Lleida (Catalunya)

Els crancs recuperats en els estrats margosos de la formació Roda (Ipresiana), a Isàvena (Osca, Aragó) així com a l'Ipresiana de Lleida (Catalunya), presenten un conjunt de caràcters, principalment en els quelípeds i en la closca dorsal que permeten la seva assignació a la superfamília Portunoidea, al mateix temps que confirmen una relació propera amb la família Portunidae. Tanmateix, la presència de structures fàcilment distingibles com les carenes dorsals molt marcades o l'estèrnum estret, ens duu a erigir un nou gènere i espècie, *Archeoportunus isabensis*, així com una nova família, *Archeoportunidae*. Les estructures ventrals del nou tàxon, en particular l'estèrnum toràcic que s'estreix posteriorment, les esternites toràciques 1-4 fortament arquejades i amb prominents inflors, i l'adaptació general de l'estèrnum, plèon i pereopodis, corrobora la condició basal del nou tàxon dins dels Portunoidea i a la vegada contribueix al coneixement de l'evolució d'aquest grup.

La present publicació serveix per a validar els actes de nomenclatura establerts en Artal et al. (2013) per tal de complir els requisits descrits a ICZN (2012).

**Mots clau:** *Crustacea, Decapoda, Portunoidea, Archeoportunus, Archeoportunidae, nova família, Ipresiana.*

The well-exposed uppermost levels of the Ilerdian-Cuisian (Ypresian, Lower Eocene) sequence all across the territory of the municipality of Isàvena (Huesca, Aragon, Spain) have yielded a few crabs of relatively large size and portunoid-like appearance. As seen in Artal et al. (2013: 308, figs. 1, 2), the

crab-bearing strata occur around La Puebla de Roda, the main village in the municipality. The layers outcropping consists of grey marls and yellow-grey marly limestones with abundant nummulitids, common echinoids and very rare crab remains. Lithostratigraphically, they correspond to the Roda Formation

(Cuevas-Gozaló et al., 1985) which is dated as early 'Cuisian' (Serra-Kiel et al., 1994). The strata discussed in the present paper invariably occur at the top of the sequence, just above the two carbonated complexes of Areniscas de Roda or Complejo Detrítico Superior (Tosquella, 1988).

Underlying the upper strata are beds with abundant crabs; *Zanthopsis dufourii* (H. Milne-Edwards in d'Archiac, 1850) and *Periacanthus ramosus* Artal & Castillo, 2005 have been documented. On top of the beds that are rich in the majoid *P. ramosus*, there are some well-developed, local patch reefs, still with a highly diverse decapod crustacean fauna, numerous large-sized oysters and abundant coralgal debris. The upper levels become more terrigenous, with abundant nummulitids and faunal indicators of deeper settings, which illustrates subsidence and a relatively fast change of environmental facies. This could explain the sudden change in decapod crustacean assemblages. The common *Z. dufourii* diminishes in overall size and abundance towards the top of the Eocene sequence, thereby gradually disappearing and finally missing from strata that yield the relatively large, portunid-like crabs described in the present paper. These rare crabs are scattered, never occurring in concentrations, but usually well preserved, disarticulated to moderate degree, co-occurring with large-sized, also well-preserved echinoids, suggesting a quiet habitat, lacking high-energy conditions. Tosquella (1988) interpreted the depositional setting to have been within the shelf photic zone.

Recently prepared material from the MGSB and the MGB collections have confirmed the presence of the same species in Perauba (Vilanova de Meià, Lleida, Catalonia). The outcrops consist of brown coloured marls, assigned to the Ypresian (Llompert, 1977). The associated fauna in Perauba, mainly consist of large assemblages of gastropods, and the crustaceans are more abundant and of smaller size in average. The environmental conditions are clearly distinct from the outcrops in Huesca, where the echinoids are abundant, and the gastropods nearly absent.

The studied specimens are housed in the Museu Geològic del Seminari de Barcelona, under acronym MGSB and the Museu de Geologia de Barcelona-Museu de Ciències Naturals de Barcelona, under acronym MGB.

This publication principally serves to validate the nomenclatural acts in Artal et al. (2013), in order to fulfil the requirements outlined in ICZN (2012).

## Results

### *Systematic palaeontology*

Order DECAPODA Latreille, 1802

Superfamily PORTUNOIDEA Rafinesque, 1815

Family ARCHAEOPORTUNIDAE fam. nov.

*Type genus:* *Archaeoportunus* gen. nov.

*Etymology:* related to the type genus.

*Diagnosis:* Large-sized carapaces, transversely subhexagonal in shape, notably wider than long, maximum width at position of epibranchial spine; orbits small, directed forwards, with two slight indentations at supraorbital margins, infraorbital margins bearing two notable teeth, fairly well visible in dorsal view; front advanced, relatively broad, with four lobes, with deep axial notch; anterolateral margins arched, bearing numerous spines including outer-orbital and epibranchial, the latter being extremely long; dorsal regions of carapace well defined by swellings and grooves; gastric, branchial and cardiac regions inflated, bearing marked ridges on top; epibranchial region defined by long, arched and salient ridge; hepatogastric and cardiobranchial grooves well marked, continuous, without interruptions; sternum relatively narrow, fairly narrowing posteriorly, strongly convex in longitudinal section; sternites 1-2 clearly separated from sternites 3-4 by complete suture; sternites 3-4 bearing three pairs of strongly marked swellings; in males, only small portion of sternite 7 visible in ventral view, sternite 8 totally covered by male pleon; male pleon with distinct pleonal segments 3-5, clearly defined by complete sutures; pleonal segment 3 not much wider than 4, reaching fifth coxa; ventral regions of carapace large, without swellings or grooves; buccal frame large; chelipeds large, stout, with thin and long fingers bearing numerous denticles; propodus ridged; pereopods P2-P4 long and flattened, P5 shorter, paddle-like.

*Discussion:* The subhexagonal carapace outline, being notably wider than long, the broadly arched anterolateral margins with numerous spines, the last posterior being extremely elongated, thin and arched; the features of the front, not very produced, with four lobes and a median notch, the small, forwardly directed orbits, with supraorbital fissures; the dorsal ridges, mainly the arched epibranchial keel; the large and robust chelipeds, with ridges on the propodus, and with long fingers bearing numerous denticles,

are characteristic features that permit inclusion in the superfamily Portunoidea (*sensu* Karasawa et al., 2008 and Spiridonov, 2020) and indicate affinities with the family Portunidae. However, the extremely swollen and ridged dorsal regions, the markedly narrow sternum, fairly elongated and narrowing backwards, the fused sternites 3-4, with three pairs of extreme protuberances, only a small portion of sternite 7 visible in ventral view, sternite 8 being entirely covered by the male pleon, the weakly differentiated sexual dimorphism in pleon structure, the male pleon segments 3-5 being fairly distinct, defined by marked and complete sutures, are a peculiar set of characteristics never seen in extant or fossil members assigned to this family to date. No other families placed in the Portunoidea exhibit a similar set of features, thus the erection of a new family within the Portunoidea appears warranted. Of special interest is the fact that pleon segment 3 is not much wider than 4, with lateral margins converging posteriorly, not extending laterally (as typical in portunids), and pleonal segment 6 is rather short in comparison to the usually elongated segment 6 in extant portunids.

#### Genus *Archaeoportunus* gen. nov.

**Type species:** *Archaeoportunus isabenensis* sp. nov.

**Etymology:** The prefix *Archaeo-* indicates a primitive condition.

**Diagnosis:** as for the family

#### *Archaeoportunus isabenensis* sp. nov.

Fig. 1, 2

2013 *Archaeoportunus isabenensis* Artal, Ossó & Domínguez: 307-317, figs. 3-5.

2015 *Archaeoportunus isabenensis* Artal, Ossó & Domínguez. Jagt et al.: 888.

2016 *Archaeoportunus isabenensis* Artal, Ossó & Domínguez. Ossó: 243.

2017 *Archaeoportunus isabenensis* Artal, Ossó & Domínguez. Ferratges: 78, fig. 40, pl. 26A, B.

2020 *Archaeoportunus isabenensis* Artal, Ossó & Domínguez. Spiridonov: 150, 157.

2020 *Archaeoportunus isabenensis* Artal, Ossó & Domínguez. Sasaki: 9073.

**Type locality:** Isàvena, Huesca province (Aragon, Spain).

**Type strata:** Roda Formation.

**Etymology:** From Isàvena (Isábena in Spanish language), the municipality of the province of Huesca where the crabs were collected.

**Diagnosis:** As for genus.

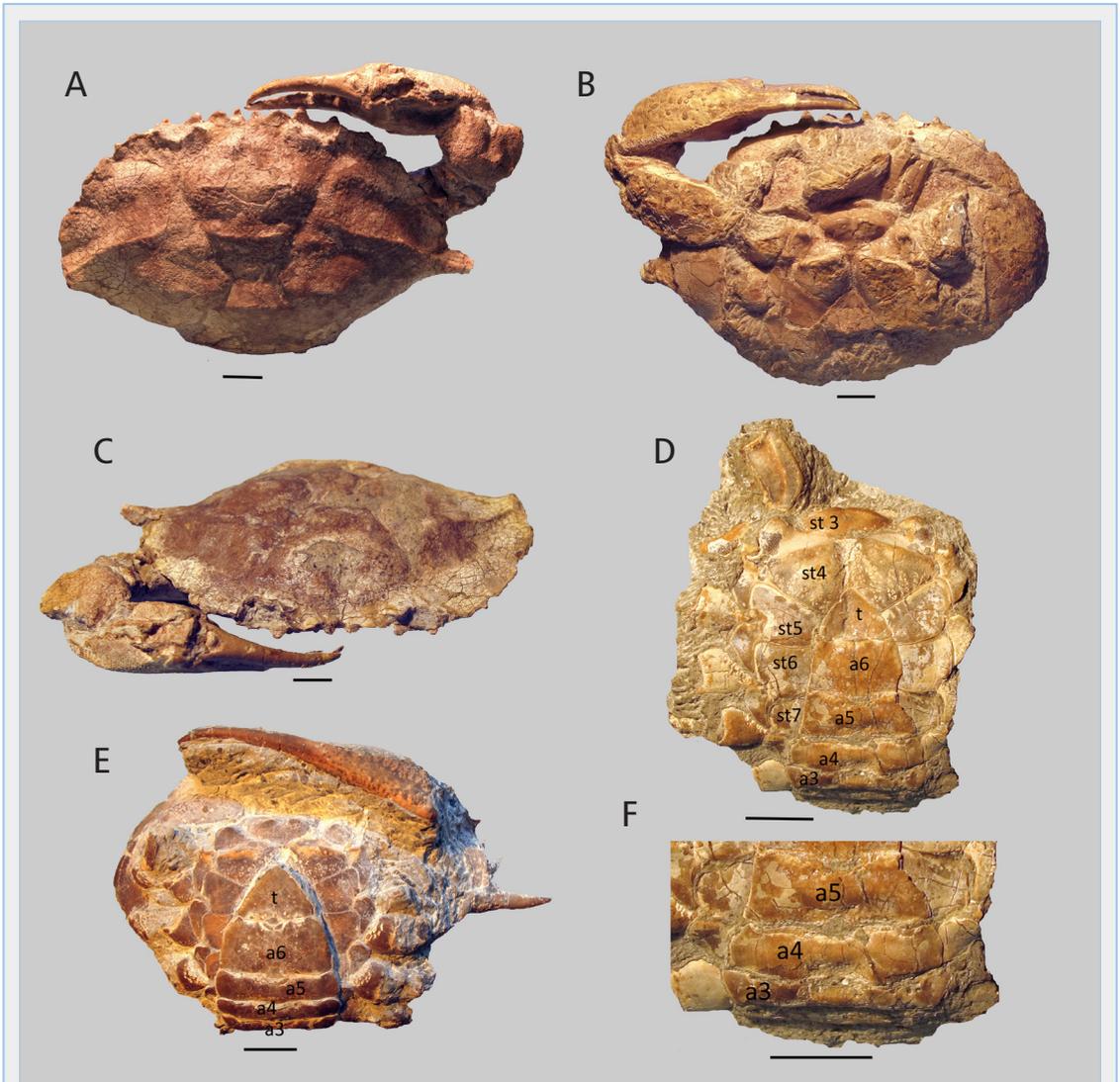
**Material.** Holotype is MGSB68576; paratypes are MGSB68578a-b and MGSB78341. Additional material is MGSB68577, from the Ypresian layers of Isàvena. Additional material MGSB85985, MGSB85986, and MGB63775, MGB56963b from the outcrops of Perauba. Holotype MGSB68576. Carapace length = 102, width = 68, orbitofrontal width = 45.

**Description:** Carapace of large size, greater than 100 mm in width, transversely subhexagonal, much wider than long (L/W ratio about 0.65), maximum width at position of epibranchial spine; dorsal surface moderately convex in both directions. Orbits small in comparison to carapace size, directed forwards, bounded by discrete lobes; supraorbital margin with two slight indentations bounding a median lobe; infraorbital margin bearing two strong subtriangular teeth, fairly well visible in dorsal view. Front slightly advanced, relatively broad, with four unequal lobes, the two axial ones being slender, separated by a deep notch, the two exterior ones broadly triangular, with a sinuous base, extending towards axis. Orbitofrontal width about 0.45 of maximum carapace width.

Anterolateral margins long, arched, bearing nine spines, including outer-orbital; first seven small, discrete, last one extremely long, arched and directed outwards and downwards (see Fig. 1A-C). Posterolateral margins slightly shorter, nearly straight, converging posteriorly. Posterior margin near straight, well defined by marked ridge, of similar size as orbitofrontal width. Dorsal regions of carapace well defined by regions and grooves. Epigastric regions distinguished by small inflations. Protogastric regions large, swollen, crossed by marked transverse ridges. Mesogastric region subtrapezoidal, raised, bearing marked transverse ridge; no clear anterior process. Urogastric region slightly inflated. Hepatic region slightly swollen, bounded transversely by shallow depressions. Epibranchial region with arched, oblique ridge directed posteriorly. Mesobranchial region bearing strong ridges. Cardiac region large, inverted subpentagonal in shape, with transverse ridge. Intestinal region small, depressed. Gastrohepatic and branchiocardiac grooves deep, well defined, continuous, without interruptions. Ventral portions of carapace large, flat, without marked swellings or grooves. Pterygostomial region large, flat.

Sternum subovate, elongated, relatively narrow, strongly convex longitudinally, clearly narrowing posteriorly. Sternites 1-2 fused, small, triangular, fairly well separated by suture from sternite 3. Sternites 1-3 strongly downturned. Sternites 3-4 large, of robust appearance, with strong inflations and marked grooves. Sternite 3 bearing two raised swellings medially separated by a depression. Sternites

3-4 clearly differentiated by a notable lateral notch and deep oblique grooves. Sternite 4 bearing two raised, slightly oblique and strongly marked ridges separated by longitudinal groove; lateral margins of sternite 4 bearing strong, raised protuberance. Sternites 5-7 clearly bounded by sutures, episternites well developed, with broadly rounded sides. Sternite 7 only partially visible in ventral view. Sternite 8 not visible

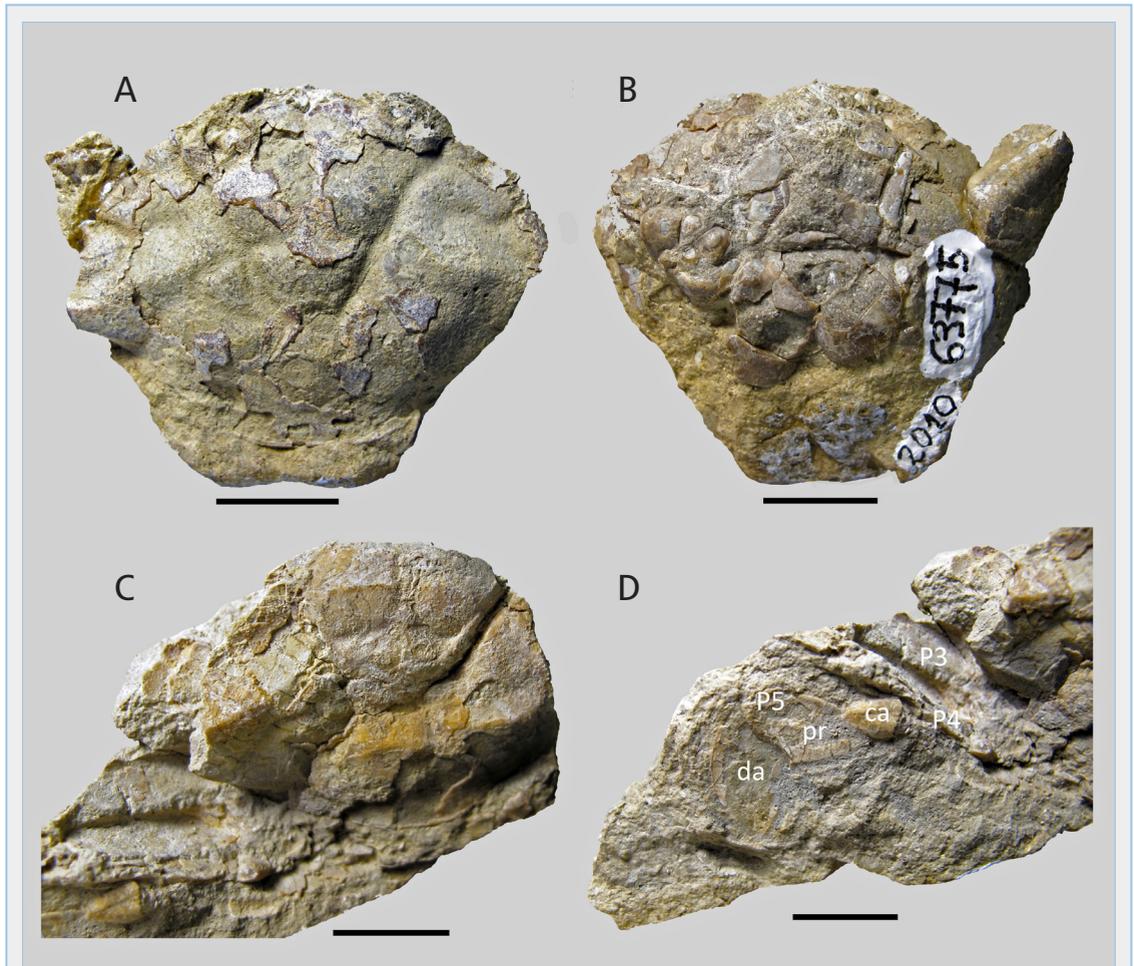


**FIGURE 1.** A-F, *Archaeoportunus isabenensis* gen. nov., sp. nov. from the Ypresian of Isàvena (Huesca, Spain). Holotype MGSB68576, female **A:** dorsal view; **B:** ventral view; **C:** frontal view. Paratype MGSB78341, female, **E:** ventral view. Paratype MGSB68578a, male, **D:** ventral view; **F:** close-up of pleonal somites 3-5. Abbreviations, **a:** pleonal somites; **st:** thoracic sternites; **t:** telson. Scale bar equal to 10 mm.

A-F, *Archaeoportunus isabenensis* gen. nov., sp. nov. de l'Ipresità d'Isàvena (Osca, Espanya). Holotip MGSB68576, femella **A:** vista dorsal; **B:** vista ventral; **C:** vista frontal. Paratip MGSB78341, femella, **E:** vista ventral. Paratip MGSB68578a, mascle, **D:** vista ventral; **F:** detall de les somites pleonals 3-5. Abreviatures, **a:** somites pleonals; **st:** esternites toràciques; **t:** tèlson. Barra d'escala igual a 10 mm.

in ventral view, totally covered by male pleon. Pleon clearly differentiated in both sexes, with all segments fairly well separated by complete sutures; female pleon subovate, with lateral margins broadly arched; male pleon subtriangular. Telson triangular, reaching posterior portion of sternite 4. Pleonal segment 6 somewhat longer than 3-5. In males, pleonal segments 3-5 of similar size, with outer margins slightly arched, separated by clear sutures, with slight inflation in median portion. Pleonal segment 3 not much wider than 4, with margins converging posteriorly and reaching fifth coxae. Buccal frame large. Maxillipeds long, narrow,

endopodite with relatively deep longitudinal groove; exopodite smooth, without grooves. Chelipeds large, robust; merus long, stout, dorsoventrally depressed; carpus short, globular; propodus stout, with rounded sides, ridge in lower portion; fingers very long, inner margins with numerous denticles; first denticle of moveable finger being large. Pereiopods P2-P4 only partially preserved, long, thin, depressed; P5 shorter, paddle-like (Fig. 2D). Second to fifth coxae of similar size. Dorsal surface covered by small granules in decorticated specimens, may be smooth when cuticle appears intact.



**FIGURE 2.** A-D: *Archaeoportunus isabenensis* gen. nov., sp. nov. from the Ypresian of Perauba (Vilanova de Meià, Catalonia). MGB63775 (Vela coll.), **A**: dorsal view; **B**: ventral view. MGB56963b (Vela coll.), **C**: dorsal view; **D**: detail of paddle-like fifth pereopod. Abbreviations, **P3-P5**: pereopods; **ca**: carpus of P5; **da**: dactylus of P5; **pr**: propodus of P5. Scale bar equal to 10 mm.

A-D, *Archaeoportunus isabenensis* gen. nov., sp. nov. de l'Ypresià de Perauba (Vilanova de Meià, Catalunya) MGB63775 (Col. Vela), **A**: vista dorsal; **B**: vista ventral. MGB56963b (Col. Vela), **C**: vista dorsal; **D**: detall del cinquè pereopodi en forma de pala. Abreviatures, **P3-P5**: pereopodis; **ca**: carp del P5; **da**: dàctil del P5; **pr**: propodi del P5. Barra d'escala igual a 10 mm.

**Remarks.** *Archaeoportunus* gen. nov. is here compared with both fossil and extant related families, genera and species. Eocene and Oligocene portunids from the Tethyan Realm, such as *Colneptunus hungaricus* Lörenthey in Lörenthey & Beurlen, 1929, *Euronectes* Karasawa, Schweitzer & Feldmann, 2008 (see also De Angeli & Beschin, 2008, figs 4-6), *Portunus catalaunicus* Via, 1941 (pl. 1), *P. kochi* (Bittner, 1893) (Bittner, 1893: 22; pl. 1, fig. 1; see also Beschin et al., 1996: 14, pl. 1, fig. 3), *P. larteti* (A. Milne-Edwards, 1860) (A. Milne-Edwards, 1860: 111; pl. 5, fig. 2), *P. suessi* Bittner, 1875 (Bittner, 1875: 80, pl. 4, fig. 1a-d), *P. vectensis* (Carter, 1898) (Carter, 1898, pl. 2, fig. 2; Quayle, 2020, fig. 1.1, 2), *P. vicentinus* (A. Milne-Edwards, 1860) (A. Milne-Edwards, 1860: 112, pl. 6, fig. 1) all present similar carapace outlines, as well as similar orbitofrontal and anterolateral features as *Archaeoportunus* gen. nov. However, all of them differ from the new genus in having less marked dorsal ridges, a wider sternum (widest across sternite 6), sternite 8 being visible in ventral view, and pleonal somites 3-5 completely fused. In addition, all of them have well-marked keels on the outer side of the propodus, whereas this is rounded in *Archaeoportunus* gen. nov.

The heterogeneous group of Eocene-Oligocene portunoid genera, referred to the former family Macropidae Stephenson & Campbell, 1960 by Karasawa et al. (2008), presents notable differences. Despite the fact that most members exhibit a long epibranchial spine, similar to the one in *Archaeoportunus* gen. nov., these extinct genera are clearly distinct from the new taxon in having a different carapace outline, larger orbits, a different frontal construction and fewer anterolateral spines. In addition, the maximum carapace width is found at a more anterior position and strongly marked ridges on the dorsal carapace surface usually are absent.

*Archaeoportunus* gen. nov. is also compared with extant former portunoid families (*sensu* Schubert & Reuschel, 2009), although several of which have been relegated to subfamily status by subsequent works (see Spiridonov et al., 2014; Davie et al., 2015; Evans, 2018; Spiridonov, 2020). Members of the family Carcinidae MacLeay, 1838 have sternite 8 covered by the male pleon, as in *Archaeoportunus* gen. nov., but somites 3-5 are completely fused, with pleonal segment 3 widened laterally, while in *Archaeoportunus* gen. nov. these are distinct, with market complete sutures. Carcinids are also distinguished by an utterly different carapace

outline, not much wider than long, a trifold front and fewer anterolateral spines (Števcíć, 2005; Karasawa et al., 2008; Spiridonov et al., 2014). The family Geronidae Colosi, 1923 presents characteristics such as pleonal segments 3-5 with complete sutures, and sternite 8 not well visible in ventral view; these are features shared with the new taxon. However, this group clearly differs from *Archaeoportunus* gen. nov. in general carapace outline, being more subquadrate, and in having fewer anterolateral spines, broader orbits and different frontal features (Karasawa et al., 2008: 96; Spiridonov et al., 2014: 419-421). The subfamily Pirimelinae Alcock, 1899 differs from *Archaeoportunus* gen. nov. by its produced and trilobed front, an utterly different carapace outline, being about as long as wide and pleonal somites 3-5 fused (Števcíć, 2005; Spiridonov et al., 2014: 421, 422). The subfamily Polybiinae Ortmann, 1893 is set apart from *Archaeoportunus* gen. nov. in displaying a carapace of near-equal width and length, fewer anterolateral spines, different frontal features, usually with a median spine, an uncovered sternite 8 and fused pleonal segments 3-5 (Karasawa et al., 2008: 100; Spiridonov et al., 2014: 422, 423). The subfamily Thiinae Dana, 1852 is easily distinguished by general carapace outline, being transversely suboval, with non-defined dorsal regions, an entire front, and all carapace margins lacking lobes or denticles, chelipeds short, adapted to the carapace, not very salient from the outline when contracted, pereopods much shorter and more flattened than in *Archaeoportunus* gen. nov. (Števcíć, 2005: 33; Spiridonov et al., 2014: 422).

The new taxon exhibits a set of characteristics that confirms a close relationship to the family Portunidae (*sensu* Spiridonov, 2020). *Archaeoportunus* gen. nov. is also compared to extant portunids, such as *Portunus pelagicus* (Linnaeus, 1758), *Callinectes sapidus* Rathbun, 1896 and *Arenaeus cribarius* (Lamarck, 1818), which were amongst the true portunids unfailingly used by authors in the latest revisions of the family (see Schubert & Reuschel, 2009: 536; Spiridonov et al. 2014: fig. 2; Evans, 2018, fig. 11; Spiridonov, 2020: 423). Extant portunids have the general carapace shape of the carapace, the anterolateral margins, the small orbits and a similar frontal construction in common with the new genus, but present notable differences as indicated in the general discussion (see below).

**Discussion.** The main features of *Archaeoportunus* permit inclusion in the superfamily Portunoidea,

*sensu* Karasawa et al. (2008: 94, 95). In their diagnosis of the Portunoidea, sternite 8 was noted to be “usually visible in ventral view” (see also Davie et al., 2015: 1099). However, it should be noted that the same was indicated for the families Longusorbiidae Karasawa, Schweitzer & Feldmann (2008: 95), Geryonidae and Carcineretidae Beurlen, 1930 to be “not visible in ventral view” (see Karasawa et al., 2008: 95, 96, and 98, respectively). This is a character shared with the new genus.

Amongst families included by authors (e.g. Karasawa et al., 2008; Spiridonov et al., 2014), the new taxon presents notable similarities to the family Portunidae, e.g., the large carapace size and subhexagonal outline, being markedly wider than long; the arched anterolateral margins, bearing nine spines, the epibranchial one being very long, thin and arched; small orbits, with two fissures; a quadrilobate front and large, stout chelipeds with ridges. All these characteristics match the family Portunidae as diagnosed by Karasawa et al. (2008: 103) and by Spiridonov et al. (2014: 423). Of special interest is the fact that the insertion of the first coxa is at about the median portion of the lateral margin of sternite 4, a feature seen in *Archaeoportunus* gen. nov. and in common with all portunids, both fossil and extant, that have been checked for the present study. However, it is easily distinguished from all extant and fossil portunids, presenting important differential features, as outlined below.

The extant *P. pelagicus* is notably different (see Lai et al., 2010), in having a near-circular, broader sternum, sternites 1-4 with grooves, but not complete sutures; a large portion of sternites 7 and 8 fairly well visible in ventral view; episternites markedly angular, inserted between coxae; sexual dimorphism very accentuated; pleon in males very narrow, with inverted T-shape; pleonal segment 3 strongly widened laterally, pleonal segment 6 markedly long, nearly the same size as set 3-5, which are completely fused; pleon in females broadly ovate. With regard to dorsal features, the extant form has a front with noticeable median tooth in a lower plane, dorsal regions with less marked ridges and anterolateral margins with better developed spines. Similar ventral differences can be confirmed in a comparison with *C. sapidus* and *A. cribrarius* (see Rathbun, 1930: 134). In addition, *C. sapidus* differs from *Archaeoportunus* gen. nov. in having a dorsal surface without ridges, with the exception of a well-marked epibranchial keel and strongly

developed anterolateral spines. The dorsal carapace of *A. cribrarius* has poorly defined regions and much better-developed anterolateral spines. Instead, *Archaeoportunus* gen. nov. has fairly swollen dorsal regions, with numerous and strongly marked ridges. Anterolateral margins of *Archaeoportunus* gen. nov. bear very small, discrete, anterolateral spines, with the exception of the epibranchial which is similar in size to the one in extant portunids. The front has four different lobes, the two median ones slender, the two exterior ones wider, with the base extending medially. There is a clear axial notch, without median spine. Supraorbital margins have two slight indentations; deep fissures are lacking. The infraorbital margin bears two strong teeth, fairly well visible in dorsal view. The sternum is narrow, narrowing further posteriorly, with the maximum width at the position of the fifth sternite. Sternites 1-2 fused, clearly separated from 3-4 by a complete suture. Sternites 3-4 with strongly marked ridges, two axial ones in sternite 3, two oblique in sternite 4, two strong inflations at the margins of sternite 4. Episternites well developed, with broadly rounded margins, not angular. The coxae are fairly well separated. Sexual dimorphism is weak, the male and female pleon are nearly subtriangular, of similar width. The male pleon has pleonal segments 3-5 distinct, clearly defined by complete and well-marked sutures. Somites 3-5 have slight medial inflations, no marked keels. Somite 3 is not much wider than somite 4, does not extend laterally, and has lateral margins converging posteriorly. Somite 6 is short, only slightly longer than somite 5, and much shorter than set 3-5. Only a small portion of sternite 7 is visible in ventral view, sternite 8 being entirely covered by the male pleon. In both sexes, only a discrete portion of the sternum is visible. Chelipeds have rounded lateral sides to the propodus, only a marked ridge in the lower portion of the hand.

Karasawa et al. (2008) diagnosed the superfamily Portunoidea as having poorly or moderately defined dorsal regions, an inconstant character, mainly in extinct taxa, which present distinct, fairly areolated regions (see also Spiridonov et al., 2014: 423; Davie et al., 1099). With regard to dorsal regions, *Archaeoportunus* gen. nov. resembles other Iberian Eocene fossil portunids such as *Colneptunus hungaricus* and *Portunus catalaunicus*, but can be clearly differentiated by the more marked dorsal ridges, the peculiar shape of the front and the number, shape and size of anterolateral spines. *P. catalaunicus* exhibits small, yet marked,

protuberances on the regions, rather than ridges; the anterolateral spines are robust, salient and subtriangular, the chelipeds strongly ridged; *C. hungaricus* exhibits only 5 salient anterolateral teeth, which are robust and subtriangular; only present faint, not strongly marked ridges on epibranchial and protogastric regions. As to ventral regions, the new taxon has in common with *C. hungaricus* and *P. catalaunicus* the position of cheliped insertion in sternite 4; sternites 1-2 are separated from sternites 3-4 by a complete suture, pleonal somite 6 being short. However, *Archaeoportunus* gen. nov. is easily distinguished on account of the strong protuberances in sternites 3-4, sternite 8 being entirely covered by the male pleon, pleonal somites 3-5 defined by clear, complete sutures, and a regularly subtriangular male pleon, while the general shape of the male pleon in *C. hungaricus* and *P. catalaunicus* is an inverted T, and pleonal somites 3-5 are fused. Despite the fact that differences are important, features in common indicate a possible evolutionary lineage from *Archaeoportunus* gen. nov. to fossil portunids, which are intermediate forms, and to modern portunids, the more derived forms. The Cretaceous fossils assigned to the Portunoidea, present as well some shared features, as the notable dorsal ridges in similar regions, that could indicate possible evolutionary issues.

It is worthy of note that, despite the well-marked and complete sutures on somites 3-5, we have a specimen in which ventral features are poorly preserved (see Artal et al., 2013, figs. 5, b-b'), with displaced portions of pleon and coxae, somites 3-5 appearing to form an entity, while sternite 6 is separated. In fossil crabs, it is difficult to be certain when exactly a pleonal segment is free or not, moveable or not, but this example might suggest a degree of fusion in the pleonal segments.

Here we propose a new extinct family, Archaeoportunidae fam. nov., to accommodate the new genus which is both similar to extant and fossil members of the family Portunidae, and also exhibits important distinguishing features (see above).

Some of the extinct families proposed by Karasawa et al. (2008), and some of the fossil genera assigned to extant families, appear to be very different from the Archaeoportunidae fam. nov. However, a closer comparison is not devoid of interest, in order to check possible evolutionary ties. Despite the fact that most of the fossils do present some shared features, such as the swollen and ridged dorsal regions or sternite 8 not

covered, are easily distinguished by the general carapace outline, the orbits or the frontal construction, as indicated below. Although differences are remarkable, it is interesting to see how they are related, i.e., which characteristics they have in common and how they might have evolved.

Some features are shared with members of the family Carcineretidae (*sensu* Karasawa et al., 2008: 98), e.g., the transverse dorsal swellings on the protogastric, mesogastric, hepatic, epibranchial and cardiac regions; sternites 1-2 being separated from sternites 3-4 by a marked and complete suture; sternite 8 not visible in ventral view; and, pleonal segment 3 completely filling the space between the coxae of the fifth pereopods. However, notable differences include the subquadrate carapace outline, the extremely wide orbits, the downturned front, the insertion of the coxae of the chelipeds in the lower portion of sternite 4, a broad portion of sternite 7 being exposed, pleonal segment 3 much wider than 4-5, extending laterally, pleonal somites 3-5 fused (see Vega et al., 2001: 321, fig. 3), but with clear evidence of sutures according to Karasawa et al. (2008: 98).

*Archaeoportunus* gen. nov. also has features in common with representatives of the family Longusorbiidae Karasawa, Schweitzer and Feldmann, 2008 (Karasawa et al., 2008: 95), such as the relatively narrow sternum, sternite 8 not being visible in ventral view, all male pleonal segments distinct, with notably complete sutures, entirely filling the space between the coxae of the fifth pereopods. The sternum is narrow (Schweitzer et al., 2003: 46, fig.15), with a marked, complete suture separating sternites 1-2 from 3-4, similar to *Archaeoportunus* gen. nov., but the insertion of the coxae of the chelipeds in sternite 4, presents an utterly different picture. As to dorsal characteristics, despite the fact that regions are strongly differentiated, as in *Archaeoportunus* gen. nov., the genus *Longusorbis* exhibits important differences, such as the subtrapezoidal carapace outline, a much greater orbital width and utterly different frontal features.

Representatives of Lithophylacidae Van Straelen, 1936 (Icriocarcininae Števčić, 2005 and Lithophylacinae Van Straelen, 1936), in spite of the similar pattern of transverse dorsal ridges that exhibit, clearly differ from *Archaeoportunus* gen. nov., sp. nov. by its large orbits and narrow rostrum, subtrapezoidal inverted carapace, wider thoracic sternum and deeper sternopleonal cavity. As well, the pereopods P5 are not

paddle-like as in *Archaeoportunus* gen. nov., and in some cases, as in Lithophylacinae, it is clearly reduced (see Téodori et al., 2013; Nyborg et al., 2014; Kornecki, 2014; Kornecki et al., 2017; Vega et al., 2018).

The genus *Ophthalmoplax* Rathbun, 1935, which was assigned to the former family Macropipidae by Karasawa et al. (2008), shares the position of the dorsal keels and the fact that male pleonal segments all have distinct sutures (see Schweitzer et al., 2003: 17, fig. 1; Ossó et al., 2010; Vega et al., 2013). It is striking to see how the Moroccan species has keels and grooves on similar regions as in *Archaeoportunus* gen. nov. However, *Ophthalmoplax* differs from the new genus in having a subquadrate carapace outline, broader orbits, a downturned front, a wider sternum, a small portion of sternite 8 not covered by the male pleon, and insertion of the chelipeds is in the lower portion of sternite 4. The family was diagnosed by Karasawa et al. (2008: 100, 101) as having a moderately broad carapace, usually with longitudinal branchial ridges parallel to the axis, often with a carapace ornament of large granules or tubercles, and pleonal segments 3-5 fused or with different degrees of fusion. In short, the new genus cannot be accommodated in that family. However, this family has been, in fact, disregarded in latest phylogenies based on molecular studies (see Schubart & Reuschel, 2009; Spiridinov et al. 2014; Evans, 2018; Spiridonov, 2020).

The potential portunoid *Eogeryon* Ossó, 2016 (*Eogeryonidae* Ossó, 2016) is easily distinguishable from *Archaeoportunus* gen. nov. by its dorsal morphology and carapace outline, which is just slightly wider than long, in contrast of *Archaeoportunus* gen. nov. which is notably wider than long; the regions are not so marked as in the new genus and only has transverse ridge on both protogastric lobes, in contrary that *Archaeoportunus* gen. nov.; as well, its epi-branchial spine is just a small blunt node, while that of *Archaeoportunus* gen. nov. is extremely long. Ventrally, the differences are also evident, *Eogeryon* lacks of the prominent swellings that *Archaeoportunus* gen. nov. bears on sternites 3 and 4, among other differences (see Ossó, 2016, fig. 5).

In common with geryonids, *Archaeoportunus* gen. nov. has sternite 8 not visible and pleonal segments 3-5 distinct, with complete sutures in males. However, geryonids have a different general carapace outline, i.e., not much wider than long, with weakly defined dorsal regions, convex anterolateral margins bearing 3-5

spines, and a well-marked suture delimiting sternites 3-4 (see Karasawa et al., 2008: 96). *Chaceon peruvianus* (d'Orbigny, 1842) has a transversely ovoid sternum, uniformly elongated, with the greatest width at sternite 6 (episternite 5), sternites 1-2 are fused, suture complete 2-3, sternite 8 completely covered by the pleon, male pleon triangular, broad, segment 3 broader than 4-5, but not extended laterally in the way that is seen in typical extant portunids (i.e., *P. pelagicus*). The pleon is subtriangular in males, pleonal segment 3 being the widest, but not much extended laterally. Segments 3-5 are fairly distinct, with complete sutures (Schweitzer & Feldmann, 2000; Casadío et al., 2005).

On account of the extreme variability of members of the family Portunidae, detailed studies in future need to determine a clearer distinction, mainly in fossil genera, in order to make general characteristics of the family more constant. In addition, our comparison with other extinct portunoids demonstrates that additional work is needed to arrive at a more reliable subdivision in families. Some general traits appear to be shared amongst fossil portunoids, such as the fact that pleonal somite 6 is short, sternites 1-2 clearly separated by a complete suture from sternites 3-4, and, in some genera, the dorsal regions are strongly areolated, with very swollen regions or ridges. The elongation and width of the sternum, the shape of the pleon, and the position of the pereopods also indicate how a crab is modified functionally. In *Archaeoportunus* gen. nov. the sternum is elongated, narrowing posteriorly; pleon, both male and female, are subtriangular, weakly differentiated, pleonal somite 3 not extending laterally, sternite 8 being covered by the male pleon, and the coxae of the five pereopods markedly separated. In extant portunids, the sternum is very wide, subcircular, sexual dimorphism being very pronounced: extremely narrow in males, with a typical inverted T-shape, and somite 6 very long, extremely wide in females, covering a large portion of the sternum, with episternites being angular, connected to the coxae of the five pereopods, the coxae are approximated, which implies a clearly defined functional morphology. The shape of pleonal somite 3, expanded laterally, being adapted to sternite 8 with a typical indentation, and the lateral margins adapted to the fifth coxae, implying an advanced degree of evolution (see Crosnier & Moosa, 2002; Lai et al, 2010). Fossil portunids clearly demonstrated an intermediate evolutionary stage, while Cretaceous portunoids assigned to the superfamily display more primitive characteristics.

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