

# New fossil decapod crustaceans from the Remy Collection, Muséum national d'Histoire naturelle, Paris

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## ABSTRACT

Unpublished material originally identified by J.-M. Remy, as well as evaluation of his type material deposited in the Muséum national d'Histoire naturelle, Paris, has resulted in two new genera, *Remyranina* n. gen. and *Planobranchia* n. gen.; two new species, *Liocarcinus heintzi* n. sp. and *Szaboa lamarei* n. sp., and five new combinations, *Remyranina ornata* n. comb., *Calappilia? gorodiskii* n. comb., *Mursia simplex* n. comb., *Planobranchia simplex* n. comb., and *Planobranchia laevis* n. comb. These taxa include the first Oligocene record for the Matutidae, and the extinct genus *Szaboa* is re-diagnosed. The Remy collection, comprised primarily of fossils from France and equatorial Africa, consists of numerous Calappidae and Carpilioidea, especially abundant today in tropical environments, suggesting that at least for some taxa in these groups, environmental tolerances have changed little since the Eocene.

## KEY WORDS

Crustacea,  
Decapoda,  
Brachyura,  
Cretaceous,  
Eocene,  
Oligocene,  
France,  
Africa,  
new species,  
new genera,  
new combinations.

## RÉSUMÉ

*Nouveaux crustacés décapodes fossiles de la Collection Remy, Muséum national d'Histoire naturelle, Paris.*

L'étude du matériel non publié et la révision du matériel type de J.-M. Remy déposé au Muséum national d'Histoire naturelle, Paris, a permis de proposer deux genres nouveaux, *Remyranina* n. gen. et *Planobranchia* n. gen., deux espèces nouvelles, *Liocarcinus heintzi* n. sp. et *Szaboa lamarei* n. sp., et cinq combinaisons nouvelles, *Remyranina ornata* n. comb., *Calappilia? gorodiskii* n. comb., *Mursia simplex* n. comb., *Planobranchia simplex* n. comb., et *Planobranchia laevis* n. comb. Un Matutidae de l'Oligocène est identifié pour la première fois et une nouvelle diagnose du genre éteint *Szaboa* est proposée. La collection Remy, principalement constituée de fossiles de France et d'Afrique équatoriale, regroupe de nombreux Calappidae et Carpilioidea. Ces crustacés, particulièrement abondants dans les environnements tropicaux actuels, suggèrent que les tolérances environnementales de certaines espèces de ces groupes ont peu changé depuis l'Éocène.

## MOTS CLÉS

Crustacea,  
Decapoda,  
Brachyura,  
Crétacé,  
Éocène,  
Oligocène,  
France,  
Afrique,  
espèces nouvelles,  
genres nouveaux,  
combinaisons nouvelles.

## INTRODUCTION

The Muséum national d'Histoire naturelle, Paris houses a collection of decapod specimens described or preliminarily identified by Jean-Marcel Remy during the mid-twentieth century. Our work and that of others over the past decade has already revised and illustrated some of the taxa described in Remy's works, bringing them up-to-date with the most recent classifications (see Collins & Morris 1975; Schweitzer 2003, 2005; Feldmann & Portell 2007; Ah Yong 2008; Karasawa *et al.* 2008). Herein we evaluate the remainder of the taxa described or preliminarily identified by Remy, resulting in several new taxa and combinations.

Remy's work has been particularly important for decapod studies because it includes some of the few decapod crustaceans known from the continent of Africa (Remy 1960; Remy & Tessier 1954; Gorodiski & Remy 1959). Some other works have described taxa from Egypt (Noetling 1885; Lörenthey 1909; Anderson & Feldmann 1995) and other areas, but relatively few decapods are known from the continent.

## LOCALITIES AND GEOLOGIC SETTING

Discussed here are the localities for the previously unpublished specimens described herein. Remy's published work contains localities for the specimens from Africa and Israel.

### MONSÉGUR (GIRONDE, FRANCE)

Two decapod specimens were collected from Monségur, *Liocarcinus heintzi* n. sp. and *Szaboa lamarei* n. sp. This locality belongs to the Calcaire à Astéries Formation (Rupelian). This formation is composed of carbonates in the northern region of Aquitaine (France), including calcilutites, calcarenites, and calcirudites, in that stratigraphic order (Puechmaillé & Vigneaux 1966; Maillet & Puechmaillé 1967). Magne (1947) confirmed the Oligocene age based upon various fossils. The calcarenite has been noted to contain abundant miliolid foraminiferans (Maillet & Puechmaillé 1967), and indeed,

the matrix of the specimen of *Liocarcinus heintzi* n. sp. contains what appears to be miliolids. The calcilutite and calcirudite both have been reported to contain abundant terrigenous input (Puechmaillé & Vigneaux 1966), seen in the matrix of the specimen of *Szaboa lamarei* n. sp. Thus, the label information corresponds well with the actual lithology of the rock surrounding the specimens, so we can only assume it to be correct.

### DAX (LANDES, FRANCE)

Remy reported that the specimen collected from this locality, simply noted as Dax (Landes) was of Eocene age, and an old label noted it as having been part of the Nummulitique de Dax, collection of A. Milne-Edwards. The Eocene age was probably derived from the association with a nummulitic rock unit. Indeed, Eocene rocks are well known from that region of France, the southwestern region of Aquitaine (Sztràkos *et al.* 1997, 1998). Fossil crabs have previously been reported from the region (A. Milne-Edwards 1862-1865; Burger *et al.* 1945; Daguin 1948; Boulanger *et al.* 1967; Sztràkos *et al.* 1998; Odin 2005). We herein simply refer to the age of the specimen as Paleogene until more material with more precise locality data is collected.

## ABBREVIATIONS

BSP	Bayerische Staatsammlung für Paläontologie und historische Geologie München, Munich;
IMDASlf.Nr.	Staatliches Museum für Naturkunde, Stuttgart;
KSU	decapod collections, Kent State University, Kent, Ohio;
MR	Természettudományi Múzeum, Föld-és Ősléntár, Stéfanía ut 14, Budapest (Hungarian National Museum, Paleontological and Geological Collection);
MNHN	collections de Paléontologie du Muséum national d'Histoire naturelle, Paris.

## SYSTEMATICS

Order DECAPODA Latreille, 1802  
 Infraorder BRACHYURA Linnaeus, 1758

Section EUBRACHYURA  
de Saint Laurent, 1980

Subsection RANINOIDA De Haan, 1839

Superfamily RANINOIDEA De Haan, 1839

Family RANINIDAE De Haan, 1839

Subfamily RANININAE De Haan, 1839

Genus *Remyranina* n. gen.

TYPE SPECIES. — *Raninella ornata* Remy, 1960.

ETYMOLOGY. — The generic name combines the name of the author of the type species and prominent French paleontologist, Jean-Marcel Remy, and *Ranina*, the type genus of the family.

OCCURRENCE. — The sole specimen was collected from probable Eocene rocks of Ivory Coast, Africa.

DIAGNOSIS. — Small raninid with expanded, moderately broad fronto-orbital margin; ovoid, slightly longer than wide, with carapace ornamentation granular in anterior half and strongly terraced in posterior half.

DESCRIPTION. — As for emended description of species.

DISCUSSION

Although the specimen referred to the new genus clearly allies it with the Ranininae, the combination of characters is unique and readily justifies creation of the new taxon. The genus to which it is most closely allied is *Lophoranina* Fabiani, 1910. These two genera are the only ones in the Raninidae that are characterized by possession of a trifold rostrum and development of terraced ornamentation. However, *Lophoranina* tends to be widest near the front or at the level of the last anterolateral spine, whereas *Remyranina* n. gen. is broadest at the midlength, well posterior to the anterolateral spines. Furthermore, the anterolateral spines and the postorbital spines on *Lophoranina* are generally small, whereas those on *Remyranina* n. gen. are large. Finally, the terraced lines of *Lophoranina* extend nearly to the front of the carapace, well in advance of the branchiocardiac grooves, whereas those on *Remyranina* n. gen. are confined to the posterior half of the carapace. There seems to be no other genus of raninids with which *Remyranina* n. gen. could be confused.

*Remyranina ornata* (Remy, 1960) n. comb.  
(Fig. 1A)

*Raninella ornata* Remy, 1960: 57, fig. 2; figs 8, 9 of the unnumbered plate.

TYPE MATERIAL. — Holotype (dorsal carapace) by monotypy (MNHN R03847, coll. Tessier).

TYPE LOCALITY. — From probable Eocene rocks on the seaciff below Kraïebouen hill, near Fresco, 5.03°N, 5.31°W, Ivory Coast, Africa (Remy 1960).

MEASUREMENTS. — Measurements (in mm) taken on the holotype of *Remyranina ornata* n. comb.: maximum carapace length, > 18.7; maximum carapace width, 14.3; frontal width, 21.0; fronto-orbital width, 10.0.

EMENDED DESCRIPTION

Carapace small for family, longer than wide, moderately vaulted transversely, weakly arched longitudinally; regions not well defined; surface granular in anterior half and strongly terraced posteriorly. Front narrow, about 17% carapace width; fronto-orbital margin moderately broad, about 68% carapace width; maximum carapace width, measured at midlength, less than 80% maximum carapace length; posterior margin broken, estimated to be about 54% maximum width. Front projected slightly in advance of postorbital spines; rostrum sulcate, trifold, with axial spine projected in advance of lateral spines; axis of rostrum with subtle granular ridge. Orbital margin not well preserved; apparently sinuous with at least one orbital fissure at about midpoint; terminating laterally in prominent outer orbital spine. Lateral margin of outer orbital spine convex, widest near tip and narrowing to tip and to intersection with anterolateral margin. Anterolateral margin widening posteriorly; with two spines (broken) dividing margin into thirds; general outline of carapace widest posterior to spines. Posterolateral margins nearly straight, converging posteriorly, rimmed by beaded marginal rim. Posterior margin broken.

Surface of carapace divided into granular anterior half and terraced posterior half. Mesogastric region discernable as extremely subtle pyriform swelling widening posteriorly from rostral ridge to anterior termination of prominent, deep, arcuate branchiocardiac pits. Regions on remainder of front half of carapace indistinguishable; surface with fine gran-

ules, somewhat coarser axially and finer laterally. Posterior half of carapace crossed by prominent, continuous to discontinuous, digitate, sinuous terrace structures; terrace structures generally concave forward; tips of digitations broken, fine, about 2.6 digitations per mm, forward-directed. Regions not defined in posterior half.

Remainder of carapace, ventral surface, and appendages not observed.

#### DISCUSSION

The description of this species given by Remy (1960: 57) is quite complete and little can be added to it. The emended description has been written to use consistent, modern terminology to facilitate comparison with other raninids.

The nature of the fine structure developed on the terraced ornamentation on *Remyranina ornata* n. comb. is very much like that seen on *Lophoranina georgiana* (Rathbun, 1935) (Feldmann *et al.* 1996: fig. 5), *L. precocia* Feldmann, Vega, Tucker, García-Barrera & Avendaño, 1996 and *L. cristaspina* Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer & Waugh, 2001. In those three species and, in all likelihood, other species within the genus, the digitate margins of terraced structures are broken ends of fine spines that are directed anteriorly (Vega *et al.* 2001: fig. 4.7). These small spines were interpreted by Feldmann *et al.* (1996) to function as hooks to anchor the organism in very fine sediment or to capture bits or organic debris as camouflage (Savazzi 1981). It is possible that *Remyranina ornata* n. comb. also possessed small spines that had a similar function.

Subsection HETEROTREMATA Guinot, 1977  
Superfamily CALAPPOIDEA De Haan, 1833  
Family CALAPPIDAE De Haan, 1833

Genus *Calappilia* A. Milne-Edwards, 1873

TYPE SPECIES. — *Calappilia verrucosa* A. Milne-Edwards, 1873, by subsequent designation of Glaessner (1929).

SPECIES INCLUDED. — See Feldmann *et al.* (2005).

DIAGNOSIS AND DISCUSSION. — See Feldmann *et al.* (2005) for a recent discussion.

#### *Calappilia? gorodiskii*

(Remy *in* Gorodiski & Remy, 1959) n. comb.  
(Fig. 1B)

*Atelecyclus gorodiskii* Remy *in* Gorodiski & Remy, 1959: 318, pl. 19, fig. 2. — Salva & Feldmann 2001: 49.

TYPE MATERIAL. — Holotype (dorsal carapace; MNHN R03840, coll. Gorodiski), paratype of M'Bathié (Senegal) not present in the MNHN Collections.

TYPE LOCALITY. — Pognar (Senegal), Upper Lutetian (Gorodiski & Remy 1959).

#### DISCUSSION

The type specimen originally referred to *Atelecyclus gorodiskii* is quite incomplete. All of the margins are broken, and nothing remains of the front and orbits. Dorsal carapace regions are reasonably well preserved, however, and indicate narrow, elongate axial regions bordered by deep axial grooves; small, narrow protogastric regions; and large, granular ornamentation on all of the carapace regions. The carapace appears to have been ovate, but it is not possible to know for certain because of the broken margins. Comparison of the nature of the carapace regions with members of the Atelecyclidae (e.g., illustrations in Salva & Feldmann 2001) indicates that the species is not a member of that family. Species of *Atelecyclus* Leach, 1814, have arcuate swellings parallel to the lateral margins of the cardiac region, which are absent in *Atelecyclus gorodiskii*. Other genera within the Atelecyclidae and the related Cancridae Latreille, 1802, have narrow axial regions, but they are not as long as those of *Atelecyclus gorodiskii*, and the cardiac and intestinal regions are never as long in those families as in *Atelecyclus gorodiskii*.

The Calappidae can better accommodate *Atelecyclus gorodiskii*. Members of that family possess narrow, elongate axial regions bordered by deep axial grooves; small, narrow protogastric regions; and often possess large, granular ornamentation on all of the carapace regions, all of the observable features on *Atelecyclus gorodiskii*. Herein we tentatively refer the species to *Calappilia*, a common Eocene genus characterized by all of these features. In addition, *Calappilia* possesses spines on the posterolateral margin as does *A. gorodiskii*, and lacks a posterolateral flange of spines, as is seen in many species of

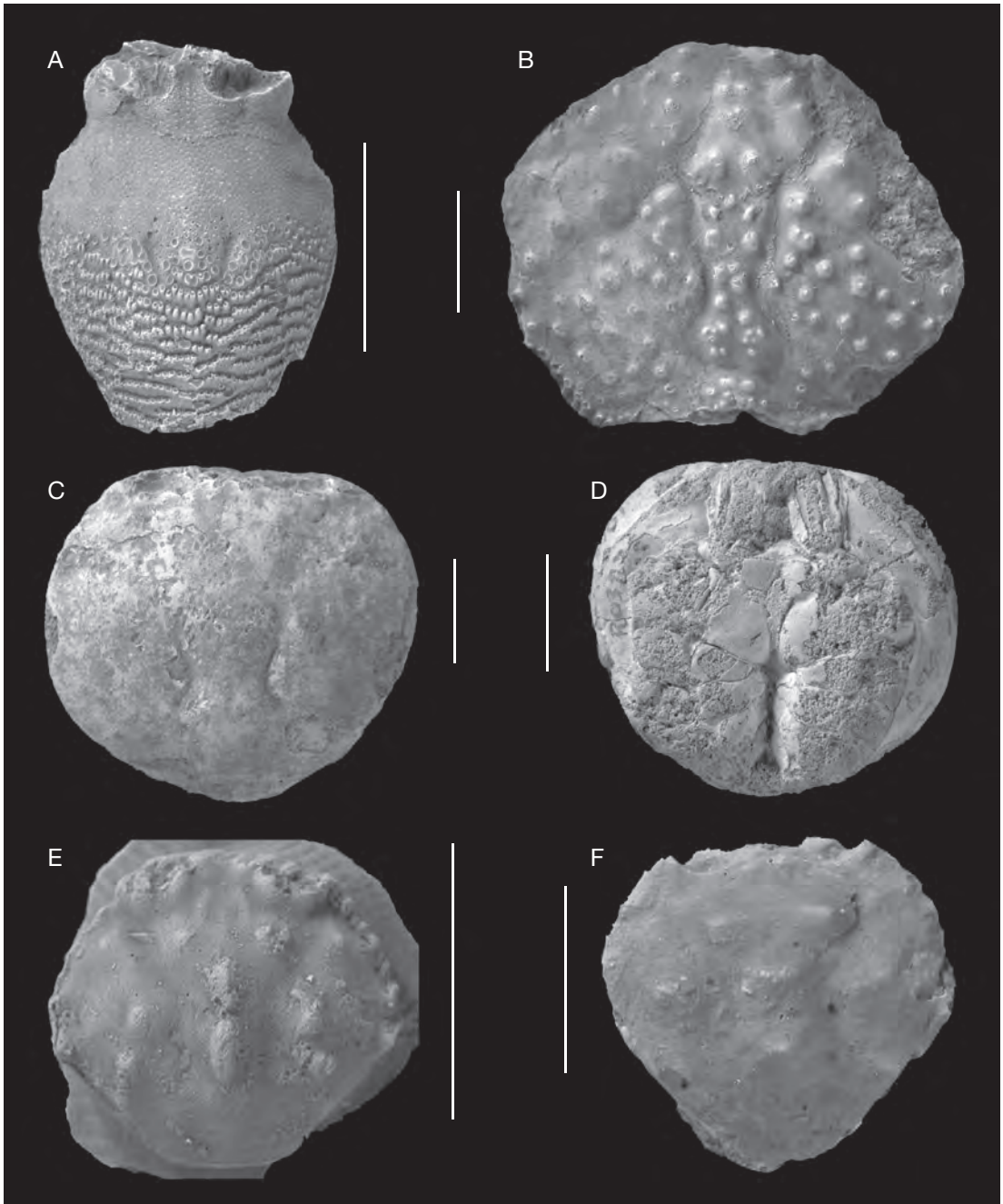


FIG. 1. — Fossil Brachyura from Monségur (Gironde, France) : **A**, *Remyranina ornata* (Remy, 1960) n. comb., cast of holotype, MNHN R03847, dorsal carapace; **B**, *Calappilia? gorodiskii* (Remy in Gorodiski & Remy, 1959) n. comb., cast of holotype, MNHN R03840, dorsal carapace; **C**, **D**, Calappidae gen. et sp. indet., dorsal (**C**) and ventral (**D**) surfaces, MNHN R03836; **E**, *Mursia simplex* (Remy, 1960) n. comb., cast of holotype, MNHN R03849, dorsal carapace; **F**, *Szaboa lamarei* n. sp., holotype, MNHN R03779, dorsal carapace. Scale bars: 1 cm.

*Calappa* Weber, 1795. More complete specimens will be necessary to confirm generic placement for this species; however, placement within the Calappidae seems reasonable.

### Genus *Mursia* Leach, 1823

TYPE SPECIES. — *Mursia cristiata* H. Milne Edwards, 1837, by subsequent monotypy (see Ng *et al.* 2008).

FOSSIL SPECIES INCLUDED. — *Mursia armata* De Haan, 1837 (also extant); *M. aspina* Schweitzer & Feldmann, 2000; *M. australiensis* Campbell, 1971 (also extant); *M. bekenuensis* Collins, Lee & Noad, 2003; *M. circularis* (Karasawa, 1989); *M. creutzbergi* Collins & Donovan, 2004; *M. granulosa* Collins & Donovan, 2002; *M. lienharti* (Bachmayer, 1962); *M. marcusana* Rathbun, 1926; *M. macdonaldi* Rathbun, 1918; *M. minuta* Karasawa, 1993; *M. obscura* Rathbun, 1918; *M. simplex* (Remy, 1960) n. comb.; *M. takahashii* Imaizumi, 1952; *M. yaquinensis* Rathbun, 1926.

DIAGNOSIS. — Carapace about as wide as long or wider than long, ovate; orbits circular, directed forward, front narrow; anterolateral margins with small spines and long lateral spine or entire; carapace ornamented with five or seven ridges, one axial and two or three on each side; ridges can be granular; carapace may be granular between ridges; merus of cheliped may have long distal spine; manus with spines on upper margin; sternum ovate, narrow.

### DISCUSSION

*Mursia* is easily diagnosed by the presence of well-developed carapace ridges and generally granular ornamentation. It has been a widespread genus from Eocene to recent time, recorded from tropical to temperate regions (Schweitzer & Feldmann 2000).

Remy (1960) referred a small, ovate specimen to *Cenomanocarcinus simplex*. This species cannot be referred to *Cenomanocarcinus* for several reasons (see illustrations in Schweitzer *et al.* 2003 and Guinot *et al.* 2008). Species of *Cenomanocarcinus* are characterized by ridges on the carapace, but they are arrayed both transversely and longitudinally. *Cenomanocarcinus simplex* has carapace ridges that are axially and obliquely arrayed on the lateral regions of the carapace. Species of *Cenomanocarcinus* have well-defined axial, protogastric, and hepatic regions, whereas *C. simplex* has axial regions that are defined only by a deep lateral groove

along the entire axial region. *Cenomanocarcinus* spp. have a transverse ridge on the cardiac and branchial regions which *C. simplex* lacks. *Cenomanocarcinus* spp. have an arcuate epibranchial ridge extending from the last anterolateral spine and terminating along the axis, which *C. simplex* lacks.

*Cenomanocarcinus simplex* is better accommodated within the Calappidae and *Mursia*. *Cenomanocarcinus simplex* possesses large, circular, rimmed orbits; a granular anterolateral margin with a small lateral spine; and five dorsal carapace ridges with large transverse granules. These features are typical of *Mursia* spp.; thus, we refer the species to *Mursia*, resulting in *Mursia simplex* n. comb. *Mursia simplex* n. comb. differs from other species of the genus in having less granular ornamentation overall.

### *Mursia simplex* (Remy, 1960) n. comb. (Fig. 1E)

*Cenomanocarcinus simplex* Remy, 1960: 56, text-fig. 1, fig. 3 of the plate.

TYPE MATERIAL. — Holotype (dorsal carapace) by monotypy (MNHN R03849, coll. Tessier).

TYPE LOCALITY. — Probable Eocene rocks on the seacliff below Kraïebouen hill, near Fresco, 5.03°N, 5.31°W, Ivory Coast, Africa (Remy 1960).

### DISCUSSION

One other Eocene species of *Mursia* is known, from Pacific coastal North America (Schweitzer & Feldmann 2000). The records for the genus span tropical and temperate localities, so the occurrence of an Eocene species in West Africa extends the geographic range of the genus but not the geologic or ecological range. The North American occurrence is late Eocene in age; it is not possible at this time to determine whether the African occurrence is older as it is simply reported as probably Eocene.

### Calappidae gen. et sp. indet. (Fig. 1C, D)

MATERIAL EXAMINED. — Carapace (MNHN R03836, coll. Milne-Edwards).

MEASUREMENTS. — Measurements (in mm) taken on the dorsal carapace of MNHN R03836: maximum carapace width = 35.8; maximum carapace length > 33.0; fronto-orbital width = 19.7; frontal width = 7.5.

OCCURRENCE. — Paleogene rocks of Dax, Landes, in Aquitaine, France.

#### DESCRIPTION

Carapace ovate, about as wide as long, widest at about midlength; moderately vaulted both longitudinally and transversely. Front narrow, about 20% maximum carapace width, broken. Orbits directed forward; rims unknown; fronto-orbital width 55% maximum carapace width. Anterolateral and posterolateral margins confluent; anterolateral portion appearing to have had small spines or protuberances; posterolateral portion possibly rimmed; posterior margin broken.

Protogastric regions weakly inflated, merged with mesogastric region. Metagastric and urogastric regions confluent, about same height as mesogastric region, lateral margins concave. Cardiac region rounded-triangular, elongate, two swellings anteriorly. Lateral margins bounded by deep, lateral groove. Intestinal region poorly defined. Hepatic region weakly inflated centrally. Epibranchial region arcuate, weakly inflated. Remainder of branchial regions undifferentiated.

Third maxillipeds elongate.

Male sternum long, narrow. Sternites 1-2 fused, no evidence of suture, triangular, separated from sternite 3 by complete suture. Sternite 3 about as long as wide, deeply depressed axially, separated from sternite 4 by deep, oblique grooves. Sternite 4 much longer than wide, deeply grooved axially, sterno-abdominal cavity extending about one-quarter the distance onto sternite, with short episternal projections, directed anterolaterally. Sternite 5 wider than long, suture 4/5 incomplete, with short episternal projections, directed laterally; sternite 6 wider than long, suture 5/6 incomplete, with short episternal projections, directed posterolaterally; sternite 7 wider than long, suture 6/7 incomplete, directed strongly posterolaterally; sternite 8 short, wide; directed strongly posterolaterally, suture 7/8 may or may not have been incomplete: preservation insufficient to determine.

Remainder of carapace and appendages unknown.

#### DISCUSSION

The specimen described here appears to be referable to the family based upon its ovate shape; closely spaced, circular orbits; well-defined axial regions that are bounded by deep grooves; narrow sternum with deep sterno-abdominal cavity; and sternal sutures 4/5 and 5/6 definitely interrupted. The specimen described here seems to lack posterolateral spines, eliminating it from the speciose Eocene genus *Calappilia* and also from *Calappa*, but those margins are heavily damaged. Species of *Mursia* generally have granular ornamentation on the dorsal carapace, which the specimen described here lacks. However, the specimen is damaged on all of the margins, so it is not possible to place it within a genus. Although the dorsal carapace is poorly preserved, the sternum is quite well preserved. Recovery of more specimens will help to place this specimen within a taxon.

Superfamily LEUCOSIOIDEA Samouelle, 1819

Family MATUTIDAE De Haan, 1841

Genus *Szaboa* Müller & Galil, 1998

TYPE SPECIES. — *Matuta inermis* Brocchi, 1883 by monotypy.

OTHER SPECIES INCLUDED. — *Szaboa lamarei* n. sp.

MATERIAL EXAMINED. — Cast of *Szaboa inermis*, MR45-2-1.

EMENDED DIAGNOSIS. — Carapace wider than long, length about 95% maximum width, widest 35-45% the distance posteriorly on carapace; front with axial spine, about 20% maximum carapace width; orbits deepest axially, outer-orbital spine triangular, directed forward; fronto-orbital width about 60% maximum carapace width; lower orbital rim extending well beyond upper-orbital rim, with two blunt spines, pterygostomial regions with sub-orbital swelling; anterolateral margin with several small spines; posterolateral and posterior margins rimmed; protogastric, mesogastric, cardiac, epibranchial, and branchial regions with swellings; stridulating ridges on inner surface of manus.

#### DISCUSSION

We herein follow Schweitzer & Feldmann (2000) and Martin & Davis (2001) in placing the Ma-

tutidae within the Leucosioidea. Galil & Clark (1994) extensively revised the matutid genera, and Martin & Davis (2001) recognized the family status of the Matutidae. Schweitzer & Feldmann (2000) followed Bellwood (1996) in recognizing the Matutidae and applied the family to the fossil record as had Müller & Galil (1998). Despite this work, there is a limited fossil record for the family. Only four fossil species are known, the two species of *Szaboa* mentioned here, *Eomatuta granosa* De Angeli & Marchiori, 2009, and one unnamed species attributed to the genus *Ashtoret* by Karasawa (2002).

### *Szaboa lamarei* n. sp. (Fig. 1F)

TYPE MATERIAL. — Holotype (carapace; MNHN R03779, coll. Remy).

MEASUREMENTS. — Measurements (in mm) taken on the holotype and sole specimen of *Szaboa lamarei* n. sp.: maximum carapace width = 20.3; maximum carapace length = 19.3; fronto-orbital width = 11.3; posterior width = 6.3; length to position of maximum width = 6.7.

ETYMOLOGY. — The trivial name is that used by Jean-Marcel Remy on the label but that was never published, in honour of Pierre Lamare (French geologist). We honor the work of both geologists by using Remy's intended name.

TYPE LOCALITY. — Monségur, Gironde, Rupelian, Calcaire à Astéries Formation.

DIAGNOSIS. — Outer-orbital spines triangular, directed forward; carapace swellings large; lower orbital margin with large swelling.

### DESCRIPTION

Carapace obovate, about as wide as long, length about 95% maximum carapace width, widest about 35% the distance posteriorly on carapace at about level of posterior edge of protogastric regions; flattened transversely and moderately vaulted longitudinally.

Front abraded, broken. Orbits wide, outer orbital spine triangular, directed forward; upper orbital margin sinuous; lower orbital margin extending well anterior of upper orbital margin, with central swelling. Anterolateral margins with several rounded

spines, at least one with granular ornament. Posterolateral margin weakly concave, probably weakly rimmed. Posterior margin narrow, about 30% maximum carapace width, weakly rimmed.

Epigastric region weakly inflated, spherical. Protogastric regions triangular, apex directed posteriorly, with transverse swelling centrally. Mesogastric region with weak anterior extension, highly inflated posteriorly. Urogastric region depressed below level of mesogastric and cardiac regions. Cardiac region most inflated of all regions, produced into conical elevation. Intestinal region very long, not well differentiated. Hepatic region small, flattened. Epibranchial region with large spherical swelling centrally. Remainder of branchial regions undifferentiated, with small swelling just adjacent to posterolateral margin.

Pterygostomial region with suborbital swelling. Remainder of carapace and appendages unknown.

### DISCUSSION

*Szaboa lamarei* n. sp. is easily distinguished from the only other species in the genus, *S. inermis*, in possessing much larger carapace swellings and apparently larger anterolateral swellings, although the latter is difficult to determine because the sole specimen of *S. lamarei* is abraded. The features of the two species are essentially identical except that the ornamentation of *S. lamarei* is much more robust. Because the species of *S. lamarei* is an abraded mold of the interior, collection of additional material could provide more details of the morphology of this species.

The new species of *Szaboa* is accommodated within the Matutidae based upon its lower orbital margins extending well beyond the upper orbital margins, seen in extant species (Galil & Clark 1994) and in *Szaboa inermis* (Müller & Galil 1998: fig. 1); its obovate carapace that is about as wide as long; and its wide orbits that occupy most of the frontal margin of the carapace. The new species is superficially similar to species of *Eriosachila* Blow & Manning, 1996, of the Aethridae Dana, 1851, but *Eriosachila petiti* Blow & Manning, 1996, the type species of the genus, has small orbits with a lower orbital margin that does not extend beyond the upper orbital margin and has well-defined carapace regions not typical of the Matutidae. Thus, the new species is best accommodated within the Matutidae.



Of the Matutidae, the new species is the only one of early Oligocene age. *Eomatuta granosa* is early Eocene in age, known from Italy (De Angeli & Marchiori 2009). The other two fossil species are Miocene in age (Müller & Galil 1998; Karasawa 2002). The occurrence extends the geographic range somewhat, although *Szaboa inermis* was already known from Hungary; thus, the probable range and distribution pathway to the current Indo-Pacific occurrences remains Tethyan.

Superfamily MAJOIDEA Samouelle, 1819  
Family MAJIDAE Samouelle, 1819

Subfamily MICROMAIINAE Beurlen, 1930

#### DISCUSSION

Beurlen (1930) provisionally united the genera *Micromaia* Bittner, 1875, *Mithracia* Bell, 1858 and *Pisomaia* Lörenthey in Lörenthey & Beurlen, 1929, within the subfamily Micromaiinae. The basis for this placement is not clear and the comparison of referred taxa suggests that they bear little resemblance to one another. The conformation of axial regions on the type species of the three genera are totally different from one another; the outlines, particularly with reference to the posterior margin are dissimilar; and the orbital architecture of the two taxa on which it is present on the type species, *Micromaia tuberculata* Bittner, 1875, and on *Pisomaia tuberculata* Lörenthey in Lörenthey & Beurlen, 1929, are different. Thus, there seems to be no unifying set of morphological criteria to justify the Micromaiinae. Further, Glaessner (1969) characterized the orbital structure of the subfamily as being like the Inachinae which he described as lacking orbits. That is certainly not the case in the several examples of *Micromaia* examined by us and well illustrated by Beschin *et al.* (1985). Investigation into the composition and validity of the subfamily is ongoing.

Discussion of the Micromaiinae is warranted because the type species of the new genus, *Planobranchia* n. gen., was originally placed within *Micromaia*. As discussed below, the species referred to the new genus bear close resemblance to members of the Majinae, and that placement is adopted here. Because we have

not examined all available representative specimens of all species of *Micromaia*, *Mithracia*, and *Pisomaia*, it is premature to comment on their relationships in detail. That work is in progress.

Subfamily MAJINAE Samouelle, 1819

Genus *Planobranchia* n. gen.

TYPE SPECIES. — *Micromaja laevis* Lörenthey, 1909: 119, pl. 1, fig. 2a, b, by present designation.

INCLUDED SPECIES. — *Planobranchia laevis* (Lörenthey, 1909); *P. simplex* (Remy in Gorodiski & Remy, 1959).

ETYMOLOGY. — The generic name alludes to the depressed and flattened metabranchial region which serves to readily distinguish the genus from closely related forms. The gender is feminine.

DIAGNOSIS. — Carapace pyriform, widest at midlength of branchial region; moderately vaulted transversely and longitudinally. Gastric regions only weakly differentiated; defined laterally by prominent V-shaped groove converging from anterior margin of orbits to urogastric region, the narrowest part of axial regions. Cardiac region nearly as wide as widest part of gastric regions, hexagonal to ovoid in outline; bearing two nodes on medial transverse ridge. Intestinal region well defined, long, approximately as wide as urogastric region. Epibranchial and mesobranchial regions strongly inflated, separated from one another by subtle arcuate attachment scar expressed on mold of the interior of the carapace; widest part of these regions converge as angular projections toward urogastric region. Metabranchial region extends from widest part of cardiac region posterolaterally around posterior margin of metabranchial region and clearly defined axially by posterior margin of cardiac region and intestinal region; depressed below other regions. Surface of carapace weakly ornamented by fine granules or pits; lacking strong tubercles.

#### DISCUSSION

*Planobranchia laevis* n. comb. and *P. simplex* n. comb. were both originally assigned to *Micromaia* based upon overall similarities in outline and, in the absence of other majid genera that the species more closely resembled, the assignments seemed reasonable. However, the two species exhibit several morphological features that readily distinguish them from other species assigned to *Micromaia*. Bittner (1875) originally defined *Micromaia tuberculata*, both the genus and

species, simultaneously. Thus, species referable to *Micromaia* must conform to the concept of the genus as defined by Bittner (1875: 76) within his species-level description. The elements of his description of *Micromaia tuberculata* that we take as characterizing the genus *Micromaia* include a pyriform outline; very poorly defined regions, sometimes defined only by the pattern of tubercles; axial regions that are more or less uniform in width, and with the intestinal region being very short or not differentiated; branchial regions that are undifferentiated and uniformly inflated; and a uniform, dense array of coarse, often truncated-conical tubercles over the entire carapace. The orbits are within the range of typical majids: directed anterolaterally and arising posterior to the bifid, weakly downturned rostrum.

The two species herein removed from *Micromaia* referred to *Planobranchia* n. gen. have regions that are weakly defined by grooves, rather than tubercle patterns; axial regions that are quite variable in width, and with the cardiac region being nearly the widest region; a distinct, long, narrow intestinal region; a depressed, flattened metagastric region that is clearly differentiated from the epibranchial and mesobranchial regions; and an overall absence of strong ornamentation. Although the fronts of both type specimens of *P. laevis* n. comb. and *P. simplex* n. comb. are absent, the orbital margin appears to be quite similar to other majids and, at least on *P. simplex* n. comb., there appears to be a slight indication of a bifid rostrum. Thus, representatives of the two genera are readily distinguishable, based upon characters that are taxonomically important at the generic level in majids.

*Planobranchia simplex* n. comb.  
(Remy in Gorodiski & Remy, 1959)  
(Fig. 2A)

*Micromaia simplex* Remy in Gorodiski & Remy, 1959: 317, fig. 2.

TYPE MATERIAL. — Holotype (carapace) by monotypy (MNHN R03839, coll. Gorodiski). Casts of the type (KSU D1097) are deposited in the Department of Geology, Kent State University.

TYPE LOCALITY. — N'Gueyène, western Senegal, Upper Lutetian (Gorodiski & Remy 1959).

## DISCUSSION

The description by Remy in Gorodiski & Remy (1959: 317) adequately describes the species and will not be repeated here. The genus *Planobranchia* n. gen. embraces two species that are quite similar to one another and confirm their affinities and their distinction from species of *Micromaia* as discussed above. *Planobranchia simplex* n. comb. has a broader, more inflated epibranchial and mesobranchial region than does the type species. The cardiac region of the Senegal specimen is narrower, about 21% maximum width, whereas the cardiac region of *P. laevis* n. comb. (Fig. 2B) is about 27% maximum width. The transverse ridge on the cardiac region of *P. simplex* n. comb. is more subtle than that of *P. laevis* n. comb., and the ridge on the latter species extends laterally to intersect the margin of the mesobranchial region. Finally, the metabranchial region on *P. simplex* n. comb. is irregularly elevated but smooth, whereas that surface on *P. laevis* n. comb. is also irregularly elevated but is covered with tiny pits or perforations. The frontal regions on both type specimens are broken, so that comparison is not possible.

Both species of *Planobranchia* n. gen. were collected from Eocene rocks in North and West Africa, on the south margin of the Tethyan seaway. The type species was collected near Cairo, Egypt (Lörenthey 1909). Species of *Micromaia* are known primarily from Italy, but also from other localities on the northern margin of the Tethys seaway.

Superfamily PORTUNOIDEA Rafinesque, 1815  
Family MATHILDELLIDAE  
Karasawa & Kato, 2003  
Genus *Branchioplax* Rathbun, 1916

*Branchioplax? ballingi*  
Remy in Remy & Tessier, 1954  
(Fig. 2C)

*Branchioplax ballingi* Remy in Remy & Tessier, 1954: 189, text-fig. 1, pl. 11, fig. 6. — Karasawa *et al.* 2008: 125.

TYPE MATERIAL. — Holotype (fragmental dorsal carapace) by monotypy (MNHN R03793, coll. Tessier).

TYPE LOCALITY. — Marigot de Balling, Senegal, Paleocene (Remy & Tessier 1954).

## DISCUSSION

The holotype is only a partial specimen, retaining the urogastric, hepatic, branchial, and parts of the mesogastric and cardiac regions. The anterolateral margin is broken, but shows the bases of four relatively robust spines. The arcuate epibranchial region and the marked muscle scars on the mesogastric region and along the urogastric region are what probably led Remy to refer the species to *Branchioplax*, which is characterized by both features. However, the apparently large anterolateral spines are larger than those seen in species of *Branchioplax*. In addition, the holotype of *B. ballingi*, while broken, has a length to width ratio of about 67%. Other species of *Branchioplax*, including *B. washingtoniana*, the type species, are more equant, having ratios of 80–85%. It is possible that *B. ballingi* is more closely related to members of the Portunidae or Macropipidae, but more complete material will be necessary to fully assess its placement. For now, we questionably refer it to *Branchioplax*.

Family CARCINIDAE MacLeay, 1838

Subfamily POLYBIINAE Paul'son, 1875

## DISCUSSION

Karasawa *et al.* (2008) provided diagnoses for the Carcinidae and Polybiinae. The new species described below is well accommodated within the Polybiinae based upon its length to width ratio of about 80%; front occupying about 30% maximum carapace width; fronto-orbital width of about 75% maximum carapace width; well-developed posterolateral reentrants; five anterolateral spines including the outer-orbital spine; and hexagonal shape. No other portunoid family accommodates this combination of features.

Genus *Liocarcinus* Stimpson, 1871

TYPE SPECIES. — *Portunus holsatus* Fabricius, 1798, by original designation.

INCLUDED FOSSIL SPECIES. — *Liocarcinus atropatanus* (Aslanova & Dschafarova, 1975); *L. corrugatus* (Pen-

nant, 1777), also Recent; *L. depurator* (Linnaeus, 1758), also Recent; *L. holsatus* (Fabricius, 1798), also Recent; *L. kuehni* (Bachmayer, 1953); *L. lancetidactylus* (Smirnov, 1929) (see Garassino & Novati 2001); *L. marmoreus* (Leach, 1814), also Recent; *L. oroszyi* (Bachmayer, 1953); *L. praearcuatus* Müller, 1996; *L. pusillus* (Leach, 1815), also Recent; *L. rakosensis* (Lörenthey, 1929).

DIAGNOSIS. — Carapace wider than long, length about 80% maximum width measured about half the distance posteriorly on carapace; front variably ornamented; orbits with two fissures on upper orbital margin; anterolateral margins with five flattened spines including outer-orbital spine, first four spines directed forward, last spine may be directed laterally or anterolaterally; regions generally well defined, epibranchial region markedly arcuate and inflated; regions may be ornamented with transverse ridges or granules; posterolateral reentrant large; posterior margin nearly straight; merus of cheliped without distal spine on inner margin, carpus with large spine on inner angle, dactylus with three ridges; dactyl of pereopod 5 lanceolate (after Poore 2004).

## DISCUSSION

Species of the genus are quite variable in their dorsal carapace ornamentation, both fossil and extant. The extant *Liocarcinus corrugatus* is characterized by transverse ridges on the dorsal carapace, and such ornamentation is seen on the fossil species *L. kuehni* and possibly on *L. rakosensis*. The illustration of *L. rakosensis* in Lörenthey & Beurlen (1929: pl. 13, fig. 1a) shows six anterolateral spines; however, it has been reported that some of the illustrations in that volume are inaccurate (P. Müller pers. comm. 2004). *Liocarcinus oroszyi* is less well preserved than some other species and appears to have had some granular ornamentation on the dorsal carapace (Bachmayer 1953). The other fossil specimens are compression specimens, making details of the carapace and ornamentation difficult to interpret.

The new species is referred to *Liocarcinus* based upon its possession of a wider than long carapace; five anterolateral spines, the first four of which are directed forward; marked posterolateral reentrants; granular ornamentation; and well-defined carapace regions. These are typical of *Liocarcinus*. The referral of the new material to *Liocarcinus* marks the second Oligocene occurrence of the genus. *Liocarcinus lancetidactylus* had already been noted from the Oligocene of the Caucasus (Smirnov 1929; Karasawa *et al.* 2008). Species of this genus are known

from the fossil record in Europe and what is now southern Russia, and extant species are Atlantic and Indo-Pacific in distribution (Ingle 1980; Poore 2004). Thus, the genus may have had a Tethyan distribution and dispersal route in the past.

*Liocarcinus heintzi* n. sp.  
(Fig. 2D)

TYPE MATERIAL. — Holotype (dorsal carapace; MNHN R03778, coll. Remy).

ETYMOLOGY. — The trivial name is that used by Jean-Marcel Remy on the museum label in honour of Émile Heintz of the MNHN, Paris, a specialist of fossil mammals, but that was never published. We honour both scientists by using Remy's intended name.

TYPE LOCALITY. — Monségur, Gironde, Aquitaine, SW France, Rupelian (Stampian), Calcaire à Astéries Formation.

DIAGNOSIS. — Carapace with granular ornamentation on inflated areas of regions; lateral margins crispate; anterolateral spines curving anteriorly.

MEASUREMENTS. — Measurements (in mm) taken on the dorsal carapace: maximum carapace width = 8.4; maximum carapace length = 6.9; length to position of maximum width = 3.3; fronto-orbital width = 6.4; frontal width = 2.5.

DESCRIPTION

Carapace hexagonal, wider than long, length about 80% maximum width, widest at position of last anterolateral spine, about half the distance posteriorly on carapace; carapace weakly vaulted longitudinally and transversely; inflated areas granular; lateral margins crispate, upturned.

Front damaged, about 30% maximum carapace width. Orbits wide, apparently with two fissures, outer-orbital spine triangular, directed forward; fronto-orbital width 75% maximum carapace width.

Anterolateral margins with five spines including outer-orbital spine; second spine broad, triangular, directed forward; third spine smaller, triangular, directed forward; fourth spine about same size as third; fifth spine apparently directed anterolaterally. Posterolateral margin appearing to be weakly

concave; posterolateral reentrant large, rimmed; posterior margin nearly straight, rimmed.

Epigastric region inflated, equant. Mesogastric region with long anterior process terminating at posterior end of epigastric regions, widened posteriorly, posterior portion pentagonal, posterior margin nearly straight. Protogastric regions hexagonal, weakly inflated. Urogastric region short, wide. Cardiac region wide, triangular, apex directed posteriorly, with two large, circular swellings anteriorly. Hepatic region depressed, small, flattened. Epibranchial region arcuate, extending from last anterolateral spine to near cardiac region, ornamented with granules. Mesobranchial region with longitudinal, granular swelling parallel and adjacent to axis, smooth laterally. Metabranchial region inflated parallel to posterior margin axially, disappearing laterally, granular.

Remainder of carapace and appendages unknown.

DISCUSSION

*Liocarcinus heintzi* n. sp. differs from all other species in the genus in possessing granular ornamentation on the most inflated portions of the carapace regions and in having crispate anterolateral margins terminating in upturned, forward directed anterolateral spines. The specimen is rather incomplete, with a broken front and damaged orbits so a complete description is not possible. However, it seems that *Liocarcinus* is the best generic placement for it at this time.

Family MACROPIPIDAE

Stephenson & Campbell, 1960

Genus *Pleolobites* Remy, 1960

*Pleolobites erinaceus* Remy, 1960

(Fig. 2E, F)

*Pleolobites erinaceus* Remy, 1960: 59, text-figs 4, 5; figs 10, 11 of the plate. — Glaessner 1969: R513, fig. 321.3. — Karasawa *et al.* 2008: 101.

TYPE MATERIAL. — Holotype (MNHN R03782, coll. Tessier); paratypes, 12 specimens (MNHN R03781, coll. Tessier).

OCCURRENCE. — Eocene of Fresco, Ivory Coast (Remy 1960).

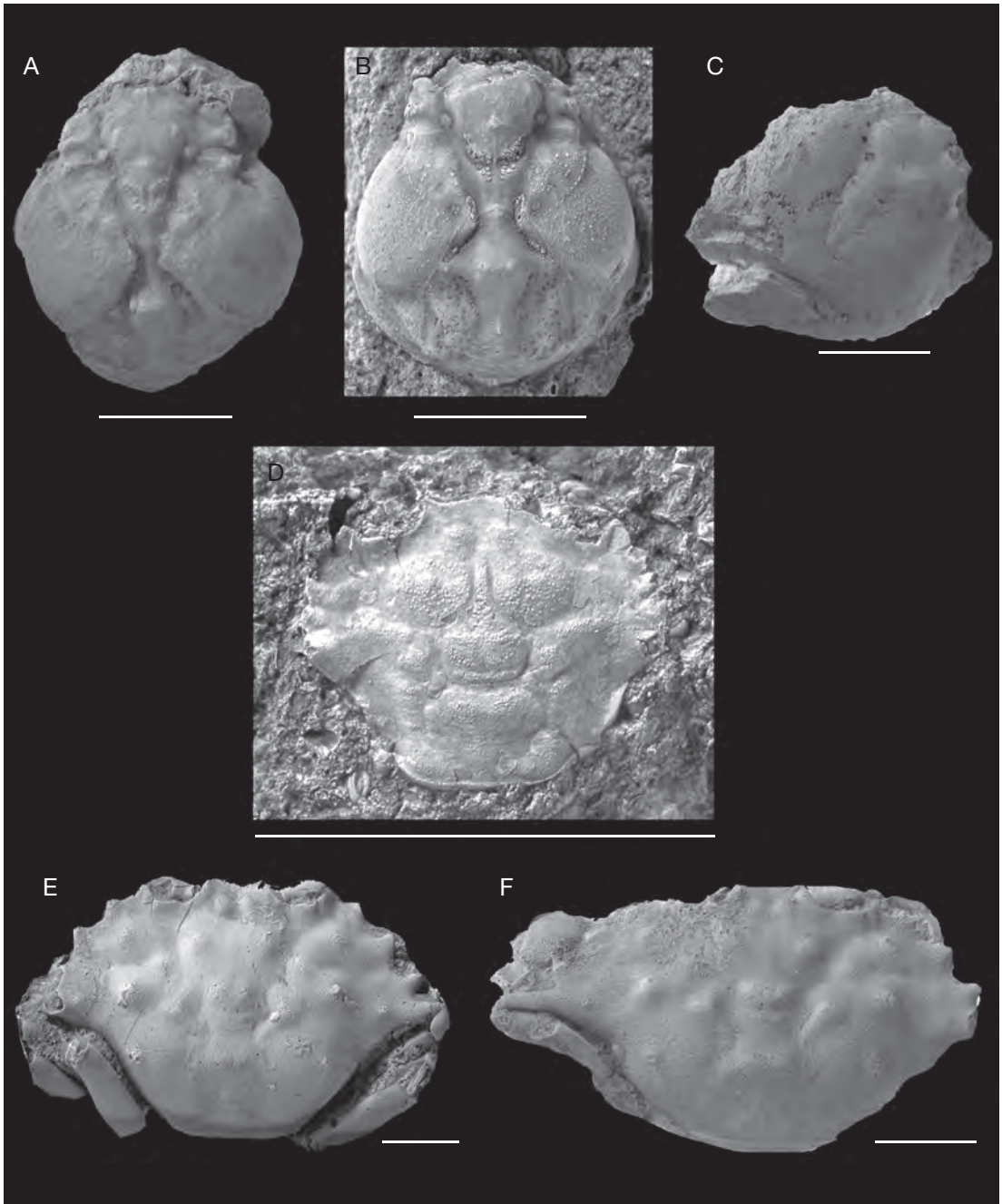


FIG. 2. — Fossil Brachyura from Monségur (Gironde, France): **A**, *Planobranchia simplex* (Remy, 1960) n. comb., cast of holotype, MNHN R03839, dorsal carapace; **B**, *Planobranchia laevis* (Lörenthey, 1909) n. comb., cast of holotype, IMDASif.Nr.25520/2005 (dorsal carapace); **C**, *Branchioplax? ballingi* Remy in Remy & Tessier, 1954, cast of holotype, MNHN R03793, fragmental dorsal carapace; **D**, *Liocarcinus heintzi* n. sp., holotype, R03778, dorsal carapace; **E**, **F**, *Pleolobites erinaceous* Remy, 1960, casts of holotype, MNHN R03782 (**E**), and MNHN R03781 (**F**). Scale bars: 1 cm.



FIG. 3. — Fossil Stomatopoda from Monségur (Gironde, France), *Ursquilla yehoachi* (Remy & Avnimelech, 1955), cast of holotype, MNHN R62691. Scale bar: 1 cm.

TYPE LOCALITY. — Probable Eocene rocks on the sea-cliff below Laga-Ghirobo hill, near Fresco, Ivory Coast, Africa (Remy 1960).

#### DISCUSSION

Karasawa *et al.* (2008) distinguished *Pleolobites* from the similar *Rhachiosoma* Woodward, 1871. They also noted the undocumented specimen in BSP indicating a Paleocene age for the genus and species. However, because the only well-documented material for *Pleolobites erinaceus*, the sole species of the genus, is indicated as Eocene, we can only regard it as Eocene at this time.

Subclass HOPLOCARIDA Calman, 1904  
Order STOMATOPODA Latreille, 1817  
Suborder UNIPELTATA Latreille, 1825  
Superfamily SQUILLOIDEA Latreille, 1802  
Family SQUILLIDAE Latreille, 1802

Genus *Ursquilla* Hof, 1998

TYPE SPECIES. — *Eryon yehoachi* Remy & Avnimelech, 1955, by original designation.

*Ursquilla yehoachi* (Remy & Avnimelech, 1955)  
(Fig. 3)

*Eryon yehoachi* Remy & Avnimelech, 1955: 311, pl. 14a.

*Ursquilla yehoachi* – Hof 1998: 258, figs 2-4.

TYPE MATERIAL. — Holotype by monotypy (MNHN R62691, coll. Yehoach).

Hof (1998) listed additional specimens.

TYPE LOCALITY. — Road from Beersheba to Mount Sedom, valley of Wadi Seiyal, Israel, Campanian (Upper Cretaceous) (Remy & Avnimelech 1955: 312).

#### DISCUSSION

At the time of preparation of the *Treatise on Invertebrate Paleontology*, classification of the stomatopods was considered to be quite simple (Holthuis & Manning 1969: R543). Holthuis & Manning (1969) referred the 24 genera of fossil and extant stomatopods to only two families. Since that time, extensive work on the group has resulted in a proliferation of suprageneric taxa so that Martin & Davis (2001) recognized seven superfamilies and 17 families of living forms. Far less proliferation of fossil taxa has resulted owing to the paucity of work on fossil stomatopods since 1969.

Hof (1998) restudied the type material of *Eryon yehoachi* as well as additional unidentified specimens and placed them into a new family and genus of stomatopod. Holthuis & Manning (1969: R541) had already tentatively assigned the holotype of *Eryon yehoachi* to *Squilla*; thus, recognition that it belonged within the Stomatopoda and not the Decapoda had been recognized for quite some time. Later, Ahyong (2008) synonymized Ursquillidae Hof, 1998, with Squillidae based upon comprehensive phylogenetic analysis including most fossils.

#### DISCUSSION

Remy's work has provided some of the few fossil decapods known from Africa. The collections he described from Africa, as well as the specimens he identified but never published from France, document a fauna with strong tropical influence as might be expected. The entire fauna contains three species

of the Calappidae, a matutid, and three members of the Carpilioidea, each from different families (Schweitzer 2003). Modern members of these groups are predominantly found in tropical areas (Rathbun 1930; Galil & Clark 1994; Schweitzer & Feldmann 2000). The region of western Africa and France has thus embraced a fauna tending toward the modern, at least in terms of family and ecological composition, since the Eocene.

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