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FIRST REPORT OF EARLY EOCENE DECAPODS IN MOROCCO:
DESCRIPTION OF A NEW GENUS AND A NEW SPECIES OF CARPILIIDAE
(DECAPODA: BRACHYURA) WITH REMARKS ON ITS
PALEOBIOGEOGRAPHY.

New early Eocene Carpiliidae from Morocco. (Running head)

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ABSTRACT

A new decapod brachyuran, *Maurocarpilus bispinosus* n. gen., n. sp. (Carpiliidae Ortmann, 1893), from the Ait Ouarhitane Formation (early Eocene, Ypresian) of Tamalout (Ouarzazate, Morocco) is described herein. This is the first record of a decapod from the Eocene of Morocco formally reported, and represents an addition to the large record of carpiliids from the Paleogene of the western margin of the Tethys. The new taxon is characterized as follows: a strongly vaulted and smooth carapace, a front strongly downturned, anterolateral margins broadly convex with two small nodes, and concave posterolateral margins. *Maurocarpilus bispinosus* n. gen., n. sp. presents clear morphological similarities with coeval taxa from the northern Iberian Peninsula and northern Italy, and the origins of those taxa and their possible phylogenetic relationships are discussed. Moreover, the paleobiogeography of the populations of carpiliids during the early Eocene in the western end of the Tethys is analyzed, and a possible connection between the Tethys Sea and the Bay of Biscay, that could have

avored the faunal exchange between the North Atlantic and the Tethyan domains, is proposed.

KEYWORDS Carpiliidae; Eubrachyura; Morocco; early Eocene; Ypresian; Tethys

RÉSUMÉ

Un nouveau Brachyura décapode, *Maurocarpilus bispinosus* n. gen., n. sp. (Carpiliidae), de la formation géologique d'Ait Ouarhitane (Yprésien) de Tamalout (Ouarzazate, Maroc) est décrit ici. Il s'agit du premier signalement d'un crustacé décapode de l'Éocène au Maroc et il constitue un ajout au vaste nombre de carpiliidés du Paléogène de la marge occidentale de la Téthys. Ce nouveau taxon se caractérise par: une carapace lisse fortement voûtée, un front avant fortement inclinée, des marges antérolatérales largement convexes à deux petits nodules et des marges postérolatérales concaves. *Maurocarpilus bispinosus* n. gen., n. sp., présente des similitudes morphologiques nettes avec les taxons contemporains du Nord de la péninsule ibérique et de l'Italie du Nord. Les origines de ces taxons et leurs possibles relations phylogénétiques sont discutées. La paléobiogéographie des populations de carpiliidés au cours de l'Éocène inférieur est aussi étudiée dans la partie ouest de la Téthys montrant ainsi un lien possible entre la Téthys et le golfe de Gascogne qui aurait favorisé les échanges fauniques entre l'Atlantique Nord et la Téthys.

MOTS CLES Carpiliidae; Eubrachyura; Maroc; Eocène inférieur; Yprésien; Téthys.

INTRODUCTION

The Carpiliidae are recognized by their strongly vaulted ovoid carapaces and strong chelae. The Carpiliidae, appeared in the late Paleocene/early Eocene, inhabited during the Eocene to Miocene in warm and generally shallow waters, usually associated with carbonate reefs. Fossil carpiliids were widespread from the south-east coast of North America and Gulf of Mexico and, along the Tethys, to Japan (e.g. Feldmann et al., 2011, and references therein), and even further north, such as the surprising finding of a *Palaeocarpilius* sp. in the fiords of the Norwegian Coast (see Smelror & Ossó 2016: 3-5). In the western area of the Tethys Realm, comprising northern Italy, Hungary, Romania, the northern of Iberian Peninsula, and North Africa, a robust stock of carpiliids arises during Eocene, which contrast with the paucity of recent representatives of this family, reduced to one sole genus and three species, also associated to reefal environments (Ng *et al.* 2008).

The greatest number of genera and species of this family from the early Eocene has been recorded in the northern Italy, of Tethyan affinity (e.g. De Angeli & Garassino 2006: 62-63; Feldmann *et al.* 2011: 338-348), but also in the Pyrenean basins (Artal & Van Bakel 2018), which are of Atlantic affinity. This fact suggests that the area of origin of the family was the occidental portion of the Tethys Sea. Therefore, the presence of *Maurocarpilius bispinosus* n. gen., n. sp., in the Ypresian (early Eocene) of northern Morocco, in addition to the carpiliids in south Pyrenean basins (Aragon and Catalonia) described by Artal & Van Bakel (2018), reinforces this idea. However, the presence of carpiliid populations that dwelt, more or less simultaneously, both in the

Atlantic and the Tethyan domains, raises the question how those populations were interconnected, given that it is assumed that both domains were not connected in that area during Ypresian, because the continental Corso-Sardinian block separated them. All of these observations would suggest that, a hypothetical connection between the Atlantic and Tethyan domains through the northeast of the Iberian Peninsula could have existed, as it was pointed out by Colombo & Caus (1984).

LOCATION AND STRATIGRAPHY

The Neogene basin of Ouarzazate corresponds to the foreland basin of the Central High Atlas in Morocco (Görler *et al.* 1988; El Harfi *et al.* 2001). Between the Ouarzazate basin and the High Atlas lies a fold and thrust belt, the Sub-Atlas zone, where highly deformed Cretaceous to Paleogene strata are outcropping (Tesón & Teixell 2006; Fig. 1A-B). There, Paleogene consists mainly of marine and continental marls and limestones. This area is particularly known for the palaeontological richness of its Eocene strata. The two sites that are cited most in the literature are Aznag for selacian and mammal fossils (Tabuce *et al.* 2005) and Ifar for its palaeo-flora (Depape & Gauthier, 1952). In 2008 and 2009, two geological fieldtrips were organized by geologists from the UniLaSalle Institute (Beauvais, France). The goal was to detail geological sections between Hdida and Aznag. The studied specimens were discovered in the Tamalout geological section (Fig.1C). This section comprises the Thanetian Jbel Ta'louit Formation (Tabuce *et al.* 2005), composed of continental red marls with gypsum, overlain by the Ypresian strata of the Ait Ouarhitane Formation (Despierrez & Etienne, 2010; Fig.2A-B). The total thickness of the Eocene interval is around 400 meters, including the Lutetian Jbel Tagout Formation on top. The Ait Ouarhitane Formation is represented by bioclastic and fossiliferous limestones intercalated with

massive gray and blue marls. The deposits are capped by one deltaic sandstone body which contains many fossils of both marine and continental vertebrates (Fig.2C). The marine fossils are numerous and highly diversified: molluscs (gastropods, bivalves, cephalopod nautiloids), urchins, isolated corals, bryozoans, crustaceans (Carpiliidae, *Callianassa* sp.) and shark teeth. Irregular urchins are of particular interest (urchins determination made by H. Soudet in Despieres & Etienne 2010): *Rhyncholampas tuder* Lambert, 1937, *Rhyncholampas* sp., *Echinolampas* sp., *Gitolampas* sp., *Gitolampas scutella* (Lamarck, 1816), *Gitolampas* aff. *pouechi* (Cotteau, 1889), *Gitolampas issyavensis* (Klein in de Loriol, 1875), *Gitolampas desmoulinsi* (Delbos in Agassiz & Desor, 1847). According to Soudet in Despieres & Etienne (2010), this echinoderm fauna confirms an early Eocene (Ypresian) carbonate shelf (Despieres & Etienne 2010). The Carpiliidae specimens come from the blue marls second layer of the Ait Ouarrhitane Formation (Fig.2B-D). These strata correspond to a decantation period in a shallow and calm marine environment. No coral reefs were observed near the Carpiliidae specimens.

ABBREVIATIONS

MCZ: Museo Civico “G. Zannato” (Montecchio Maggiore, Italy) MSGB: Museu de Geologia del Seminari de Barcelona (Barcelona, Catalonia). UB: Universitat de Barcelona (Barcelona, Catalonia). ULB: UniLasalle paleontological collections (Beauvais, France). L: length. W: width. FOW: fronto-orbital width. F: frontal width

SYSTEMATIC PALEONTOLOGY

Order DECAPODA Latreille, 1802

Infraorder BRACHYURA Latreille, 1802

Section EUBRACHYURA Saint Laurent, 1980

Subsection HETEROTREMATA Guinot, 1977

Superfamily CARPILIOIDEA Ortmann, 1893

Family CARPILIIDAE Ortmann, 1893

***Maurocarpilus* n. gen.**

TYPE SPECIES. — *Maurocarpilus binodosus* n. gen. n. sp. by monotypy

ETIMOLOGY. — From *mauri*, the name given to the people who lived in Mauritania Province, during the Roman Empire, which is the part of the current Morocco where the studied specimens were recovered. Gender: masculine.

DIAGNOSIS. — Carapace transversely ovate, wider than long, L/W ratio about 0.72, smooth. Vaulted in both senses, mainly anteriorly. Maximum width at half-length of carapace. Front slightly subtriangular, bilobed, strongly downturned. Orbits small, rounded, supraorbital margin entire, slightly rimmed. Anterolateral margin strongly convex, acute, bearing two small nodes, one at half-length level and a second at the angle with the posterolateral margin. Posterolateral margin concave, entire, acute in anterior half, starting about 60° respect to the axis. Posterior margin slightly convex. Regions not defined. Branchiocardiac grooves defined by muscle scars. Gastric pits visible. Ventral features and appendages no preserved.

REMARKS

Arose in the early Eocene, carpiliids are defined by a transversely ovate and broad carapace with well demarcated margins, a usually smooth surface of carapace, anterolateral margins entire or with blunt teeth or nodes, and from poorly to not defined regions (e.g. Karasawa & Schweitzer 2006: 43; Davie *et al.* 2015: 1074; Schweitzer *et al.* 2018: 2). The inexpressiveness of the dorsal carapaces of members of Carpiliidae, often leaves comparisons between their different genera and species reduced to subtle details, as the number of anterolateral teeth, if present, to length/width or fronto-orbital ratios, shape of them, or the angle degrees of posterior margins. Feldmann *et al.* (2011: t. 3) in the revision of *Palaeocarpilius* A. Milne-Edwards, 1862, summarized the aforementioned characters of all the genera placed within Carpiliidae, which will be used in the following comparisons as well. Therefore, *Maurocarpilius* n. gen. is compared with all the known carpiliid genera as follow.

Braggicarpilius Beschin, Busulini & Tessier, 2015, from the Ypresian of northern Italy differs from *Maurocarpilius* n. gen. in having entire anterolateral margins, and convex posterolateral margins (see Beschin *et al.* 2015; Schweitzer *et al.* 2018: 3, fig. 3.1). An array of carpiliids, such as *Bryocarpilius* Feldmann, Schweitzer, Bennet, Frantescu, Resar & Trudeau, 2011, from the Eocene; *Ocalina* Rathbun, 1929, from the Eocene; *Palaeocarpilius*, from the Eocene to Miocene; and *Paraocalina* Beschin, Busulini, De Angeli & Tessier 2007, from Eocene, all of them with wide Tethysian and also Atlantic distribution; *Proxicarpilius* Collins & Morris, 1978, from the Eocene of Pakistan; and *Tethyscarpilius* De Angeli & Alberti, 2016, all those genera clearly differ from *Maurocarpilius* n. gen., in having the anterolateral margins armed from four, to up to nine nodes or teeth, instead of only two small nodes in the new genus and different ratios (see Feldmann *et al.* 2011: t. 3), and furthermore, in the case of *Ocalina*, in having a tuberculated dorsal surface (see Feldmann *et al.* 2011; 345-346, fig. 13;

Rathbun 1929; A. Milne-Edwards 1862: 51-53; Beschin & De Angeli 2006: 11-23, figs. 2-5, pls. 1-4; Beschin *et al.* 2007: 42-43, pl. 6, figs. 1b, b; Collins & Morris 1978: 972; Schweitzer *et al.* 2004: 100-102, fig. 6; Schweitzer *et al.* 2018; De Angeli & Alberti, 2016). *Carpilius* Desmarest, 1823, from the early Eocene to recent, differs from *Maurocarpilius* n. gen. in having only one anterolateral tooth instead of two, and a short but well-developed oblique carina that extends from that tooth (epibranchial) to the dorsal surface (see Desmarest 1823: 227-228; Schweitzer *et al.* 2018: 3, fig. 2a-b). *Corallicarpilius* De Angeli & Ceccon, 2015, from the early Eocene of northern Italy, differs clearly from *Maurocarpilius* n. gen. in having a broader and more ovate carapace, without distinction between the posterolateral and posterior margin, and in having the dorsal surface ornated with irregular tubercles, instead of smooth in the new genus (see De Angeli & Ceccon 2015: 125-126, fig. 4; Schweitzer *et al.* 2018: 5, fig. 3, 3a-b). *Eocarpilius* Blow & Manning, 1996 from the Eocene of eastern North America and westernmost Tethys, differs from *Maurocarpilius* in having a longer ovoid carapace, anterolateral margins entire with only a small protuberance at the corner with antero- and posterolateral margin, posterolateral margins straight, and by its punctulate surface (see Blow & Manning 1996: 20-22, pl. 5, figs. 2a, 2b; Feldmann *et al.* 1998: 11-12, figs. 13-14; Schweitzer *et al.* 2018: 5, fig. 3, 3a-b). *Holcocarcinus* Withers, 1924, from the Eocene of Nigeria, differs clearly for the new genus in having the carapace with two marked transverse dorsal ridges (see Withers 1924: 94, pl. 5, figs. 1-2; Schweitzer *et al.* 2018: 5, fig. 4.1). *Laticarpilius* Feldmann, Schweitzer, Bennet, Frantescu, Resar & Trudeau, 2011, from the Eocene of Egypt, differs from *Maurocarpilius* in having a broader carapace, and a less downturned and completely triangular front (see Feldmann *et al.* 2011: 342-344, fig. 12; Schweitzer *et al.* 2018: 5, fig. 4, 2a, 2b). *Liopsalis* von Meyer, 1862 from the Eocene of western Tethys and India,

differs from the new genus in having a completely entire margins, and a triangular front not lobed (see von Meyer 1862: 161-163, pl. 17, figs. 9-12; Stoliczka 1871 pl. 5, figs. 6, 6a-b; Vía 1969: 231-237, fig. 28, t 23, figs. 3-4; Feldmann *et al.* 2011: 344-345; Schweitzer *et al.* 2018: 5, fig. 4, 3). *Lovaracarpilius* Beschin, De Angeli, Checchi & Zarantonello, 2016 from the Eocene of northern Italy, differs from *Maurocarpilius* in having shorter anterolateral margins, convex posterolateral margins, strongly punctulate surface and a triangular front (see Beschin *et al.* 2016: 55-56, fig. 47, pl. 9, figs. 4A-B; Schweitzer *et al.* 2018: 5, fig. 4, 4a-b). *Oscacarpilius* Artal & Van Bakel, 2018 from the northern of Iberian Peninsula, differs from the new genus in having a completely entire anterolateral margin, rounded lateral corners and a densely pitted surface (Artal & Van Bakel 2018: 23-29, figs. 1-2).

As mentioned above, the Moroccan specimens match perfectly with the general diagnosis of Carpiliidae. However, as can be seen in the comparisons, they do not fit completely with the characters or ratios of any of the aforementioned genera. Therefore, we propose the new genus, *Maurocarpilius*, to accommodate them.

***Maurocarpilius binodosus* n. sp.**

(Fig. 3)

MATERIAL AND MEASUREMENTS (IN MM). — Holotype ULB-IV-A(1a), L= 17; W= 23; FOW= 12,5; F= 7. Paratype ULB-IV-A(1b), L= 16; W= 23; FOW= 11; F= 6,5. Paratype ULB-IV-A(1c) (deformed) L= 19,5; W= 25,5; FOW= 13; F= 7,5.

TYPE LOCALITY AND HORIZON. — Tamalout section, northern face of the Jbel Talouit, North of Kelâa M'Gouna (East of Ouarzazate, Maroc). Ait Ouarhitane Formation, Ypresian (early Eocene).

ETIMOLOGY. — In allusion to the two anterolateral nodes of the anterolateral margin.

DIAGNOSIS. — as for the genus.

DESCRIPTION. — Carapace transversely ovate, wider than long, L/W ratio about 0.72; surface of carapace smooth. Carapace vaulted transversely, strongly vaulted longitudinally in the anterior part of carapace. Maximum width at half-length of carapace, between the first and second (epibranchial) anterolateral teeth. Front strongly downturned, bilobed, slightly rimmed, forms a very flattened inverted isosceles triangle; the two median lobes, with the inner orbital lobes, gives a quadrilobate appearance; slightly arched and produced in dorsal view. Orbits small, rounded, supraorbital margin entire, slightly rimmed only at the inner half of the supraorbital margin; inner orbital tooth blunt, outer orbital tooth short, acute subtriangular; visible dorsally. Anterolateral margin largely convex, acute, bearing two small nodes, one at half-length level, weakly visible, and a second more prominent (epibranchial tooth) at posterolateral junction. Posterolateral margin concave, entire, acute rounded rim in anterior half, starting about 60° respect to the axis. Posterior margin slightly convex. Regions not defined; cardiac region bounded by the branchiocardiac grooves. Gastric pits visible. Branchiocardiac grooves defined by muscle scars. Ventral features and appendages no preserved.

REMARKS

The dorsal carapace and the general outline of *Maurocarpilus binodosus* n. gen., n. sp., greatly recall several species present in the early Eocene, which present unarmed

anterolateral margins and a smooth carapace, but differing, however, in the absence or presence of subtle, but distinctive characters, that precludes a congeneric relationship.

For instance, *Braggicarpilius marginatus* Beschin, Busulini & Tessier, 2015, from the Ypresian (early Eocene) of northern Italy, differs from the new species by its more produced front, completely unarmed and rimmed anterolateral margin, and convex posterolateral margins. In contrary, *Maurocarpilius binodosus* n. gen. n. sp. presents two anterolateral nodes and their posterolateral margins are clearly concave (Beschin *et al.*, 2015: 82, fig-text. 11, t. 5, fig. 1; Schweitzer *et al.* 2018: 3, fig. 3.1; Fig. 4A).

Carpilius petreus Beschin, Busulini, De Angeli & Tessier, 2007, from the middle-late Ypresian of northern Italy, differs from the new species because presents only one anterolateral tooth (epibranchial), instead of two in *Maurocarpilius binodosus* n. gen. n. sp., and by the presence of the short oblique carina, typical for the genus, that extends from that tooth to the dorsal surface, which is absent in the new species, and in having a shorter posterior margin (Beschin *et al.* 2007: 41-42, pl. 7, fig. 7a-b, 8a-b; Fig. 4B).

Eocarpilius ortegai Artal & Van Bakel, 2018, from the Ilerdian (early Ypresian) of northeastern of the Iberian Peninsula, presents a different L/W ratio, about 0,77/080 *vs.* 0,73 in the new species. As well, their anterolateral margins are unarmed, with only a small node at the anterolateral/posterolateral angle, and its dorsal surface is densely covered by small granules, instead of the two clear anterolateral nodes and completely smooth dorsal surface of *Maurocarpilius binodosus* n. gen. n. sp., which makes the difference between the two species (Artal & Van Bakel 2018: 30-34, figs. 3-6; Fig. 4C-D). *Oscacarpilius rotundus* Artal & Van Bakel, 2018, also from the Ilerdian of northeastern of the Iberian Peninsula, shows a very similar dorsal and outline pattern than *Maurocarpilius binodosus* n. gen. n. sp., however, differs from the latter in having a different L/W ratio, 0,80 *vs.* 0,73, completely entire antero- and posterolateral margin,

without nodes or sharp angles and by its dorsal surface pitted (Artal & Van Bakel 2018: 23-29, figs. 1-2; Fig. 4E-F).

PALAEOBIOGEOGRAPHIC REMARKS

The presence of the numerous typical carpiliid forms in the early Eocene of western Tethys area, would suggest that, likely, it was the origin area of this group, in view of the large number of species described from northern Italy (cf. Schweitzer *et al.* 2018: 2-8; and references therein), to which we must add those recently described by Artal & Van Bakel (2018) from Aragon and Catalonia, and the new specimens from the northern Morocco studied here (Fig. 5).

Several of the Ypresian species from northern Italy, such as *Braggicarpilius marginatus* and *Carpilius petreus*, the Pyrenean species *Eocarpilius ortegai* and *Oscacarpilius rotundus*, and the Moroccan *Maurocarpilius binodosus* n. gen., n. sp., described here, are only differentiated by minimal morphological details, which suggests a clear phylogenetic relationship. Moreover, the paleogeographic reconstructions of the occidental area of Tethys, show how the Moroccan and the Italian populations were apparently geographically separated from the populations of the South Pyrenean basins, by the continental Corso-Sardinian Block during the Ypresian, as it is assumed in all the paleogeographic reconstructions (e.g. Plaziat 1981; Meulenkamp *et al.* 2000; Barrier *et al.* 2018), which leads us to ask how and from where those populations were moving.

Plaziat (1981: fig. 14), drew the maximum of the Ilerdian (early Ypresian) transgression, extending the Atlantic waters of the Bay of Biscay towards the east and south-east, through the South Pyrenean basins to the Corso-Sardinian Block continental

region, only few tens of kilometers before the current coastline. As well, and according with the work of Benzaquen *et al.* (1973), who interpreted as Thanetian in age the alveolinid and orbitolitid faunas found in the coastline of the Cap de Salou (southern Catalonia), Plaziat (1981: 299, fig. 19B, F), discarded a hypothetic connection with the Tethys Sea.

Colombo & Caus (1984), reviewed the faunas of the Cap de Salou, which are related with those of Egypt (Hottinger 1960), and finally discarded a Thanetian age for them. Based on the presence of *Orbitolites* aff. *gracilis*, they gave an Ilerdian age for those faunas. Consequently, they suggested a probable extension of the Ilerdian transgression beyond of the current coastline by the north-east and the south of Catalonia (Colombo & Caus 1984: fig. 2). In the Corso-Sardinian Block itself, the marine lower Eocene, related with the Ilerdian transgression, has been reported both in Corsica (e.g. Amaudric du Chaffaut *et al.* 1969) and Sardinia (e.g. Carmignani *et al.* 2012).

Given the dispersal capability of brachyurans (Anger *et al.* 2015: 352), carpiliids could have reached the Pyrenean basins from the western Tethys, using a connection through the Corso-Sardinian Block, or vice versa, via the Atlantic waters of the Bay of Biscay, along the southern and western coast of the Iberian Peninsula. But it would imply, for instance, that carpiliids could have also reached the south of British Isles and Belgium. Largui (2002: 65-67, figs. 4-5) also suggested a possible faunal exchange through the Pyrenean basins during the Ypresian. However, carpiliids are not present among the decapod faunas of the Ypresian outcrops of Isle of Sheppey (UK), Eggen, Marke, Forest (Belgium), neither further north, in Trelde Næs (Denmark) nor in Greenland (e.g. Bell 1858; Collins & Smith 1993; Collins & Jakobsen 2003; Collins & Rasmussen 1993). Although this absence could be explained whether by latitudinal thermic differences, by the presence of barriers such an isthmus or by the paleocurrent effects (Plaziat 1981:

308; Haq 1981). Given the presence of a robust stock of carpiliids in the western Tethys, it looks more likely parsimonious that the geographical origin of the Pyrenean carpiliids is related with the Tethys domain.

CONCLUSIONS

The presence of *Maurocarpilus binodosus* n. gen., n. sp., in the Ypresian outcrops of northern Morocco, increases the list of Carpiliidae species recorded in the Paleogene of the westernmost Tethys, which was the area and epoch with the greatest number of taxa of this family in all times. In addition, it represents the first report of an Eocene brachyuran from Morocco.

Maurocarpilus binodosus n. gen., n. sp., presents great morphological similarities with coeval taxa from the South Pyrenean basins in the Iberian Peninsula, and from northern Italy. Regions that, however, were supposed to be separated by the continental Corso-Sardinian Block at that time.

To discuss the paleogeography of the western Tethys is beyond of the main scope of the present work, nevertheless, considering the present evidences it is interesting to propose that a kind of connection could have existed in the eastern end of the Pyrenees basins, allowing the faunal exchange between the Atlantic and the Tethyan domains during the early Eocene, as it was suggested by Colombo & Caus (1984). Further works would help to answer this question.

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FIGURE CAPTIONS

Figure 1: The geographical and geological contexts- A) location map of the Paleogene formations between Ouarzazate and Kelâa M'Gouna (Tabuce *et al.* 2005, modified), B) location of Tamalout paleontological site (Tabuce *et al.* 2005, modified), C) sedimentological section of the Tamalout site, 1: calcarenite, 2: sandstone, 3: bioclastic

limestone, 4: gypsum, 5: marls, 6: urchins, 7: cephalopod nautiloids, 8: others molluscs, 9: vertebrates, 10: *Maurocarpilius binodosus* n. gen., n. sp.

Figure 2: Field photographs from the Jbel Talouit area. A: Tilted strata of the Jbel Talouit outcropping in the Tourbict gorges. This shows the high degree of tectonic deformation within the sub-Atlas thrust belt. B: View of the Tamalout section on the northern face of the Jbel Talouit. The dot line corresponds to the limit between the Thanetian and Eocene sedimentary units. The white arrow shows the location of the Carpiliidae site. C: vertebrate bone fragments coming from the beds that overlies the Carpiliidae marls. Those beds are the lateral equivalent of those of the Aznag vertebrate site. D: In the white box is *Maurocarpilius bispinosus* n. gen., n. sp. holotype, *in situ*, that is outcropping within the Eocene marls of the Ait Ouarhitane Formation.

Figure 3 . *Maurocarpilius binodosus* n. gen. n. sp., from the Ypresian (early Eocene) of Kelâa M'Gouna (Morocco). A-D: holotype ULB-IV-A(1a), A: dorsal view (digitally cut out of the matrix); B: frontal view; C: right lateral view; D: posterior view. E-H: paratype ULB-IV-A(1b), E: dorsal view; F: frontal view; G: posterior view; H: right lateral view. I-J: paratype ULB-IV-A(1c), I: dorsal view; J: frontal view. Arrows indicate the two anterolateral teeth distinctive of the species. Scale bar equal to 10 mm

Figure 4 . A: *Braggicarpilius marginatus* Beschin, Busulini & Tessier, 2015, holotype MCZ 3998, from the Ypresian (early Eocene) of Vestenanova (NE Italy) (digitally cut out of the matrix). B: *Carpilius petreus* Beschin, Busulini, De Angeli & Tessier, 2007, holotype MCZ 1809, from the Ypresian of Contrada Gecchelina (NE Italy) (digitally cut out of the matrix). C-D: *Eocarpilius ortegai* Artal & Van Bakel, 2018, topotype MGSB 77906a, from the Ilerdian (early Ypresian) of Isábena (N Spain); C: frontal view; D: dorsal view. E-F: *Oscacarpilius rotundus* Artal & Van Bakel, 2018, from the Ilerdian of Isábena (N Spain); E: topotype MGSB 77905b; F: topotype MGSB 77905a. Scale bar equal to 10 mm, except for A which is 5 mm.

Figure 5: The paleogeographic map of the Tethys sea during the Ypresian (lower Eocene). 1: continental domain, 2: shallow marine domain, 3: deep marine domain, 4: oceanic crust boundary, 5: major thrust fault, 6: active subduction zone, 7: present-day coastlines, 8: *Maurocarpilius binodosus* n. gen., n. sp., 9: *Eocarpilius ortegai* and *Oscacarpilius rotundus*, 10: *Braggicarpilius marginatus* and *Carpilius petreus*. This map also shows a hypothetical connection between the Tethys sea and the Bay of Biscay through the South Pyrenees. This is suggested by the spatial distribution of fossil carpiliids sites and imply a shallow marine corridor in the south of the Corso-Sardinian Block as also proposed by Colombo & Caus (1984). Adapted from Barrier *et al.* (2018).