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A re-appraisal of the middle-late Miocene fossil decapod crustaceans of the 'Faluns' (Anjou-Touraine, France)

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ABSTRACT
The access to a new collection of decapod crustaceans collected from the middle-late Miocene 'Faluns', and examination of new specimens available, have allowed to expand the previous compilations by Couffon (1908) and Ossó & Gagnaison (2019), elevating to nineteen the species reported, representatives of seventeen genera and fourteen families. Squat lobsters and parthenopid crabs are reported for the first time in the Atlantic Miocene of France. The expected presence of *Xantho moldavicus* (Yanakevich, 1977) and *Lobocarcinus sismondai* (von Meyer, 1843), hitherto known only by chelae, is confirmed herein. The status of *Haydnella pulchellus* (A. Milne-Edwards, 1864) is discussed. Moreover, the ventral features of *Necronectes michelini* (A. Milne-Edwards, 1861) are described for the first time. This decapod assemblage presents clear affinity with coeval decapod faunas from the Mediterranean and Paratethys realm, as evidenced by the presence of identical species such as *Liocarcinus kuehni* (Bachmayer, 1953) or *Pilumnus mediterraneus* (Lőrenthey, 1897), which is by far, the most common decapod in the 'Faluns' outcrops. Several different chelae and carapace remains are left in open nomenclature.

KEY WORDS
Decapoda,
Anomura,
Brachyura,
Paratethys,
Mediterranean,
Miocene,
faluns.

RÉSUMÉ
Réévaluation des crustacés décapodes du Miocène moyen-supérieur des 'Faluns' (Anjou-Touraine, France).
L'accès à une nouvelle collection de crustacés décapodes collectés dans les faluns du Miocène moyen-supérieur associé à l'examen de nouveaux spécimens, permettent d'élargir les synthèses précédentes de Couffon (1908) et Ossó & Gagnaison (2019), augmentant le nombre des espèces (dix-neuf) représentatives de dix-sept genres et de quatorze familles. Des Galathéidés comme *Galathea weinfurteri* Bachmayer, 1950 et des Parthénopidés sont signalés pour la première fois dans le Miocène de l'Atlantique français. La présence attendue de *Xantho moldavicus* (Yanakevich, 1977) et de *Lobocar-*

MOTS CLÉS
Decapoda,
Anomura,
Brachyura,
Paratéthys,
Méditerranée,
Miocène,
faluns.

cinus sismondai (von Meyer, 1843), jusque-là connus uniquement par des pinces, est confirmée ici. Le statut d'*Haydnella pulchellus* (A. Milne-Edwards, 1864) est discuté. De plus, les caractéristiques ventrales de *Necronectes michelini* (A. Milne-Edwards, 1861) sont décrites pour la première fois. Cet assemblage de décapodes présente une affinité évidente avec les faunes contemporaines de la Méditerranée et de la Paratethys, comme en témoigne la présence d'espèces identiques telles que *Liocarcinus kuehni* (Bachmayer, 1953) ou *Pilumnus mediterraneus* (Lőrenthey, 1897), qui est de loin, le décapode le plus classique des faluns. Plusieurs pinces et carapaces sont laissées dans une nomenclature ouverte.

INTRODUCTION

The compilation of decapods of the 'Faluns' by Couffon (1908) was expanded by Ossó & Gagnaison (2019), who also updated the systematics of the taxa known to date. In the latter work, a total of seven genera and eight species of eubrachyuran crabs, undetermined chelae, and one anomuran species, were reported. Access to a new collection of decapod crustaceans collected mainly in the 'La Blandinerie' quarry near Breil in the Anjou region (Maine-et-Loire, France), allows us to increase our knowledge of the 'Faluns' decapod fauna. This collection, composed of fifty-one remains that, have been identified for the most part, despite the fragmentary and worn condition of many of them. Here we present a selection of them, keeping aside several isolated dactyli, most of them likely belonging to *Pilumnus mediterraneus* (Lőrenthey, 1897) and *Necronectes michelini* (A. Milne-Edwards, 1861).

In the present work, some genera of different families of decapods are reported for the first time in the European Atlantic Miocene, for instance squat lobsters and parthenopids. Likewise, we confirm the expected presence of several taxa previously known from chelae remains only, by the discovery of identifiable carapaces, e.g., *Xantho moldavicus* (Yanakevich, 1977) and *Lobocarcinus sismondai* (von Meyer, 1843). The obscure systematic status of the *Haydnella pulchellus* (A. Milne-Edwards, 1864), whose holotype was lost, is revisited, concluding that one of the specimens attributed by Couffon (1908) to that species, was in fact a sample of *Xantho moldavicus,* and that the lost holotype could have actually been a sample either of the latter or of *Pilumnus mediterraneus*. A new specimen of *Hebertides jurassica* Guinot, De Angeli & Garassino, 2007 is reported, confirming thus its origin in the 'Faluns'. The enigmatic large cheliped from Doué-la-Fontaine described and depicted by Couffon (1908: t. 2, figs 3-4), was examined at the Muséum national d'Histoire naturelle (Paris, France), and its possible systematic affinity is discussed herein. A large but incomplete sample of *Necronectes michelini* A. Milne-Edwards, 1881 has allowed to extend the description of this species, known hitherto only by chelipeds, to the ventral features opening the debate on possible synonyms of this species.

As a result of the present appraisal and of the previous works by Couffon (1908) and Ossó & Gagnaison (2019), a total of seventeen genera, comprising nineteen different species, that tentatively represent fourteen families, are reported from the Miocene of the 'Faluns' (Table 1). As pointed out by Ossó & Gagnaison (2019), the similarity between the Miocene 'Faluns' fauna and the Mediterranean and Central Paratethys coeval faunas is remarkable, with which – except for a few exceptions – the Miocene 'Faluns' fauna shares genera and even species. However, it contrasts the relatively low species richness reported in the 'Faluns', when compared to the high species richness reported from the localities with reefal environments (e.g. Müller 1984, 1993; Hyžný 2016) or non-reefal (siliciclastic) environments of the aforementioned areas (e.g. Müller 1993; Artal & Gilles 2007). This could be due to the strong underwater currents of 'Faluns' shallow infralittoral environment, precluding the rapid burial of decapod corpses and molts that otherwise disarticulate rapidly, as evidenced by the absence of articulated specimens and the higher percentage of hardest parts such as isolated chelae compared to the number of carapaces.

The specimens described in the present work are housed in the collections at the Muséum d'Histoire naturelle du Havre (Le Havre, France) (MHNH); the Muséum national d'Histoire naturelle (Paris, France) (MNHN); the UniLaSalle Institute (Beauvais, Oise, France) (ULB), and the Musée du Savignéen (Savigné-sur-Lathan, Indre-et-Loire, France) (MS).

TABLE 1. — Decapods reported in the 'Faluns' Miocene outcrops (see Couffon 1908; Ossó & Gagnaison 2019; and this article) and in the circum-Mediterranean and Western-Central Paratethys areas (see Müller 1984; Hyžný 2016). Symbols: ●, species reported; ○, genus reported; –, not reported.

Family	Genus/Species	'Faluns'	Mediterranean and Western-Central Paratethys
Galatheidae	*Galathea weinfurteri*	●	●
? Porcellanidae	Undetermined chela	●	–
Diogenidae	*Paguristes gagnaisoni*	●	○
? Paguridae	Undetermined chelae	●	–
Calappidae	*Calappa praelata*	●	●
Calappidae	*Calappa* sp.	●	○
Cancridae	*Lobocarcinus sismondai*	●	●
Corystidae	*Hebertides jurassica*	●	–
Leucosiidae	'*Ebalia*' cf. *hungarica*	●	●
Majidae	*Maja orbignyana*	●	●
? Majidae	Undetermined majoid	●	○
Parthenopidae	*Derilambrus* cf. *szaboi*	●	●
Pilumnidae	*Pilumnus mediterraneus*	●	●
Carcinidae	*Liocarcinus* sp.	●	○
Carcinidae	*Liocarcinus kuehni*	●	●
Carcinidae	Undetermined chelae	●	○
Portunidae	*Necronectes michelini*	●	○
Xanthidae	*Xantho moldavicus*	●	●
? Xanthidae	Undetermined cheliped	●	–

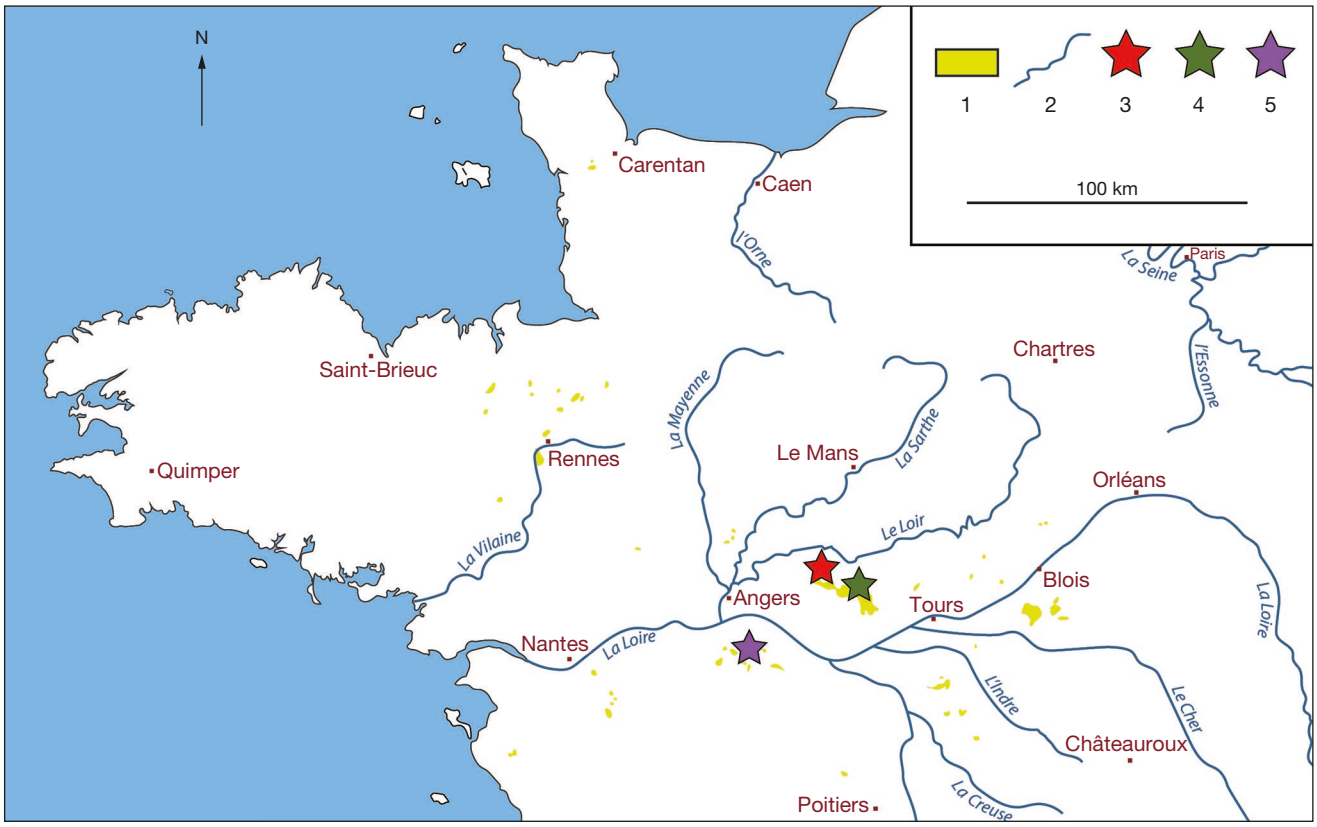

FIG. 1. — Location map of the three quarries: **1**, the marine Miocene outcrops; **2**, the river network; **3**, the 'Blandinerie' quarry (Breil); **4**, the 'Sonneterie' quarry (Meigné-le-Vicomte); **5**, the 'Noyant-la-Plaine' quarry (Doué-la-Fontaine).

LOCATION AND STRATIGRAPHY

The specimens studied herein were recovered from three different localities from the Anjou region (Maine-et-Loire, France): the 'Blandinerie' quarry (Breil), the 'Sonneterie' quarry (Meigné-le-Vicomte) and the 'Noyant-la-Plaine' quarry (Doué-la-Fontaine) (Fig. 1).

During the late Burdigalian to the Tortonian, a transgression came from the west to the east until the Blésois region in the Loire Valley, and resulted in the deposition of bioclastic sands locally named 'Faluns' (Lecointre 1947) in a tidally-influenced hydrodynamic regime (André & Gagnaison 2012). 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 a mixture of marine and continental faunas (invertebrates and vertebrates).

The 'Faluns' substratum is composed of Mesozoic rocks (Jurassic carbonate platforms, Cenomanian gravelly sands and marls, and finally Turonian chalks, named 'tuffeau') (André & Gagnaison 2012) and Paleogene-Early Miocene fluvial to lacustrine deposits (Gagnaison 2017). Quaternary-to-recent soils cover all the Miocene formations.

In the Anjou region, three Miocene marine facies are present: 1) a clinostratified calcarenite with sea urchins of the late Burdigalian-early Langhian; 2) the clayey shelly sands with bryozoans ('Savignean facies') which present a diachronism between the Savigné-sur-Lathan/Noyant-sous-le-Lude sedimentary basin (Langhian-Serravallian) and the Doué-la-Fontaine sedimentary basin (Tortonian) (Ginsburg 1990); and 3) the bioclastic calcarenite with the Tortonian *Anadara turonica* (Dujardin, 1837) ('Lublean facies') in the Savigné-sur-Lathan/Noyant-sous-le-Lude sedimentary basin (Courville & Bongrain 2003; Gagnaison 2020).

The fossils reported and described herein were recovered from the the base of the clayey shelly ('Savignean facies') sands with bryozoans: Langhian for the 'Blandinerie' quarry (Breil) and the 'Sonneterie' quarry (Meigné-le-Vicomte); and, Tortonian for the 'Noyant-la-Plaine' quarry (Doué-la-Fontaine). These facies are composed of clayey, shelly sand with many bryozoan fragments (mainly celleporiforms and reteporiforms) and mollusc shells (Buge 1948; Courville & Bongrain 2003). In these three quarries, the 'Savignean facies' begins with many bryozoan bioconstructions in place or slightly broken (Fig. 2). Many fragile invertebrate fossils have been found in these facies such as molluscs with their connecting valves, sea urchins with their spines and sometimes, well-preserved crab remains. This biotope integrates into a warm underwater environment typical of shallow (upper infralittoral) bryozoan colonies (Ossó & Gagnaison 2019). 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).

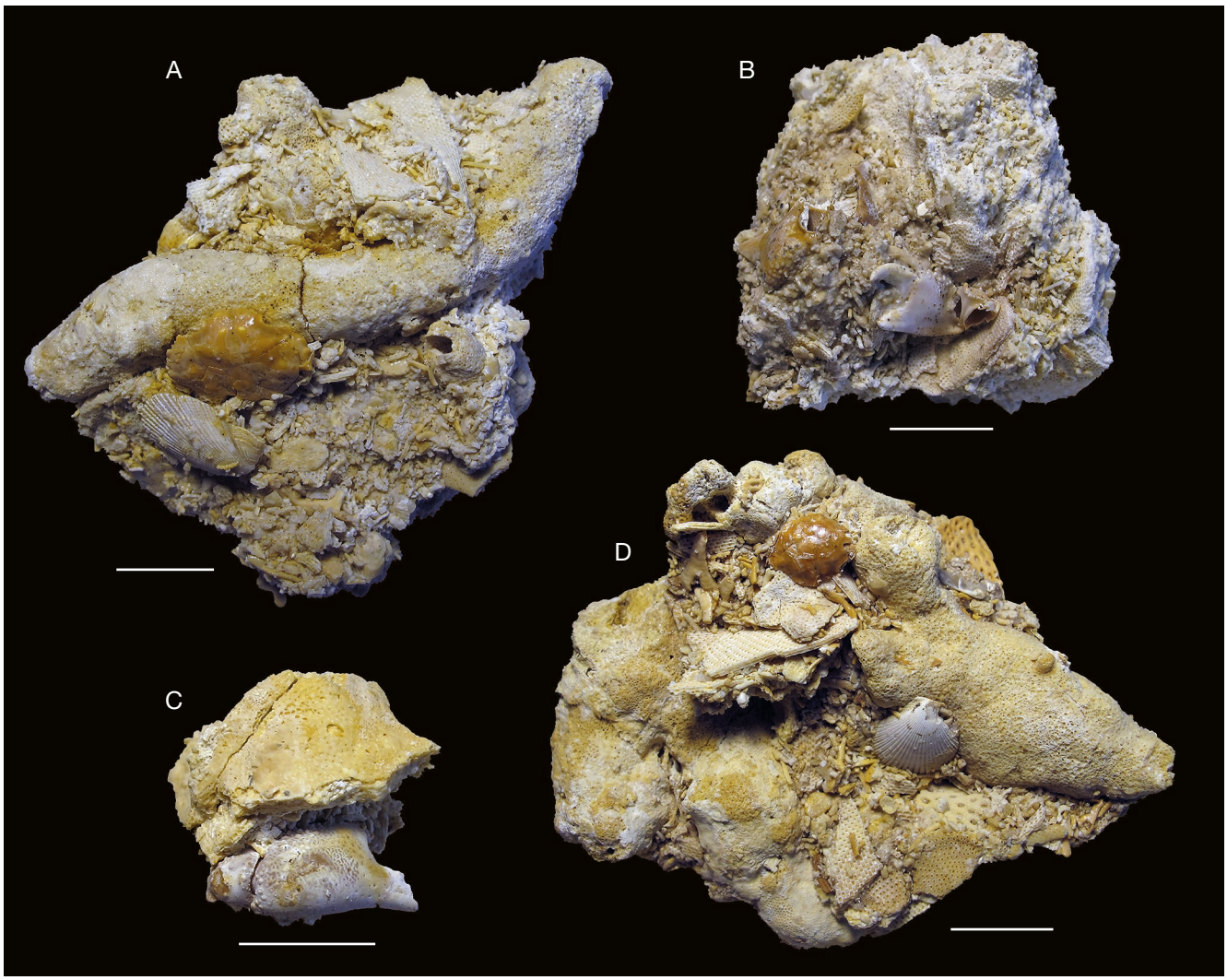

FIG. 2. — Typical aspect of the clayey shelly sands with bryozoans of the 'Savignean facies' (Langhian) from the 'Blandinerie' quarry Breil (Maine-et-Loire), with embedded remains of *Pilumnus mediterraneus* (Lőrenthey, 1897): **A**, ULB-IV-A (37), dorsal carapace; **B**, ULB-IV-A (39), right chela; **C**, ULB-IV-A (40), right chela; **D**, ULB-IV-A (38), dorsal carapace. Scale bars: 10 mm. Photographs by À. Ossó.

ABBREVIATIONS

L	carapace length;
W	carapace width;
FOW	fronto-orbital width;
H	maximum height (for chelae);
T	maximum thick (for chelae).

SYSTEMATIC PALAEONTOLOGY

Order DECAPODA Latreille, 1802
Infraorder ANOMURA MacLeay, 1838
Superfamily GALATHEOIDEA Samouelle, 1819
Family GALATHEIDAE Samouelle, 1819

Genus *Galathea*
Fabricius, 1793

TYPE SPECIES. — *Cancer strigosus* Linnaeus, 1761, by subsequent designation of Latreille (1810).

Galathea weinfurteri Bachmayer, 1950
(Fig. 3A, B)

Galathea weinfurteri Bachmayer, 1950: 135-137, pl. 1, figs 2-4; 1953a: 242-243, pl. 5, figs 3, 4, 6. — Müller 1974b: 276, pl. 1, fig. 4; 1984: 60, pl. 21, figs 4, 5, pl. 22, figs 1-5; 1996: 8. — Radwański *et al.* 2006: pl. 2, fig. 1. — Gatt & De Angeli 2010: 1326, pl. 2, fig. 4. — Ossó & Stalennuy 2011: text-fig. 3.7. — Collins 2014: 33-34, pl. 1, figs 3, 4. — Hyžný *et al.* 2014a: 243-247, text-fig. 2, pl. 1, figs 1-7, pl. 2, figs 1-8. — Hyžný 2016: text-fig. 10.F. — Hyžný & Dulai 2021: 126-128, fig. 44.1-14.

MATERIAL EXAMINED AND MEASUREMENTS (in mm). — One fragmentary carapace preserving only the central portion and part of right lateral, ULB-IV-A (9): L = 4; W = 6.5.

LOCALITY AND HORIZON. — 'Blandinerie' quarry, Breil (Maine-et-Loire). 'Savignean facies', Langhian (middle Miocene).

DESCRIPTION

Anterior portion of carapace transversely vaulted, crossed by transverse striae. Cervical and branchiocardiac grooves well

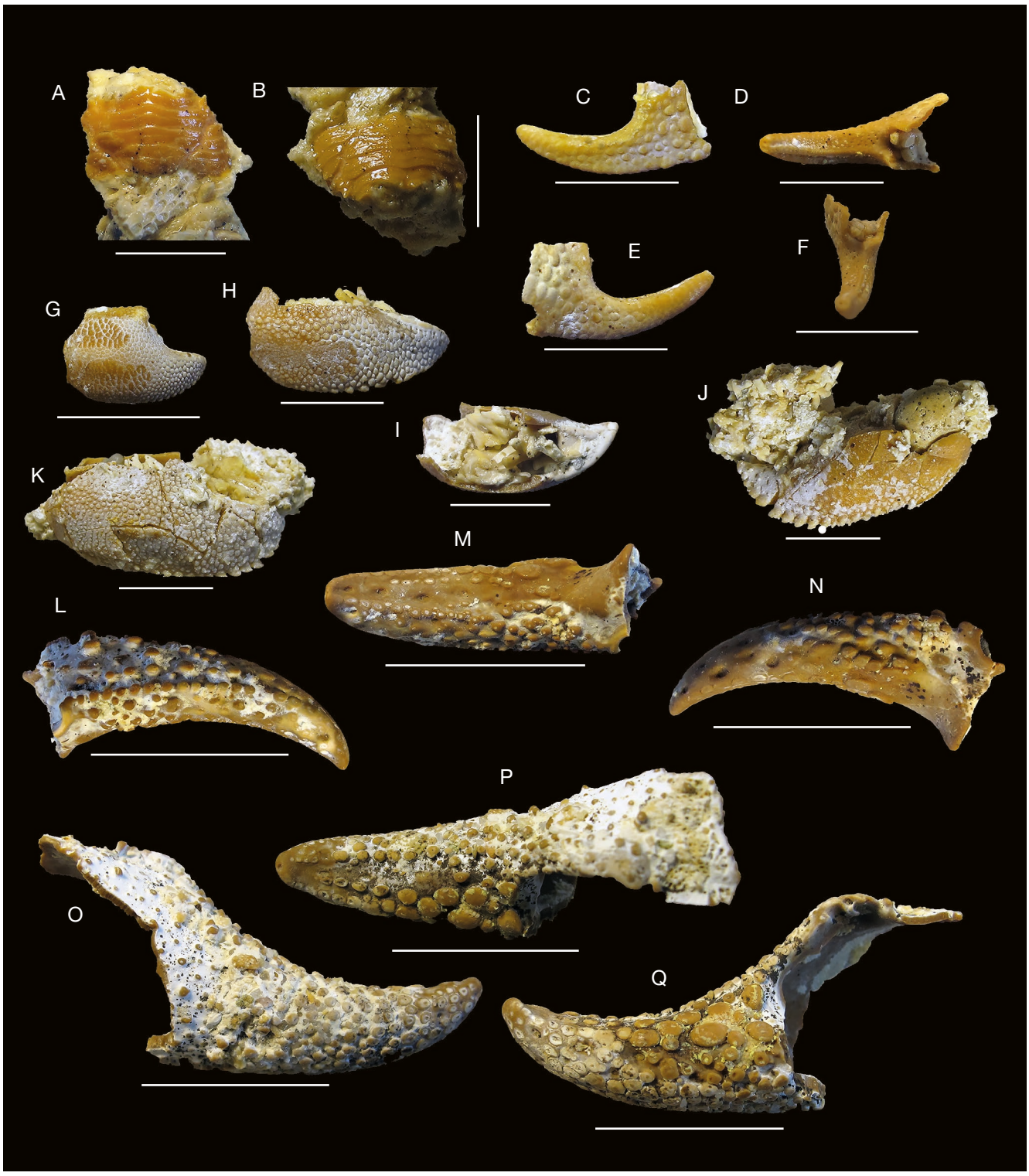

Fig. 3. — Decapods from the 'Savignean facies' (Langhian) of the 'Blandinerie' quarry, Breil (Maine-et-Loire): **A**, **B**, *Galathea weinfurteri* Bachmayer, 1950, ULB-IV-A (9): **A**, dorsal view; **B**, frontal view; **C**-**F** undetermined ?porcellanid; **G**-**K,** *Paguristes gagnaisoni* Gagnaison, 2012: **G**, ULB-IV-A (19), right chela; **H**, ULB-IV-A (19.2), right chela outer margin; **I**, occlusal margin; **J**, ULB-IV-A (17), right chela inner margin; **K**, right chela outer margin; **L**-**Q**, undetermined paguroid: **L**, ULB-IV-A (49), right dactylus outer margin; **M**, occlusal margin; **N**, inner margin; **O**, ULB-IV-A (44), left index, inner margin; **P**, occlusal margin; **Q**, outer margin. Scale bars: A-J, 5 mm; L-Q, 10 mm. Photographs by À. Ossó.

marked. Gastric region with sinuous and continuous main striae, raised, axially curved forward. Mesogastric region with secondary transverse striae between the main striae. Protogastric lobes weakly defined, at lower level that the axis. Epigastric striae sinuous, short. Hepatic region subtriangular. Epibranchial regions triangular, with two short

striae, defined by cervical groove anteriorly and branchial groove posteriorly. One hepatic spine and two epibranchial spines preserved.

Remarks

Despite of the fragmentary condition of the studied sample, lacking specific characters such as the rostrum, it conserves enough characters to assign it to *Galathea weinfurteri*. The set of continuous transverse striae and the position of the secondary ones, and the shape of the cervical groove and branchiocardiac groove, fit with the holotype figured by Bachmayer (1950: pl. 1, figs 2, 3) and subsequent works (see synonymies list above). Hyžný *et al.* (2014a: 244, pl. 1, figs 1-5) emended the original diagnosis and also depicted Bachmayer's images of the holotype. *Galathea weinfurteri* is by far the most widely distributed squat lobster in the Miocene of the Central Paratethys (Hyžný *et al.* 2014a: 254). This report extends the presence of this species in the Atlantic Coast of Europe.

Family ?Porcellanidae Haworth, 1825

Undetermined chela
(Fig. 3C-F)

Material examined and measurements (in mm). — Fragment of left chela preserving part of palm and index, ULB-IV-A (15): L = 8; H = 4; T = 3.

Locality and horizon. — 'Blandinerie' quarry, Breil (Maine-et-Loire). 'Savignean facies', Langhian (middle Miocene).

Description

Portion of palm preserved covered by coarse rounded granules, becoming squamous near the index; outer and inner margins slightly convex. Index slender, strongly curved upwards, slightly curved inwards, covered by squamous rounded granules; occlusal margin with acute cutting edge, not toothed.

Remarks

The slender and curved left index does not match with that of the squat lobster, usually spinose, neither with that of the porcellanids, such as the typical Miocene species of *Petrolisthes*, wich have more robust and straighter index (cf. Górka 2018: text-fig. 3, 4a-b, 6, 7, 8a-b). Notwithstanding, some extant species of *Pisidia* Leach, 1920, possesses pollex of left chela somewhat slender and curved. Lacking of complete specimens, we place this chela within Porcellanidae with reservations.

Superfamily Paguroidea Latreille, 1802
Family Diogenidae Ortmann, 1892

Genus *Paguristes* Dana, 1851

Type species. — *Paguristes hirtus* Dana, 1851, by subsequent designation of Stimpson (1858).

Paguristes gagnaisoni Gagnaison, 2012
(Fig. 3G-K)

Paguristes gagnaisoni Gagnaison, 2012: 69-71, figs 3-5.

Material examined and measurements (in mm). — One complete right chela, ULB-IV-A (19): L = 6; H = 4.5; T = 3. — Two incomplete right chelae ULB-IV-A (19.2): L = 11; H = 6; T = 5.5. ULB-IV-A (17): L = 12.5; H = 7; T = 7.

Locality and horizon. — 'Blandinerie' quarry, Breil (Maine-et-Loire). 'Savignean facies', Langhian (middle Miocene).

Description

Palm almost subtrapezoidal, slightly wider than high, thick, ovoid in section. Upper margin straight, ornated with a row of bluntly rounded granules; lower margin clearly convex, sharp-edged, armed with a row of raised tubercles, varying from blunt to pointed triangular forwardly directed giving a dentate aspect. Outer margin convex, densely covered by blunt granules of different sizes; inner margin strongly convex at the mid, smooth. Index inverted triangular in section, somewhat shorter than half the palm, gently curved inwards; outer occlusal margin with large flattened molariform teeth; inner occlusal margin with a row of smaller blunt teeth.

Remarks

Paguristes gagnaisoni was the first paguroid found and described from the 'Faluns' (Gagnaison 2012), albeit the presence of hermit crabs was already expected, in view of the findings of gastropod shells covered by bryozoans (Lecointre 1947). It was assigned to *Paguristes* by its similarity with the right chela of *P. santamartaensis* Feldmann, Tshudy & Thomson, 1993 (Paguridae Latreille, 1802) from the Upper Cretaceous of the Antarctica. It is assumed that the studied remains belong to the major chela.

The chela ULB-IV-A (17) (Fig. 3J, K), present an apparently different ornamentation in the lower half and distal part of its outer margin, formed by elongate and serrate granules, forming short terraces forward directed of squamous aspect, reminiscent of the ornamentation of some porcellanids chelae. However, this fragment of chela shows the same general features that *Paguristes gagnaisoni,* therefore it is tentatively left within this species.

Paguristes gagnaisoni presents strong similarities such as similar outline, strongly granulate surface, and dentate lower margin of palm, with *Anisopagurus leganyii* Müller, 1984 (Paguridae), from the middle Miocene of the Central Paratethys (Hungary), whose fossil decapods population has great affinities with the decapod population of the 'Faluns'.

Family and genus indeterminate
(Fig. 3L-Q)

Material examined and measurements (in mm). — One right dactylus, ULB-IV-A (49): L = 17; H = 6; T = 5. — One left index, ULB-IV-A (44): L = 25; H = 12; T = 7.

Locality and horizon. — 'Blandinerie' quarry, Breil (Maine-et-Loire). 'Savignean facies', Langhian (middle Miocene).

Description
Index elongate, stout, rounded in section except in the occlusal margin, which is flattened. Cuticle densely covered by rounded granules, larger in outer side. Small portion of palm appears largely concave laterally. Portion of upper margin, broad, flattened. Dactylus curved, proximally ornated with pointed granules, decreasing distally.

Remarks
Except *Paguristes gagnaisoni*, no other paguroid has been reported from the Miocene sediments of the 'Faluns'. Neither, no other paguroid species reported in the Miocene of the Mediterranean or the Central Paratethys, with which the Faluns shares great fauna affinity, shows morphological similarities with the studied dactylus and index. Comparison with recent paguroid taxa does not clarify their identity as well. The lack of a complete palm prevents us from making a generic and even familiar assignation of these remains.

Infraorder BRACHYURA Latreille, 1802
Section EUBRACHYURA de Saint Laurent, 1980
Subsection HETEROTREMATA Guinot, 1977
Superfamily Cancroidea Latreille, 1802
Family Cancridae Latreille, 1802

Genus *Lobocarcinus* Reuss, 1867

Type species. — *Cancer paulino-würtembergensis* von Meyer, 1847, by original designation.

Lobocarcinus sismondai (von Meyer, 1843)
(Fig. 4A-C)

Cancer sismondae von Meyer, 1843: 590.

Cancer punctulatus – Desmarest 1822: 92, pl. 7, figs 3-4.

Platycarcinus antiquus – Sismonda 1846: 58-60, pl. 3, figs 1, 2. — Meneghini 1857: 528, pl. H, fig. 11.

Platycarcinus sismondai – Vinassa de Regny 1896: 124-127, pl. 2, fig. 1 a, b.

Cancer deshayesii – A. Milne-Edwards 1864: 74-76, pl. 4, figs 1, 2, pl. 5, fig. 2. — Couffon 1908: 5, pl. 2, fig. 11. — Van Straelen 1927: 87, pl. 3, fig. 2, pl. 4, figs 1, 2.

Cancer sismondai – A. Milne-Edwards 1864: 76-78, pl. 6, figs 1, 1a, pl. 7, fig. 1. — Ristori 1886: 95-99, pl. 2, fig. 1. — Varola 1981: 16-26, pl. 3, figs 5, 6, pl. 4, figs 1, 2, pl. 5, figs 1, 2, pl. 6, figs 2, 4. — Bonfiglio & Donadeo 1982: 270-291, figs 5-27, pls 33-44. — Bonfiglio 1982: 5-18, figs 1-4, pls 1-7. — Vía Boada *et al.* 1982: 245-254, pl.1, figs 1-3, pl. 2, figs 1, 2. — Moissette & Müller 1990: 739, 740, pl. 1, fig. 1, pl. 2, figs 1, 2. — Beschin & Santi 1997: 13, fig. 2, pl. 1, figs 1, 2. — Garassino & Fornaciari 2000: 29, fig. 1.

Lobocarcinus sismondai – Reuss 1858: 41, pl. 9, figs 1, 2. — Garassino & De Angeli 2004: 42, 43, figs 9-11. — Ferratges 2017: 58, pl. 16, figs A-B. — Baldanza *et al.* 2017: 59, fig. 15B. — Górka 2018: 523-522, text-fig. 5.1, 5.2.

Lobocarcinus sismondae – Maestre *et al.* 2005: 107-108.

Lobocarcinus imperator – Reuss 1858: 41, pls 7, 8, pl. 9, fig. 1; Garassino, Hyžný & Pasini *in* Baldanza *et al.* 2013: 346, fig. 11.

Cancer sismondai var. *antiatina* – Maxia 1946: 134-147, fig. 1, pl. 1, figs 2-5.

Material examined and measurements (in mm). — One carapace almost complete, cuticle partially preserved, ULB-IV-A (3): L = 42; W = 59.5; FOW = 23.

Locality and horizon. — 'Noyant-la-Plaine' quarry, Doué-la-Fontaine (Maine-et-Loire), Tortonian (upper Miocene).

Description
Medium sized carapace, transversely ovate, clearly wider than long, gently convex transversely and longitudinally; regions weakly marked, axial regions more elevated; endocuticle preserved, exocuticle partially preserved; surface smooth. Maximum width about two thirds posteriorly of carapace. Front slightly raised and produced, armed with three sharp triangular teeth, the mesial one smaller, at lower level than the others. Orbits small, rounded, deep. Supraorbital margin raised; inner orbital tooth trifid, produced, adjacent to the frontal teeth; two pointed mesial teeth at higher level than the supraorbital teeth; closed fissures that ending in a small hole, separate these mesial teeth. Infraorbital margin concave, serrate, bearing an inner tooth, dorsally visible, coalescent with basal antennal article, fissure separating them is visible internally; and an outer tooth separated laterally from the outer orbital tooth by a notch. Anterolateral margins widely convex. Right margin preserves six subrectangular lobes bearing three triangular teeth, the mesial the larger; closed fissures that ending in a small hole separate the lobes. Left margin with not preserved lobes or teeth. Left posterolateral margin concave, bearing two post epibranchial teeth, subtriangular, serrated, decreasing in size; rest of the margin rimmed by a row of granules. Posterior margin short, broken, rim of granules partially preserved. Gastric process slightly swollen, faintly raised over adjacent regions. Mesogastric anterior lobe slender, at lower level than protogastric lobes; posterior portion of region broader, subtrapezoidal, undifferentiated from meta- and urogastric regions. Protogastric lobes swollen, anterior portion confluent with distal frontal and inner orbital teeth. Cardiac region subhexagonal, swollen. Intestinal region subrectangular, not well defined, narrower than cardiac region. Epi-, meso-, and metabranchial regions, slightly swollen, weakly differentiated. Hepatic regions subtriangular, slightly swollen. Sternopleonal features and appendages not preserved.

Remarks
The specimen of Noyant-la-Plaine, is herein attributed to *Lobocarcinus sismondai* with confidence. In despite of the partial incompleteness of its margins, it matches perfectly with the descriptions or figures seen in the literature (see synonymies list above). For instance, although the lateral margins are partially incomplete, it is possible to see the ten anterolateral lobes (included the outer orbital tooth), or scars of them, diagnostic character of the species as it is stated, in

particular in the description of A. Milne-Edwards (1864) or in the exhaustive and detailed work by Bonfiglio & Donadeo (1982) (see also the specimen MNHN.F.A24543).

Couffon (1908: 5, pl. 1, fig. 11), reported a palm of a left chela from Le Haguineau (Maine-et Loire), and assigned it to *Cancer deshayesii* (syn. of *Lobocarcinus sismondai*; cf. specimen MNHN.F.B39264). Ossó & Gagnaison (2019: 379, fig. 6G) in face of the absence of known carapaces of that species from the 'Faluns' outcrops, and neither in the Miocene of the Atlantic of Europe, left this chela tentatively as *Lobocarcinus* sp. in view of the similarity with the chelae of *L. sismondai*.

Lobocarcinus sismondai, is widespread in deposits from the Miocene to the Pleistocene in the Mediterranean Sea and related basins (see Garassino, Hyžný & Pasini *in* Baldanza *et al.* 2013: 346). However, in the Miocene of the Atlantic margin of Europe, *Lobocarcinus sismondai* it is reported based upon only isolated dactyli from the Miocene-Lower Pleistocene of the Netherlands (Holthuis 1949). Therefore, its presence in the Atlantic margin of Europe from the Miocene, is completely confirmed by the report of the carapace described herein.

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. 4D, E)

Hebertides jurassica Guinot, De Angeli & Garassino, 2007b: 241-260, figs 1-3. — Van Bakel *et al.* 2009: 80. — Taylor *et al.* 2012: 71-83, fig. 1. — Taylor 2012: 9-11, fig. 2. — Jagt *et al.* 2015: 882. — Emmerson 2017: 323. — Ossó & Gagnaison 2019: 372-373, fig. 3F-J. — Schweitzer & Feldmann 2019: 12, fig. 8.5.

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

Material examined and measurements (in mm). — Fragment of less than a left half of the carapace. ULB-IV-A (5): L = 19; W = 7.5.

Locality and horizon. — 'Blandinerie' quarry, Breil (Maine-et-Loire). 'Savignean facies', Langhian (middle Miocene).

Description
Left half of carapace longitudinally ovate, convex in both sections. Cuticle well preserved. Regions relatively well defined, slightly swollen and separated by weak, smooth grooves; medial regions faintly distinct. Dorsal surface of carapace covered by rounded granules at anterior half, grouped and aligned at posterior half. Orbit broad; inner orbital tooth blunt, as a fold; supraorbital margin sinuous, finely serrate, with two V-shaped fissures; outer orbital tooth triangular, acute, prominent. Supraorbital area slightly depressed, smooth. Anterolateral margin convex, with three granular teeth (excluding the extraorbital one); the third the smallest. Posterolateral margin slightly convex. Protogastric regions slightly swollen, with two tubercles obliquely aligned at each lobe. Hepatic region subtriangular, well delimited by cervical and hepatic groove. Branchial regions slightly swollen. Ventral parts and appendages not present.

Remarks
A complete specimen of *Hebertides jurassica* was reported by Ossó & Gagnaison (2019), which allowed a complete description of the species, and at the same time to confirm its Neogene age rather than Jurassic – as suspected (Taylor 2012; Taylor *et al.* 2012) –, and the area of origin of the holotype, which was unknown at that time. The material of *H. jurassica* herein studied confirms the geographical origin and Miocene age of this species.

Superfamily Leucosioidea Samouelle, 1819
Family Leucosiidae Samouelle, 1819
Subfamily Ebaliinae Stimpson, 1871

Genus *Ebalia* Leach, 1817

Type species. — *Ebalia bryerii* Leach, 1817, subsequent designation by Rathbun (1922).

'***Ebalia***' cf. ***hungarica*** Müller, 1974
(Fig. 4F, G)

'*Ebalia*' cf. *hungarica* Müller, 1974a: 121, 126, pl. 1, figs 5-7.

'*Ebalia*' *hungarica* – Müller 1984: 70, pl. 44, fig. 5, pl. 45, figs 1-5. — Hyžný & Dulai 2021: 171, figs 64.1-9.

Material examined and measurements (in mm). — One small carapace almost complete, with preserved cuticle, ULB-IV-A (7): L = 8.5; W = 7.5.

Locality and horizon. — 'Blandinerie' quarry, Breil (Maine-et-Loire). 'Savignean facies', Langhian (middle Miocene).

Description
Carapace small, subhexagonal slightly elongate, longer than wide, strongly convex longitudinally and transversely; regions strongly swollen, axially more elevated, well separated by grooves; whole carapace surface uniformly covered by close minute perliform granules. Front broken, but appears to be narrow and produced. Orbits not completely preserved, only the right orbit partially preserved, very close to the front; supraorbital margin raised, with medial tooth, separated from outer orbital corner by a closed fissure; outer orbital corner subtriangular in dorsal view; infraorbital margin visible in dorsal view, bearing a subtriangular distal tooth separated from the corner by a fissure. Anterolateral margin with prominent hepatic lobe. Posterolateral margin convex, rounded in section. A groove notching the margin separates both margins. Posterior margin short, appears to be bilobate, albeit only the right lobe in preserved. Meso-, meta-, and urogastric regions elevated, weakly differentiated. Protogastric lobes inflated,

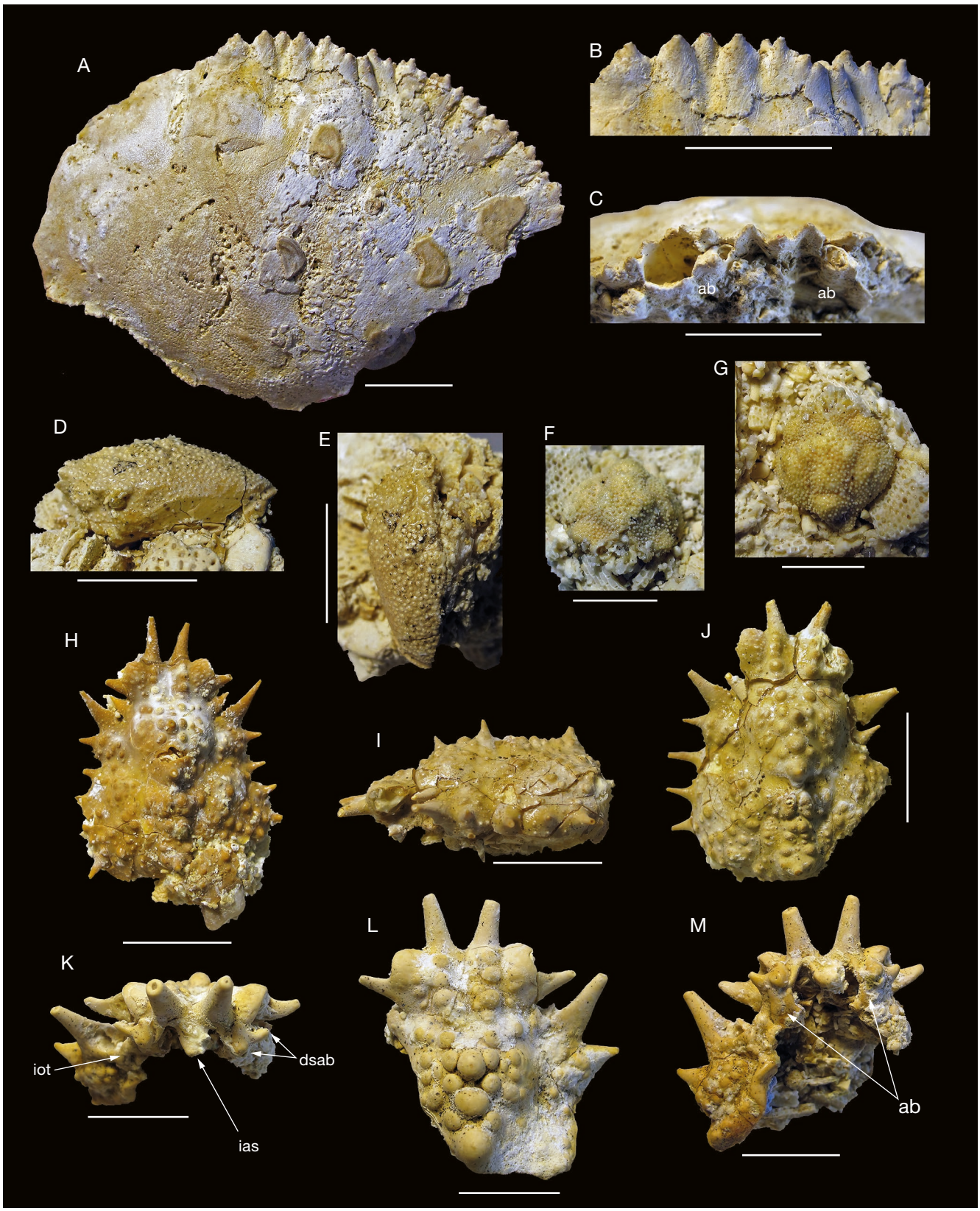

FIG. 4. — Decapod from the Tortonian of the 'Noyant-la-Plaine' quarry, Doué-la-Fontaine (Maine-et-Loire): **A**-**C**, *Lobocarcinus sismondai* (von Meyer, 1843), ULB-IV-A (3): **A**, dorsal view; **B**, close-up of front in dorsal view; **C**, close-up of front and orbits in frontal view. Decapods from the 'Savignean facies' (Langhian) of the 'Blandinerie' quarry, Breil (Maine-et-Loire): **D**, **E**, *Hebertides jurassica* Guinot, De Angeli & Garassino, 2007, ULB-IV-A (5): **D**, left lateral view; **E**, dorsal view; **F**, **G**, '*Ebalia*' cf. *hungarica* Müller, 1974a, ULB-IV-A (7): **F**, frontal view; **G**, dorsal view; **H**-**M**, *Maja orbignyana* Millet de la Turtaudière, 1865: **H**, ULB-IV-A (1), dorsal view; **I**, ULB-IV-A (2), left lateral view; **J** dorsal view; **K**, ULB-IV-A (23), frontal view; **L**, dorsal view; **M**, ventral view. Abbreviations: **ab**, basal antennal article; **dsab**, distal spines of basal article; **ias**, interantennular spine; **iot**, infraorbital tooth. Scale bars: A-E, H-M, 10 mm; F, G, 5 mm. Photographs by À. Ossó.

with central tubercle. Cardiac region rounded strongly raised. Intestinal region very short, depressed. Hepatic lobes strongly inflated. Branchial regions swollen, undifferentiated, with one central tubercle.

Remarks

This small carapace fits largely with the diagnosis and figures of '*Ebalia*' *hungarica* (see Müller 1974a: 121, 126, pl. 1, figs 1-5; 1984: 70, pl. 44, fig. 5, pl. 45, figs 1-5), in particular with the holotype. However, the French form appears to be more rounded and vaulted. A close examination of the type series, and additional material from the 'Faluns', would be necessary to stablish the conspecificity of both forms, and also to review the generic attribution of this species. Meanwhile, we place the 'Faluns' specimen tentatively as '*Ebalia*' cf. *hungarica*.

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. 4H-M)

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. — Ossó & Gagnaison 2019: 373, figs 4A-F.

Maïa orbigniana – Couffon 1910: 130, fig. 4.

Maia sp. – Vía 1932: 9.

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

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

Material examined and measurements (in mm) (length measurements taken from the basis of the pseudorostral spines). — Two complete carapaces, ULB-IV-A (1): L = 23; W = 17.5. — ULB-IV-A (2): L = 22.5; W = 17.5. — Five fragments of carapaces, ULB-IV-A (23): L = 22.5; W = 22. — ULB-IV-A (24): L = 21; W = 17. — ULB-IV-A (27): L = 22; W = 18. — ULB-IV-A (28): L = 17; W = 18. — ULB-IV-A (29): L = 22; W = 18.5.

Locality and horizon. — 'Blandinerie' quarry, Breil (Maine-et-Loire). 'Savignean facies', Langhian (middle Miocene).

Description

Carapace pyriform with spiny outline, longer than wide, strongly vaulted transversely; regions well defined, inflated; surface coarsely tuberculate except in the cervical and gastrohepatic grooves. Front narrow with two long, sharp and conical pseudorostral divergent spines. Orbits shallow, rounded, opened; supraorbital eave broad, strongly vaulted; antorbital spine sharp, laterally directed; intercalated spine subtriangular, short; postorbital spine the longer, sharp, conical, obliquely and slightly upwardly directed; suborbital tooth blunt. Hepatic spine short, laterally directed. Lateral margins with three sharp spines laterally directed. Frontal and epigastric regions defined by two rows of tubercles, separated by a shallow groove, that end at the base of the pseudorostral spines. Gastric process raised over the other regions. Proto-, meso- and metagastric regions strongly swollen, weakly differentiated between them; mesogastric lobe defined by longitudinal rows of coarse rounded tubercles, with medial spine; metagastric lobe with sharp spine; protogastric lobes sloping laterally, with scattered tubercles. Urogastric region transversely narrow, slightly swollen, with prominent tubercles; separated from metagastric lobe by cervical groove. Cardiac region swollen, rhomboidal elongate, prominent sharp central spine. Branchial regions strongly swollen, indistinct, sharp branchial spine upward and laterally directed at posterior part. Intestinal region not preserved. Hepatic region slightly swollen, ornate with rounded granules, the biggest ones at the basis of the hepatic spine. Interantennular spine prominent. Basal antennal article broad with two distal spines.

Remarks

Two almost complete small carapaces, and remains of anterior pars of carapace of five larger specimens, allows us to attribute them all with confidence to *Maja orbignyana* (cf. Couffon 1908: figs 1, 2, 4). Likewise, the new material preserves elements not described previously such as, some cephalic appendages and frontal spines, which allows a more detailed description of the species (Fig. 4K, M). A clear distinction between *Maja orbignyana* and *M. biaensis* Lőrenthey *in* Lorenthey & Beurlen, 1929, can be established not only by the strong, rounded and raised tubercles in the protogastric lobes and hepatic regions in the former (see Müller 1993: 13), but also by the more distinct branchial regions in the latter (see Müller 1993: pl. 48, figs 1-6, t. 49, fig. 1). The general shape and the conformation of the regions of *Maja orbignyana*, strongly recalls those of the extant *M. crispata* Risso, 1827, which, like the fossil species, inhabits the Mediterranean and the Atlantic coast of Europe (e.g. Ng & Richer de Forges 2015: 126-127, fig. 6A-B).

Family and genus indeterminate
(Fig. 5A)

Material examined and measurements (in mm). — Remains of a central portion of dorsal carapace, ULB-IV-A (26): L = 10; W = 13.

Locality and horizon. — 'Blandinerie' quarry, Breil (Maine-et-Loire). 'Savignean facies', Langhian (middle Miocene).

Description

Central portion of dorsal carapace, strongly vaulted, regions defined by inflations with tubercles and coarse granules, well divided by grooves. Mesogastric region with posterior portion subpentagonal bearing a large and prominent granulate tubercle, anterior portion elongate and narrow, bearing a tubercle medially. Protogastric lobe swollen posteriorly, with

scattered coarse granules and small tubercles. Urogastric region depressed, defined by two transverse rows of rounded granules, two the anterior one and four the posterior one. Cardiac region large, swollen, with large rounded granules. Epibranchial lobes well differentiated, prominent, with coarse granules and small tubercles, obliquely directed to the anterolateral margin. Cervical and branchiocardiac grooves well marked, smooth, the latter the deeper.

Remarks

It's difficult to assign this fragmentary remain to a known fossil crab. Nonetheless, its regions conformation is reminiscent of majids, in particular the ornamentation and the strong constrictions at the urogastric-cardiac level. For instance, it strongly recalls *Micippa hungarica* Lőrenthey in Lőrenthey & Beurlen, 1929 (cf. Müller 1984: pl. 52, figs 4-6, pl. 53, figs 1-4; Hyžný & Dulai 2021: fig. 67.1-6). However, the absence of other carapace portions, prevent us from assigning this remain to any genera or family. or family. Thus, we place it within Majoidea, with reservations.

Superfamily Parthenopoidea MacLeay, 1838
Family Parthenopidae MacLeay, 1838
Subfamily Parthenopinae MacLeay, 1838

Genus *Derilambrus* Tan & Ng, 2007

Type species. — *Cancer longimanus* Linnaeus, 1758, subsequent designation by Rathbun (1904).

Derilambrus cf. ***szaboi*** (Müller, 1974)
(Fig. 5B-E)

Parthenope szaboi Müller, 1974b: 277, 283, pl. 1, figs 8-9; 1976b: 152, pl. 4, fig. 2; 1984: 74, pl. 53, fig. 5, pl. 54, figs 1-9.

Derilambrus szaboi – Hyžný & Dulai 2021: 190, 191, figs 72.1-10.

Material examined and measurements (in mm). — Three right propodi, ULB-IV-A (33): L = 14, H = 5.5, T = 3.5; ULB-IV-A (34): L = 15.5, H = 5.5, T = 4. — One left propodus ULB-IV-A (35): L = 13, H = 7.5, T = 6. — Two merus, ULB-IV-A (32): L = 9.5, H = 3, T = 4; ULB-IV-A (36): L = 16, H = 6, T =5.

Locality and horizon. — 'Blandinerie' quarry, Breil (Maine-et-Loire). 'Savignean facies', Langhian (middle Miocene).

Description

Propodus long, subtriangular in cross-section, acute edges; upper margin armed with acute spines irregularly placed; lower margin bearing a continue row of granules or spines; outer margin with a transverse row of continuous acute spines; inner margin coarse granulate, with a medial row of granules; index short, obliquely downward directed. Merus elongate, subrhomboidal in section, lateral angles coarsely spiny.

Remarks

The 'Faluns' parthenopid chelae are reminiscent of those attributed to *Derilambrus szaboi*, from several localities of the middle Miocene of Hungary (see Müller 1984: pl. 54, figs 6-9; Hyžný & Dulai 2021: fig. 72.7-10), and in lesser extend of those of *Parthenopoides tetenyensis* (Müller, 1984), which are shorter than the former species (Müller 1984: 74-75, pl. 66, fig. 3; Hyžný & Dulai 2021: fig. 71.6-15). The 'Faluns' chelae have been found isolated, and no carapace attributable to Parthenopidae has been recovered in those outcrops to date, and moreover, it's hard to assign an isolated chela to a carapace of any particular species. However, despite the poor degree of preservation of the 'Faluns' parthenopid chelae, which are strongly reworked, they still preserve some main characters that allow to check the similarities with the chelae described as *Derilambrus szaboi,* to which, they are assigned tentatively.

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

Genus *Pilumnus* Leach, 1815

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

Pilumnus mediterraneus (Lőrenthey, 1897)
(Fig. 5F-K)

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; 1984: 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. — Ossó & Gagnaison 2019: 373, 374, fig. 4G-L. — Hyžný & Dulai 2021: 192-194, fig.73.1-6.

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). — Six complete dorsal carapaces with cuticle well preserved, ULB-IV-A (4) L = 8, W = 9, FOW = 7; ULB-IV-A (8): L = 6.5, W = 8, 8, FOW = 6.5; ULB-IV-A (14): L = 11, W = 14.5, FOW = 10.5; ULB-IV-A (18): L = 8.5, W = 11, FOW = 8; ULB-IV-A (37): L = 10, W = 13, FOW = 11; ULB-IV-A (38): L = 7.5, W = 9.5, FOW = 7. —Two right chelae, ULB-IV-A (39): L = 12.5, H = 6; ULB-IV-A (40): L = 11, H = 7. — One left chela, ULB-IV-A (20): L = 25.5, H = 11.5, T = 7.

Locality and horizon. — 'Blandinerie' quarry, Breil (Maine-et-Loire). 'Savignean facies', Langhian (middle Miocene).

Description

Carapace relatively small, 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 serrate, 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 elongate 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 pleonal features not preserved. Right chela stout, palm slightly wider than high, 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 chela length; dactylus curved with blunt teeth in occlusal margin; index 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

As pointed out by Ossó & Gagnaison (2019: 380), the decapods population of the 'Faluns' appears clearly dominated by *Pilumnus mediterraneus*, as the new collection of decapods from the 'Blandinerie' quarry also confirms. This species, represented usually by undetermined cheliped remains in the 'Faluns' outcrops, was confirmed as such by the report of two complete dorsal carapaces (Ossó & Gagnaison 2019: 373-374, figs 4G-J). In the same text, the authors suggested that the type of *Haydnella pulchellus*, figured in A. Milne-Edwards (1863: pl. 9, figs 2, 2a, as *Titanocarcinus pulchellus*) was likely a specimen of *P. mediterraneus,* based upon the drawings of the holotype, which is lost (see Couffon 1908: 1), and on the description of it (see A. Milne-Edwards 1864: 33, 34). A careful reading of the French text of the description, reveals details such as: "*La surface est ornée, sur toutes ses parties, de petites granulations, qui sont plus nombreuses près des bords* [...] *Les régions branchiales sont décomposées en leurs lobes antérieurs, moyens et postérieurs, par des sillons peu profonds*" (The surface is adorned in all its parts with small granulations, which are more numerous near the edges [...] The branchial regions are decomposed into their anterior, middle and posterior lobes, by shallow furrows), characters that are more typical, for instance, of *Xantho moldavicus,* whose presence in the 'Faluns' is confirmed herein (see below), rather than of *Pilumnus mediterraneus*. Thus, it is plausible that the holotype was in fact, a small sample either of *Pilumnus mediterraneus* or *Xantho moldavicus* instead of a third species. In any case, the continuity of *Haydnella pulchellus* as a valid taxon, based on a lost holotype and two schematic drawings, appears problematic now, and should be considered as *nomen nudum*.

Superfamily Portunoidea Rafinesque, 1815
Family Carcinidae Macleay, 1838

Subfamily and genus indeterminate
(Fig. 5L, M)

Material examined and measurements (in mm). — One right chela, ULB-IV-A (52): L = 30; H = 16; T = 11. — One left chela, ULB-IV-A (50): L = 20; H = 10.5; T = 6.5.

Locality and horizon. — 'Blandinerie' quarry, Breil (Maine-et-Loire). 'Savignean facies', Langhian (middle Miocene).

Description

Palm stout, subtrapezoidal, longer than high, higher distally; subhexagonal elongate in cross section; surface coarsely granulate; upper margin straight, flattened, with keeled lateral angles, scar of spinule at inner distal corner, over the dactylus insertion; outer margin convex, with two transverse keels, one at halfway up of palm, the second below, near the lower margin and continues along the index; inner margin convex medially, with two transverse weak keels; lower margin slightly convex, flattened, rounded lateral angles. Index straight, slightly concave proximally, keeled, occlusal margin with serial conical teeth.

Remarks

The two chelae described herein exhibit the typical long and keeled 'portunid' shape, but no 'portunid' carapace to which they can be related has been found in the 'Faluns'. Strictly, although both chelae possess very similar construction and ornamentation, we cannot affirm that they are conspecific. Despite this, the absence of spines in their upper margin, mainly at the proximal articulation with carpus, discards their affinities with Portunidae *s.s.* (Spiridonov *et al.* 2014: 423). Nevertheless, the general shape of that chelae, shorter as in Portunidae, and the "lacking spines except for a distal spinule on upper face of manus", exactly in the inner distal corner over the dactylus insertion, is characteristic for

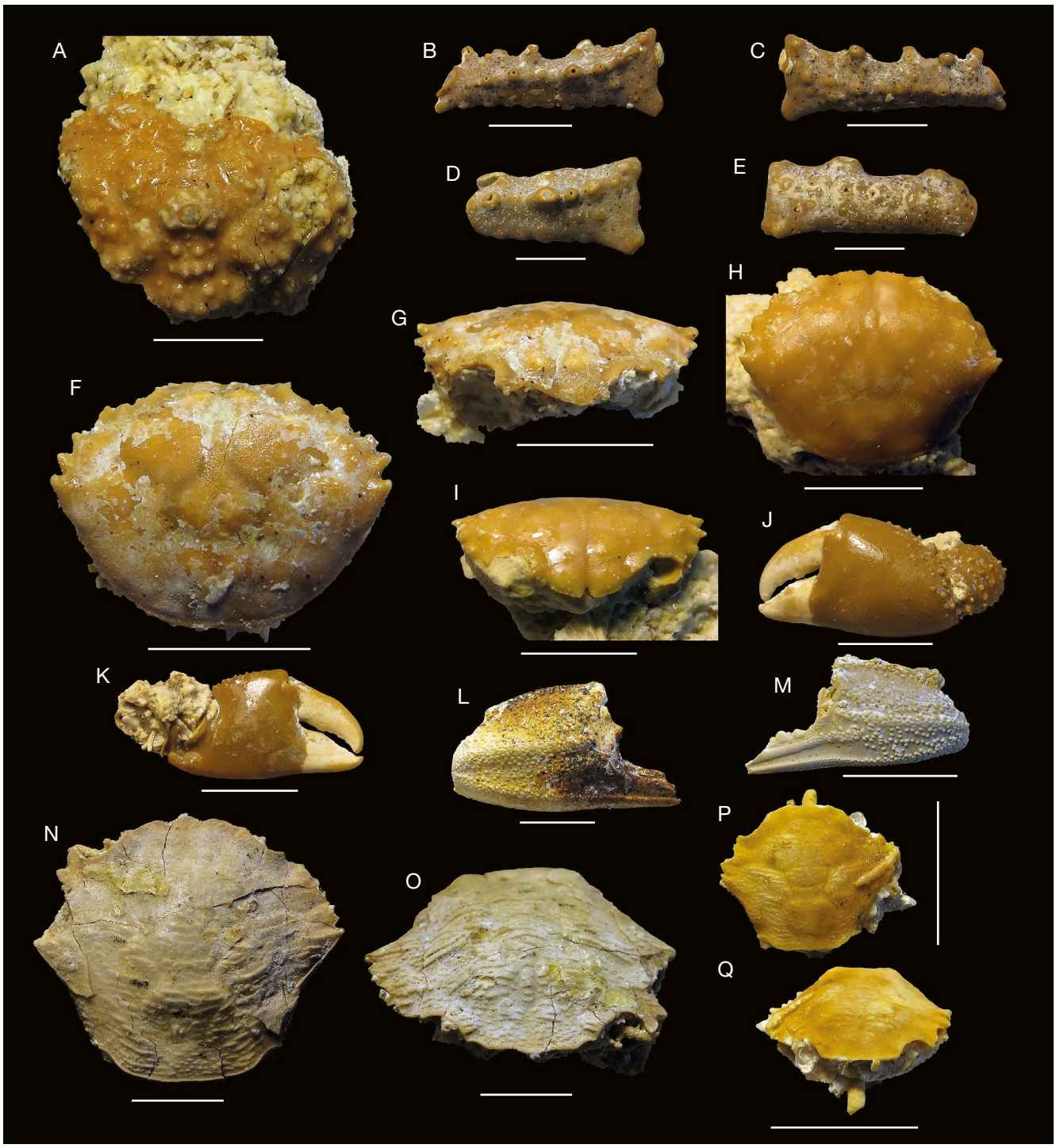

Fig. 5. — Decapods from the 'Savignean facies' (Langhian) of the 'Blandinerie' quarry, Breil (Maine-et-Loire): **A**, indeterminate majoid, ULB-IV-A (26): dorsal view; **B**-**E**, *Derilambrus* cf. *szaboi* (Müller, 1974): **B**, ULB-IV-A (33), right propodus, outer margin; **C**, inner margin; **D**, ULB-IV-A (35), right propodus, outer margin; **E**, right propodus, inner margin; **F**-**K**, *Pilumnus mediterraneus* (Lőrenthey, 1897): **F**, ULB-IV-A (14), dorsal view; **G**, frontal view; **H**, ULB-IV-A (18), dorsal view; **I**, frontal view; **J**, ULB-IV-A (20), left chela, outer margin; **K**, inner margin; **L**-**M**, undeterminated Carcinidae: **L**, ULB-IV-A (52), right chela; **M**, ULB-IV-A (50) left chela; **N**-**Q**, *Liocarcinus kuehni* (Bachmayer, 1953a): **N**, ULB-IV-A (10), dorsal view; **O**, frontal view; **P**, ULB-IV-A (13), dorsal view; **Q**, frontal view. Scale bars: A-I, N-Q, 5 mm; J-M, 10 mm. Photographs by À. Ossó.

the Carcinidae, and for at that time considered full family Polybiidae, now subfamily of Carcinidae (Spiridonov *et al.* 2014: 422).

In view of the aforementioned, we assign both chelae to Carcinidae, which in fact, as seen below, has representatives in the 'Faluns' such as *Liocarcinus* spp., albeit the small size of the specimens available prevent us from relating them at a generic or specific level with confidence.

The two fragments of dactyli attributed by Couffon (1908: 2, pl. 1, fig. 5) to *Neptunus* aff. *monspeliensis* A. Milne-Edwards, 1861 (sic), could likely belong to the chelae of Carcinidae species such as the described herein.

Subfamily Polybiinae Ortmann, 1893

Genus *Liocarcinus* Stimpson, 1871

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

Liocarcinus kuehni (Bachmayer, 1953)
(Fig. 5N-Q)

Portunites kühni Bachmayer, 1953a: 249-251, pl. 2, fig. 2. — Karasawa 1990: 17.

Liocarcinus kuehni – Müller 1984: 84, pl. 71, figs 2, 3. — Hyžný *et al.* 2015: 226. — Hyžný & Dulai 2021: 208, fig. 80.14.

Material examined and measurements (in mm). — Two dorsal carapaces, ULB-IV-A (10): L = 15, W = 17, F = 7, FOW = 12. — ULB-IV-A (13): L = 6, W = 6.5, F = 3, FOW = 5,5.

Locality and horizon. — 'Blandinerie' quarry, Breil (Maine-et-Loire). 'Savignean facies', Langhian (middle Miocene).

Description

Small sized carapace, subhexagonal, slightly wider than long; carapace surface covered by transverse rows of minuscule granules forwardly directed, forming terraces of different sizes. Regions weakly defined. Front gently trilobate, edge finely serrate, medial tooth slightly more advanced than the lateral teeth. Orbits relatively large; supraorbital margin arched, finely serrate, with two closed fissures, first at mid length second near outer orbital tooth; inner orbital tooth blunt; outer orbital tooth broad subtriangular, forwardly directed; infraorbital margin not preserved. Anterolateral margin slightly arcuate, with four subtriangular teeth (excluding the outer orbital tooth), the latest (epibranchial tooth) the sharper. Posterolateral margin slightly concave; anterior half sharp edged, with serrate keel; posterior half blunt edged; reentrant of fifth pereiopod well marked, gently concave. Posterior margin slightly convex, finely rimmed. Frontal region flattened. Gastric process poorly defined. Epigastric lobes slightly marked. Protogastric lobes slightly swollen. Mesogastric region weakly marked, very narrow anteriorly, subrhomboidal posteriorly, slightly elevated above the rest of regions. Metagastric region faintly defined. Urogastric region slightly depressed. Cardiac region broad, swollen anteriorly. Intestinal region depressed. Hepatic region depressed. Epibranchial region sigmoidal, interrupted medially, defined by long terraces, and a sharp ridge distally that ends in the epibranchial tooth. Mesobranchial region slightly swollen internally. Metabranchial region depressed. Cervical groove faintly marked. Branchiocardiac groove weakly marked. Ventral parts and appendages not preserved.

Remarks

The dorsal morphology of the two samples of decapods described herein correspond exactly with the holotype of *Liocarcinus kuehni* from the upper Miocene of Austria, described and depicted as *Portunites kühni* by Bachmayer (1953a: 249-251, pl. 2, fig. 2) (see also Müller 1984: 84, pl. 71, figs 3, 4). The carapace outline, same number and shape of anterolateral teeth, shape of the orbits, similar size, and in particular the squamous carapace surface formed by transverse terraces of different sizes, in despite that the holotype and paratypes does not preserve the front, allows to consider the 'Faluns' specimens conspecific of *Liocarcinus kuehni* with confidence.

Strikingly, the dorsal carapace, the only part preserved of our specimens and of Bachmayer's types, seems identical to that of the extant *Liocarcinus corrugatus* (Pennant, 1777). However, they apparently differ in having a much smaller size than the extant species. In this respect, it is interesting to know that molecular analyses by Plagge *et al.* (2016), concluded that the European and the Asian populations of *Liocarcinus corrugatus*, only separated morphologically by subtle dorsal and penial differences, are in fact two genetically separated species, as the results of their analyses demonstrated, thus recognizing the Asian population as *L. strigilis* Stimpson, 1858. In view of that, and given the scarce number of specimens of the fossil form, the two samples herein studied, and the three Bachmayer's samples seen by Müller, is not sufficient to infer that *Liocarcinus kuehni* is the same species that *L. corrugatus*. In addition, Plagge *et al.* (2016: 386) suggested that both extant species are relict of a former range of the eastern Tethys Ocean", *Liocarcinus kuehni* would confirm it.

Ossó & Gagnaison (2019: 374-376, fig. 5A-B) reported and described a specimen from the 'Faluns' as *Liocarcinus* sp., and compared it with all the known fossil forms of *Liocarcinus*. However, it was left in open nomenclature due to its poor preservation and the sole available specimen. Now, compared with the two new specimens of *Liocarcinus kuehni*, it still appears to be different. Its smooth carapace surface could be due to the reworking, but the specimen of *Liocarcinus kuehni* ULB-IV-A (13) (Fig. 5P, Q) although it is also strongly worn, it retains still the terraces in the carapace, absent in *Liocarcinus* sp. In addition, the three characteristic tubercles, longitudinally aligned three tubercles at both sides of carapace that *Liocarcinus* sp. exhibits, are not present, or at least not interpreted as such, in the specimens of *L. kuehni* described herein. Consequently, we retain the former in open nomenclature.

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. 6A-C)

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. — Ossó & Gagnaison 2019 : 376-378, fig. 5C-D.

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

MATERIAL EXAMINED AND MEASUREMENTS (in mm). — Ventral carapace preserving chelipeds MHNH-2016-79-2003, W (from carpus to carpus) = 150. — Right dactylus, ULB-IV-A (51): L = 41.5, H = 16. — Right dactylus ULB-IV-A (41): L = 20, H = 9.5. — Fragment of right epibranchial portion of dorsal carapace bearing two last anterolateral teeth, ULB-IV-A (42): L = 17.5, W = 9.5.

LOCALITY AND HORIZON. — 'La Sonneterie' quarry, Meigné-le-Vicomte (Maine-et-Loire). 'Savignean facies', Langhian (middle Miocene): MHNH-2016-79-2003 and ULB-IV-A (51); and, 'Blandinerie' quarry, Breil (Maine-et-Loire). 'Savignean facies', Langhian (middle Miocene): ULB-IV-A and ULB-IV-A (42).

DESCRIPTION (EMENDED)

Large ventral carapace preserving sternum and chelipeds, surface smooth. Sternum relatively large, flattened, maximum width at level of sternite 6. Sternite 2 subtriangular; sternite 3 inverted subpentagonal; sternite 4 subtrapezoidal; sternite 5, 6 and 7 subrectangular transversely elongate, distal margin rounded; sternite 5 placed in acute angle respect the axis of sternum, sternite 6 almost in right angle, and sternite 6 in slightly obtuse angle. Episternites posteriorly directed. Suture 2/3 complete, horizontal; suture 3/4 inverted V-shaped, weakly distinguishable, only laterally. Sutures 4/5, 5/6, and 6/7 appear complete. Pleon not preserved. Sternopleonal cavity deep, narrow, almost reaching suture 3/4. Pterygostome subtrapezoidal elongate. Ischium of third maxilliped large, with medial longitudinal groove, inner margin strongly convex; exopod subrectangular elongate, narrower than ischium. Chelipeds strong, slightly heterochelous. Merus robust, subtriangular in section, outer margin strongly vaulted, wider at mid length. Carpus strong, embedded in matrix. Right chela strong, dactyli curved distally; palm about 0.70 of length of chela, subtrapezoidal, longer than high, higher distally; upper margin rounded, slightly convex; lower margin rounded, straight; outer margin strongly convex, smooth; dactylus stout, gently curved forward, strong proximal knobstick molariform tooth followed by six serial rounded conical teeth of different sizes, and rounded tip; index stout straight with rounded tip, strong flattened proximal molariform tooth, followed by three blunt teeth. Left chela strong, elongate, slightly shorter than right chela, dactyli gently curved distally; palm subrectangular, longer than high, about 0.68 of length of chela, upper and lower margins straight, rounded, outer margin strongly convex; cutting edge of dactyli with serial conical teeth.

REMARKS

Erected by A. Milne-Edwards (1861), to place fragmentary large chelipeds found in the 'Faluns', *Necronectes michelini*, was originally placed within *Scylla* De Haan, 1833 due to its similarity to the strong chelipeds of the extant *S. serrata* (Forskål, 1775), albeit the author already considered the differences between the chelae of both species such as the rounded upper margin of palms, which are flattened and angled in *Scylla* spp., and the absence in *N. michelini* of the two typical distinct spines on the distal upper part of the palm, near the insertion of dactylus (see Fig. 6B; Couffon 1908: pl. 1, figs 6-10, t. 2, figs 1, 2; MNHN.F.B25950), which are usually present in *Scylla* spp. (e.g. Keenan *et al.* 1998; Trivedi & Vachhrajani 2013; Vincecruz-Abeledo & Lagman 2018). Glaessner (1933: 5), included *S. michelini* within *Necronectes* A. Milne-Edwards, 1881, in view of the similarities of the chelae of both taxa. Subsequent authors assigned this species indistinctly to both genera, *Scylla* and *Necronectes*, as explained in Ossó & Gagnaison (2019: 376-378, and references therein). Since the chelipeds of the studied specimen are identical to the type series MNHN.F.B25950 described by A. Milne-Edwards (1861), the conspecificity between them is beyond doubt.

For the first time, a specimen of *Necronectes michelini* preserving features other than the chelipeds, is available for study, although important diagnostic features, such as the dorsal carapace is not preserved. Nevertheless, the sternum of the studied specimen fits well with the sternums of other representatives of *Necronectes*, such as *N. proavitus* (Rathbun, 1918) and *N. schafferi* Glaessner, 1928 (e.g. Rathbun 1918: pl. 55; De Angeli & Berti 2017: fig. 2, 1b).

The absence of specimens formally available for study with the preserved dorsal carapace, although some of them are known in private collections (e.g. Gagnaison *et al.*, 2020: fig. 2A), prevents us from going further in our considerations. For instance, to explore the possible conspecific relationship between the circum-Mediterranean and Paratethyan Miocene species of *Necronectes*, such as *N. schafferi* and *N. batalleri* (Vía, 1941), almost identical morphologically, and *N. michelini* (cf. Vía 1941: figs 3, 4, pl. 5, figs 31, 32, pl. 6, figs 33, 34; De Angeli & Marangon 1992: pl. 1, figs 1, 2, pl. 2, figs 1a, 1b; Ferratges 2017: fig. 43, pl. 29, fig. C).

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 moldavicus (Yanakevich, 1977)
(Fig. 6D-G)

Medaeus moldavicus Yanakevich, 1977: 80, pl. 10, fig. 4.

Titanocarcinus pulchellus Couffon, 1908: 4-5, pl. 2, fig. 6, text-fig. unnumbered p. 4.

Titanocarcinus vulgaris Glaessner, 1928: 185, pl. 3, figs 9-11. — Bachmayer 1953b: 254, pl. 4, figs 1-9, pl. 6, figs 1-2.

Xantho cfr. *X. incisus* – Müller 1974a: 123, pl. 3, figs 1-2; 1979: 274, pl. 20, figs 1-5.

Xantho cf. *X. vulgaris* – Förster 1979: 263-264, pl. 5, fig. 4.

Xantho moldavicus – Müller 1984: 92, figs 5-8, pl. 86, figs 1-5, pl. 87, fig. 1.

Xantho cf. *moldavicus* – Friebe 1987: 61, pl. 2, fig. 5.

Xantho moldavicus – Vía 1988: 351. — Solé & Via 1989: 35. — Marras & Ventura 1991: 110, pl. 2, fig. 2. — Müller 1996: 11, pl. 2 fig. 6; 1998: 34. — Radwański *et al.* 2006: 96, pl. 2, figs 5, 6. — Gatt & De Angeli 2010: 1339, figs 8G-K. — De Angeli *et al.* 2011: 114-115, fig. 6. — Ossó & Stalennuy 2011: 37, figs 3.11-12, 9.1-2. — Górka *et al.* 2012: 171, fig. 21D. — Hyžný *et al.* 2014b: 226, pl. 1, fig. 6. — Górka *in* Wysocka *et al.* 2016: 379, fig. 14F-G. — Hyžný 2016, text-fig. 14F, G. — Ferratges 2017, pl. 33, fig. B. — Górka 2018: 528-529, text-fig. 8.3-8.4a-b. — Hyžný & Dulai 2021: 245-247, figs 98.1-11.

Material examined and measurements (in mm). — One almost complete carapace, ULB-IV-A (6): L = 9.5, W = 14, FOW = 8.5. — Right half of carapace, ULB-IV-A (11): L = 14.5, W= 12.

Locality and horizon. — 'Blandinerie' quarry, Breil (Maine-et-Loire). 'Savignean facies', Langhian (middle Miocene).

Description

Carapace transversely subhexagonal, regions well marked, surface rugose; ratio length/width about 0.67. Front straight, bilobed, medial notch, edges granulated. Orbits complete, small, rounded, forwardly directed; supraorbital margin finely granulate with two fissures, one of them medially placed, the other close to the outer-orbital tooth; inner orbital tooth acute triangular, separated from the frontal lobe by a deep notch, outer orbital tooth blunt triangular; infraorbital margin, visible dorsally, finely granulate ends in a produced tooth. Ratio fronto-orbital margin/width about 0.60. Anterolateral margin bearing four subtriangular teeth with serrated margins, the fourth the smaller. Posterolateral margins straight, rounded in section. Posterior margin incomplete, rim of small granules. Frontal region divided medially by groove. Protogastric region swollen, anterior portion of lobes divided medially, the inner part confluent with epigastric lobes. Mesogastric region slightly swollen, slender anteriorly, broader rhomboidal posteriorly. Metagastric region not differentiated from mesogastric region. Urogastric region very narrow, separated from meso- metagastric by a groove with two gastric pits visible. Cardiac region broadly T-shaped, slightly swollen, laterally confluent with metabranchial lobes. Intestinal region narrow, transversely swollen, medially depressed. Epibranchial region transversely elongate, sigmoidal, bearing three lobes, the inner one smaller, the medial is separated from the distal lobe that ends at the epibranchial tooth, by an oblique groove. Mesobranchial region short, laterally placed, confluent with the distal lobe of epibranchial lobe. Metabranchial region broad, swollen, separated from epi- and mesobranchial regions by transverse grooves. Hepatic region slightly swollen. All regions covered by granules or rows of granules giving a rugose or squamous aspect. Cervical, branchiocardiac and accessory grooves delimiting regions and lobes well marked but shallow, smooth. Sterno-pleonal elements and appendages not preserved.

Remarks

Ossó & Gagnaison (2019: 378, figs 5F-I), reported two left chelae likely referable to *Xantho moldavicus*, but without carapace remains, they left them in open nomenclature. Likewise, they suggested that the specimen figured by Couffon (1908: t. 2, fig. 6, text-fig. unnumbered), from Doué-la-Fontaine, could actually be a sample of *Xantho moldavicus*, which is confirmed by the new materail herein described, which fits perfectly with the carapaces described and depicted in the literature (e.g. Yanakevich 1969: pl., fig. 6; Müller 1984: pl. 86, figs 1-2, 4, pl. 87, fig. 1; Ossó & Stalennuy 2011: fig. 3, 11-12; Górka 2018: text-fig. 8.3, 4a-b).

Xantho moldavicus is widely present in middle/upper Miocene outcrops of the Central Paratethys and the Mediterranean (see Górka 2018: 530 and references therein). The occurrence of *Xantho moldavicus* in the Miocene of the 'Faluns', extends the presence of this species to the northeastern Atlantic waters, in a similar palaeogeographic distribution and environments of the extant representatives (e.g. Drach & Forest 1953; Reuschel & Schubart 2006)

Undetermined cheliped
(Fig. 6H-J)

Cancer sismondae – Couffon 1908: 5, pl. 2, figs 3-4.

Eriphia? sp. – Glaessner 1933: 6-7, pl. 1, fig. 2.

Undetermined cheliped – Ossó & Gagnaison 2019: 378-379, fig. 6E-F.

Material examined and measurements (in mm). — One left cheliped with complete propodus and dactyli, and carpus attached, MNHN.F.B39266: (palm) L = 65.3, H = 31.55, T = 15.80.

Locality and horizon. — Doué-la-Fontaine (Maine-et-Loire), probable Tortonian.

Description

Palm subtrapezoidal, robust, wider than high, higher distally. Outer side convex, surface smooth, five transverse rows of weakly marked spaced spines more pointed proximally. Inner side slightly convex, smooth. Upper margin flattened, with rounded edges, with two rows of spaced spines, irregularly aligned. Lower margin slightly convex, rounded. Dactyli about one third of the length of the chela. Dactylus gently curved with strongly curved spooned tip; upper margin spiny proximally; occlusal margin with four weakly prominent blunt teeth. Index robust, with rounded lower margin; occlusal margin, longitudinally depressed with spooned tip, with three blunt teeth in the outer edge. Carpus rounded subtriangular, robust, surface smooth; armed with spaced spines placed irregularly; inner angle with a prominent spine, and a second spine placed below.

Remarks

Couffon (1908) reported this large left cheliped for the first time and attributed it to *Lobocarcinus sismondai* (as *Cancer sismondae*). Subsequently, Glaessner (1933) examined the cheliped and an additional right chela and discarded its belonging to *Cancer*, based on the absence of a cutting-edge in that cheliped, point-

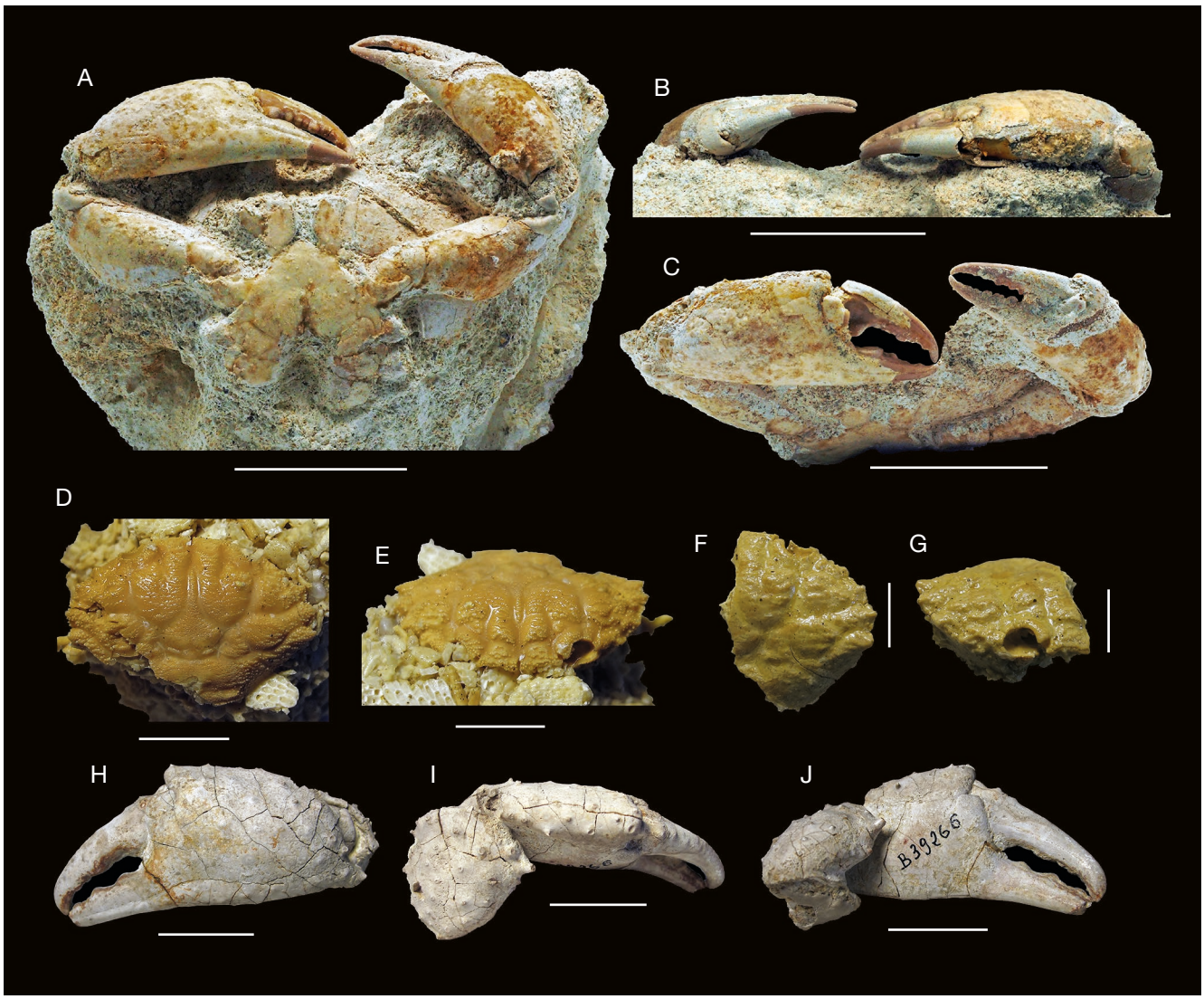

FIG. 6. — Decapod from the 'Savignean facies' (Langhian) of 'La Sonneterie' quarry, Meigné-le-Vicomte (Maine-et-Loire): **A**-**C**, *Necronectes michelini* (A. Milne-Edwards, 1861), MHNH-2016-79-2003: **A**, ventral view; **B**, view of upper margin of chelipeds; **C**, frontal view of chelipeds. Decapods from the 'Savignean facies' (Langhian-Serravallian) of the 'Blandinerie' quarry, Breil (Maine-et-Loire): **D**-**G**, *Xantho moldavicus* (Yanakevich, 1977): **D**, ULB-IV-A (6), dorsal view; **E**, frontal view; **F**, ULB-IV-A (11), dorsal view; **G**, frontal view. Decapod from the probable Tortonian of Doué-la-Fontaine (Maine-et-Loire): **H**-**I**, Undetermined cheliped MNHN.F.B39266: **H**, outer margin; **I**, upper margin; **J**, inner margin. Scale bars: A-C, 50 mm; D-G, 5 mm; H-J 20 mm. Photographs of: A-C, by P. Saulet; D-J, by À. Ossó.

ing out to a possible relationship with xanthids and particularly with *Eriphia* Latreille, 1817, but with a question mark. Ossó & Gagnaison (2019) discussed on this cheliped, discarding any relationship with Cancridae and avoiding any systematic assignation without prior examination of the specimen. Personal examination of this cheliped at MNHN, also did not clarify a clear identification. However, it cannot be attributed to *Eriphia* due to the lack of cutting-edge in its dactyli, that *Eriphia* spp. possess. No remains of carapace have been found in the 'Faluns' outcrops, that give us any clue. Nevertheless, the general construction of the cheliped, the weakly spiny in the upper portion of the palm, and the absence of cutting-edge, and the slightly spooned tips of the dactyli, recall that of some species of xanthids, for instance *Etisus* H. Milne-Edwards, 1834. Therefore, this cheliped is left as Xanthidae *sensu lato*, with reservations.

CONCLUSIONS

This new compilation of all the known decapods collected in the Miocene of the 'Faluns' in Anjou-Touraine, yields as a result a total of nineteen different species, possibly representatives of seventeen genera and fourteen families.

The previously pointed out faunal similarity with the Miocene faunas of the Mediterranean and Paratethys, is supported by the results of the present work (Table 1). The relative homogeneity of the middle Miocene Mediterranean and Paratethys decapod assemblages (Hyžný 2016), is also observed in the 'Faluns' decapod assemblage, with the exception of Corystidae. Since during the middle Miocene there was no marine communication north of the Atlantic coast of France (Rögl 1998; Popov *et al.* 2004), the Mediterranean-

Paratethyan fauna likely reached the Atlantic coast of France through southern the Iberian Peninsula, probably during the Langhian transgression.

The true diversity and richness of the decapod fauna of the 'Faluns' could be blurred by not very favorable conditions of fossilization of decapods, if compared with that of the reefal or siliciclastic deposits of the Mediterranean and Paratethys Miocene.

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