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Couverture / *Cover* :
Left specimen: *Hebertides jurassica* Guinot, De Angeli & Garassino, 2007, in dorsal view; Right specimen: *Xantho* cf. *moldavicus* (Yanakevich, 1977), in outer lateral view; Background: Panoramic view of the Museum quarry 'la carrière-musée' (Channay-sur-Lathan).

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An appraisal of the Middle-Late Miocene fossil decapod crustaceans of the 'Faluns' (Anjou-Touraine, France)

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ABSTRACT
A detailed report of the decapod crustaceans discovered in the Middle-Late Miocene outcrops of the 'Faluns' of Anjou-Touraine (West of France) is here presented. The Couffon's compendium (1908) is reviewed, and the systematics updated. A total of seven genera and eight species of eubrachyuran crabs, undetermined chelae, and one anomuran species, are reported. The varied decapod assemblage, dominated by *Pilumnus mediterraneus* (Lőrenthey, 1897), shows clear affinity with coeval decapod faunas from the Mediterranean and Paratethys realm. This fauna dwelt in a shallow warm and agitated environment of bryozoan meadows. The age of *Hebertides jurassica* Guinot, De Angeli & Garassino, 2007, is confirmed, and the probable provenance of the holotype is suggested. We also discuss the generic status of *Scylla michelini* A. Milne-Edwards, 1861 transferred herein to *Necronectes* A. Milne-Edwards, 1881.

KEY WORDS
Decapoda,
Brachyura,
Paratethys,
Mediterranean,
Miocene,
Faluns.

RÉSUMÉ
Évaluation des crustacés décapodes fossiles du Miocène moyen-supérieur des 'Faluns' (Anjou-Touraine, France).
Une présentation détaillée d'une série de crustacés décapodes provenant de différents affleurements des faluns du Miocène moyen-supérieur de l'Anjou-Touraine (ouest de la France) est présentée dans cet article. Un total de sept genres et huit espèces d'eubrachyures et une espèce d'anomure sont décrits ici. Cet assemblage de décapodes est varié, dominé par *Pilumnus mediterraneus* (Lőrenthey, 1897), montrant une affinité claire avec les faunes de décapodes contemporaines de la Mer Méditerranée et du domaine paratéthysien. Cette faune vivait dans un environnement peu profond, chaud et agité, dans des prairies à bryozoaires. L'âge de *Hebertides jurassica* Guinot, De Angeli & Garassino, 2007 est confirmé, et la provenance éventuelle de l'holotype est ici suggérée. Le statut générique de *Scylla michelini* A. Milne-Edwards, 1861 est discuté et transféré à *Necronectes* A. Milne-Edwards, 1881.

MOTS CLÉS
Decapoda,
Brachyura,
Paratéthys,
Méditerranée,
Miocène,
Faluns.

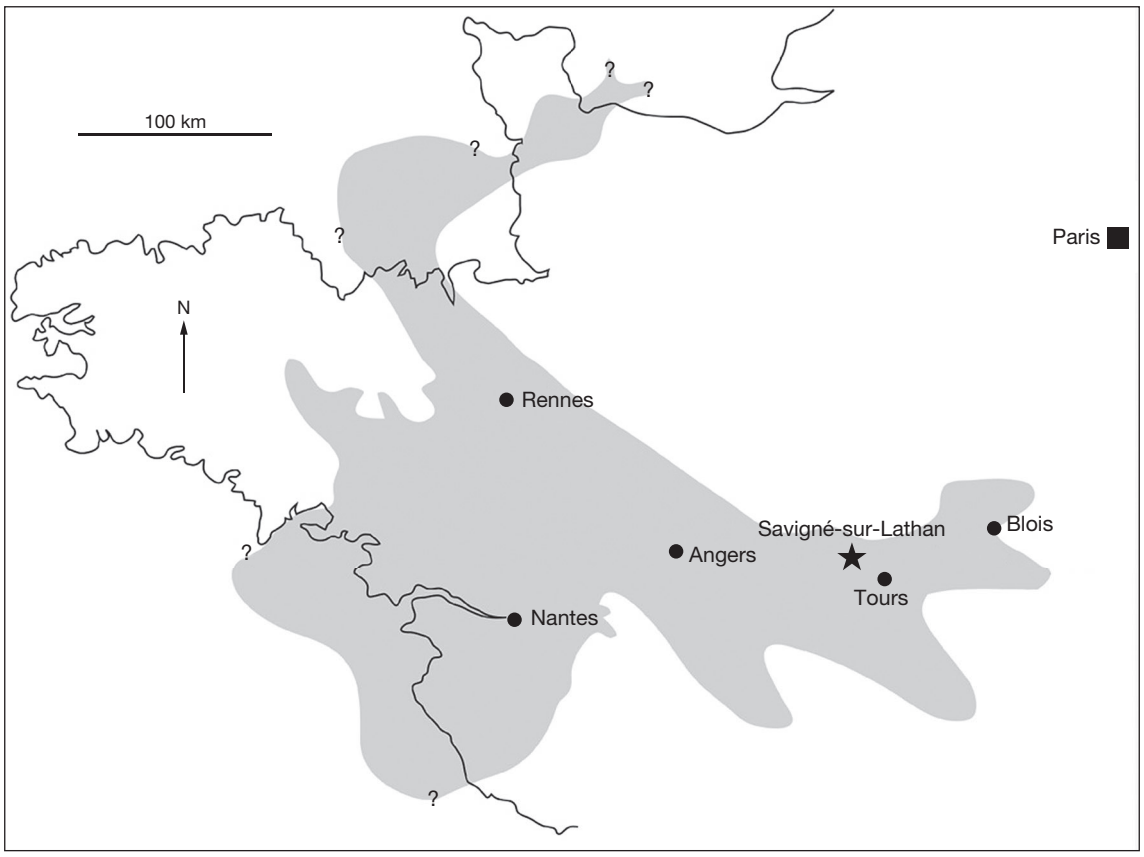

Fig. 1. — Location map of the outcrops area, and extension of the Falun's Sea during the Middle-Late Miocene (**shaded area**). Map from Gagnaison *et al.* 2012. ?, limits of the "Faluns sea" probable extension.

INTRODUCTION

Since Couffon (1908, 1934), little has been written on the crustaceans of the Miocene of the 'Faluns' of Anjou-Touraine (France). Couffon (1908), summarized the known species of decapods found in the 'Faluns' up to that time: *Scylla michelini* A. Milne-Edwards, 1861, *Maja orbignyana* Millet de la Turtaudière, 1865, *Titanocarcinus pulchellus* A. Milne-Edwards, 1864, *Cancer deshayesii* A. Milne-Edwards, 1865 (sic), *Cancer sismondai* Meyer, 1843 (sic) and also reported fragments of dactyli as *Neptunus* aff. *monspeliensis* A. Milne-Edwards, 1864 (sic). Herein, that work is reviewed and the systematics discussed and updated. Gagnaison (2012) described *Paguristes gagnaisoni* (Fig. 5E) from the Middle Miocene of 'La Sonneterie' quarry, Meigné-le-Vicomte (Anjou, France).

As a result of excavations carried out by J. C. Gagnaison and J. P. Hartmann, in 'La Sonneterie' quarry, between 1993 to 1997, one hundred and thirty-five disarticulated decapod crustacean remains, mainly chelae, fragments of carapaces, and a few complete dorsal carapaces, were recovered after sieving the bioclastic sands. From this assemblage, and from other collections recovered in different quarries of this region, eight families of decapods, containing seven genera and eight species of brachyurans, are identified: *Calappa praelata* Lőrenthey *in* Lőrenthey & Beurlen, 1929; *Calappa* sp. (Calappidae De Haan, 1833); *Hebertides jurassica* Guinot, De Angeli & Garassino, 2007 (Corystidae Samouelle, 1819); *Maja orbignyana* (Majidae Samouelle, 1819); *Pilumnus mediterraneus* (Lőrenthey, 1897) (Pilumnidae Samouelle, 1819); *Liocarcinus* sp. (Polybiidae Ortmann, 1893); *Necronectes michelini* (Portunidae Rafinesque, 1815); *Xantho* cf. *X. moldavicus* (Yanakevich, 1977) (Xanthidae MacLeay, 1838), several undetermined brachyuran chelae, and the anomuran *Paguristes gagnaisoni* Gagnaison, 2012 (Paguridae Latreille, 1802). From these, an array of twenty-three specimens, the best preserved of each species, are described and figured herein. The assemblage is clearly dominated by *Pilumnus mediterraneus* (Lőrenthey, 1897), the most abundant species in the 'Faluns', whereas other species are represented by unique specimens.

The present work represents a complete overview of the fossil decapods recovered in the 'Faluns' outcrops of Anjou-Touraine expanding our knowledge of several aspects of the assemblage. For instance, the age and the probable area of occurrence of *Hebertides jurassica* is suggested, the systematic placement of *Scylla michelini* is rehabilitated, and the true nature of *Titanocarcinus pulchellus* is discussed.

The specimens described in the present work are housed in the collections at the Musée du Savignéen (Savigné-sur-Lathan, Indre-et-Loire, France), under acronym MS, and the paleontological collections of UniLaSalle Polytechnic Institute (Beauvais, Oise, France) under acronym ULB.

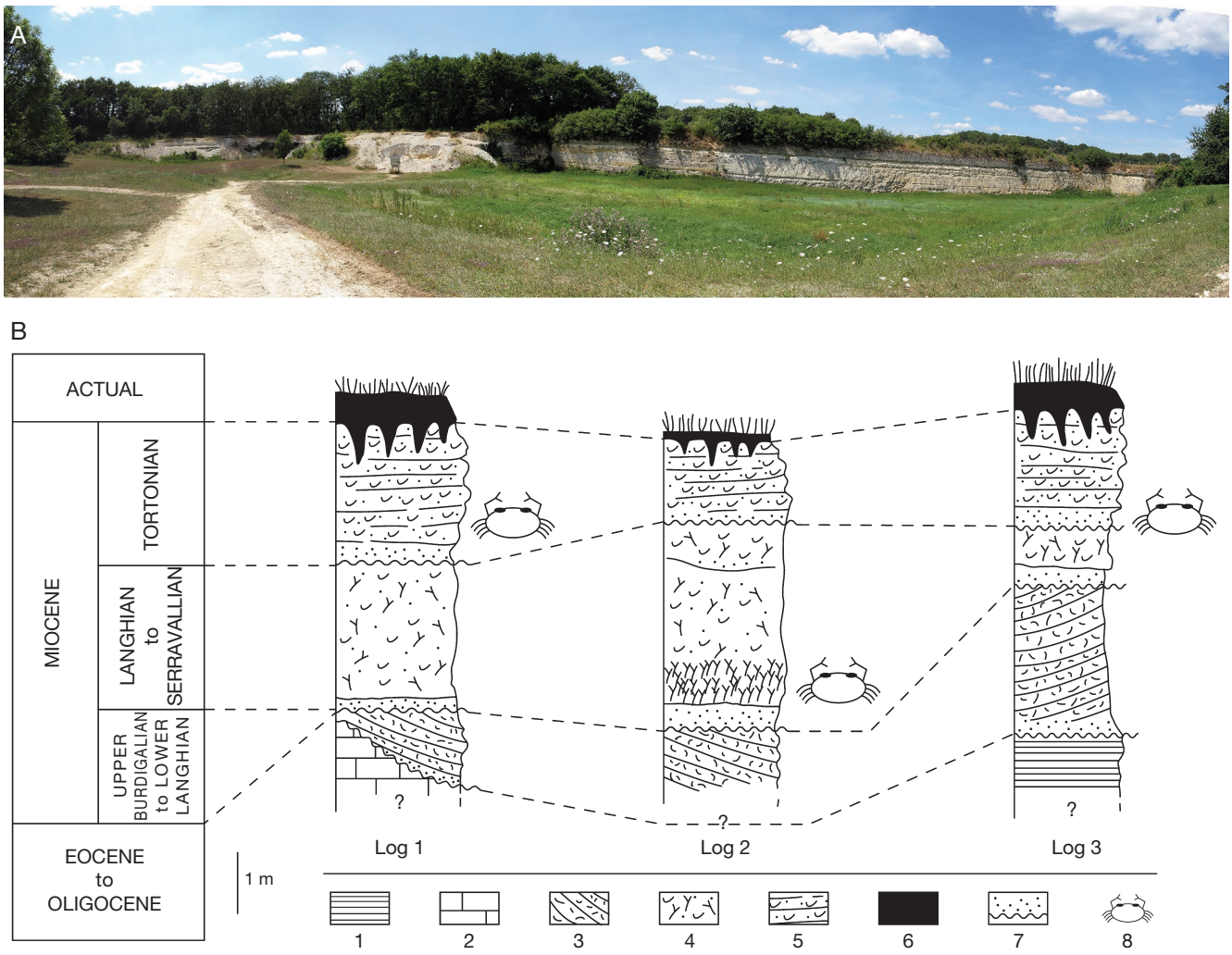

Fig. 2. — **A**, Panoramic view of the Museum quarry 'la carrière-musée' (Channay-sur-Lathan); **B**, lithostratigraphic columns from the differents shelly sands quarries. **Log 1**, 'la carrière-musée' (Channay-sur-Lathan, Indre-et-Loire); **Log 2**, 'La Sonneterie' (Meigné-le-Vicomte, Maine-et-Loire); **Log 3**, 'Les Bournais' (St-Laurent-de-Lin, Indre-et-Loire). Cells: **1**, Eocene green marl; **2**, Oligocene limestone; **3**, clinostratified calcarenite (Upper Burdigalian to Lower Langhian); **4**, Bryozoans clayey shelly sands, 'Savignean facies' (Langhian to Serravallian); **5**, Bioclastic calcarenite with *Anadara turonica* (Tortonian); **6**, modern soils (Quaternary-Actual); **7**, Miocene erosive surface; **8**, Fossil occurrences. Photograph by A. Ossó; drawing by C. Gagnaison.

LOCATION AND STRATIGRAPHY.

The specimens studied herein were recovered from different localities around Savigné-sur-Lathan (Indre-et-Loire, France) (Fig. 1).

Between the late Burdigalian and the Tortonian (Miocene), the transgressing sea in the Loire Valley (from West to East until the Blésois region) and the Savigné-sur-Lathan/Noyant-sous-le-Lude (South-West of the Paris Basin, Anjou-Touraine) deposited shelly, sandy sediments locally named 'Faluns' (Lecointre 1947) (Fig. 1). This sedimentary formation is found in different French regions: Vendée-Bretagne, Poitou, Normandy, Anjou-Touraine and Blésois (Temey 1996).

Excavations in these deposits locally reveal the presence of numerous marine fossils invertebrates and vertebrates. These Miocene shelly sands were deposited over different Paleogene-Early Miocene continental formations: Eocene green marl, Oligocene-Agenian lacustrine limestone, and Orlanian fluvial sands (Gagnaison 2017; Gagnaison *et al.* 2018). Quaternary-recent soils cover all the Tertiary formations (Fig. 2). Three Miocene marine facies are present in the sedimentary basin of Savigné-sur-Lathan/Noyant-sous-le-Lude: 1) clinostratified calcarenite with sea urchins (late Burdigalian-early Langhian); 2) the clayey shelly sands with bryozoans ('Savignean facies') of the Langhian-Serravallian; and 3) the bioclastic calcarenite with the Tortonian *Anadara turonica* ('Lublean facies') (Courville & Bongrain 2003).

The fossils reported and described herein were recovered from two facies: the clayey shelly sands with bryozoans (Langhian-Serravallian) and the bioclastic calcarenite with *Anadara turonica* shells (Tortonian) (Fig. 2).

The clayey shelly sands with bryozoans (Langhian-Serravallian), also called 'Savignean facies':

Its thickness varies between 0.5 to 5 meters (Fig. 2). These facies are composed of clayey, shelly sand with many bryozoan fragments (mainly celleporiforms and reteporiforms) and

molluscs shells (Buge 1948; Courville & Bongrain 2003). Most of the decapod specimens reported here, come from the lower part of these shelly sand ('La Sonneterie' quarry near Meigné-le-Vicomte; Fig. 2). In this quarry, this geological formation begins with many bryozoan bioconstructions in place or slightly broken. Many fragile invertebrate fossils have been found in these facies such as molluscs with their connecting valves, sea urchins with their spines, and well-preserved crab remains. This biotope integrates into a warm underwater environment typical of shallow (upper infralittoral) bryozoan colonies (Gagnaison 2012). The classic clay shelly sand with bryozoan debris and oblique strata covers this bioconstruction. This unit is interpreted as a warm and shallow infralittoral environment (Gagnaison 2012),

The bioclastic calcarenite with *Anadara turonica* (Tortonian):

Corresponds to the last Miocene formation in this sedimentary basin. The facies is visible in all three quarries of this study (Fig. 2). Its thickness does not exceed 4 meters and its top is always marked by Quaternary-Recent brown clays dissolution pockets (Fig. 2). This calcarenite is composed by rolled and broken fossils (bryozoans, molluscs, echinoderms and marine vertebrates) and rolled quartz grains. Many oblique bi-directional strata are visible on all the outcrops. Several of the crustacean remains reported herein, come from the base of this formation. This calcarenite is interpreted as a warm sea of shallow depth (intertidal) very agitated by underwater currents (Temey 1996).

Abbreviations

L	length;
W	width;
FOW	fronto-orbital width;
H	height;
T	thick.

SYSTEMATIC PALAEONTOLOGY

Order DECAPODA Latreille, 1802
Infraorder BRACHYURA Latreille, 1802
Section EUBRACHYURA de Saint Laurent, 1980
Subsection HETEROTREMATA Guinot, 1977
Superfamily Calappoidea De Haan, 1833
Family Calappidae De Haan, 1833

Genus *Calappa* Weber, 1795

Type species. — *Cancer granulatus* Linnaeus, 1758, subsequent designation by Latreille (1810).

Calappa praelata Lőrenthey *in* Lőrenthey & Beurlen, 1929 (Fig. 3A-C)

Calappa praelata Lőrenthey *in* Lőrenthey-Beurlen, 1929: 132, 133, pl. 6, fig. 3. — Glaessner 1929: 71. — Müller 1984a: 66, pl. 35, figs 1-2, 7; pl. 36, fig. 6; 1984b: pl. 2, fig. 4; 1996: 9, pl. 1, fig. 11; 1998: 22. — Gatt & De Angeli 2010: 1329, pl. 2, fig. 2. — Schweitzer *et al.* 2010: 83. — Pasini *et al.* 2012: 135-140, fig. 1A-C. — Collins 2014: 37-36, t. 1, pl. 2, fig. 9. — Díaz-Medina *et al.* 2017: 180, 181, fig. 9A-C.

Calappa heberti – Glaessner 1928: 174, 175. — Veiga Ferreira 1958: 203-207, text-figs 1-3, pl. 1, figs 1-3 (*non* Brocchi, 1883).

Calappa cf. *heberti* – Da Carvalho 1959: 79, pl. 2, figs 4-6.

Calappa heberti sp. 2 – Bachmayer 1962: 41, pl. 2, fig. 1.

Calappa aff. *granulata* – Bachmayer 1962: 42.

Calappa aff. *heberti* – Förster 1979: 255, 257, pl. 1, figs 2, 3 (*non* fig. 4).

Calappa sp. – Artal & Gilles 2007: fig. 2a.

Carapace de crabe – Gagnaison *et al.* 2009: 1, fig. 2.

Material examined and measurements (in mm). — Complete dorsal carapace embedded of bioclastic limestone, cuticle preserved, MS2006 FS 134a: L = 30, W = 39.5, FOW = 13.

Locality and horizon. — 'La Sonneterie' quarry, Meigné-le-Vicomte (Maine-et-Loire). 'Savignean facies', Langhian-Serravallian (Middle Miocene).

Description

Carapace medium sized, transversely subovate in outline, expanded clypeiform process (wing-like extension) in posterolateral angles; wider than long, maximum width at posterolateral angle; strongly vaulted longitudinally and transversely. Cuticle well preserved. Maximum width at level of third posterolateral tooth. Front narrow, medial notch; orbits small, rounded; supraorbital margin entire. Anterolateral margin strongly arcuate, ornate with blunt teeth and nodes. Posterolateral margin strongly convex; wing-like extension with largest tooth at posterolateral angle, preceded by three teeth progressively smaller, and followed by two teeth that decrease in size progressively; all of them triangular with an axial elevated ridge. Posterior margin short, slightly convex, bounded by two blunt teeth. Carapace surface covered anteriorly by large tubercles and swellings, smaller posteriorly, forming longitudinal rows. Central regions bounded longitudinally by two parallel grooves running from orbits to cardiac region. Ventral parts and appendages not present.

Remarks

The carapace outline, toothed posterolateral wing-like extension, and dorsal features of the 'Faluns' specimen, fit well with the description and images of the holotype figured by Müller (1984a: 66, pl. 35, figs 1-2), as well as with the specimens in literature, widely described and depicted by diverse authors through time (see for instance the synonymies list above). Further, comparisons with specimens of the collection of the first author (AO), allow us to place the French specimen within this species with confidence. Differences of the French specimen with *Calappa heberti* Brocchi, 1883 from the Middle Miocene of the Paratethys are clear, since the dorsal surface of the carapace of *C. heberti* is ornate with short squamous ridges in the posterior portion and have less produced teeth in its posterolateral angle (e.g. Lőrenthey *in* Lőrenthey & Beurlen 1929: pl. 6, fig. 3; Müller 1984a: pl. 35, figs 1-2, 7; pl. 36, fig. 6). It differs as well with *C. saheliensis* Van Straelen, 1937, from the Late Miocene of North Africa and Southern Iberian Peninsula, in having large tubercles in the anterior half of carapace and by the absence of longitudinal grooves, more or less marked, in the branchial regions

Fig. 3. — **A**-**C**, *Calappa praelata* Lőrenthey *in* Lőrenthey & Beurlen, 1929, MS2006 FS 134a: **A**, dorsal view; **B**, frontal view; **C**, close-up of posterolateral margin; **D**, **E**, *Calappa* sp., MS2018-2-1: **D**, left chela, MS2018-2-2; **E**, right chela; **F**-**J**, *Hebertides jurassica* Guinot, De Angeli & Garassino, 2007; **F**-**H**, MS2018-1-1: **F**, right lateral view; **G**, frontal view; **H**, dorsal view; **I**, **J**, ULB-SO-1: **I**, fragment of right dorsal carapace; **J**, the same fragment showing bryozoans incrusted. Scale bars: A-H, 10 mm; I, J, 5 mm. Photographs by À. Ossó.

(Van Straelen 1937: pl. 32, fig. 1; type series from MNHN: MNHN.F.R03768). *Calappa zurcheri* Bouvier, 1899 from the Oligocene-Miocene of Mexico and Panama, also differs clearly from the studied specimen in having stronger tuberculation along almost all the dorsal carapace surface (e.g. Bouvier 1899: 189-192 text-fig. 1; Luque *et al.* 2017: fig. 12M).

Calappa praelata is widespread during the Miocene along the Paratethys and Proto-Mediterranean; it is also present in the Atlantic along the southern coast of Portugal. Díaz-Medina *et al.* (2017: 181) summarized the known previous records of this species. *Calappa praelata* is morphologically very close to the extant *C. granulata*, mainly dorsally; however, different features in chelae and in the posterior margin distinguish both species (see Müller 1984a: pl. 36, figs 1-5).

Calappa sp.
(Fig. 3D, E)

MATERIAL EXAMINED AND MEASUREMENTS (in mm). — Two palms of a right (embedded in shell-grit matrix) and a left chelipeds, dactyli not preserved. Right chela, MS2018-2-1: H = 28; left chela, MS2018-2-2: H = 30.5; W = 33; T = 8.5.

LOCALITY AND HORIZON. — 'La carrière-musée' (Channay-sur-Lathan, Indre-et-Loire). Bioclastic calcarenite with *Anadara turonica*, Tortonian (Late Miocene).

DESCRIPTION
Palm subtrapezoidal, much higher distally. Upper margin strongly convex distally, cockscomb like; armed with six to eight teeth, being the distal ones acute and the medial ones blunt and larger. Lower margin straight, sharp edged. Outer surface of palm with coarse granules in the lower half, being smaller and tight in the upper half.

REMARKS
The two described chelae were recovered on a different stratigraphic level (Tortonian) than the *Calappa praelata* carapace described above (Languian-Serravallian), which does not allow us to assign with certainty those chelae to that species. They could be likely attributable to *C. praelata*, but the dense granulation of the outer surface of the palm differs from the less ornamented surface of the right chela figured by Müller (1984a: pl. 36, fig. 6) and attributed to *C. praelata*. The granules that stipple the outer surface of the palm, the shorter teeth of the upper margin of chelae, and the unrimmed lower margin precludes the attribution of the 'Faluns' chelae to *C. granulata* (see Müller 1984a: pl. 36, fig. 1). Consequently, we prefer to leave these chelae as *Calappa* sp.

Superfamily CORYSTOIDEA Samouelle, 1819
Family CORYSTIDAE Samouelle, 1819
Subfamily CORYSTINAE Samouelle, 1819

Genus *Hebertides*
Guinot, De Angeli & Garassino, 2007

TYPE SPECIES. — *Hebertides jurassica* Guinot, De Angeli & Garassino, 2007 by original designation.

Hebertides jurassica Guinot, De Angeli & Garassino, 2007
(Fig. 3F-J)

Hebertides jurassica Guinot, De Angeli & Garassino, 2007b: 241-260, fig. 1-3. — Van Bakel *et al.* 2009: 80. — Schweitzer *et al.* 2010: 104. — Taylor *et al.* 2012: 71-83, fig. 1; — Taylor 2012: 9-11, fig. 2. — Jagt *et al.* 2015: 882. — Emmerson 2017: 323.

Corystid – Guinot *et al.* 2007a: 53-55, fig. 1.

MATERIAL EXAMINED AND MEASUREMENTS (in mm). — Carapace, MS2018-1-1: L = 16.5, W = 13, FOW = 13. — Fragment of carapace, ULB-SO-1: L = 11.4; W = 5.8.

LOCALITY AND HORIZON. — Carapace: 'La carrière-musée' (Channay-sur-Lathan, Indre-et-Loire). Bioclastic calcarenite with *Anadara turonica*, Tortonian (Late Miocene). Fragment of carapace: 'La Sonneterie' quarry, Meigné-le-Vicomte (Maine-et-Loire). 'Savignean facies', Langhian-Serravallian (Middle Miocene).

DESCRIPTION (modified from Guinot *et al.* 2007b)
Carapace longitudinally ovate, longer than wide, convex in both sections; maximum width at the epibranchial teeth level; W/L ratio about 0.75. Cuticle well preserved. Regions relatively well defined, slightly swollen and separated by weak, smooth grooves; medial regions faintly distinct, forming a continuous medial area. Dorsal surface of carapace covered by rounded tubercles in anterior half, grouped and aligned in posterior half. Front narrow, broken, medially V-notched. Orbits broad; inner orbital tooth blunt, as a fold; supraorbital margin sinuous, finely serrated, with two V-shaped fissures; outer orbital tooth triangular, acute, prominent. Supraorbital area slightly depressed, smooth. Anterolateral margin convex, with three granular teeth (excluded the extraorbital one); the second sunken, placed at lower level that the rest; the third the larger; the fourth the smallest. Posterolateral margin slightly convex. Posterior margin convex, with marked granular rim. Protogastric regions slightly swollen, with two tubercles obliquely aligned at each lobe. Mesogastric region subpentagonal, slender and elongate anteriorly, broad posteriorly. Metagastric region indistinct from mesogastric region. Urogastric region subrectangular elongate, separated from meso-, metagastric regions by two gastric pits. Cardiac region subhexagonal, somewhat raised respect to urogastric region. Meta-, urogastric and cardiac regions, bounded laterally by well-marked branchiocardiac groove. Intestinal region indistinct. Hepatic region subtriangular, well delimited by cervical and hepatic groove. Branchial regions slightly swollen, epi- and mesobranchial lobes delimited by a weak oblique groove. Ventral parts and appendages not present.

REMARKS
Hebertides jurassica was erected based on a unique specimen found as a loose block in a quarry of Ranville (Normandy). In spite of the strikingly fine preservation of the specimen, its age was considered as the same as the rocks of the quarry, i.e., Bathonian (Middle Jurassic) (Guinot *et al.* 2007a, b). Further examination of the matrix of this specimen revealed that the bryozoans (mainly cheilostomes) attached to the matrix and specimen were not Jurassic in age but younger,

Cenozoic, and probably Miocene in age. Therefore, it was assumed that the specimen was accidentally discarded in the quarry by a fossil collector. Thus, the provenance of that specimen remained unknown (Taylor 2012; Taylor *et al.* 2012).

Despite this, complete specimens of *Hebertides jurassica* are known among French collectors' private collections, which regularly collect in the 'Faluns' of Anjou-Touraine. Fragmentary remains of their carapaces are relatively common among the typical shell grit of the 'Faluns' (Fig. 3I-J). Therefore, the common occurrence of *H. jurassica* in the 'Faluns' leads us to suggest that, likely, the holotype comes from a locality in this region whose age is confirmed as Middle-Late Miocene.

Superfamily Majoidea Samouelle, 1819
Family Majidae Samouelle, 1819
Subfamily Majinae Samouelle, 1819

Genus *Maja* Lamarck, 1801

Type species. — *Cancer squinado* Herbst, 1788, subsequent designation by ICZN (1958).

Maja orbignyana Millet de la Turtaudière, 1865
(Fig. 4A-F)

Maia orbignyana Millet de la Turtaudière, 1865: 577. — Millet 1854: 152 (*nomen nudum*). — Couffon 1934: 171, fig. 155.

Maja orbignyana – Couffon 1908: 2, 3, pl. 1, figs 1-4. — Glaessner 1929: 247.

Maja orbigniana – Couffon 1910: 130, fig. 4. — Schweitzer *et al.* 2010: 95.

Maia sp. – Via 1932: 9.

Maia cfr. *orbingyana* – Vía 1941: 118, 119, pl. 10, fig. 70.

Maja cf. *orbigniana* – Müller 1993: 13, fig. 6E.

Material examined and measurements (in mm). — One fragment of anterior part of carapace preserving left rostral spine, left orbit and protogastric lobe, MS2012 0 172a: L = 26.3; W = 21. — Three fragments of left orbital region, ULB-SO-3: L = 9.5, W = 16; ULB-SO-3: L = 17, W = 11; ULB-SO-2: L = 19, W = 14.5. — Merus of ambulatory leg ULB-SO-4: L = 23; W = 5. — Dactylus of ambulatory leg ULB-SO-5: L = 21; W = 4.

Locality and horizon. — 'La Sonneterie' quarry, Meigné-le-Vicomte (Maine-et-Loire). 'Savignean facies', Langhian-Serravallian (Middle Miocene).

Description
Rostrum bifid with long, conical and acute rostral spines. Orbits shallow, rounded, opened; supraorbital margin with medial, flattened, acute subtriangular tooth, bounded by two fissures, the outer one deepest; outer orbital tooth long, conical, acute, slightly upward directed; inner orbital tooth subtriangular, acute; infraorbital margin with a blunt, prominent inner tooth, separated from the outer lateral orbit margin by a deep fissure. Protogastric region strongly swollen, ornate with strong and raised rounded tubercles. Hepatic region slightly swollen, ornate with rounded granules, the biggest ones at the basis of the hepatic spine, which is conical, acute and laterally directed. Merus of ambulatory leg subcircular in cross section, slightly compressed laterally; dactylus of ambulatory leg conical, subcircular in proximal cross section, slightly compressed distally.

Remarks
The recovered specimens are fragmentary portions of the left anterior parts of several carapaces (mainly orbits and front). After comparison with images of the holotype (Couffon 1908: figs 1, 2, 4; 1934: pl. 1, fig. 155), and of the fragmentary left orbit figured there (Couffon 1908: pl. 1, fig. 3), it is clear that the recovered remains can be attributed to *M. orbignyana* with confidence. The strong, rounded and raised tubercles in the protogastric lobe and hepatic region are distinctive for the species (see Müller 1993: 13).

Superfamily Pilumnoidea Samouelle, 1819
Family Pilumnidae Samouelle, 1819
Subfamily Pilumninae Samouelle, 1819

Pilumnus Leach, 1815

Type species. — *Cancer hirtellus* Linnaeus, 1761, by monotypy.

Pilumnus mediterraneus (Lőrenthey, 1897)
(Fig. 4G-L)

Pilodius mediterraneus Lőrenthey, 1897: 160, 167, 169; 1898a: 105, 113, 115; 1898b: 126-129, pl. 8, figs 5, 6; 1898c: 99-101, pl. 8, figs 5, 6. — Glaessner 1929: 315.

Pilumnus sp. – Glaessner 1928: 190.

Chlorodopsis mediterraneus – Lőrenthey *in* Lőrenthey & Beurlen 1929: 34, 225-227, pl. 12, figs 13-17, 19.

Chlorodopsis mediterranea – Bachmayer 1953a: 253, pl. 3, fig. 5. — Bachmayer & Tollmann 1953: 314.

'*Pilodius*' *mediterraneus* – Müller 1974a: 122, pl. 3, fig. 3.

Pilumnus mediterraneus – Müller 1974b: 280; 1976a: 510; 1976b: 152; 1979: 274, pl. 21, fig. 3; 1984a: 93-94, pl. 87, figs 2-5, pl. 88, figs 1-5. — Radwański *et al.* 2006: 96, pl. 2, fig. 7. — Ossó & Stalennuy 2011: 37, fig. 9.3. — Górka *et al.* 2012: 171. — Górka *in* Wysocka *et al.* 2016: 379, fig. 14E.

Pilumnus sp. – Förster 1979: 260-261, pl. 3, fig. 6, pl. 5, fig. 1, 3, text-figs 8, 9.

Pince d'une patte de crabe – Gagnaison *et al.* 2009: 1, fig. 3.

Pilumnus cfr. *P. mediterraneus* – De Angeli *et al.* 2011: 112, fig. 4.

Material examined and measurements (in mm). — Two complete dorsal carapaces with cuticle well preserved, ULB-SO-6: L = 19.5, W = 27, F = 8, FOW = 15.5; MS2012 0 170: L = 14, W = 20, F = 8, FOW = 13.5. — Two right chelae, ULB-SO-7: H = 8.72, W = 15.6; ULB-SO-8: H = 7.84; W = 12.8.

Locality and horizon. — 'La Sonneterie' quarry, Meigné-le-Vicomte (Maine-et-Loire). 'Savignean facies', Langhian-Serravallian (Middle Miocene).

Description

Carapace relatively small sized, subhexagonal, longitudinally vaulted anteriorly, regions faintly marked; surface smooth, weakly ornate with small acute granules and small clusters of acute granules of squamous aspect, spread mainly by anterior half of carapace; setal pits visible. Maximum width at level of fourth anterolateral tooth, at the anterior half of carapace. Front bilobed, medially notched, each half with inner lobes very wide, and the outer lobes smaller, and separated from the inner orbital angle by notches. Orbits small, subrectangular, complete, forward directed; supraorbital margin finely serrated, with two fissures, one median and a second close to outer orbital tooth. Anterolateral margin with four subtriangular teeth (excluding outer orbital tooth), the first one semifused with the outer orbital one, the second one broad, the third and fourth acute. Posterolateral margin slightly convex, smooth. Posterior margin clearly convex medially, rimmed. Frontal region with a short, longitudinal deep groove, lobes slightly swollen. Gastric process fairly defined. Epigastric lobes faintly swollen, ornate. Protogastric lobes rounded, swollen, faintly ornate. Mesogastric region subpentagonal elongated anteriorly, wider posteriorly. Metagastric region indistinct. Urogastric region slightly depressed and separated from meso- and metagastric lobes by two gastric pits. Cardiac region diamond shaped, weakly swollen. Intestinal region narrow, transversely elongate, faintly swollen laterally. Hepatic region with a short granulate ridge paralleling the anterolateral margin. Epibranchial region with a short, acute, half-moon ridge not reaching the fourth (epibranchial) anterolateral tooth. Meso- and metabranchial regions indistinct, swollen. Gastrohepatic groove well marked; cervical and branchiocardiac grooves slightly marked. Thoracic and abdominal features not preserved. Right chela stout, palm slightly wider than long, outer side smooth, spiny in the upper margin and the distal portion of palm, mainly in smaller individuals; articulation with the dactylus strong; dactyli stout, about one third of propodus length; dactylus curved with blunt teeth in occlusal margin; pollex strong, with three to four massive acute teeth in the occlusal margin; setal pits visible in both dactyli. Carpus stout, angle of upper and outer surface with scattered spiny tubercles; upper inner angle with prominent tooth.

Remarks

The specific assignation of the French specimens to *Pilumnus mediterraneus* is unequivocal, in view of their stout, short palm with spiny upper margin and distal part, as well as their short dactyli (cf. Müller 1984a: 94, pl. 87, figs 2-5, pl. 88, figs 1-5; Radwański *et al.* 2006: fig. pl. 2, figs 7A, B; Ossó & Stalennuy 2011: fig. 9.3). Couffon (1908: 4, pl. 2, figs 5-7) reported a fragment and complete carapace and referred them to *Titanocarcinus pulchellus* (currently *Haydnella pulchellus* (A. Milne-Edwards, 1864)) and reproduced the diagnosis and the figures of the type of Milne-Edwards (Couffon 1908: pl. 2, figs 5a-5b). The type specimen was found on the 'Faluns' of Maine-et-Loire, and is currently lost (Couffon 1908: 1; Müller 1984a: 90). Strikingly, the diagnosis of *H. pulchellus* (see A. Milne-Edwards 1864: 33, 34), as well as its small size, fits well with that of *P. mediterraneus*. Given the abundance of chelae of *P. mediterraneus* in the 'Faluns' outcrops, it would be plausible that the small carapace described by A. Milne-Edwards as *T. pulchellus* was likely a specimen of *P. mediterraneus.* Since the transfer of this species from *Titanocarcinus* to *Haydnella* was made based on the drawings of A. Milne-Edwards (see Müller 1984a: 90; Schweitzer *et al.* 2007: 281, t. 1, fig. 1I), we suggest a revision of the systematic status of this taxon.

Pilumnus mediterraneus is by far the most abundant brachyuran of the 'Faluns' outcrops, in view of the great number of chelae remains found; although, complete carapaces, or even fragments of them, are very scarce. Müller (1984a: 94) pointed out already, referring to the Central Paratethys realm, that this species "is probably the most common crab in the Badenian [Langhian/Serravallian]. It occurs in all types of studied biotopes, even in reefs, but it is the most abundant in very shallow, almost eulittoral environments", and stated: "*P. mediterraneus* occurs in all substages of the Badenian". It is present, furthermore, in the Proto-Mediterranean during the Late Miocene, in the Messinian reefal outcrops of Spain and Italy (e.g. De Angeli *et al.* 2011). As stated by Müller (1984a: 94), *P. mediterraneus* is very close morphologically to the extant *P. hirtellus* Linnaeus, 1761 that lives in the Eastern Atlantic and Mediterranean Sea. We concur.

Superfamily Portunoidea Rafinesque, 1815
Family Carcinidae Macleay, 1838
Subfamily Polybiinae Ortmann, 1893

Genus *Liocarcinus* Stimpson, 1871

Type species. — *Portunus holsatus* Fabricius, 1798, by original designation.

Liocarcinus sp.
(Fig. 5A, B)

Material examined and measurements (in mm). — Partially preserved carapace, MS2012 0 172b: L = 10.5, W = 12, FOW = 8.5, F = 4.

Locality and horizon. — 'La Sonneterie' quarry, Meigné-le-Vicomte (Maine-et-Loire). 'Savignean facies', Langhian-Serravallian (Middle Miocene).

Description

Small sized carapace, subhexagonal, smooth, slightly wider than long. Regions weakly defined. Three longitudinally aligned tubercles at each side of carapace. Front incomplete, straight, but appears to be slightly produced medially. Orbits

Fig. 4. — **A**-**F**, *Maja orbignyana* Millet de la Turtaudière, 1865: **A**, ULB-SO-2, frontal view of left orbit; **B**, MS2012 0 172a, dorsal view of anterior part of carapace; **C**, ULB-SO-3, frontal view of left orbit; **D**, ULB-SO-3, frontal view of left orbit; **E**, ULB-SO-4, merus of ambulatory leg; **F**, ULB-SO-5, dactylus of ambulatory leg; **G**-**L**, *Pilumnus mediterraneus* (Lőrenthey, 1897): **G**, ULB-SO-6, dorsal view; **H**, frontal view; **I**, MS2012 0 170, frontal view; **J**, dorsal view; **K**, ULB-SO-7, left chela; **L**, ULB-SO-8, left chela. Scale bars: 10 mm. Photographs by À. Ossó.

relatively large; supraorbital margin with two closed fissures. Anterolateral margin slightly arcuate, with four subtriangular teeth (excluding the outer orbital tooth), the last of them (epibranchial tooth) the sharper. Posterolateral margin straight; reentrant of fifth pereiopod well marked. Posterior margin straight. Frontal region smooth, flattened. Gastric process poorly

defined. Epigastric lobes slightly marked. Protogastric lobes slightly swollen with faintly marked transverse ridge at each lobe; marked tubercle near gastrohepatic groove. Mesogastric region weakly marked. Urogastric region depressed. Cardiac region large, slightly swollen. Intestinal region depressed. Hepatic region depressed. Epibranchial region sigmoidal, weakly marked, with medial tubercle. Mesobranchial region slightly swollen, with marked tubercle, Metabranchial region depressed. Cervical groove faintly marked. Branchiocardiac groove weakly marked. Ventral parts and appendages not preserved.

Remarks

The features of the studied specimen fit with those of *Liocarcinus*, and its general outline matches well with the known Miocene *Liocarcinus* species (see Schweitzer *et al.* 2010). However, they differ in having a most decorated or rough surface of the carapace, as for instance *L. rakosensis* Lőrenthey *in* Lőrenthey & Beurlen, 1929 and *L. kuehni* (Bachmayer, 1953), whereas in the studied specimen the carapace surface is completely smooth; or in having more marked and raised regions as in the case of *L. oroszyi* (Bachmayer, 1953) and *L. praearcuatus* Müller, 1996 (see Bachmayer 1953a: pl. 2, figs 2, 5-5a; Müller 1984a: 83-84, pl. 69, figs 2-6, pl. 71, figs 1-4; 1996: 10, pl. 2, figs 2-3). *Liocarcinus ottnangensis* (Bachmayer, 1953) differs clearly in having a trifid front and a characteristic prominent transverse ridge running across the mesogastric and epibranchial regions, which is absent in the studied specimen (see Hyžný *et al.* 2015). *Liocarcinus oligocenicus* (Paucă, 1929) and *L. lancetidactylus* (Smirnov, 1929) present a different pattern of anterolateral margins and front, furthermore, their poor preservation makes difficult an accurate comparison (e.g. Jerzmańska 1967: fig. 1; Schweitzer *et al.* 2009: fig. 6; and Garassino & Novati 2001, respectively).

Regarding the extant species of *Liocarcinus* (see Ng *et al.* 2008), they have usually a more arched anterolateral margins than the studied specimen, and most of them have a trifid front, and/or a rough surface of carapace, which is smooth in the studied specimen. *Liocarcinus pusillus* (Leach, 1815) and *L. navigator* (Herbst, 1794) have a similar blunt front medially produced, similar to the studied specimen, but they differ in having a rougher dorsal surface, and by the lack of the conspicuous protogastric ridges and three characteristic tubercles, longitudinally aligned, present in the French specimen possess (e.g. Froglia & Manning 1982; Koch & Ďuriš 2016)

The general outline and dorsal sculpture of the studied specimen also resemble that of *Miopipus pygmaeus* (Brocchi, 1883) (Brocchi 1883: 1, pl. 5, figs 4-4a). However, Müller (1984a: 84, pl. 72, figs 1-4), described the front of *M. pygmaeus* as trilobed, narrow and prominent, and the carapace regions as strongly inflated, which precludes a congeneric relationship with the specimen described herein.

Therefore, in spite that the aforementioned differences could lead us to propose a new species of *Liocarcinus* for this specimen, based on the poorly preserved sole specimen, we report it as *Liocarcinus* sp., until more specimens are available for study.

Family Portunidae Rafinesque, 1815
Subfamily Necronectinae Glaessner, 1928

Genus *Necronectes* A. Milne-Edwards, 1881

Type species. — *Necronectes vidalianus* A. Milne-Edwards, 1881 by original designation.

Necronectes michelini (A. Milne-Edwards, 1861)
(Fig. 5D-F)

Scylla michelini A. Milne-Edwards, 1861: 137, pl.3., figs 3-3A. — Couffon 1908: 3, 4, pl. 1, figs 6-10, pl. 2, figs 1, 2. — Schweitzer *et al.* 2006: 122; 2010: 110. — Karasawa *et al.* 2008: 106. — Emmerson 2017: 584.

Cancer macrochelus – Millet 1854: 152 (*non* Desmarest, 1817).

Scylla cf. *michelini* – Glaessner 1928: 184, 185.

Scylla? *michelini* – Glaessner 1929: 374.

Scylla sp. (cf. *michelini*) – Lőrenthey & Beurlen 1929: 178, pl. 15, figs 5, 6.

Necronectes michelini – Glaessner 1933: 5-6. — De Angeli & Marangon 1992: 178, 179.

Scylla michelini? – Betancort *et al.* 2014: 345, pl. 1, figs K1-K2 (*non* I1-I2)

Material examined and measurements (in mm). — Two dactyli. Right dactylus, ULB-SO-9: L = 41.38, H = 25. — Left dactylus (tip broken off), ULB-SO-10: L = 32.53, H = 15.52.

Locality and horizon. — 'La Sonneterie' quarry, Meigné-le-Vicomte (Maine-et-Loire). 'Savignean facies', Langhian-Serravallian (Middle Miocene).

Description

Right dactylus stout, gently curved forward; subrectangular in section with rounded upper angles; strong proximal knob-stick molariform tooth followed by six serial rounded conical teeth of different sizes; rounded tip. Left dactylus stout, gently curved forward; subrectangular in section with rounded upper angles, proximal tooth and tip not preserved.

Remarks

Scylla michelini was erected based on fragmentary chelipeds and was referred to *Scylla* De Haan, 1833, because of its similarity to the strong chelipeds of the extant *S. serrata* (Forskål, 1775). Nevertheless, A. Milne-Edwards (1861: 136), pointed out the absence in *S. michelini* of the two typical distinct spines on the distal upper part of the palm, near the insertion of dactylus (see Couffon 1908: pl. 1, figs 6-10, t. 2, figs 1, 2; MNHN.F.B25950, which are present in *Scylla* species (e.g. Keenan *et al.* 1998; Trivedi & Vachhrajani 2013). Rathbun (1918: 168), when described *Necronectes proavitus* (as *Gatunia proavita*), pointed out as well, the absence of those spines as a differential trait with *Scylla,* and also noted the striking similarity between the cheliped of *N. proavitus* and that of *S. michelini* (Rathbun 1918: 171). Furthermore, A. Milne-Edwards (1861: 136) noted as well, that the upper

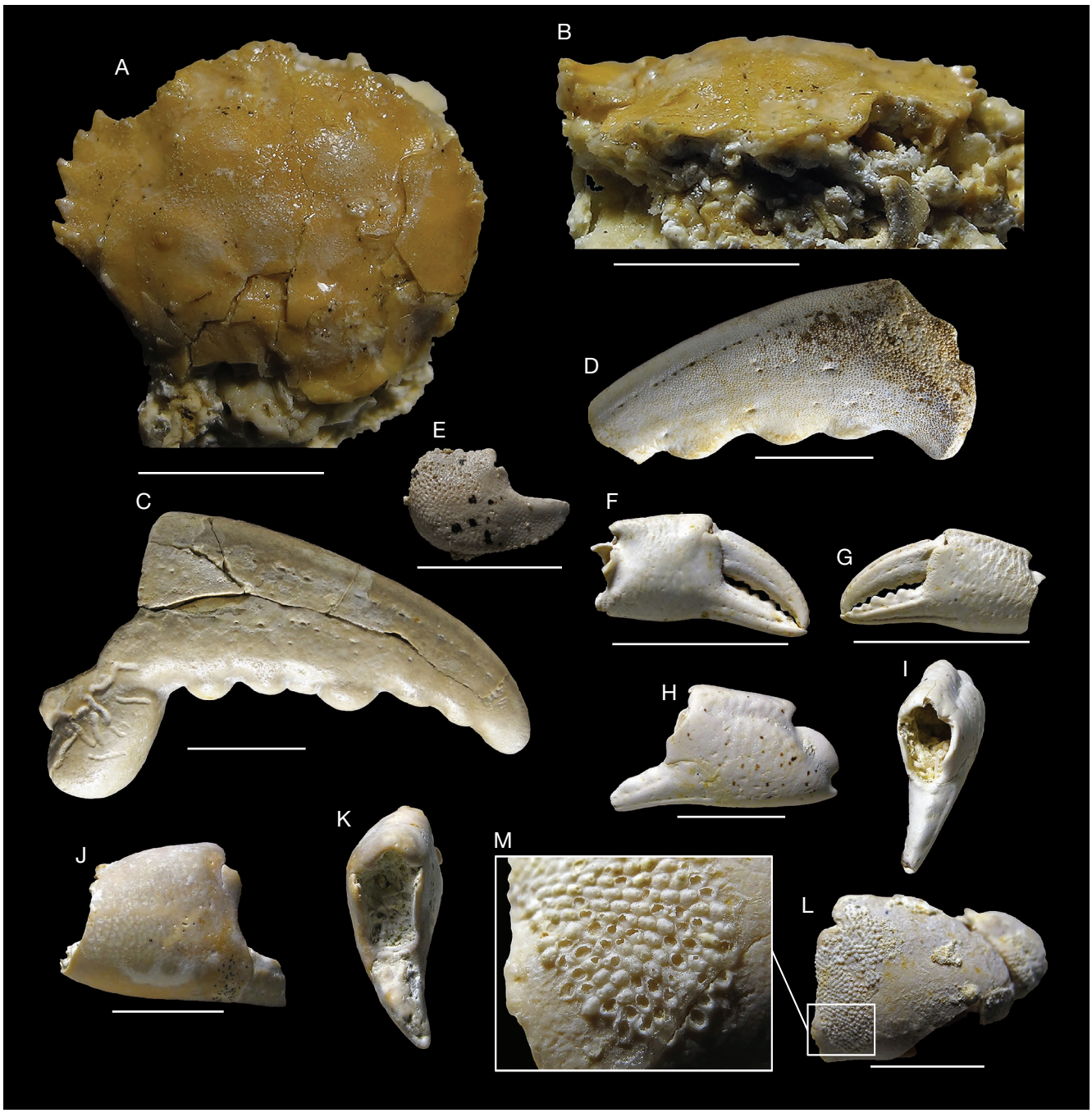

FIG. 5. — **A**, **B**, *Liocarcinus* sp., MS2012 0 172b: **A**, dorsal view; **B**, frontal view; **C**, **D**, *Necronectes michelini* (A. Milne-Edwards, 1861): **C**, ULB-SO-9, right dactylus; **D**, ULB-SO-10, left dactylus; **E**, *Paguristes gagnaisoni* Gagnaison, 2012, MS2006 FS 134b, right chela; **F-I**, *Xantho* cf. *moldavicus* (Yanakevich, 1977): **F**, ULB-SO-11, left chela, inner lateral view; **G**, outer lateral view; **H**, ULB-SO-12, left chela, outer lateral view; **I**, frontolateral view; **J-M**, undetermined chelae: **J**, ULB-SO-13, lateral view of right chela; **K**, frontal view; **L**, ULB-SO-14, lateral view of left chela; **M**, close-up showing an encrusted colony of bryozoans. Scale bars: A, B, 5 mm; C-M, 10 mm. Photographs by À. Ossó.

margin of the palm of *S. michelini* is rounded, whereas it is usually more flattened and angled in *Scylla* species (see Keenan *et al.* 1998: fig. 8).

Subsequently, several authors assigned similar fragmentary remains of dactyli y to *Scylla michelini* (see synonym list). Glaessner (1933: 5), included *S. michelini* within *Necronectes* A. Milne-Edwards, 1881, being followed by De Angeli & Marangon (1992: 178, 179). Nevertheless, this placement was questioned by Schweitzer *et al.* (2006: 121, 122), which retained *S. michelini* within *Necronectes* (see also Karasawa *et al*. 2008: 106).

The aforementioned differences in the palms, such as the absence of the outer and inner spines on distal margin, and the strong spine at carpal articulation of propodus, further, the absence of spines on the outer part of carpus, peculiar of the most species of *Scylla* possesses (e.g. Keenan

et al. 1998: fig. 8; Trivedi & Vachhrajani 2013: fig. 5a-c), allow us to confirm the generic placement of *S. michelini* within *Necronectes*, as it was previously placed by Glaessner (1928, 1933).

Superfamily XANTHOIDEA MacLeay, 1838
Family XANTHIDAE MacLeay, 1838
Subfamily XANTHINAE MacLeay, 1838

Genus *Xantho* Leach, 1814

TYPE SPECIES. — *Cancer incisus* Leach, 1814 by monotypy.

Xantho cf. ***moldavicus*** (Yanakevich, 1977)
(Figs 5F-I)

MATERIAL EXAMINED AND MEASUREMENTS (in mm). — Two left chelae, ULB-SO-11: L = 6, W = 12; ULB-SO-12: L = 11, W= 21.5.

LOCALITY AND HORIZON. — 'La Sonneterie' quarry, Meigné-le-Vicomte (Maine-et-Loire). 'Savignean facies', Langhian-Serravallian (Middle Miocene).

DESCRIPTION
Propodi transversely elongate, stout. Palm of left propodus subtrapezoidal, slightly wider than high; maximum height at the distal end. Upper margin straight, flattened, rugose. Lower margin gently convex. Outer side convex, with longitudinal rugose ridges; transverse stepped depression parallel to the upper margin, about to the three quarters of the total height. Inner side obliquely convex distally and concave in the upper proximal corner. Dactyli slightly shorter than palm; dactylus gently curved downwards with a blunt keel in upper margin, and occlusal margin with six or seven subequal triangular teeth; pollex straight, stout, lower margin slightly convex, transverse lateral keel and groove, with occlusal margin with seven or eight subtriangular teeth, the biggest ones in the middle. Tip of both dactyli spoon like. Setal pits visible.

REMARKS
We have not found carapace remains of *Xantho moldavicus* among the recovered decapod remains in the 'Faluns' outcrops, though the specimen figured by Couffon (1908: pl. 2, fig. 6) as *Titanocarcinus pulchellus* could to be referred to this species. In any case, the chelae examined match exactly the chelae of *X. moldavicus* described and depicted in the literature (e.g. Müller 1984a: pl. 86, figs 5-8, pl. 86, figs 3, 5; Ossó & Stalennuy 2011: fig. 9, 1-2; Górka *in* Wysocka *et al.* 2016: fig. 14G). Furthermore, the typically spooned occlusal surface of the dactyli tips, would allow us to assign, those chelae to the aforementioned species. A successful search of this specimen in the museum collections would confirm the assignation of both, the Couffon's carapace and the chelae reported herein to *X. moldavicus*. Meanwhile, in absence of complete carapaces, or remnants of them, with which to relate the chelae, we prefer to leave them in open nomenclature.

Undetermined chelae
(Fig. 5J-M)

MATERIAL EXAMINED AND MEASUREMENTS (in mm). — Left chela palm, ULB-SO-14: L = 14.5, W = 17. — Right chela palm: ULB-SO-13: L = 14, W = 20.

LOCALITY AND HORIZON. — 'La Sonneterie' quarry, Meigné-le-Vicomte (Maine-et-Loire). 'Savignean facies', Langhian-Serravallian (Middle Miocene).

DESCRIPTION
Propodi with massive palm slightly subtrapezoidal, stout, higher distally; outer and inner surface convex, completely smooth. Upper and lower margin rounded, smooth. Pollex broken, appears short, with flattened molariform teeth. Carpus rounded, smooth; blunt tooth at upper inner angle.

REMARKS
Due to their incompleteness and the lack of dactyli, or carapaces to they may be related, a generic or familial assignation is not clear. However, in view of the features displayed, they could belong to Carpilioidea or Xanthoidea but even to other superfamilies as well.

DISCUSSION

Couffon (1908), made a compendium of all of the species found and described from the 'Faluns' of Anjou-Touraine. He revisited the species formerly described by A. Milne-Edwards and Millet de la Turtaudière, housed in the collections of the museums of Angers and Paris, likewise, he reported and described new specimens. In his work, Couffon used in part the original diagnosis of the authors and made his own observations.

For instance, he reported three specimens of *Titanocarcinus pulchellus* (Fig. 6A-D), of which he could not locate the type species; consequently, he figured the original drawings of A. Milne-Edwards (1863: t. 9, figs 2, 2a;). With respect to the first specimen, based mainly on the diagnosis not on the drawing, which may be somewhat idealized (Couffon 1908: t. 2, figs 5, 5a; Fig. 6A, B), we suggest, as indicated above, that this specimen is likely a specimen of *Pilumnus mediterraneus*. The second specimen reported and also attributed to *T. pulchellus* (Couffon 1908: t. 2, fig. 7; Fig. 6C) is a fragment. Based on that figure, we are not able to attribute it to any genus or species. The third specimen attributed to this species (Couffon 1908: t. 2, fig. 6; Fig. 6D), an almost complete dorsal carapace, could actually be, as previously mentioned, a specimen of *Xantho moldavicus* (cf. Müller 1984a: pl. 86, figs 1, 2, 4; Ossó & Stalennuy 2011: fig. 3.11-12), a species to which we tentatively attribute the chelae (Fig. 3F-I).

Two chelae were also reported in Couffon's work. One of them, a complete right cheliped without size references (Couffon 1908: t. 2, figs 3-4; Fig. 6E-F), was attributed to *Lobocarcinus sismondai* (as *Cancer sismondae*). In our opinion, the general shape of this cheliped and the length and denti-

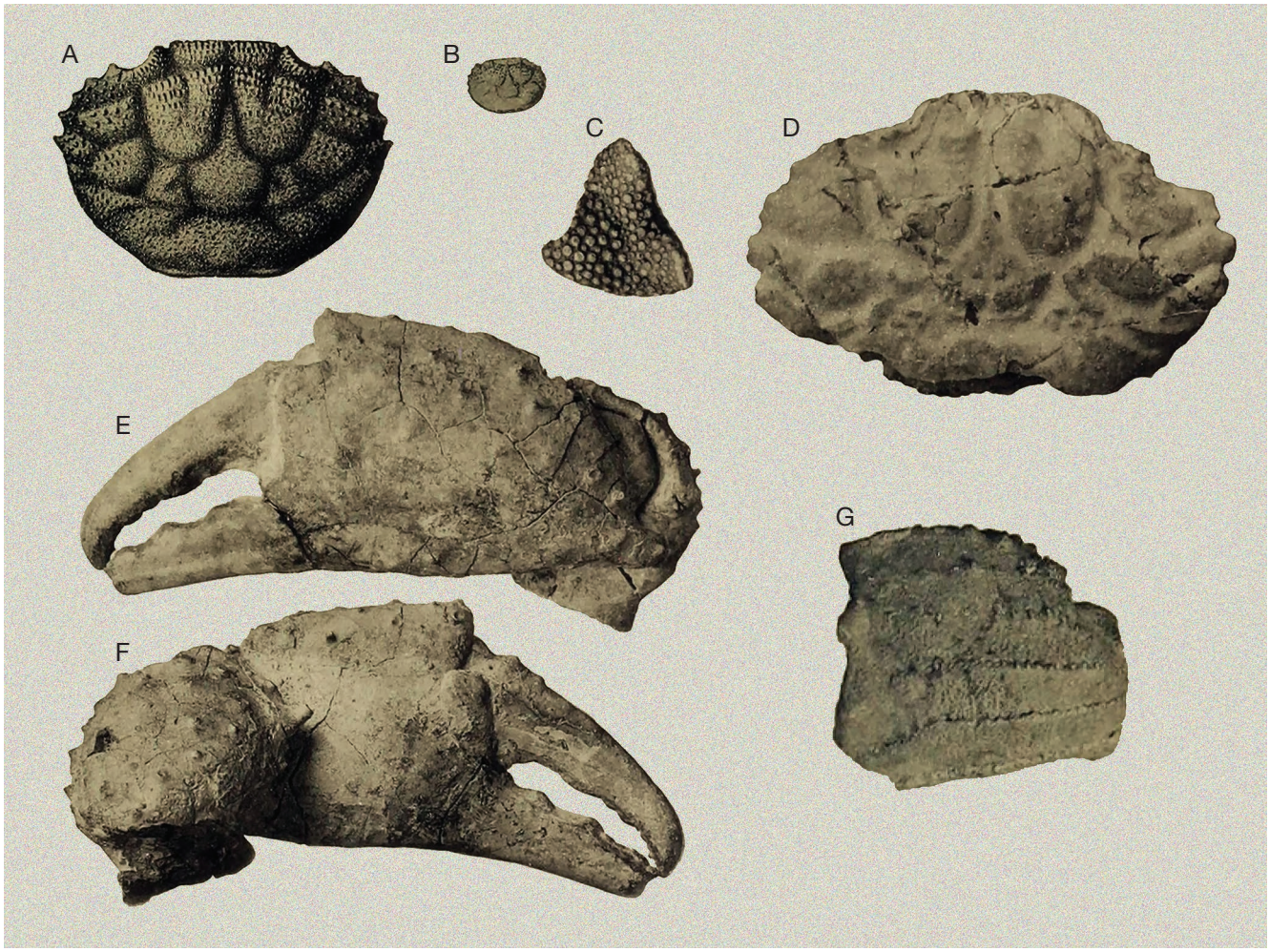

FIG. 6. — Digital reproduction of the figures from Couffon (1908) with the original nomenclature: **A**-**D**, *Titanocarcinus pulchellus* Al. Milne-Edwards, 1865 (sic); **E**, **F**, *Cancer Sismondae* Meyer, 1843? (sic); **G**, *Cancer Deshayesii* A. Milne-Edwards, 1865 (sic). Without scale.

tion of its dactyli, does not corresponds with Cancridae chelae (see Nations 1975; Schram & Ng 2012). Glaessner (1933: 6, 7) discussed on it and interpreted this chela as *Eriphia*? sp. An examination of this cheliped would be necessary to a proper identification. A second specimen, a palm of a left chela (Couffon 1908: t. 1, fig. 11; Fig. 6G), was attributed to *Cancer deshayesii* (synonymous of *Lobocarcinus sismondai* [see Glaessner 1929]). Indeed, this palm presents the typical cancrid features (cf. Nations 1975; Schram & Ng 2012) and matches well with those of *L. sismondai* (see Bonfiglio & Donadeo 1982: fig. 17). However, as far we know, *L. sismondai* has not been reported in the Miocene of the European Atlantic (see Collins 2002: 86; Van Bakel *et al.* 2003). Furthermore, given the great similarity among the palms of the Cancridae, and considering that we have not recognized any carapace remains attributable to that species among the material examined, we prefer to leave this chela tentatively as *Lobocarcinus* sp.

The two fragments of dactyli attributed by Couffon (1908: 2, pl. 1, fig. 5) to *Neptunus* aff. *monspeliensis* (sic) would belong likely to a portunid species, but their fragmentary condition does not allow any specific or even generic attribution. Therefore, we leave them as undetermined portunid.

The crab assemblage present in the Middle-Late Miocene of the 'Faluns' of Anjou-Touraine, represents species of nine families. It shows a clear affinity with Mediterranean and Paratethyan coeval faunas. Indeed, all of the genera reported herein, and even several species such as *Calappa praelata*, *Maja orbignyana*, *Pilumnus mediterraneus* and *Xantho* cf. *moldavicus*, are also present in the Mediterranean and Paratethys realms during the Miocene (e.g. Müller 1993; Hyžný 2016). The only exception is *Hebertides*, which appears to have a North Atlantic affinity, like other Neogene Corystidae, at least in view of the fossil record (e.g. Müller 1984a; Van Bakel *et al.* 2003, 2009).

CONCLUSIONS

A complete appraisal of the fossil crustacean fauna of the Middle-Late Miocene of the 'Faluns' of Anjou-Touraine is accomplished for the first time since Couffon (1908). The

preservation of the specimens, all of them disarticulated, indicates an environment of shallow, agitated waters. This decapod assemblage, clearly dominated by *Pilumnus mediterraneus*, shows strong affinities with the Miocene Mediterranean-Paratethyan faunas, with which this assemblage shares all the genera here reported, eight in total, with the exception of *Hebertides*. Thanks to new evidence, the supposed Cenozoic (Miocene) age of *Hebertides jurassica* is confirmed herein, as well as its possible geographic provenance. Finally, the portunid crab *Scylla michelini* is transferred again to *Necronectes*.

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