

***Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879 from the French Cretaceous (Cenomanian) and placement of the family Lithophylacidae Van Straelen, 1936 (Crustacea, Decapoda, Brachyura)**

Danièle GUINOT

Département Milieux et Peuplements aquatiques,
Muséum national d'Histoire naturelle,
case postale 53, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
guinot@mnhn.fr

Gérard BRETON

Laboratoire Géosciences, Université de Rennes I, campus de Beaulieu,
263 avenue du Général-Leclerc, F-35042 Rennes cedex (France)
gerardbreton@free.fr

Guinot D. & Breton G. 2006. — *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879 from the French Cretaceous (Cenomanian) and placement of the family Lithophylacidae Van Straelen, 1936 (Crustacea, Decapoda, Brachyura). *Geodiversitas* 28 (4): 591-633.

ABSTRACT

Based on numerous and remarkably preserved specimens from the Upper Cretaceous, Cenomanian, at Lamnay and Le Mans (Sarthe), France, the fossil crab *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879 is redescribed. Characters which were thought not to be easily fossilized (rostrum, vulvae, female and male abdomen, male pleopods, thoracic sternal sutures, stridulating apparatus and the reduced fifth pereopod) are present. It was possible by careful clearing of the fossil crab from the matrix to expose most of the parts, so that the structures could be studied almost as completely as in a recent species. *Lithophylax trigeri* is one of the most complete brachyuran crabs so far discovered from the Cenomanian, from the Cretaceous in general, and even more recently. The monotypic family Lithophylacidae Van Straelen, 1936 is redefined, and its relationships with the fossil and extant brachyuran families known from the Cretaceous, in particular the Carcineretidae Beurlen, 1930, Necrocarcinidae Förster, 1968, Hexapodidae Miers, 1886, Retroplumidae Gill, 1894, Palicidae Bouvier, 1897, and the Goneplacidae MacLeay, 1838, are discussed.

KEY WORDS

Crustacea,
Brachyura,
Lithophylacidae,
Lithophylax,
stridulating apparatus,
Cretaceous,
Cenomanian,
Maine (France),
taphonomy.

RÉSUMÉ

Lithophylax trigeri A. Milne-Edwards & Brocchi, 1879 du Crétacé de France (Cénomanién) et statut de la famille des Lithophylacidae Van Straelen, 1936 (Crustacea, Decapoda, Brachyura).

Grâce à la découverte de nombreux spécimens remarquablement préservés du Crétacé supérieur (Cénomanién), trouvés en France à Lamnay et au Mans (Sarthe), le crabe fossile *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879 est redécrit. Plusieurs structures (rostre, vulves, abdomen femelle et mâle, pléopodes mâles, sutures sternales thoraciques, appareil de stridulation, et dernier péréopode, réduit), supposées ne pas se fossiliser aisément, sont présentes. Un minutieux dégagement a permis d'exposer la plupart des régions du crabe, si bien que son organisation a pu être étudiée presque aussi complètement que chez une forme actuelle. *Lithophylax trigeri* est l'un des Brachyours les plus complets découverts à ce jour, du Cénomanién, du Crétacé en général, voire plus récemment. La famille monotypique des Lithophylacidae Van Straelen, 1936 est redéfinie, et ses affinités avec les familles brachyouriennes actuelles et éteintes connues depuis le Crétacé, en particulier les Carcineretidae Beurlen, 1930, Necrocarcinidae Förster, 1968, Hexapodidae Miers, 1886, Retroplumidae Gill, 1894, Palicidae Bouvier, 1897 et les Goneplacidae MacLeay, 1838, sont discutées.

MOTS CLÉS

Crustacea,
Brachyura,
Lithophylacidae,
Lithophylax,
appareil de stridulation,
Crétacé,
Cénomanién,
Maine (France),
taphonomie.

TABLE OF CONTENTS

Introduction	593	Other brachyuran crustaceans reported from the stratotypic Cenomanian with <i>Lithophylax trigeri</i>	608
Abbreviations	593	Discussion	610
Occurrence and stratigraphy	594	Lithophylacidae vs Carcineretidae Beurlen, 1930	612
Middle-upper Cenomanian	594	Lithophylacidae vs Necrocarcinidae Förster, 1968 and Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003 ...	615
Lower Cenomanian	595	Lithophylacidae vs Hexapodidae Miers, 1886 ..	617
Material examined and prepared	595	Lithophylacidae vs Retroplumidae Gill, 1894 ..	618
Middle-upper Cenomanian material	595	Lithophylacidae vs Palicidae Bouvier, 1898	620
Lower Cenomanian material	596	Lithophylacidae vs Goneplacidae MacLeay, 1838	620
Method	596	Conclusion	622
Taphonomy	597	Acknowledgements	623
Cuticular structure	597	References	623
Petroglyphy of the nodules	598	Annexe	631
Paleoecology and ethology	600		
Systematics	600		
Family Lithophylacidae Van Straelen, 19366 ...	600		
Genus <i>Lithophylax</i> A. Milne-Edwards & Brocchi, 1879	602		
<i>Lithophylax trigeri</i> A. Milne-Edwards & Brocchi, 1879	602		
Remarks on the stridulating apparatus	607		

INTRODUCTION

Abundant material of the rare and not well known fossil crab, *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879, was collected by one of us (GB) from the Upper Cretaceous (Cenomanian) of France in the Louvre quarry, Lamnay (Sarthe, France). Several specimens of the same species, from the stratotypic middle-upper Cenomanian of Le Mans (Sarthe), were also discovered in the collections of several institutions.

The genus *Lithophylax* was established by A. Milne-Edwards & Brocchi (1879: 116) for *L. trigeri* collected by J. Triger in the "Grès verts du Maine" (Cenomanian Greensand of the Maine: terminology in Rathbun 1935: 57). The same species was also collected in the same place by Guéranger but not published in his 1867 papers. A. Milne-Edwards & Brocchi (1879), based on males and females, characterized the species as having a transversally hexagonal carapace, extremely narrow front, and large and bipartite orbits that implied particularly well developed eyes, presumed to be carried on angled stalks. No figure was provided. The genus was assigned to the "tribu Gonéplaciens" H. Milne Edwards, 1837 (Goneplacidae MacLeay, 1838). *Lithophylax trigeri* was again quoted as "rather frequent" by Guillier (1886: 238, 244) in the "Sables supérieurs à *Rhynchonella compressa*" (middle-upper Cenomanian) of the Sarthe Department. Juignet (1974) provided a history and synonymy of the stratigraphic units of the Cenomanian stratotype.

Lithophylax trigeri was not recorded for a long time. A new record from the same geologic formations ("Sables à *Rhynchonella compressa*") was given by Van Straelen (1936: 43, pl. 4, fig. 9), who presumably saw the original material of A. Milne-Edwards & Brocchi and established a separate family, the Lithophylacidae Van Straelen, 1936. Unfortunately, Van Straelen's small figure of a topotype does not provide a good idea of the characters of *L. trigeri*. Neither the species nor any lithophylacid representative has had ever been found since. The hypotheses about the systematic status of the family Lithophylacidae have been rare and made with reservation, the genus *Lithophylax* being considered either *incertae sedis*,

or goneplacid, or portunid, or carcineretid with more agreement.

The present paper reports on exceptionally well preserved specimens of *Lithophylax*, where most parts were rescued by gently removing the matrix in several individuals. The under parts were visible after the matrix was removed. Male pleopods, vulvae, and the reduced fifth pereopod, characters that are believed not to be readily fossilized, were present. The antennular and antennal regions, and the distal part of the eyes were unfortunately not preserved. A spectacular stridulating apparatus has been found and prepared. It was possible to study the external structures of *Lithophylax* almost as completely as in a recent species. *Lithophylax trigeri* proved to be one of the most complete crabs so far discovered from the Cenomanian, and even from the Cretaceous. The partial elimination of the abdomen, which allowed the observation of the vulvae and gonopods, clearly allowed its placement in the Heterotremata Guinot, 1977.

Slight morphological differences between lower Cenomanian and middle-upper Cenomanian material seem to be not regarded as specific and are not sufficient to warrant naming it a new species.

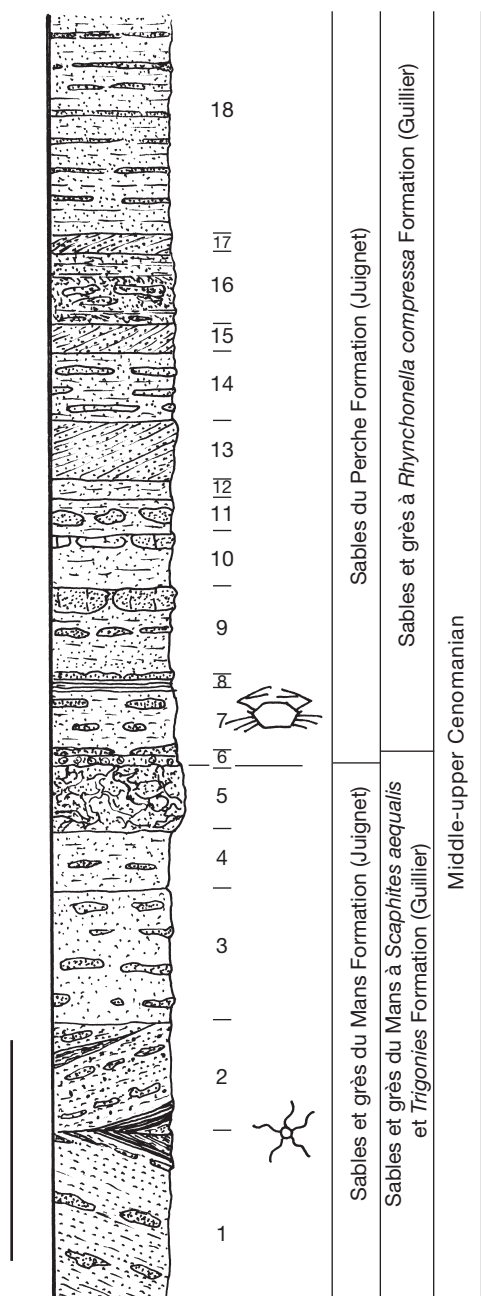
ABBREVIATIONS

A1-A6	abdominal segments (or somites) 1 to 6;
G1	first male pleopod or first gonopod;
G2	second male pleopod or second gonopod;
LC	lower Cenomanian material;
L/W	length/width;
MUC	middle-upper Cenomanian material;
mvp3	third maxilliped;
P1-P5	first to fifth pereopods;
1/2-7/8	thoracic sternal sutures 1/2 to 7/8.

The material used in this study is deposited in the following institutions:

MHNH	Muséum d'Histoire naturelle, Le Havre (Seine-Maritime);
MHN LM	Musée d'Histoire naturelle ("Musée Vert"), Le Mans (Sarthe);
MNHN	Muséum national d'Histoire naturelle, Paris, Domaine Sciences de la Terre;
LGUC	Laboratoire de Géologie, Université de Caen (Calvados);
RBINSB	Royal Belgian Institute of Natural Sciences, Brussels.

Measurements of carapace length × carapace width and coxae length × diameter are given in millimeters (mm).



OCCURRENCE AND STRATIGRAPHY

MIDDLE-UPPER CENOMANIAN (FIG. 1)

During the 19th century the stratotypic Cenomanian, in and around the French town of Le Mans (Sarthe), provided a large amount of good fossils. The so-called “carrière de la Butte” (“Butte de Gazonfier”) and the neighbouring “carrière de la Butte Sainte-Croix” within the town of Le Mans permitted local collectors such as J. Triger or E. Guéranger to gather important collections of fossils (Delaunay 1937, 1938; Breton 1996). Guéranger published in 1867 the “Album paléontologique du département de la Sarthe” in which each plate is a photograph of one drawer of his collection. One “normal” (1867b) and one “miniature” (1867a) edition, plus some unpublished plates housed in the “Musée Vert” of Le Mans, show echinoderms, worms, sponges, corals, bryozoans, foraminifera, brachiopods, and mainly molluscs, but no crustaceans. Guéranger (1867a: 9) stated that his “Album paléontologique” was a beginning and that forthcoming books would appear. Nevertheless, this work remained unfinished.

In the 1970s, one of us (GB) saw in the Guéranger collection (at that time housed at the Laboratoire de Géologie of the Université du Maine) a drawer prepared to be photographed, with seven brachyuran specimens (MHN LM 2005.1.1 to 1.7) and several other crustaceans, all from the “couches à Crustacés” (see below). Nicolas Morel, curator of the “Musée Vert” (pers. comm.), confirmed that Edouard Guéranger was in the habit of collecting fossils in the “Butte de Gazonfier” quarry between 1845 and 1865.

The “Butte de Gazonfier” quarry exposed about 30 m of middle-upper Cenomanian (Fig. 1), according to Guillier (1886) and Juignet (1974: fig. 124): – 12 m of sand, with 1.5 m thick bed of coarse glauconitic sandstone at the top (the hard ground “Jalais”) (beds 1 to 5 of Juignet [1974]: upper part of the “Sables et Grès du Mans” Fm; Jukesbrownei biozone).

FIG. 1. — Butte de Gazonfier quarry, Le Mans (Sarthe), lithostratigraphic section, modified from Juignet (1974) and Guillier (1886): **1, 2**, cross-bedded sand and sandstone with lenses of grey clay with perfectly preserved echinoderms (*Konservat-Lagerstätte*); **3**, yellowish sand with ferruginous sandstones; **4**, green sand and sandstone; **5**, hard ground “Jalais”; **6**, calcareous sandstone with nullipores; **7**, argillaceous sand and sandstone, phosphatic nodules with crustaceans [original bed of specimens MHN LM 2005.1.1 to 1.7]; **8**, compact clay; **9-11**, argillaceous sand and sandstone [**11** has provided *Raninella trigeri*]; **12**, coarse sand; **13, 15, 17**, cross-bedded coarse sand; **14, 16, 18**, argillaceous sand, beds of clay and sandstone. Scale bar: 5 m.

– 17 m of sand, sand with clay, clay and sandstone, beginning with 0.15 m of calcareous sandstone with nullipores (beds 6 to 18 of Juignet [1974]: “Sables du Perche” Fm; top of the Jukesbrownei and Guerangeri biozones). The so-called “couche à Crustacés” is located in the first lower meter of the Sables du Perche.

LOWER CENOMANIAN (FIG. 2)

The Louvre quarry was opened during the 1970s and 1980s. It was located at Lamnay (Sarthe), halfway along the road towards Saint-Maixent (Lambert coord.: x = 476.45; y = 346.55). This quarry is now closed.

Juignet (1974: fig. 114) gave a section of the upper beds of this quarry. One of us (GB) drew a section of the lower part of the quarry in 1983 while collecting the crabs:

– 3.50 m (observable, bed 1a): dark grey sand with ferruginous beds in the lower part, becoming in the upper 1.50 m a fine medium grey sand with a bit of clay, glauconite and mica. The top is a very thin, 1 cm thick, discontinuous bed of white clay. The crabs are located in nodules, scattered in the two upper meters, but are more abundant about 0.80 m under the white clay.

– 0.25 m (bed 1b = couche 1 of Juignet [1974]): sand with clay, khaki coloured, with lenses of calcareous sandstone coquina at the upper part.

– (bed 2 = couche 2 of Juignet [1974]): glauconitic calcareous sand to sandstone, with numerous internal moulds of molluscs.

The whole section (Fig. 2) is lower Cenomanian, Sables et Grès de Lamnay Fm, Mantelli (Saxbii) and Dixoni biozones. According to Juignet (1980), the Sables et Grès de Lamnay Formation constitutes, off the Armorican Massif, a sandy bar in a strong hydrodynamic environment, and periodically close to emersion. Our crab bearing fine grained sand may represent a lower energy bed, in the open sea, well oxygenated and photic.

MATERIAL EXAMINED AND PREPARED (ANNEXE: TABLE 1)

It was possible to trace the original material collected by J. Triger and described by A. Milne-Edwards &

Brocchi (1879) (see Type material of *L. trigeri* in Systematics).

MIDDLE-UPPER CENOMANIAN MATERIAL

– Seven specimens, collected by Guéranger, “Butte de Gazonfier” quarry, Le Mans; “Sables du Perche” Formation, middle-upper Cenomanian, Jukesbrownei-Guerangeri biozones (MHN LM 2005.1.1 to 1.7).

– Five specimens, same origin and collection, originally attached to a green cardboard, labelled “*Palaeoplax Trigeri* Milne-Edw. Zône de la *Rhynchonella compressa*. Localité: Le Mans (‘Carrière de la Butte’)”. The precise stratigraphic origin is not the same for all the specimens: four specimens (MHN LM 2005.1.9 to 1.12) come from the “couche à Crustacés” and are preserved in phosphatic nodules; and one specimen (MHN LM 2005.1.8), without appendages, from unknown precise origin, is preserved in a glauconitic sandstone.

– Ten specimens, same origin and collection, without original label (MHN LM 2005.1.13 to 1.22). The specimen MHN LM 2005.1.13, which shows a ventral surface, is preserved in a glauconitic sandstone; the other ones are preserved in phosphatic nodules.

– Two additional specimens and one plaster cast, same origin, unregistered (MHN LM).

– Five specimens, Boutillier collection, unregistered (LGUC), labelled: “Fragments de Crustacés (Le Mans) – Sarthe – Cénomaniens. Rare”. Probable origin: Butte de Gazonfier Quarry, Le Mans (Sarthe), Sables du Perche Fm, “couches à Crustacés”, middle-upper Cenomanian, Jukesbrownei-Guerangeri biozones. All are preserved in phosphatic nodules, and one specimen is fossilized holding a coprolite (Breton 2006).

– One specimen from the Van Straelen collection (RBINSB), labelled: “coll. Bosquet I.g. 4285 / Van Straelen déterm. 1936. Ce spécimen provient vraisemblablement du Cénomaniens, sables à *Rhynchonella compressa* du Mans (départ. de la Sarthe)”. We consider that it is a topotypical specimen of *Lithophylax trigeri*. Conversely, we think that a second specimen (in study) from the Van Straelen collection RBINSB does not correspond to *Lithophylax trigeri*. It is labelled “101

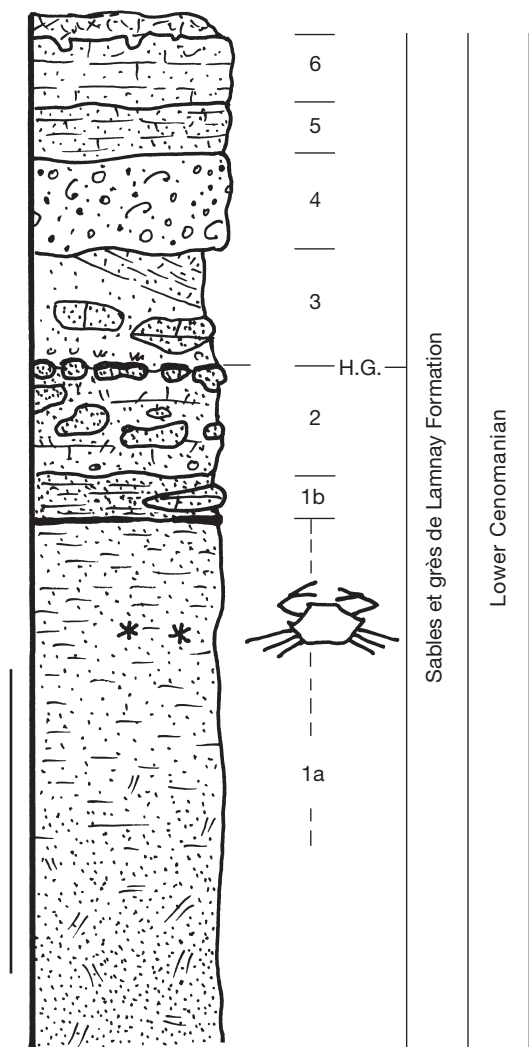


FIG. 2. — Louvre quarry, Lamnay (Sarthe), lithostratigraphic section (2-6 from Juignet 1974: fig. 14): **1a**, dark to medium grey fine sand (the two asterisks indicate the level where phosphatic nodules with crabs have been collected *in situ*; dash line indicates the overall vertical extension of nodules containing crabs); **1b**, sand and calcareous sandstone with clay, khaki coloured; **2**, glauconitic calcareous sand to sandstone with internal moulds of molluscs; surface at the top (**H.G.**) is lateral equivalent to hard-ground Lamnay; **3**, sand and sandstone with gravels, locally cross-bedded; **4**, massive sandstone bivalve coquina, with gravels and pebbles; **5**, **6**, calcareous sandstone. Scale bar: 2 m.

Arthr. Second. II Et. Cénomanién Loc. Prat Périé (Corbières méridionales) Don: V. Van Straelen IG 12692 / Van Straelen déterm. 1938 *Lithophylax trigeri* A Milne-Edwards & Brocchi ?".

LOWER CENOMANIAN MATERIAL

– Thirty six specimens, Louvre Quarry, Lamnay (Sarthe); Sables et Grès de Lamnay Formation, lower Cenomanian, limit of the Mantelli-Dixoni biozones, all collected by one of us (GB) in 1983 and all prepared. Five additional specimens, same origin, were unprepared. These specimens have been shared out between:

- Muséum d’Histoire naturelle du Havre, Le Havre (MHNH 9186 to 9209 and 9211 to 9217);
- Muséum national d’Histoire naturelle, Paris, Domaine Sciences de la Terre (MNHN A 24793 to 24797).

METHOD

The specimens MHN LM 2005.1.1 to 1.7 and most of the specimens collected in 1983 in the Louvre quarry were prepared (by GB) using a hand-held needle under a Leica MZ6 stereomicroscope. At each significant step, a camera-lucida drawing and/or a photograph was made. Fossils were cleaned in an ultrasonic tray. One specimen, hollow and thus less resistant than the embedding nodule, was broken in the attempt to prepare it quickly by squeezing it in a vice. The fossil was crushed, revealing delicate fossilization of all thoracic endophragmes, but it was inadequate for good preparation of the external morphology. A thermic shock was administered to two fossils by dropping them in cold water after heating with a gas-torch: the preparation seemed to be a little easier but the fossils became very brittle, and this technique was not carried on further. A thin section in a crab-bearing nodule from Lamnay was examined under transmitted-light and polarized-light microscope (see Taphonomy).

A very delicate cast in order to reveal the course of the thoracic sternal sutures 4/5 to 6/7, in particular at the level of their deep depressions, was made with silicone rubber under vacuum.



FIG. 3. — Unprepared phosphatic nodule containing *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879, frontal view; Gazonfier quarry, Le Mans (Sarthe); Cenomanian; coll. Guéranger, MHN LM 2005.1.14. Scale bar: 5 mm.

Drawings, with a camera lucida on the Leica MZ6 stereo-microscope, were made (GB) either as seen under the microscope, or turning the fossil under the microscope in order to always keep the optical axis of the microscope perpendicular to the observed part: this peculiar technique better displays the exact shape of every part, and is quoted as “same-plane view” in the drawings captions. Photographs were taken with a macro-objective for the low magnifications up to 2 \times , or with the stereo-microscope: the last decimal figure is thus not significant, but results from the conversion of the micrometric scale into millimeters.

TAPHONOMY (BY GB) (FIGS 3; 4)

A thin section in a phosphatic nodule, obliquely intersecting the merus of three pereopods of *Lithophylax trigeri*, partly exposed at the surface of the nodule (see Occurrence and stratigraphy, Louvre quarry), permitted description of the structure of the cuticle and the petrography of the nodule (Fig. 4).

CUTICULAR STRUCTURE

The cuticular structure of fossil brachyuran crabs has been rarely studied (see Roer & Dillaman 1984; Feldmann & Thsudy 1987 for details on crustacean cuticle). Comparative cuticle microstructure of fossil decapods have been studied (Waugh & Feldmann 2002, 2003) with a classification aim. Comparison of cuticular ultrastructure of the Miocene homolodromiid *Antarctidromia inflata* Förster, 1985 with that of the confamilial, extant *Homolodromia paradoxa* A. Milne-Edwards, 1880 suggests that the more rigid carapace of the fossil form results from a relatively thicker, more strongly calcified exocuticle (Feldmann & Gazdzicki 1998). Structure, patterns, and function of cuticular terraces in Recent and fossil have been summarized (Schmalfuss 1978); carapace terraces in the Raninidae and, more generally, in Recent sand-dwelling crabs are associated with penetration into a loose substrate or burrowing (Savazzi 1981, 1982). Vega *et al.* (1994) gave an excellent account of the cuticular structure of the Maastrichtian retroplumid *Costacopluma mexicana* Vega & Perrilliat, 1989, and its phosphatic epigeny. The cuticle structure in several Late Cretaceous and

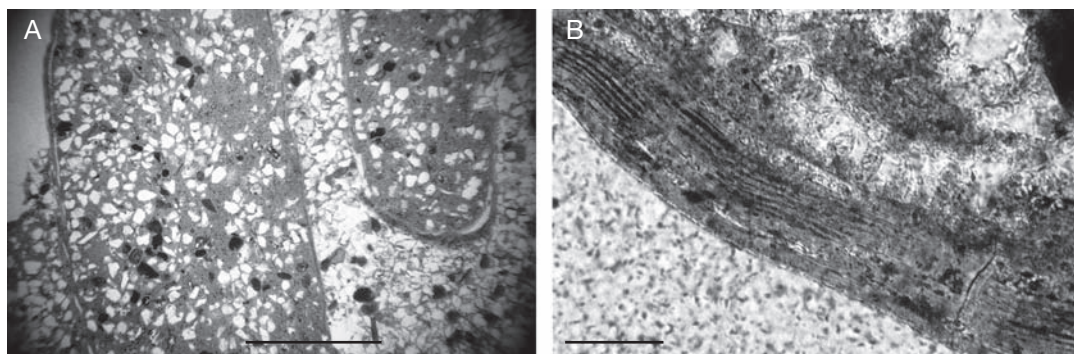


FIG. 4. — Thin sections in a nodule containing *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879; Louvre quarry, Lamnay (Sarthe), lower Cenomanian; transversal section of pereopods; bright field; **A**, overall view; **B**, cuticle structure. Scale bars: A, 1 mm; B, 50 µm.

Early Tertiary crabs was recently reviewed (Vega *et al.* 2005b).

The cuticle of *Lithophylax trigeri* shows:

– 1) an external layer, here interpreted as the exocuticle, is 12 µm thick (at one precise point, the thickness being variable), homogeneous but locally lamellar (lamellae are underlain by dark pigments parallel to surface). An external lamella 2-3 µm thick is locally visible and interpreted as the epicuticle. It is either more birefringent than the rest of the external layer, or epigenetically altered in silica (low birefringent calcedonite). Contrary to *Costacopluma mexicana*, no cellular or cellular-like structure can be seen in this external lamella.

– 2) an internal layer, interpreted as the endocuticle is 60 µm thick (measured at the same point, laminated with 10 to 20 lamellae underlined by: a) dark pigmented grains 2-3 µm, sprinkled between the laminae, and b) local peeling between the laminae, as well as between the internal and the external layers.

Locally, canals perpendicular to the surface (possible tegumental ducts, see Vega *et al.* 1994) cross the endocuticle. They are most visible in the thinnest parts of the cuticle.

PETROGRAPHY OF THE NODULES

The matrix of the fossils is a phosphatic sandstone.

The particles include: well calibrated, 100-150 µm quartz clasts, rounded 100-150 µm grains of glauco-

nite, brown ferruginous alteration frequent; grains of limonite are the final step of the alteration of the glauconite grains; and calcite grains and micas (muscovite and altered biotite) are rare.

The cement is collophane. Locally, crystals (carbonate-hydroxyapatite?) 2-5 µm are visible in pores, cavities or peelings between the laminae of the cuticle. Phosphatic cement is more compact and darker (dark brown) inside the pereopods. Outside the pereopods, it is honey-coloured and located around the particles, but leaving pores. At high magnification, the dark pigments scattered in the cement are *pro parte* argillaceous minerals, but mainly evoke a biological origin: micro-organisms or bacteria as rod-shaped bacilla, myceloid bacteria, and ring-shaped forms. Allison (1988: 1096) described possible bacterial microspheres in the cement of phosphatic concretions bearing crustaceans from the London Clay, and stated that the early precipitation of phosphates is due to microbial activity.

On the whole surface of the thin section, “traditional” microfossils are rare (because they are not preserved?) and often reworked: one sponge spicule (acanthostyle), some foraminifera, bryozoa, and unidentified spheroradiate structures.

Average shape of phosphatic nodules bearing *Lithophylax trigeri* specimens is roughly concentric to the fossil, ellipsoidal, often flattened and with a concavity between the claws (Fig. 3). As a rule, the extremities of the pereopods P1-P4 are truncated at the surface of the nodules and thus are

not preserved. Within each nodule, cementation on average increases toward the centre (practically, the beginning of the work of preparation is always much easier than the end). However, this increase is irregular, and more cemented zones, 1–5 mm wide, neighbour weakly cemented ones, from the surface up to the contact of the fossil. The difficulty of the final preparation in contact with the cuticle of the crab is increased both by the hardening of the matrix and by the fact that parts of the crab can be hollow, not infilled with sediment. This is particularly true with appendages, antero-lateral and posterior parts of the cephalothorax.

As already noted by Mertin (1941), Schäfer (1951) and Glaessner (1969), Bishop (1986: 329) wrote: “One of the challenges in interpreting decapod remains is attempting to distinguish those that were corpses from those that were molts at the time of burial”.

The position of the crabs from the Louvre quarry as well as those from the Butte de Gazonfier quarry is nearly always the same: sternal and dorsal parts of the cephalothorax in anatomical connection; carapace weakly shifted with respect to the thoracic sternum (always less than 2 mm) and most frequently not shifted at all, rarely slightly lifted posteriorly; P1 tucked along the front, exhibiting the propodi in frontal view, claws semi-closed; P2–P4 extended laterally (P5 is much reduced). This is nearly a “normal” position as defined by Bishop (1986: 331), which may constitute proof that fossils were corpses at the time of the burial, but this position could also result from the burial of molts.

Breton (2001) and Breton *et al.* (2004) have described the exuviae found in a similar position for an extant majoid crab, *Inachus phalangium* (Fabricius, 1775). In a discussion about the taphonomy of the Upper Cretaceous *Longusorbis cuniculosus* Richards, 1975 assemblage, Richards (1975) asserted that exuviae of crabs can fossilize in a normal, relaxed position and not necessarily in the Open Molt Position (Bishop 1986), also called Salter’s position (Schäfer 1951). On one hand, molts being open are readily infilled with sediment after burial. On the other hand, the production of gas during the decay of the soft part of the corpse acts as an obstacle to the penetration of sediment. Hollow parts of the

appendages or the cephalothoracic cavity would then speak in favour of burial of corpses, instead of molts. Our unsuccessful attempt to prepare one specimen by squeezing it in a vice showed that its cephalothoracic cavity was partly empty, and partly infilled with tiny coprolites.

More often, the cephalothorax cavity is only partly infilled. One individual from the Louvre quarry exhibits a carapace and some articles of the legs filled with a sediment rich in microcoprolites. These microcoprolites appear, where the cuticle is not preserved, as dark brown phosphatized pellets measuring 0.5×0.35 mm under the carapace, slightly smaller in the legs, and packed tight locally under the posterior part of the carapace. Some other specimens exhibit, to a lesser extent, similar microcoprolites. This indicates that corpses – not molts – were buried, and the organic matter was exploited *in situ* by small scavengers. Collins & Jakobsen (2003: 65, pl. 8, fig. 1a, b) and Collins *et al.* (2003: 222, pl. 7, fig. 9a, b) have described carapaces of phosphatized Eocene crabs (*Panopeus bessmani* Collins & Jakobsen, 2003) and Pleistocene crabs (*Macrophthalmus (Mareotis) wilfordi* Morris & Collins, 1991) filled with possible even-sized faecal pellets *c.* 2 mm in length. Collins *et al.* (2003) therefore remarked that “another interpretation of these pellets could be that they are the result of bacterial induced phosphatizations of soft anatomy”. Among the specimens of *Lithophylax trigeri* that were examined, one individual (Boutillier coll., LGUC, unregistered) contains a long, cylindrical coprolite (1 mm in diameter), in which ovoid pellets are approximately helically tight (Breton 2006). These pellets, here with an obvious faecal origin, in a very close sedimentological context, are identical to those infilling the carapace of several *Lithophylax trigeri*, which are thus interpreted to be true coprolites of a scavenger.

The supposed absence of exuviae among our fossils would be consistent with the fact that decaying organic matter facilitates phosphate precipitation and nodulization (Benmore *et al.* 1983; Allison 1988). Contrary to molts, corpses contain more organic matter and are thus able to be preserved in early phosphatic concretions. The absence of exuviae in our material would then be preservational.

Disarticulation and other distortions of the body are weak or rare. Coxo-basis elongation(s), buccal parts displacement, disarticulation or absence of abdominal somites, distortion of the abdomen can be observed, but only weakly and not as a rule. They can always be explained either by a decay-produced gas inflation or by the preburial or postburial action of a scavenger. No peculiar ichnological feature – no burrow, no boring – was observed in the field, in the phosphatic nodule or in the surrounding sand. No mechanical action (hydrodynamics, compaction) was observed. Carapace and P1-P4 are almost never broken; the body is never flattened nor crushed. This indicates that phosphatization and hardening of the fossil took place very early in the diagenetic process and predate compaction.

This early phosphatization permitted an exceptional preservation. All the originally calcitic parts are phosphatized. As a result, delicate organs have been preserved: eyestalks, mxp3, buttons of the press-button, male gonopods, with in one case G2 *in situ* inserted inside G1, and circular hole on P5 coxa, interpreted to be the male gonopore, preserved in one individual. Consequently the work of preparation has resembled the dissection of a living crab – hardness of the matrix apart. The parts of the body that were not preserved are the uncalcified parts in crabs (e.g., the extremities of the eyes, the female pleopods) or the parts external to the nodules (e.g., the distal parts of P2-P4).

PALEOECOLOGY AND ETHOLOGY

Without any preserved burrow, contrary to *Longu-sorbis cuniculosus* Richards, 1975 (Richards 1975) and without any special burrowing adaptative feature, *Lithophylax trigeri* was probably not a burrower. We suggest that *L. trigeri* lived on a soft, fine-grained bottom, under infratidal conditions and buried itself in the soft sediment (for the distinction between the burying and burrowing behaviours, see Bellwood 2002). The developed eyes (stout stalks, thick basophthalmite and presumably long podophthalmite) could be adaptative in order to

let only the eyes stick out when the crab is buried (see Discussion).

One of us (GB) has often observed living infratidal crabs (see Vincent & Breton 1999). Their behaviour, when stressed, falls into four kinds of responses to danger: 1) run away, sometimes after a tentative intimidation position (e.g., *Carcinus maenas* (Linnaeus, 1758); 2) shelter under a stone, or among algae, sea grasses or a sea-anemone (e.g., *Pilumnus birtellus* (Linnaeus, 1761) and *Eriphia verrucosa* (Forsskål, 1775)); 3) remain still (e.g., *Cancer pagurus* Linnaeus, 1758; *Dromia personata* (Linnaeus, 1758)); and/or have a specific posture interpreted, in the case of *Inachus phalangium*, as an automimicry of the exuvia (Breton *et al.* 2004); and 4) if the sediment is soft, bury themselves rearwards, up to the front, so that the eyes just point out of the sediment (e.g., *Carcinus maenas*, *Polybius depurator* (Linnaeus, 1758), *Rithropanopeus harrisi* (Gould, 1841), *Hemigrapsus penicillatus* (De Haan, 1835)); this last behaviour is constant for *Corystes cassive-launus* (Pennant, 1777) (see Hartnoll 1972).

SYSTEMATICS

Order DECAPODA Latreille, 1802

Infraorder BRACHYURA Latreille, 1802

Section EUBRACHYURA Saint Laurent, 1980

Subsection HETEROTREMATA Guinot, 1977

Family LITHOPHYLACIDAE Van Straelen, 1936

Lithophylacidae Van Straelen, 1936: 43. — Stenzel 1953: 215. — Glaessner 1969: R514.

TYPE GENUS. — *Lithophylax* A. Milne-Edwards & Brocchi, 1879 by monotypy. No other genus included.

DESCRIPTION

Carapace broad, hexagonal to inverted trapezoidal, widest at outer-orbital angles, each marked by strong tooth. Antero-lateral margins strongly diverging anteriorly, markedly slanted. Dorsal surface lobulated throughout surface. Cervical, gastro-cardiac, branchio-cardiac grooves deep, resulting in H-shaped depression on each side. Gastric pits deep.

Front long, straight, not toothed, projecting medially in narrow, ventrally deflected, non-grooved rostrum. Frontal and orbital margins forming same line, with only minute fissure at mid- of supra-orbital margin. Orbits extremely broad (long orbital margins posteriorly sloping), deep, obliquely directed towards the axis of carapace, divided into two fossae. Eyes with stout stalks, basophthalmite thick; podophthalmite presumably much developed, presumably with inflated cornea. Well defined area (“shutter”) beneath suborbital region. Endostome wide. Mandibles extremely strong. Mxp3 clearly diverging, directed obliquely, with large gap between. Endopodite with rectangular ischion and wide merus; palp articulating on anteromesial corner of merus; exopodite broad. Pleural line typically ventral. Thoracic sternum wide. Sternal sutures 1/2 and 2/3 marked, complete; suture 3/4 replaced by sinuous ridge; sutures 4/5 to 7/8 marked by depressions, deep for 4/5 and 5/6, terminal for 4/5 and 7/8; suture 4/5 interrupted axially; suture 5/6 prolonging beyond deep depressions, thus presumed to be complete; suture 6/7 not interrupted axially, complete; suture 7/8 extremely short, only lateral. Sternites 1 and 2 narrow, not fused; sternites 4–6 widened; most of sternite 7 covered by male abdomen; sternite 8 subdorsal, reduced, narrow, covered by abdomen in both sexes, not visible dorsally. Median line on sternite 7. Wide sterno-abdominal cavity. Male and female abdomens only weakly dimorphic. Male abdomen with all segments free, covering most part of sternite 4, widely triangular; first segments (1–3) completely filling space between coxae of pereopods; telson triangular. Sexual openings typically heterotreme: vulvae on sternites 6; male gonopores located on P5 coxae. G1 long, slender, with simple apex; G2 relatively long, only slightly shorter than G1. Configuration of press-button type for abdominal maintaining. Chelae massive, clear heterochely, weak homodonty; hand not carinated. P2–P4 markedly long, elongated, merus thick, enlarged, compressed. P5 subdorsal, markedly reduced; merus narrow, slender; other articles not preserved. Specialized stridulatory apparatus may be present: pars stridens on merus of P1 consisting of well defined, elongated area bearing several prominent striae;

plectrum consisting of row of spaced tubercles on the suborbital region.

REMARKS

The family Lithophylacidae was established by Van Straelen (1936: 44, pl. 4, fig. 9) for the sole *Lithophylax*, with a small illustration of a topotype, showing the large orbits. It was characterized by a subhexagonal carapace, straight fronto-orbital margin and grooves on the branchial regions. Van Straelen (1936: 44) placed the family close to the Goneplacidae, in remarking however: “Il peut paraître étrange de trouver déjà au Cénomaniens une forme se rattachant aux phylums les plus élevés parmi les Brachyryncha”.

In absence of any new records of *Lithophylax trigeri*, the placement of this Cenomanian fossil was rarely evoked. The family has remained poorly known because of the insufficient illustration, and the relationships of the family have not been discussed in the carcinological literature. *Lithophylax* was initially attributed to the Goneplacidae by A. Milne-Edwards & Brocchi (1879) and later included in the tribu “Goneplacidea” by Van Straelen (1936), then considered *incertae sedis* by Glaessner (1929: 236), and finally placed with reservation within the Carcineretidae Beurlen, 1930 by Glaessner (1969: R514: “Wide carapace and narrow front, comparable with the distinction of Podophthalminae among Portunidae”), Bishop (1988: 247), Vega & Feldmann (1991: 172, 173), Vega *et al.* (1995: 345) and, with confidence, by Schweitzer *et al.* (2002a: 21; 2003a: 44), based on wide carapace, dorsal areolation, narrow and deflected front, large orbits, developed eyestalks and massive chelae. According to Feldmann & Villamil (2002: 721), who followed Rathbun (1935: 52), *Lithophylax* was “probably a portunid”. Presently, *Lithophylax* is referred to the Carcineretidae, one of the heterotreme families that appeared during or before the Cretaceous and became extinct during the Late Cretaceous (Schweitzer & Feldmann 2005: 35, 42, tables 4, 7).

Main characters of the Cenomanian crab studied herein support the recognition of a distinct family, Lithophylacidae, and its relationships with other known fossil and extant brachyuran families are reviewed (see Discussion).

Genus *Lithophylax*

A. Milne-Edwards & Brocchi, 1879

Lithophylax A. Milne-Edwards & Brocchi, 1879: 116. — Van Straelen 1936: 43. — Stenzel 1953: 215. — Glaessner 1969: R514. — Bishop 1988: 247. — Vega & Feldmann 1991: 172, 173. — Vega *et al.* 1995: 345; 1997: 619. — Feldmann & Villamil 2002: 721. — Schweitzer *et al.* 2002a: 21; 2003a: 44. — Schweitzer & Feldmann 2005: 35, 42, tables 4, 7.

TYPE SPECIES. — *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879 by monotypy.

DESCRIPTION

As for the species.

REMARKS

Guillier (1886: 238 pro 338, 244) quoted *Lithophylax trigeri* with the reference: “*Palaeoplax Trigeri*, M.-Edw. Notes inédites (5)”, a footnote which referred to “Guillier. Notice géologique agricole etc. 1869, p. 32”. *Palaeoplax Trigeri* and *Petrocarcinus Trigeri*, used by A. Milne-Edwards in his personal handwritten notes (see Guillier 1886: 338 pro 238, 244) and on the labels (see Van Straelen 1936: 44), are *nomina nuda*.

Palaeoplax A. Milne-Edwards & Brocchi, 1879 (Milne-Edwards & Brocchi 1879: 114), with *Goneplax incerta* (Desmarest, 1819) (Desmarest 1819: 501 as *Ocypode incerta*; see also Desmarest 1822: 104, pl. 8, fig. 9 as *Goneplax incerta*) as type species, shows superficial similarities with *Lithophylax* (large orbits, narrow front, marked areolation on whole carapace) but is clearly distinct. *Palaeoplax incerta* (Desmarest, 1819), based on a single worn specimen, was indicated, despite absence of any clear indication of provenance (Desmarest 1819: 501: “I ignore from where this crab has been recorded, but its aspect somewhat evokes that of the Indian species”), to be a subfossil from the Indo-Pacific (Glaessner 1969: R532). The assertion of Van Straelen (1936: 44) that *Palaeoplax* “was established to designate a subfossil goneplacid species named *Goneplax incisa* Desmarest” was erroneous (a lapsus) since the type species of *Palaeoplax* is *Goneplax incerta* (Desmarest, 1819) (1819, instead of 1822 as in the literature; the Latin name *Ocypode incerta*

was published already in 1819 with the vernacular name “*Ocypode incertain*” in the *Nouveau Dictionnaire d’Histoire naturelle*). *Palaeoplax* has been considered a good goneplacid genus (Glaessner 1929: 300) or of uncertain systematic position (Glaessner 1969: R532). The holotype of *P. incerta* (a female, about 29 mm width, MNHN B 41496; only a – supposedly subsequent – label “subfossile des Indes”), that we have examined, bears some resemblance to fossil thoracotreme crabs as the Macrophthalminae Dana, 1851, for example to the figure of *Macrophthalmus vindobonensis* Glaessner, 1924 (see Glaessner 1969: fig. 338.1), synonymised with *M. aquensis* A. Milne-Edwards & Brocchi, 1879 by Schweitzer *et al.* (2002a: 40). Even if the lateral borders of *P. incerta* are incomplete, the presence of the three deep transversal grooves on each side of the carapace are sufficiently characteristic to prevent its affiliation with the Lithophylacidae. We agree with Desmarest (1819) in thinking that it is related to Indo-Pacific crabs, and suggest that it is post-Cretaceous.

Lithophylax trigeri A. Milne-Edwards & Brocchi, 1879
(Figs 5-14)

Lithophylax Trigeri A. Milne-Edwards & Brocchi, 1879: 117. — Guillier 1886: 238 [and not 338], 244.

Palaeoplax Trigeri – Guillier 1869: 32; 1886: 238 (and not 338) (Non *Palaeoplax* A. Milne-Edwards & Brocchi, 1879; type species: *Ocypode incerta* Desmarest, 1819).

Petrocarcinus Trigeri – Guillier 1869: 32; 1886: 244 (*nomen nudum* of A. Milne-Edwards).

Lithophylax trigeri – Glaessner 1929: 236, 431; 1969: R514. — Rathbun 1935: 52. — Van Straelen 1936: 43, pl. 4, fig. 9. — Juignet 1974: 669. — Vega *et al.* 1997: 619.

TYPE MATERIAL. — Despite Rathbun’s (1935: 52, and footnote) statement: “The holotype is not to be found in the Paris Museum, according to M. Boule et C. Gravier”, we found in the paleontological collections of the MNHN 36 specimens from Le Mans and Saint-Mars-sous-Ballon (Sarthe), registered as B16566 (3 specimens), B16567 (3 specimens), B16576 (9 specimens), B16577 (3 specimens), and B16595 (18 specimens) which very probably

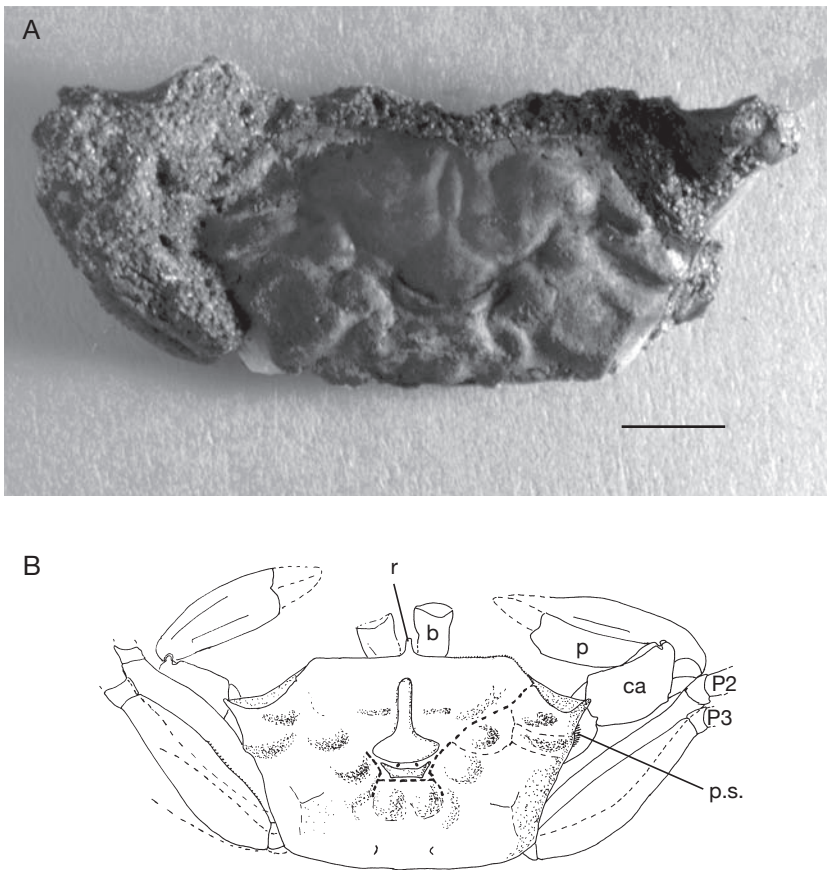


FIG. 5. — *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879, dorsal surface: **A**, MHN LM 2005.1.3; **B**, semi-diagrammatic reconstruction, restored from many specimens (bold dash lines indicate the deepest grooves). Abbreviations: **b**, basophthalmite; **ca**, carpus of P1; **p**, propodus of P1; **P2**, **P3**, pereopods 2 and 3; **p.s.**, pars stridens of the stridulating apparatus; **r**, rostrum. Scale bar: A, 5 mm.

constitute the original material (of both sexes) studied by A. Milne-Edwards & Brocchi (1879), i.e. the type series. The topotype figured by Van Straelen (1936: pl. 4, fig. 9) has not been found; the specimen of the Bosquet's collection (RBINSB) is not the topotype figured by Van Straelen (1936).

Amongst the syntypes we select from B16566 one lectotype which receives the new number MNHN A25835 (original label "Cénomaniens St Mars-sous-Ballon (Sarthe) Coll. A. Milne-Edwards, 1902-3". Other label "Van Straelen determ. 1938"). We were not able to include the material of the type series in our Table 1 (Annexe) because of its very late re-discovery.

ADDITIONAL MATERIAL. — See Material examined and prepared, and Annexe: Table 1.

DESCRIPTION

Size moderate (maximum width 28 mm). Carapace much wider than long, transversally hexagonal to inverted trapezoidal, widest at position of the outer-orbital teeth; length about 0.53 to 0.59 maximum carapace width in average. Dorsal carapace obviously lobulate; regions well distinct throughout surface. Rather deep grooves clearly differentiating regions, in particular the deeply impressed cervical, branchio-cardiac and gastro-cardiac grooves. A strong H-shaped mark on each side (Figs 5; 6; 14), and a "human face" sometimes depicted (formed by attractor epimeralis muscle apodeme, posterior gastric muscle scar, median part of cervical groove,

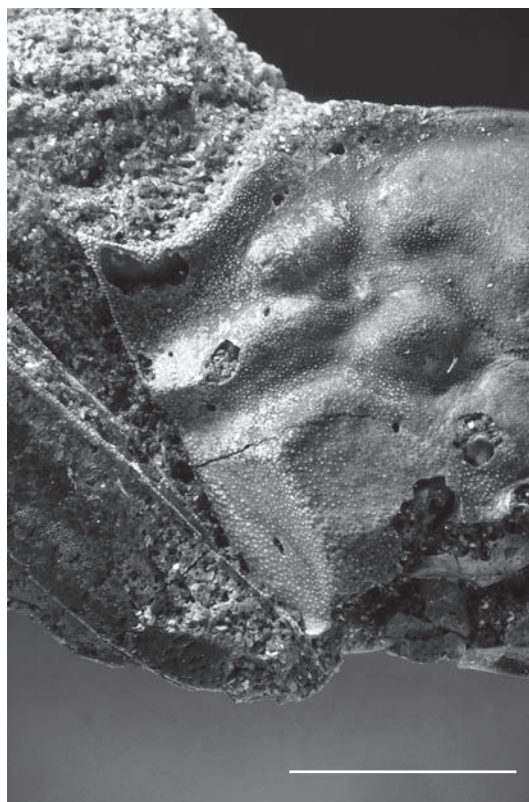


FIG. 6. — *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879, MHN LM 2005.1.6, left side of carapace, dorsal view, showing the developed outer-orbital tooth. Scale bar: 5 mm.

and branchio-cardiac groove). Two deep gastric pits along cervical groove.

Areolation (Fig. 5) as follows: mesogastric (funnel-shaped and extending forward almost to the frontal) and metagastric regions well defined and forming an undivided, single plate; urogastric region elongated transversally, arched, crescent-shaped, separated from metagastric region by deep furrow; protogastric regions large, expanded laterally, may be crossed by elevated transverse ridge (that marks the maximum height of the carapace), with two more or less marked nodes on each side; hepatic region with two unequal lobes: anteriorly, a prominent, rounded bump; posteriorly, a narrow, elongated ridge reaching carapace lateral margin and separated from branchial region by shallow groove; paragastric region (or branchial lobe) semicircular,

well differentiated, prominent; cardiac region with two elevations; epibranchial region with salient internal lobe and external marked ridge, posterior to hepatic swelling; mesobranchial region broad, consisting of narrow, salient internal lobe and inflated lateral part (may be ridged on three sides) with pronounced slope along carapace postero-lateral margin; metabranchial region depressed; intestinal region poorly separated and depressed posteriorly. Ornamentation of dense but fine granules. No trace of punctuations.

Lateral margins (Fig. 6) strongly diverging anteriorly, converging posteriorly; junction of antero- and postero-lateral margins weakly marked; antero-lateral margins slanted, without tooth other than marked outer-orbital tooth, only followed by a blunt angle; postero-lateral regions steeply inclined, very oblique, with sharply defined margins; postero-lateral corners rounded; posterior margin rimmed, nearly straight to weakly concave centrally in dorsal view.

Rostrum (Figs 5; 7; 10A; 14) forming narrow, rather long, ungrooved process, inclined downwards, its distal half deflected at 90° to dorsal carapace surface; its extremity bluntly rounded. Frontal margin forming same line with supra-orbital margin, entire, except for small fissure at mid-part of supra-orbital margin; frontal margin lined by coalescent granules; supra-orbital margin lined by tubercules twice as long as frontal granules.

Orbits extremely deep, wide, long, extending from rostrum to outer-orbital tooth (total 80% carapace width; 55% for podophthalmite and corneal surface), directed obliquely rearwards, divided into two unequal fossae by small furrow, inner fossa being cylindrical, outer one being larger, elliptical and extending back to center of hepatic region; orbital margins very long, extending to outer-orbital teeth carapace corners. Infra-orbital margin lined by tubercules smaller than those of supra-orbital margin.

A pair of thick, stout, cylindrical and mobile eyestalks; basophthalmite (Figs 5; 10A; 14) present in four specimens, erected, their insertion close to base of rostrum clearly visible; rest of eye (podophthalmite and corneal surface) not present, interpreted however as sufficiently developed to fold back into orbit and to completely fill it; presumably inflated

corneal surface probably lodged in external part of orbit (Figs 5; 7; 8B; 10A; 14). Antennae and antennules not present, nor their cavities.

Below outer orbital fossa, suborbital region granular. Presence of a special plate, herein named "shutter" consisting of two parts: a quadrangular internal part, delineated by a slightly granulated to smooth rim, with marked right angle margins; and an external fan-like process (Figs 7A, B; 8A, C). Relationships of the "shutter" with suborbital and antero-lateral margins, as well as pterygostomial region, remaining unclear. Pleural line ventrally located. Buccal cavern very wide. Presence of extremely strong mandibles. Mxp3 clearly diverging, directed obliquely, leaving large gap between them. Endopodite with coxa expanding laterally; ischion rectangular; merus widened and broadly rounded at postero-external angle; palp not preserved or barely preserved; exopodite well developed.

Thoracic sternum complete, wide, oval, flat, but last sternites 7 and 8 inclined; gynglymes of mxp3 and pereopods well visible. Suture 1/2 marked, complete; sternites 1 and 2 not fused, forming narrow, relatively long and downward inclined triangle. Suture 2/3 marked. Suture 3/4 not present and replaced by sinuous ridge; sternite 3 wide, much more depressed than sternites 4 and 5. Sternite 4 well developed. Suture 4/5 extending along from the margins before turning sharply inwards, therefore interrupted axially; its extremities separated by rather wide gap and marked by deep depressions corresponding to the invagination of the two plates which form each phragma. Sutures 5/6 and 6/7 showing deep depressions, as suture 4/5; suture 5/6 (seen in four individuals) prolonging beyond depressions and thus (presumably) not interrupted axially. Suture 6/7 (weakly exposed in our material) not interrupted axially. Suture 7/8 incomplete, extremely short and thus only lateral, ending by small depressions. Sternites 4-6 normally exposed; most of sternite 7 covered by abdomen in both sexes; sternite 8 much reduced and subdorsal, covered by abdomen in both sexes. Episternites 4-6 well defined. Presence in both sexes of elongated cupules hollowed on sternites 4 to 6 on posterior margin, internal to episternites. A longitudinal median line present on sternite 7. Surface smooth, punctate.

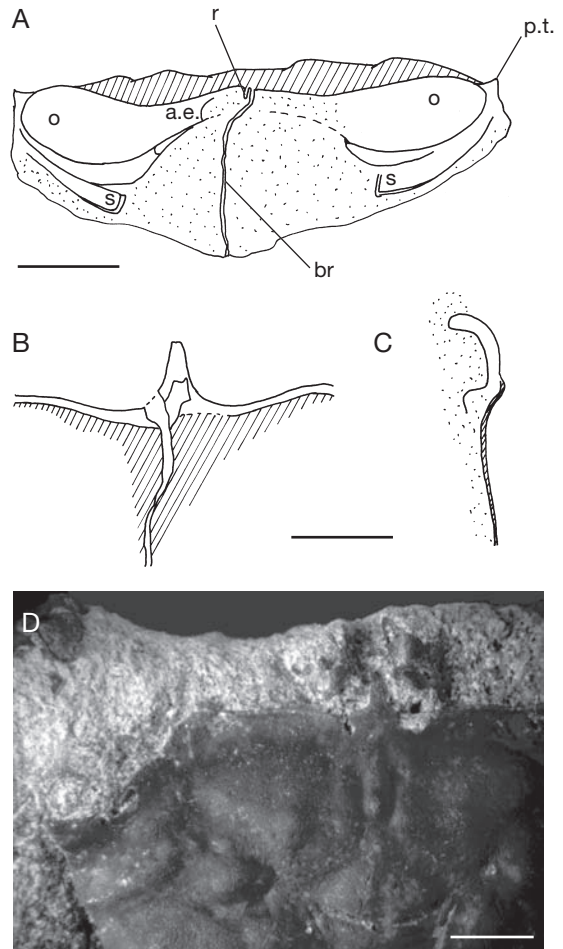


FIG. 7. — *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879, rostrum, eyes and orbits: **A-C**, MNHN 9208; **D**, MNHN A 24796; **A**, frontal view, same-plane view; **B**, rostrum, dorsal view; **C**, rostrum, profile (dorsal at right) (dotted: matrix of the fossil; hatched: carapace); **D**, dorsal view of carapace. Abbreviations: **a.e.**, accommodation for the eyestalk; **br**, break of the fossil; **o**, orbit; **p.t.**, outer-orbital tooth; **r**, rostrum; **s**, shutter. Scale bars: A, 5 mm; B-D, 2 mm.

Sterno-abdominal cavity triangular, extending the mid-length of sternite 4, not deeply excavated, without sharply delimited margins. Vulvae present on sternite 6, relatively far from each other, on oblique flanks of sterno-abdominal cavity.

Male abdomen with all somites free and telson, lodged in the cavity (except for its extreme anterior part), relatively wide, not much narrower than female

one (weak sexual dimorphism), regularly triangular; its base broad; first abdominal somites covering completely space between coxae of last pereopods. A4 elongated transversally and joining level of P3 coxae. Carapace covering first abdominal somites, at least A1 (in some cases A2 and portion of A3 apparently covered by carapace, Fig. 9E). A1-A4 ridged transversally. Telson triangular. Abdominal surface punctate, posterior axial part of each segment smooth.

Male gonopods preserved in 14 specimens at least (Annexe: Table 1); G1, or G2 or both cleared in three of these. G1 long, slender, each forming regular curve; punctuations being bases of setae. G2 relatively long, 1.4 times shorter than G1, with wide base, angled at distal fourth; tip pointed; G2 may be found in an horizontal position close to A1 or inserted inside G1.

Abdominal devices of press-button type: locking structures showing as developed and pointed prominences situated on sternite 5 about at its mid-part (but closer to suture 4/5 than to suture 5/6), remaining present and most probably effective in mature females; sockets (not seen) likely on abdominal segment 6, in postero-lateral angles.

All pereopods with their condyli often preserved (narrower for P1), their gynglymes often well visible. Chelipeds robust, with massive propodus, clearly heterochelous, right hand being distinctly larger (right hand varying from 10% to 25% wider than left, and 12-15% longer than left); palm outer surface not keeled but thickened in superior half; inferior border flat or slightly convex, not ridged; surface minutely granulate, without spines on borders. Fingers elongated, with surface minutely granulate; heterodonty rather weak but distinct, several teeth on both prehensile margins, slightly thicker at right.

Arthroal cavities of P1-P5 not aligned, P4 and P5 being progressively nearer to the mid-line, P5 coxa being completely subdorsal (Figs 11; 12B). P2-P4 very long, thick; merus wide, elongated, markedly compressed dorso-ventrally, flattened (Fig. 12D), distal part more slender than proximal, with antero-dorsal carina lined by marked tubercles; surface minutely granulated; punctate traces on posterior margin may indicate existence

of setae; carpus rarely preserved (only proximal part on P3 and P4); propodus and dactylus not preserved. Autotomy line visible on most pereopods, just distal to ischio-basis limit (Fig. 12C). P5 (only coxa and merus preserved) obviously reduced and subdorsal (Figs 11; 12B; 14); coxa very small, diameter and length half that P1-P4 coxae (Annexe: Table 2), and with male gonopore visible (Fig. 11A, below); merus (present in only one specimen), presumably cylindrical, narrow, with a main distinctive row of pointing granules and another one with weaker granules. Right and left P5 coxae closer to each other than P4 coxae and more widely separated than P3 and P2 coxae.

Stridulatory apparatus in both sexes, consisting of a well specialised pars stridens, with about marked 29 striae on flattened area at inner surface of merus of chelipeds; and a plectrum on the suborbital region, represented by at least eight blunt tubercles. In one specimen (MHNH B 9199) (Fig. 13) counterpart of five striae of the pars stridens situated in front of both suborbital blunt tubercles and tiny granules on posterior rim of quadrangular part of shutter.

See the reconstruction of dorsal carapace Figure 14.

REMARKS

Lithophylax trigeri was originally based by A. Milne-Edwards & Brocchi (1879) on material collected in the Butte de Gazonfier quarry, at Le Mans (Sarthe), Grès verts du Maine (or Sables à *Rhynchonella compressa* = Sables du Perche Fm), middle-upper Cenomanian, Jukesbrownei and Guérangeri Biozones.

Most of the material studied herein comes from the Louvre quarry, at Lamnay (Sarthe), Sables et Grès de Lamnay Formation, lower Cenomanian, Mantelli (Saxbii) and Dixoni biozones. Thus this material is 2-3 ammonites biozones (*c.* 2 my) older than the original material (not seen) and the Guéranger's topotypic specimens that we were able to examine. A few differences have been observed between the lower Cenomanian (LC) and the middle-upper (MUC) Cenomanian material. The carapace of MUC material is slightly larger and wider (average L/W 0.53 for MUC and 0.59 for LC) (Annexe:

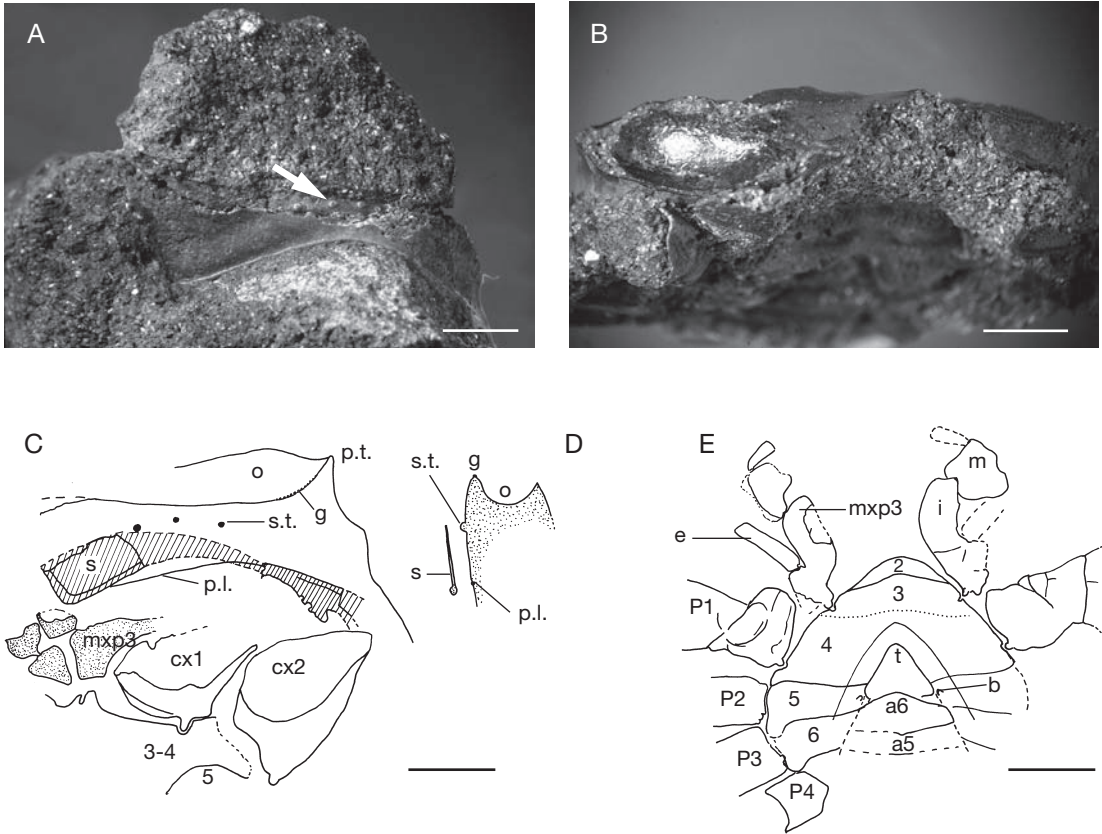


FIG. 8. — *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879, orbit, shutter, buccal parts, and sternum: **A**, MHNH 9209, ventral view, shutter (the arrow indicates tubercles of the plectrum of stridulating apparatus); **B**, MHNH 9211, frontal view, orbit; **C**, MHNH 9196, ventral side of left anterior part (lateral same-plane view); **D**, MHNH 9196, diagrammatic vertical section; **E**, MNHN A 24794, ventral side, thoracic region and part of abdomen (antero-posterior and lateral same-plane views). Tegument lacks on sternites and part of abdomen. Abbreviations: **a5**, **a6**, abdominal segments 5, 6; **b**, button of the press-button; **cx1**, **cx2**, coxae of P1, P2; **e**, exopodite of mxp3; **g**, granulation on inferior rim of the orbit; **i**, ischium of mxp3; **m**, merus of mxp3; **mxp3**, third maxilliped; **o**, orbit; **p.l.**, pleural line; **p.t.**, outer-orbital tooth; **P1-P4**, pereopods 1-4; **s**, shutter; **s.t.**, tubercles of the plectrum of the stridulating apparatus; **t**, telson; **2-6**, sternites 2-6. Scale bars: A-C, 2 mm; E, 5 mm.

Table 1); chelipeds of MUC material are more sturdy; areolation and granulation of the dorsal carapace of MUC material is more marked. Unfortunately, no new MUC material can be collected now, and the 19th century material is not located precisely enough to allow confident statistical measurements. Regardless, the differences between the MUC and the LC material are weak, and they do not seem sufficient, at this stage of our work, to distinguish two different species – or even subspecies – in the present paper.

REMARKS ON THE STRIDULATING APPARATUS

A *Lithophylax* specimen exhibits the counterpart of the pars stridens *in situ* (Fig. 13), exactly just ventral to the tubercles of the plectrum: striae of the pars stridens are exactly perpendicular to the row of eight tubercles located posteriorly to the shutter (Figs 8A, C; 12B). A similar mechanism to that of *Lithophylax* roughly involves the same areas in the Recent goneplacid *Bathypylax typhlus* A. Milne-Edwards, 1880. In *B. typhlus* (see Tavares 1996: 416, fig. 3A, B) the pars stridens consists of a

narrow area of transversal striae (about 40) on the inner face of P1 merus, and the plectrum consists of about 50 non-aligned, subhepatic granules: among these 50 granules, only those of a medial row appear to be blunt, thus are probably the only efficient ones. In *Lithophylax trigeri* the pars stridens is shorter and wider (29 striae), and the plectrum is a row of eight spaced tubercles. The anterior part of the pars stridens is supposed to be also in contact with the posterior rim of the shutter. This rim bears a minute granulation. We suggest, as an hypothesis, that this layout permitted a two-frequencies “di-phonic” stridulation with a low frequency from the suborbital tubercles and a higher frequency from the shutter granules.

The stridulating apparatus in the Recent and fossil goneplacid *Ommatocarcinus* White, 1851 (not present in all species of the genus) (see Guinot-Dumortier & Dumortier 1960; Jenkins 1975), with striated suborbital ridge and crest on P1 merus, is different from the mechanism in *Lithophylax*. The goneplacid genus *Psopheticus* Wood-Mason, 1892 (see Guinot 1990) contains also stridulating species, but with tubercles on P1 merus (instead of striae in *L. trigeri*) and pterygostomial crest and/or granules (tubercles in *L. trigeri*).

Another case of friction of the P1 merus against the subhepatic region of the carapace is known in the Recent gecarcinid *Gecarcinus quadratus* Saussure, 1853, but both parts consist of granules and/or tubercles (Abele *et al.* 1973: 148, fig. 1). The rarity of known mechanisms for sound production in fossil crabs is explainable by our incomplete knowledge, and it is probable that other extinct species were able to produce sound. Examples of stridulating species are the Miocene *Szaboa inermis* (Brocchi, 1883) (= *Matuta brocchii* Glaessner, 1969) (Müller 1984: 69; Müller & Galil 1998: fig. 2), *Ommatocarcinus* species (see Jenkins 1975: 36, 48, pl. 4, fig. 6, pl. 7, fig. 2c), and *Stevea cesarii* Beschin, Busulini, De Angeli & Tessier, 1994 from the Eocene of Italy (A. De Angeli, pers. comm.). The Maastrichtian *Megaxantho zoque* Vega, Feldmann, García-Barra, Filkorn, Pimentel & Avendaño, 2001 shows striae on the inner surface of the distal portion of the palm suggesting a “possible stridulatory mechanism” (Vega *et al.* 2001: fig. 5.3).

The stridulating apparatus, present in the fossil Hexapodidae (as in extant species), consists either of a prominent ridge of striae (e.g., in *Goniocyropa edwardsi* Woodward, 1867 and probably also in *G. quaylei* Crane, 1981, both from the Upper Eocene of Hampshire, see Crane 1981: 6, 7, fig. 8D; and in *Stevea cesarii*) or an area of pterygostomial striae (e.g., in *Hexapus pinfoldi* Collins & Morris, 1978, from Eocene of Pakistan; probably in other fossil *Hexapus* species). These striated ridges are rubbed by thin, closed striae on the inner surface of the dactylus of both chelipeds (Guinot 2006).

OTHER BRACHYURAN CRUSTACEANS REPORTED FROM THE STRATOTYPIC CENOMANIAN WITH *LITHOPHYLAX TRIGERI*

According to Guillier (1886) the other brachyuran crustaceans reported from the stratotypic Cenomanian with *Lithophylax trigeri* are:

– *Raninella trigeri* and *R. elongata*, species names mentioned by A. Milne-Edwards (1862b: 493) in establishing the genus *Raninella*; the species were described and figured by Brocchi (1877). They belong to the Raninoidea De Haan, 1839, i.e. to the Podotremata Guinot, 1977.

– *Caloxanthus formosus* A. Milne-Edwards, 1862 (A. Milne-Edwards 1862a: 44, pl. 9, fig. 1), type species of *Caloxanthus* A. Milne-Edwards, 1862, collected in the “grès verts du Maine by M. Triger”. An upper Santonian material of *C. formosus* from Aude in France was figured by Wright & Collins (1972: 104, pl. 21, fig. 9). A second species of *Caloxanthus*, *C. americanus* Rathbun, 1935, from the Albian, shows on the ventral surface a triangle inserted between the mxp3, interpreted by Rathbun (1935: 56, pl. 11, fig. 19) as “the terminal segment (female?) of the abdomen” (instead of, in our interpretation, the first thoracic sternites forming a narrow and triangular plate, inserted between the mxp3). Wright & Collins (1972: 56, 103) have suggested a derivation of *Caloxanthus* from the Lower Cretaceous *Dialulax* Bell, 1863, “a stock that diverged from Dynomenidae in the Later Jurassic” and, however, included *Caloxanthus* in the Carpiliidae Ortmann, 1893. The Early Cretaceous *Caloxanthus* was attributed to the Xanthidae *s.l.* by Schweitzer *et*

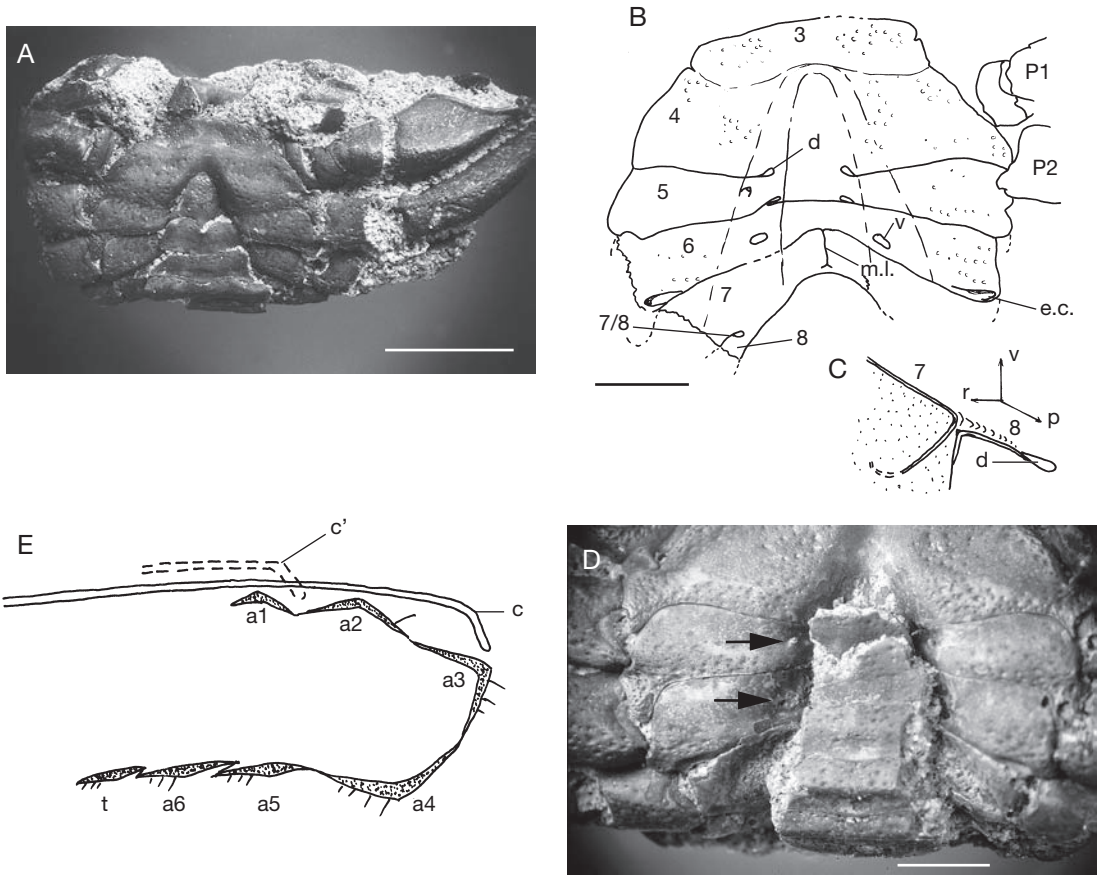


FIG. 9. — *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879; thoracic sternum, abdomen, male gonopods, vulva; **A**, MHNH 9187, ventral view; **B**, MHNH 9191, thoracic sternum, ventral view, same-plane view; **C**, diagrammatic section of the 7/8 suture, from MHNH 9191 (r, right; v, ventral; p, posterior); **D**, MHNH 9186, ventral view of a female (the arrows indicate: above, button of the press-button; below, vulva); **E**, relations between abdomen and carapace, diagrammatic sagittal section. Abbreviations: a1-a6, abdominal segments 1-6 (dotted); c, posterior part of carapace, normal position; c', maximum forwards shift of carapace (observed on several specimens); d, depressions; e.c., episternal cupules; m.l., median line; P1, P2, first and second pereopods; t, telson; v, vulva; 3-8, sternites 3-8; 7/8, thoracic sternal suture 7/8. Scale bars: A, 5 mm; B, D, 2 mm.

al. (2002a: 39, 40, table 4). At present we consider *Caloxanthus* a podotreme crab, and prefer to assign it (with reservation) to the Diaulacidae Wright & Collins, 1972 or to an undescribed family within the Podotremata.

Glaessner (1969: R488) included *Diaulax* in the dynomenids, and Schweitzer *et al.* (2003a: 18, 20) synonymized the Diaulacidae with the Dynomenidae Ortman, 1892 (see also Schweitzer & Feldmann 2005: 38). The P5 dorsal location, mentioned in *Diaulax carteriana* Bell, 1863 (Bell 1863: 7), sup-

ports the hypothesis of a podotreme condition, similar to that of the Dynomenidae. But the most reliable characters (sexual gonopores, ventral surface, and thoracic sternum/male abdomen relationships), allowing the certain assignment of a family (and more generally to distinguish podotreme crabs from heterotreme crabs), are still lacking, and it is why for the moment we prefer to consider the Diaulacidae a separate family. According to Wright (1997: 135) re-examination of the crab fauna in Austria removes “the puzzling record of *Diaulax*

from the Jurassic” and “shows that it is Cretaceous, Cenomanian”.

We agree with Wright & Collins (1972: 54, 105) that the lower Senonian *Creticarcinus* Withers, 1928 (Withers 1928: 461) is very close to *Caloxanthus*. *Graptocarcinus* Roemer, 1887 (see Stenzel 1944: 550; Wright & Collins 1972: 54; De Angeli & Garassino 2006: 279, fig. 6), with the Aptian *G. texanus* Roemer, 1887 and *G. muiri* Stenzel, 1944, the Cenomanian *G. bellonii* Collins & Dieni, 1995, shows also strong resemblance to *Caloxanthus*. Both *Graptocarcinus* and *Caloxanthus* are likely candidates to be podotreme. The lower Cenomanian *Necrocarcinus avicularis* Fritsch in Fritsch & Kafka, 1887 (Fritsch 1887: 47 *pro parte*, pl. 10, fig. 12 only) might be included in *Graptocarcinus* Roemer, 1887 (see Glaessner 1929: 261; Wright & Collins 1972: 54, 55, 106; De Angeli & Garassino 2006: 280).

– *Necrocarcinus inflatus* A. Milne-Edwards, *nomen nudum*, in Guillier (1886: 244), was figured by Boule & Piveteau (1935: 392, fig. 570), that is not sufficient to validate the name (ICZN: Art. 13.1.1). Thus the author of the species is Van Straelen (1936: 37-39, pl. 4, fig. 8) who provided a long diagnosis and established the new genus *Cenomanocarcinus* Van Straelen, 1936 for this species. This genus, considered invalid by Stenzel (1945: 447) and renamed (Stenzel 1953: 214) “*Cenomanocarcinus* Van Straelen, 1936 in Stenzel 1945”, was later synonymised with *Necrocarcinus* Bell, 1863 by Wright & Collins (1972: 62). *Cenomanocarcinus* was re-attributed to Van Straelen, 1936 and rehabilitated by Schweitzer *et al.* (2002a: table 4, fig. 29) and Schweitzer *et al.* (2003a: 36). Anyway, *C. inflatus* (Boule & Piveteau, 1935) belongs to the Necrocarcinidae Förster, 1968, an heterotreme family, appeared in Early Cretaceous (see Discussion).

– *Necrocarcinus minutus* A. Milne-Edwards, *nomen nudum*, in Guillier (1886: 244). Status unknown.

DISCUSSION (BY DG)

The abundant and extremely well preserved material at our disposal has allowed the rescue of most parts, so that the fossil crab studied herein is almost as complete as a living species. All characters of

Lithophylax trigeri (except antennules, antennae, podophthalmites of eyes, distal articles of the P2-P5, details of G1, and part of the subhepatic area) can be described. The male gonopore is visible on the P5 coxa in two individuals. Vulvae and gonopods were found exposed in several individuals, thus it was possible to be sure of the eubrachyuran nature, and heterotreme condition, of *Lithophylax*. The sex of individuals was often easily defined. The gonopods were exposed after cleaning of the matrix and partial removal of the abdomen and carapace. Autotomy line was visible on P1-P4 (Fig. 12C) (see Legendre 1908). These characters are generally not preserved or poorly preserved in most fossil crabs, the vulvae being barely known and the gonopods present only exceptionally. Consequently, the Cenomanian material studied in the present paper, with specimens collected by one of us (GB) in particular, represents a precious paleontological document.

In *Lithophylax trigeri* (see Annexe: Table 1) thoracic sternal sutures show as follows: sutures 1/2 and 2/3 complete; suture 3/4 not marked; suture 4/5 interrupted and ending by deep depressions; sutures 5/6 and 6/7 also with deep depressions but presumably complete; suture 7/8 short, only lateral, and ending by small depressions. Suture 5/6, seen in four individuals, is presumably not interrupted axially; suture 6/7 (less exposed on our material) is not interrupted axially. In *L. trigeri* the depressions at level of sutures 5/6 and 6/7, similar to those located at the extremities of the suture 4/5, perhaps correspond to the median membranous areas which are frequent at the point where both extremities of the sutures (especially in the case of suture 6/7) join medially.

At least five patterns of sternal sutures 5/6 to 7/8 are known to exist in extant eubrachyuran crabs. An interrupted suture 4/5 may be followed by: 1) sutures 5/6-7/8 complete; 2) suture 5/6 interrupted but sutures 6/7-7/8 complete; 3) sutures 5/6-6/7 interrupted but suture 7/8 complete; 4) suture 5/6 interrupted, suture 6/7 complete; suture 7/8 interrupted; 5) sutures 5/6-7/8 interrupted (see Guinot 1979: tables 2, 3; Guinot & Richer de Forges 1981). The extremities of the sutures may be sometimes close together (sometimes joining in

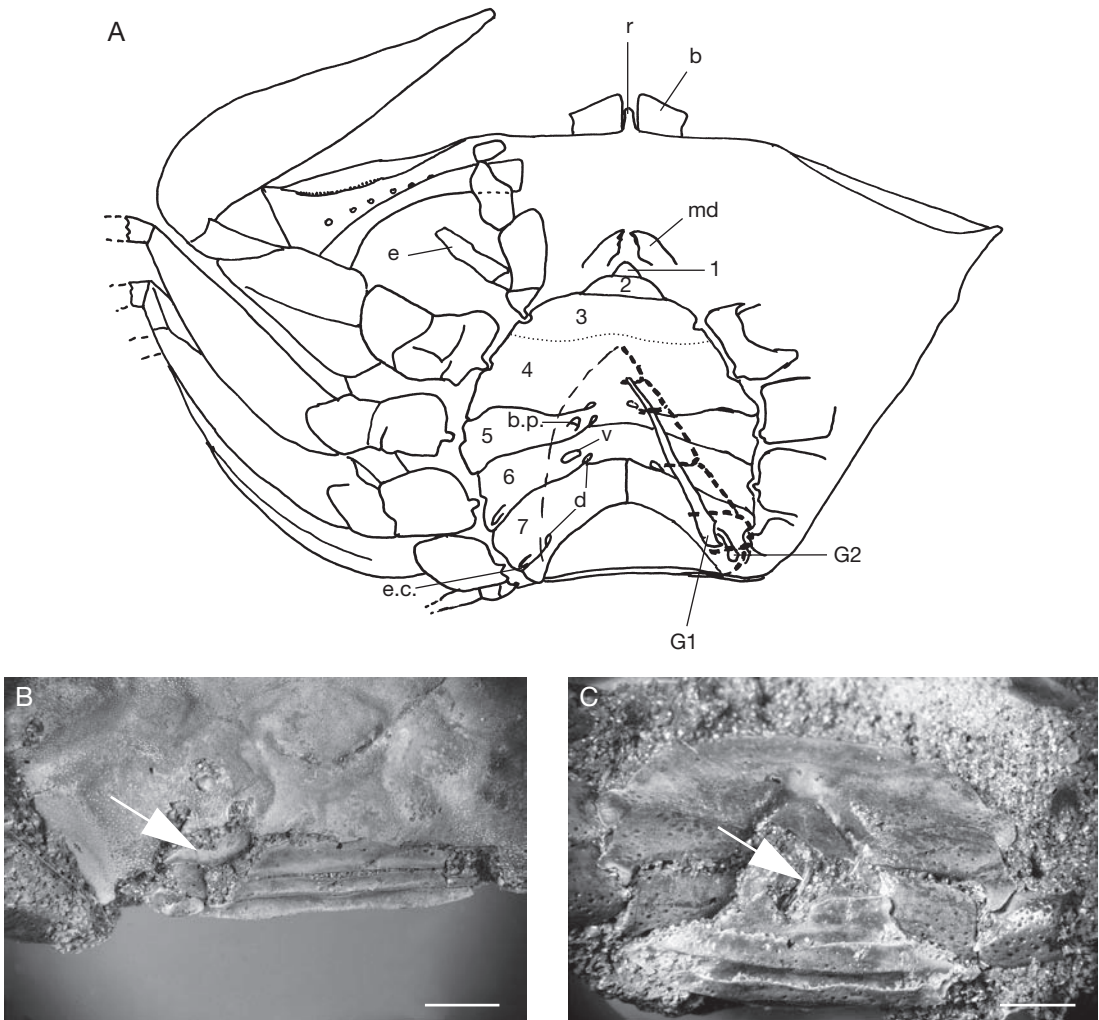


FIG. 10. — *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879, ventral side and male gonopods: **A**, ventral side, restored from many specimens, semi-diagrammatic reconstruction (left half: male; right half: female; bold dash line: extension of abdomen before clearing); **B, C**, MHN LM 2005.1.6; **B**, dorsal view, posterior part of cephalothorax cleared (the arrow indicates G2); **C**, ventral view, abdomen partly cleared (the arrow indicates G1). Abbreviations: **b**, basophthalmite; **b.p.**, button of the press-button; **d**, depressions; **e**, exopodite of mxp3; **e.c.**, episternal cupules; **G1, G2**, male gonopods 1 and 2; **md**, mandible; **r**, rostrum; **v**, vulva; **1-7**, sternites 1-7. Scale bars: 2 mm.

a median membrane area) so that they seem to be complete, and misinterpretations are possible. The Lithophylacidae shows another pattern: 6) suture 4/5 followed by complete sutures 5/6-6/7 and interrupted suture 7/8.

Considering the absence of thoracic sternal sutures in most ancient fossils, their condition cannot be

used in our comparisons of the Lithophylacidae with extinct eubrachiuran families.

In the previous placements of *Lithophylax*, the carapace was the only character available to paleontologists, often obliged to take into account the traditional features commonly preserved and described in fossils (“proxy characters” as defined

by Schweitzer 2003). *Lithophylax*, never considered a podotreme crab and finally referred to the Eubranchyura, already appeared at the limit between Lower and Upper Cretaceous. Our observations of the complete animal confirm such a placement. First referred to the Goneplacidae (see A. Milne-Edwards & Brocchi 1879) or “Goneplacidea” (see Van Straelen 1936) and then to the Portunidae Rafinesque, 1815 (see Rathbun 1935; Feldmann & Villamil 2002), *Lithophylax* was finally assigned, with more or less confidence, to the Carcineretidae (see Glaessner 1969; Bishop 1988; Vega & Feldmann 1991; Vega *et al.* 1995, 1997; Schweitzer *et al.* 2002a, 2003a).

The presence and shape of the last pereopod in *L. trigeri*, not mentioned by the preceding authors, was observed in the present material. Five individuals show a P5 coxa that is subdorsal and very small (Annexe: Table 2), in contrast to the wide coxae of preceding legs. The P5 coxae are close to each other, but by far to a lesser extent than in the Retroplumidae Gill, 1894. Only one individual of *L. trigeri* showed a preserved merus, extremely slender and cylindrical in comparison with the size and shape of the large, compressed meri of preceding legs. The P5 carpus, propodus, and dactylus are not preserved in our material. A natatory condition for P5 in *L. trigeri* is doubted, the narrow preserved (although incomplete) merus of *L. trigeri* not suggesting a paddle-shaped P5. Additionally, the subdorsal location of P5 is not reminiscent of a natatory pereopod.

Araripecarcinus ferreirai Martins-Neto, 1987, from the Brazilian Lower Cretaceous, exhibits, however, an extremely reduced P5 with a cylindrical merus and a wider and flattened article that has been presumed to be natatory (Martins-Neto 1987: 408, figs 1, 2). The small, damaged holotype specimen of 10 mm width does not provide enough information (M. Tavares, pers. comm.). The hypothesis that this crab belongs to the Podotremata Guinot, 1977 (perhaps to the Raninoidea De Haan, 1839) cannot be completely excluded. The Cretaceous Etyidae Guinot & Tavares, 2001, with a wide and areolated carapace, was considered podotreme (Guinot & Tavares 2001), in contrast to the typically heterotreme Lithophylacidae.

LITHOPHYLACIDAE VS CARCINERETIDAE BEURLEN, 1930

The widespread Cretaceous Carcineretidae (type genus *Carcinertes* Withers, 1922), within the superfamily Portunoidea, is suggested to have become extinct at the end of the Cretaceous (Feldmann *et al.* 1998; Vega *et al.* 2001; Schweitzer *et al.* 2002a; Schweitzer & Feldmann 2005). It includes: *Branchiocarcinus* Vega, Feldmann & Sour-Tovar, 1995, ?*Cancrixantho* Van Straelen, 1934, *Carcinertes*, *Mascaranada* Vega & Feldmann, 1991, *Ophthalmoplax* Rathbun, 1935, and *Woodbinax* Stenzel, 1953 (Van Straelen 1934: 3, pl. 1, fig. 2; Stenzel 1953: 215, figs 6, 8, pl. 59, fig. 11; Beurlen 1958: 1, 6; Bishop 1988: 247; Solé & Vía 1989: 25; Vega *et al.* 1995: 345; 1997: 619; Fraaye 1996: 271; Feldmann & Villamil 2002: 720; Schweitzer *et al.* 2002a: 21, 36-40, fig. 29, table 4; 2003a: 44). The Carcineretidae was already present in the Cenomanian with *Woodbinax* Stenzel, 1953, and in the Turonian with *Ophthalmoplax*, *Cancrixantho*, and *Carcinertes*.

Lithophylax was questionably included in the Carcineretidae by several authors. In the remarks concerning a new carcineretid, *Carcinertes planetarius* Vega, Feldmann, Ocampo & Pope, 1997, *Lithophylax* was considered an “authentic carcineretid crab”, with too poor a preservation to give any paleoecological interpretation of its lifestyle (Vega *et al.* 1997: 619). In a new description based on more complete new material of *C. planetarius*, Vega *et al.* (2001: 323) did not mention *Lithophylax* among the members of the Carcineretidae.

The Carcineretidae are characterized by a square or transversally extended carapace (may be urn-shaped, flat to convex longitudinally); dorsal regions well marked by grooves and transverse ridges, posterior-most regions may be ornamented; lateral margins straight, converging posteriorly, more or less diverging anteriorly; outer-orbital spines may be directed antero-laterally; rostrum narrow to broad, straight, grooved or bifid; orbits wide and eyestalks long; suborbital margins long, with fissures and ending in forwarding spines; P5 propodus flattened, paddle-like, and dactylus oval or oblancoolate; P4 may be also flattened; thoracic sternum ovate; male abdomen with 6 free segments (Withers 1922: 539,

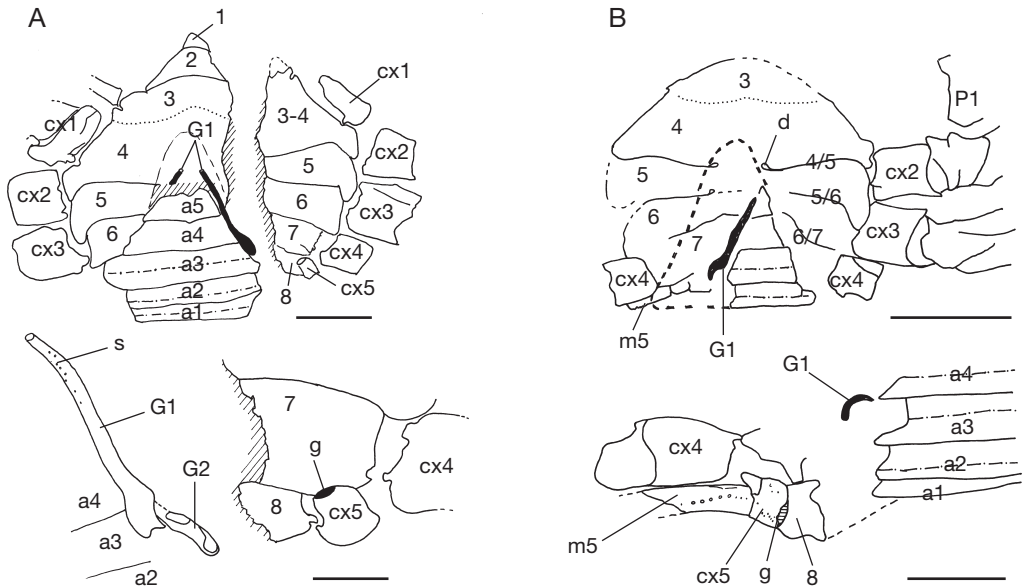


FIG. 11. — *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879, ventral side, male gonopods, and fifth pereopod: **A**, MHNH 9209, above, ventral same-plane view (the fossil is broken into two pieces, hatched); below, at left: ventro-lateral view of gonopods; below, at right, male gonopore on P5 coxa; **B**, MHNH 9202, above, ventral view; below, detailed posterior view. Abbreviations: **a1-a5**, abdominal segments 1-5; **cx1-cx5**, coxae P1-P5; **d**, depressions; **g**, male gonopore; **G1, G2**, male gonopods 1, 2; **m5**, P5 merus; **P1**, pereopod 1; **s**, setae; **1-8**, sternites 1-8; **4/5-6/7**, thoracic sternal sutures 4/5 to 6/7. Scale bars: above, 5 mm; below, 2 mm.

pls 16, 17; Glaessner 1969: R514; Schweitzer *et al.* 2003a: 44, 45).

The Carcineretidae is a brachyuran radiation witnessing the rise of a natatory mode of life during the Cretaceous (Fraaye 1996: 269). However, the flattened P5 propodus and oval dactylus may be also an adaptation for back-burrowing (Morris 1993). At present taphonomical and morphological data do not indicate that *Lithophylax* may have been a swimming or a burrowing crab; it was probably a burying crab.

Resemblance of the Carcineretidae with the Retroplumidae has been evoked, but their relationships are obscure. *Ophthalmoplax* was considered close to the retroplumid *Archaeopus* Rathbun, 1908 (see Via 1980: 5, 11, fig. 2) and a Cretaceous-Retropluma ancestor (Via 1982: 118, fig. 2) (see also Vega & Feldmann 1992: 145-148, fig. 8). *Branchiocarcinus cornatus* Vega, Feldmann & Sour-Tovar, 1995 (type species of *Branchiocarcinus*) resembles a retroplumid because of the shape and ridges of the carapace; it also has two sharp, anteriorly curved spines (forming

the widest portion of the carapace) which probably correspond to the outer-orbital spines of *Lithophylax*. *Archaeopus rathbunae* Beurlen, 1965 (Beurlen 1965: 271, fig. 4), from the Early Cretaceous (Albian) of Brazil, was not considered a retroplumid (Via 1980: 54, 64): it has a carapace that resembles that of the Carcineretidae (see Vega & Feldmann 1992: 147), and Schweitzer & Feldmann (2001b: 202) suggested that it “may be a carcineretid”.

The Lithophylacidae differs from the Carcineretidae by numerous characters: carapace much wider, in the form of an inverted trapezoid; antero-lateral margins strongly diverging anteriorly; rostrum downturned; fronto-orbital border wide and continuous; supraorbital margin very long, without teeth or spines, only with a small fissure; orbits shape; thoracic sternum wider, with sternites 1-3 broad and flattened; male abdomen relatively wide; P5 reduced, (presumably) not natatory, with subdorsal coxae.

The relatively wide, fully lobulate carapace of *Mascaranada* (see Vega & Feldmann 1991: fig. 7.1)

resembles that of *Lithophylax* but the antero-lateral margins are converging anteriorly and the P5 is paddle-like, not reduced. The narrow, not sulcate rostrum of *Lithophylax* fits the description of some Carcineretidae, such as the poorly known *Cancrinxantho* Van Straelen, 1934, from the Campanian, which was placed in the Carcineretidae (Glaessner 1969: R514, fig. 325; Vega *et al.* 1997: 619; Schweitzer *et al.* 2002a: 21; 2003a: 44 with reservation). *Cancrinxantho pyrenaicus* Van Straelen, 1934 (see Vía 1988: 351, fig. 339L; Solé & Vía 1989: 25) shows a subrectangular carapace that is deeply grooved and marked by transverse ridges, a narrow and spiniform rostrum, long orbits and eyestalks, characters which resemble those of *L. trigeri*. However, the carapace shape, the trilobate supra-orbital margin and the toothed postero-lateral margin of *C. pyrenaicus* distinguish it from *L. trigeri*.

In *Lithophylax* the developed outer-orbital teeth and the distance between these teeth (coinciding with maximum width) correspond to the condition found in some Carcineretes, *Ophthalmoplax* and *Mascaramada*, but the rest of the lateral margin is unarmed (only a small angle at the level of hepatic lobe) in *Lithophylax* instead of at least one more tooth or spine in the other genera. In the Carcineretidae (as Carcineretes, *Ophthalmoplax*) the rostrum is broader than in *Lithophylax trigeri* (Figs 5; 7; 10A; 14) and more or less grooved or bifid.

Some of the genera previously included in the Carcineretidae have been removed from the family. *Withersella* Wright & Collins, 1972 (Wright & Collins, 1972: 91, fig. 13, pl. 19, figs 4, 5; see also Fraaye 1996: 270, fig. 1.8) (type species: *W. crepitans* Wright & Collins, 1972 from the early Aptian), first regarded as the earliest known carcineretid, shows a rather concave frontal margin bounded by large outer frontal spines, supra-orbital fissures, and a spine on each side of the bifid rostrum. Collins *et al.* (1995: 200) suggested close relationships to the Maastrichtian *Binkhorstia* Noetling, 1881, and placed these two genera in the Carcineretidae. Van Bakel *et al.* (2003: 85-87, fig. 1) recently re-assigned *Binkhorstia* to the Tornyomatidae Glaessner, 1980 (Glaessner 1980: 180), based on new material of the type species, *B. ubaghsi* (van Binkhorst, 1857). *Binkhorstia*

ubaghsi has a spatulate rostrum, all abdominal segments residing in a true sterno-abdominal cavity, broad thoracic sternum, flattened P2-P4, and a P5 coxa which is reduced and situated laterally to the first abdominal segment. The difficulty of the systematic placement of early crabs is well shown by the case of *Binkhorstia*, which was considered either a podotreme or an heterotreme, being successively assigned to the Dorippidae MacLeay, 1838 (Quayle & Collins 1981: 738), the Cyclodorippidae Ortmann, 1892 (Glaessner 1969: R492; Feldmann & Villamil 2002: 721), and to the Carcineretidae Beurlen, 1930 (Wright & Collins 1972; Collins *et al.* 1995; Fraaye 1996: 272, figs 1.9, 1.10, 2; Wright 1997: 138, figs 12, 16; Jagt *et al.* 2000: 40, fig. 2). It is presently impossible to decide the status of all the Tornyomatidae without verification of their sexual gonopores. The information at our disposal does not permit recognizing affinities of the Tornyomatidae with the Lithophylacidae.

The Late Cretaceous genus *Icriocarcinus* Bishop, 1988, initially assigned to the Carcineretidae with respect to its long eyestalks, transverse ridges on the dorsal carapace and heterochelous chelipeds, was included in the Goneplacidae (Schweitzer *et al.* 2002a: 21, 28, 40). The P3-P5 meri are flattened, P5 are the smallest (but not markedly reduced and end with straight dactylus), and these characters (among others) are not carcineretid-like (see below).

Longusorbis Richards, 1975 (Richards 1975: 1850, figs 1-11), first included within the Carcineretidae (see Bishop 1988: 251), then placed in the Xanthidae (see Vega *et al.* 1997: 619; Schweitzer *et al.* 2002a: 21), was recently reassigned to the Carcineretidae (Schweitzer *et al.* 2003a: 44, fig. 15). The excellently preserved *L. cuniculosus* Richards, 1975, found buried and fossilized in its burrows (see Paleoecology and ethology), shows an almost complete eyestalk, as long as its supra-orbital margin, P2-P5 slightly compressed, "modified for crawling" (Richards 1975: 1862), and P5 shorter than precedings, with paddle-like propodus and oblongate dactylus (Schweitzer *et al.* 2003a: 45, fig. 15.1), that is a P5 very different from the reduced and subdorsal P5 of *Lithophylax trigeri* (Figs 12B; 14). See also Conclusion.

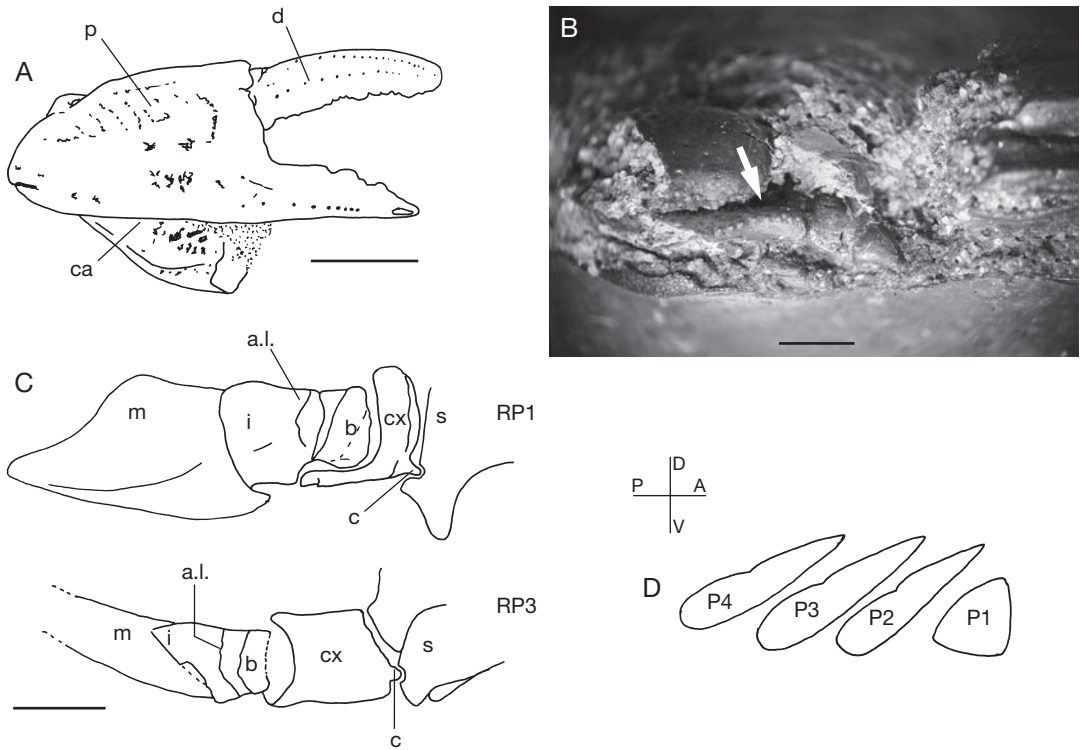


FIG. 12. — *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879, pereopods: **A**, MHN LM 2005.1.4, cheliped, frontal view; **B**, MHNH 9202, posterior view (arrow indicates proximal part of P5 merus); **C**, MHNH 8186, autotomy line on right cheliped (RP1) and right third pereopod (RP3); **D**, overlapping of P1-P4, vertical section, diagrammatic [orientation: D-V, dorso-ventral; P-A, postero-anterior]. Abbreviations: a.l., autotomy line; b, basis; c, condyle; ca, carpus; cx, coxa; d, dactylus; i, ischion; m, merus; p, propodus; **P1-P4**, pereopods 1-4; s, sternite. Scale bars: A, 5 mm; B, 1 mm; C, 2 mm.

LITHOPHYLACIDAE VS NECROCARCINIDAE
 FÖRSTER, 1968 AND ORITHOPSIDAE
 SCHWEITZER, FELDMANN, FAM, HESSIN,
 HETRICK, NYBORG & ROSS, 2003

The exclusively fossil family Necrocarcinidae Förster, 1968, with the first records occurring during the Early Cretaceous, was first considered a member of the Calappoidea De Haan, 1833 (Förster 1968; Wright & Collins 1972; Schweitzer & Feldmann 2000a; Fraaije 2002), then attributed to the Dorippoidea MacLeay, 1838 (Schweitzer *et al.* 2003a: 31, 32). According to Jagt *et al.* (2000: 40) some supposed necrocarcinids might represent parthenopids rather than calappids. The Necrocarcinidae was assigned with reservation to the Podotremata (Collins & Williams 2004: 34).

Six genera have been included in the Necrocarcinidae: *Campylostoma* Bell, 1858, *Cenomanocarcinus* Van Straelen, 1936, *Corazzatocarcinus* Larghi, 2004 (see below), *Hasaracancer* Jux, 1971, *Necrocarcinus* Bell, 1863, *Paranecrocarcinus* Van Straelen, 1936, *Pseudonecrocarcinus* Förster, 1968 (for the family diagnosis see Schweitzer *et al.* 2003a: 32), and *Shazella* Collins & Williams, 2004 (Collins & Williams 2004). The earliest known occurrences include the Hauterivian *Paranecrocarcinus hexagonalis* Van Straelen, 1936; the Barremian *P. kennedyi* Wright, 1997 and *Necrocarcinus ?olsoni* (Rathbun, 1937); the upper Aptian *Necrocarcinus undecimtuberculatus* Takeda & Fujiyama, 1983; the Aptian-Cenomanian *N. labeschii* (Eudes-Deslongchamps, 1835, as *Orithyia labeschii*); the Albian *Paranecrocarcinus graysonensis* (Rathbun, 1935), *P. moseleyi*

(Stenzel, 1945), *Necrocarcinus texensis* Rathbun, 1935, *Cenomanocarcinus renfroae* (Stenzel, 1945), *C. oklahomensis* (Rathbun, 1935), and *Pseudonecrocarcinus stenzeli* Bishop, 1983; the Albian-lower Cenomanian *N. woodwardi* Bell, 1863; and the Cenomanian *P. libanoticus* Förster, 1968, *P. digitatus* Wright & Collins, 1972, *P. mozambiquensis* Förster, 1970, *Paranecrocarcinus biscissus* Wright & Collins, 1972, and an indeterminate genus and species of Egypt (Schweitzer *et al.* 2003b).

Necrocarcinus labeschii, type species of the genus *Necrocarcinus* (Glaessner 1929: 282; 1969: R495, fig. 306.3; Wright & Collins 1972: 63, pl. 11, pl. 22, fig. 8a-c), is known by its male abdomen: six segments and telson in both sexes, a sharp dorsal rib on the first five segments, and segment 6 twice as long as segment 5 (Wright & Collins 1972: 64).

As in many fossils, necrocarcinids have a long history of taxonomic problems and transferrals. The case of *Necrocarcinus siouxensis* Feldmann, Awuota & Welshenbaugh, 1976 (Feldmann *et al.* 1976: pl. 1, fig. 5), from the Maastrichtian of North Dakota, is representative of the difficulty of the placement of crabs supposed to be necrocarcinids. Not referable to *Necrocarcinus* Bell, 1863 (Bishop & Williams 1991), of uncertain position (Fraaye 1994: 264) or tentatively assigned to *Cenomanocarcinus* (Schweitzer *et al.* 2003a: 36-39, table 1), *C. siouxensis* was assigned to the Podotremata by Guinot & Quenette (2005: 329). The Cretaceous necrocarcinid *Cenomanocarcinus vanstraeleni* Stenzel, 1945 (Stenzel 1945: 447, fig. 15, pl. 44) also seems to be typically podotreme. The two species *C. siouxensis* and *C. vanstraeleni*, as well as other necrocarcinids, might be referred to a new genus to be included in the Podotremata.

The hypothesis that certain members of the Necrocarcinidae actually prove to be non-eubrachiurans was already suggested by Larghi (2004: 529, 530), who questionably placed some of them within the Podotremata. When ventral parts exist in fossil records and have been cleared, the dimensionial relations between the male abdomen and the thoracic sternum are fundamental. A (basal) podotreme crab is characterized, besides its coxal female gonopores and the presence of spermathecae, by having most of the sternum laterally covered by male abdomen

and in contact with coxae of pereopods (Guinot & Tavares 2001).

In the supposed necrocarcinid *Corazzatocarcinus* Larghi, 2004 (Larghi 2004: 530, figs 2-4; see also Larghi & Garassino 2000: 53, fig. 1), belonging to an "uncertain superfamily", the sternum is missing, and the abdomen is probably that of a female; the dorsal and reduced P4 and P5 might support an assignation to the basal Podotremata (Dromiacea De Haan, 1833), otherwise to the Dorippoidea.

The Campanian *Hasaracancer cristatus* Jux, 1971 (Jux 1971: figs 2A, C, pl. 17, figs 1, 2), with an incompletely folded abdomen and abdominal pleurae, was first referred to the Raninidae, thus supposed to be a podotreme crab, and then included in the Necrocarcinidae within the Heterotremata (Schweitzer *et al.* 2003a: 32).

Some of the species first included in the Necrocarcinidae (Schweitzer & Feldmann 2000a: 232, 246, fig. 1) were referred to the Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetricks, Nyborg & Ross, 2003 (Schweitzer *et al.* 2003a: 33). Both Necrocarcinidae and Orithopsidae have been associated within the Dorippoidea (Schweitzer *et al.* 2003a: 39). The family diagnosis of the Orithopsidae must be completed in including the following characters: 1) thoracic sternum, known in *Goniochele angulata* Bell, 1858 and *G. madseni* Collins & Jakobsen, 2003: sternum of *G. angulata* broadly ovate, two-fifths the width of the carapace, with "Episternum [corresponding to the anterior sternites] considerably longer than wide, much produced, pointed" (Carter 1898: 23); female sternum of *G. angulata* and *G. madseni* with nodes: sternites 1-2 fused and forming a triangle between the mxp3; sternite 3 subrescentic; sternite 4 subtrapezoidal; sternites 6-7 triangular (Collins & Jakobsen 2003: pl. 3, figs 2a, 4a); 2) male abdomen of *G. angulata* very long, linear and narrow, with all free segments (see Bell 1858: 27, pl. 4, fig. 8); 3) female abdomen of *G. angulata* with segment 6 twice as long as any other of the anterior segments according to Carter (1898: 23, pl. 1, fig. 6), a feature not apparent in the figure of Bell (1858: fig. 9); and 4) subdorsal position of P4 and P5, coxae preserved in *G. angulata* (see Bell 1858: 26, 27, pl. 4, figs

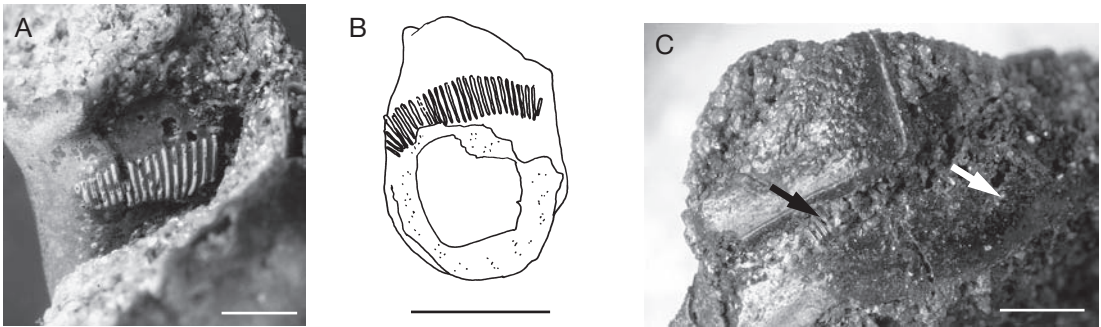


FIG. 13. — *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879, stridulating apparatus: **A**, MHN LM 2005.1.6, pars stridens; **B**, MHNH 9186, pars stridens; **C**, MHNH 9199, counterpart of a portion of the pars stridens (black arrow) in front of the tubercles of the plectrum (white arrow) and the granulous ridge of the shutter. Scale bars: 1 mm.

4, 5). This last feature generally implies reduced P4 and P5, special arrangement (mobility), and carriage over the carapace. These pereopods have so far not been preserved in other necrocarcinid genera.

The familial status of some genera with apparent similarities to the Necrocarcinidae remains questionable. For example the Paleocene *Camarocarcinus* Holland & Cvanara, 1958, placed within the Necrocarcininae or Necrocarcinidae (see Jakobsen & Collins 1979: 63; Fraaye 1994: 264; Fraaije 2002: 914) or within the Calappidae (see Collins & Rasmussen 1992: 33, fig. 19; Schweitzer & Feldmann 2000a: 234, 246, fig. 3), was finally considered most closely related to the Leucosiidae Samouelle, 1819 (Schweitzer *et al.* 2003a: 34). We have examined a cast of *C. quinquetuberculatus* Collins & Rasmussen, 1992, with well preserved ventral parts. The mxp3 are elongate and of oxystomian type, the arthrochial cavities of the chelipeds are located close together and overhang the sterno-abdominal cavity, the thoracic sternum is narrow, with a flat, undivided bottom forming “a median furrow” (Collins & Rasmussen 1992: 36) and lateral flanges oriented almost vertically. Anyway the combination of ventral characters (neither calappid nor leucosiid) does not allow a confident attribution, only suggests inclusion of *Camarocarcinus* in an extinct family.

The status of *Shazella* Collins & Williams, 2004, from the upper Turonian, known by carapace only, remains uncertain.

LITHOPHYLACIDAE VS HEXAPODIDAE

MIERS, 1886

The P5, in the course of our first investigations on *Lithophylax*, were not visible in any of the specimens that were examined, and, finally, the discovery of a P5 subdorsal coxa prolonging into a narrow merus was an important discovery. The absence of discernible P5 in fossil records makes the assignment to family and generic levels difficult, which may result in inaccurate placements. The absence of P5 may be due either to an evident absence as it is traditionally stated for the Hexapodidae (loss of all P5 articles except for the concealed, vestigial coxa in males, see Guinot 2006; Guinot, Tavares & Castro unpublished), or to a complete loss during fossilization. The fact that in many fossil crabs the legs do not readily fossilize, especially in the case of reduced, thin and subdorsal last pair, thus not preservable (see Glaessner & Rao 1960; Schweitzer & Feldmann 2001a; Larghi 2004), creates a problem for their identification. A reduced and subdorsal P5 which has been lost during fossilization risks being misinterpreted as missing. The only way of determining the presence of a P5 consists in carefully examining the P5 coxa (if preserved), the size and position of its arthrochial cavity, and the space that remains for this cavity at the posterior corners of the carapace. Reduced P5 coxae are often subdorsal (sometimes also P4); additionally, they have often a reentrant location on the carapace (also for the P4, but to a lesser extent), which corresponds to

the progressive dorsal position of P4 and P5 related to the posterior thoracic curvature. For instance, in the case of the fossil Retroplumidae, preserved P5 coxae are much closer to each other than preceding ones so that they leave a very short distance between them. It is possible that some fossil crabs supposed to be Hexapodidae actually belong to the Retroplumidae. The characters of the thoracic sternum, when present, nevertheless, permit an identification since this region is quite different in these two families.

Lithophylax does not belong to the Hexapodidae since cleaning from the matrix resulted in discovery of a P5, with a subdorsal, reduced coxa and a (presumably) narrow merus bearing a row of granules. Other features of *Lithophylax* are not at all those of an hexapodid, in particular the thoracic sternum. However, one characteristic shared by the Hexapodidae (a part of them only) and the Lithophylacidae is the presence of a stridulatory apparatus. Extant Hexapodidae (*Hexaplex* Doflein, 1904, *Hexapus* De Haan, 1835, *Stevea* Manning & Holthuis, 1981, and *Paeduma* Rathbun, 1898) as well as fossil (the Eocene *Hexapus pinfoldi* Collins & Morris, 1978 and *Stevea cesarii* Beschin, Busulini, De Angeli & Tessier, 1994; the upper Eocene *Goniocypoda edwardsi* Woodward, 1867 and probably *G. quaylei* Crane, 1981) show stridulating striae, arranged in two different patterns, either a suborbital row or a pterygostomial area (Guinot-Dumortier & Dumortier 1960; Manning & Holthuis 1981; Crane 1981: 6, 7, fig. 8D; Manning 1982; Glaessner & Secretan 1987: 8, pl. 1, fig. 5b, 6; Beschin *et al.* 1994: 194; Guinot 2006). However, the stridulating mechanism is different in the two families. In *Lithophylax triggeri* (Figs 5B; 13; 14), most of the inner part of the P1 merus bears a wide transverse area with 29 strong striae, and it is likely that the plectrum (Fig. 8A, C) consists of at least eight suborbital tubercles (versus striae on the ventral surface of the cephalothorax rubbed by striae on inner surface of P1 dactylus in the Hexapodidae).

The main differences between the Lithophylacidae and the Hexapodidae are the presence of P5 with a subdorsal coxa and narrow merus in the Lithophylacidae (Figs 11B; 12B, below; 14) (partial loss of P5 in males except for the vestigial coxa in male

hexapodids, absent in female hexapodids; see Guinot 2006; Guinot, Tavares & Castro unpublished); thoracic sternum broadly triangular; sternites 4-8 unequal, sternite 7 being smaller, and sternite 8 subdorsal and smaller, covered by abdomen in the Lithophylacidae (very wide sternum, sternites 5-7 subrectangular, similarly developed and high, sternite 8 subdorsal, reduced, and generally partly exposed in the Hexapodidae, see Glaessner & Secretan 1987; Beschin *et al.* 1994; Guinot 2006); sternal sutures 5/6 and 6/7 slightly oblique, presumably complete in the Lithophylacidae (sutures 4/5 to 6/7 nearly parallel, equidistant and interrupted in the Hexapodidae); male abdomen triangular in the Lithophylacidae (relatively narrow and with straight margins in Hexapodidae). A character shared by the Lithophylacidae and the Hexapodidae is the mxp3 condition: they are strongly divergent anteriorly, leaving the mandibles exposed.

Palaeopinnixa perornata Collins & Morris, 1976, known from Miocene and Eocene (see Feldmann & Schweitzer 2004: 19, fig. 3B-E), has inflated swellings on the carapace which contrast with the smooth carapace of most fossil and extant hexapodids (the Recent *Latohexapus* Huang, Hsueh & Ng, 2002 excepted) and shows a long male abdomen which is reminiscent of that of *Paeduma cylindraceum* (Bell, 1859) and *Stevea williamsi* (Glassell, 1938) (see Guinot 2006).

LITHOPHYLACIDAE VS RETROPLUMIDAE

GILL, 1894

The relationships of the family Lithophylacidae with the Retroplumidae merit discussion. First considered "aberrant" Catometopes among the Goneplacidae (Alcock & Anderson 1894: 180 under *Archaeoplax* Alcock & Anderson, 1894), then true Catometopes but of "an archaic type" (Alcock 1899: 78, 79 as Ptenoplacidae), near *Hexapus* (Alcock 1900: 285, 455 as Ptenoplacidae), the Retroplumidae was left, more or less explicitly, in the Catometopes by many authors (Tesch 1918: 29-33; Rathbun 1918: 15; Sakai 1976: 322, 592). The family was not included in the Thoracotremata by Guinot (1977), as stated by Schweitzer & Feldmann (2001b: 201). At present, the Retroplumidae appears as an heterotreme family (Schram 1986; Guinot 1978; Saint Laurent 1989;

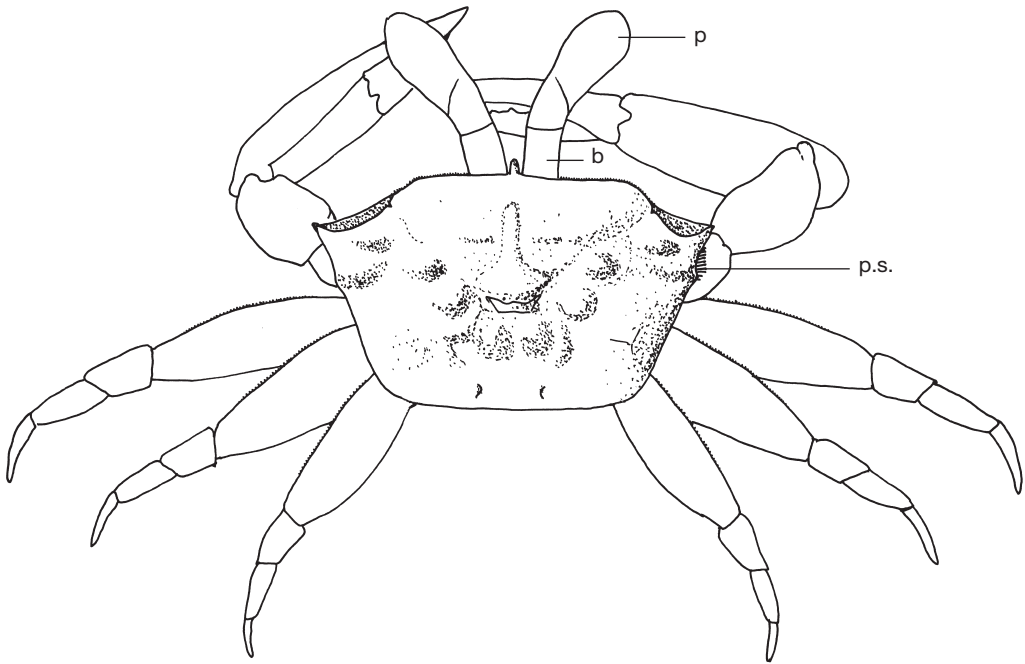


FIG. 14. — Reconstruction of *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879; subdorsal P5 not figured; podophthalmite, hypothetical, inferred from plasticine casts of the orbits. Abbreviations: **b**, basophthalmite; **p**, podophthalmite; **p.s.**, pars stridens.

Guinot & Bouchard 1998; McLay 2006), and is placed in proximity to the Dorippidae or Palicidae (Bals 1957: 1633, 1662; Guinot 1978: 214, 249, 251, 284; Guinot & Quenette 2005: 334).

Retroplumid crabs are known from many fossils, and paleontologists are faced with a rich and diverse fauna, known only from the Late Cretaceous (the Early Cretaceous *Archaeopus rathbunae* was suspected to be a carcineretid by Schweitzer & Feldmann 2001b; see above). The family was supposed to have originated during the Cretaceous in the Americas (Schweitzer & Feldmann 2001b: 202). The Retroplumidae was placed close to the Ocypodidae or within the Ocypodoidea (Beurlen 1930: 350-352; Glaessner 1969: R531; Collins & Morris 1975: 823; Vía 1957: 553; 1969: 322-328; 1980: 4, fig. 1, table 1; 1982: 115, figs 1, 2; Bishop 1983: 427), or considered a thoracotreme family (Vega & Feldmann 1992: 139; Collins *et al.* 1993: 304; 1994: 29; Feldmann & Martins-Neto 1995: 610; Vega *et al.* 1995: 347; Feldmann *et al.* 1995: 16; 1997: 126). Beschin *et al.* (1996),

Martin & Davis (2001), Collins *et al.* (2003), and Schweitzer *et al.* (2003a) followed Saint Laurent (1989) in considering a separate superfamily, Retroplumoidea. According to Saint Laurent (1989), *Archaeopus* Rathbun, 1908 (Rathbun 1908: 346, pl. 47, figs 4-7, pls 48, 49, figs 2-4), considered one of the oldest known retroplumid fossil genus (or closely allied to) (Beurlen 1930; Vía 1969; Collins & Morris 1975; Vega & Feldmann 1992; Schweitzer *et al.* 2003a) and supposed to have survived the end of the K/T event, must be removed from the Retroplumidae. According to McLay (2006) many fossil retroplumids (all *Archaeopus* species and several representatives of the genus *Costacopluma* Collins & Morris, 1975) are very likely members of the Palicidae (see below).

The differences between the Lithophylacidae and the Retroplumidae are too numerous to be enumerated. Nevertheless, the two families share some features: rostrum developed, projected (similarly downturned in *Archaeopus rostratus* Schweitzer, Feldmann, Fam, Hessin, Hetricks, Nyborg & Ross,

2003), thoracic sternum broad (sutures 4/5-7/8, however, are all interrupted in the retroplumids), mxp3 obviously diverging, sternite 8 reduced, and P5 dorsal, reduced, in the Lithophylacidae not as reentrant, however, as in the Retroplumidae.

LITHOPHYLACIDAE VS PALICIDAE BOUVIER, 1898

The only obvious resemblances between the Lithophylacidae and the Palicidae Bouvier, 1898 (see Castro 2000 for the date of publication) concern the P5, which are very reduced, nearly filiform, and dorsal in the Palicinae, instead to be represented only by a small, subdorsal coxa and a (presumed) narrow merus in *L. trigeri* (Figs 11A; 12B; Annexe: Table 2). In the Palicidae the thoracic somite 8 is strongly modified, so that sternite 8 is reduced (although nearly aligned with preceding sternites) and also pleurite 8 is modified (Guinot, Tavares & Castro unpublished). In the Lithophylacidae the sternite 8 is subdorsal, reduced, covered by the abdomen in both sexes, and not visible dorsally.

The Palicidae was regarded as a catometope or thoracotreme family (Faxon 1895: 38; Alcock 1900: 290, 450; Borradaile 1907: 482; Rathbun 1918: 15, 182; Bouvier 1940: 303; Monod 1956: 387; Balss 1957: 1633, 1661; Serène 1965: 25; 1968: 97; Sakai 1976: 592; Manning & Holthuis 1981: 191; Schram 1986: 308), and was even included in the Ocyropodoidea Rafinesque, 1815 (Martin & Davis 2001: 75). Actually the Palicidae shows a typical coxo-sternal condition of the male gonopores (Guinot 1979: fig. 30G), thus is heterotreme. A relationship with the Dorippoidea was suggested (Cano 1891; Bouvier 1897a, b; 1898; A. Milne-Edwards & Bouvier 1900, 1902; Gurney 1942; Bourdillon-Casanova 1960; Guinot 1978; Guinot & Quenette 2005). Affinities between the Palicidae and *Carcimeretes woolacotti* Withers, 1922 (see Vega *et al.* 2001; Donovan *et al.* 2003), from the Maastrichtian, were evoked by Withers (1922: 541), despite the conflicting indications of their catometope/cyclometope conditions and the different shape of their P5.

The Palicidae Bouvier, 1898 shares also with the Retroplumidae a strong modification of somite 8 and dorsal location of P5. Fossil species of *Archaeopus* Rathbun, 1908 and *Retrocyropa* Via, 1957,

presently assigned to the Retroplumidae, have been considered possible members of the Palicidae (Glaessner 1969: R531; McLay 2006). The carapace of the Eocene (lower Lutetian) palicine *Spinipalicus italicus* Beschin & De Angeli, 2003 (Beschin & De Angeli 2003: 7-12, figs 2-4) shows some similarities with the Cretaceous *Archaeopus antennatus* Rathbun, 1908 (Rathbun 1908: 346, pl. 47, figs 4-7, pl. 48, pl. 49, figs 2-4), as stated by Beschin & De Angeli (2003: 12).

Several fossil Palicidae are known: *Eopalicus* Beschin, Busulini, De Angeli & Tessier, 1996, from Eocene and Oligocene; Miocene species were attributed to the extant genus *Palicus* Philippi, 1838 by Van Straelen (1938) and Müller (1984); see Beschin & De Angeli (2003). We agree with the hypothesis that ornamentation of transverse ridges in *Eopalicus squamosus* Beschin, Busulini, De Angeli & Tessier, 1996 (Beschin *et al.* 1996: pl. 1), with a typically palicid carapace-shape, is reminiscent of the "terraces" found in raninids and indicates a similar adaptation for burying. The condition of *Spinipalicus italicus*, with a broad carapace and inflated, tuberculated dorsal regions, resembles some ancient retroplumids. The thoracic sternum, abdomen and (fragile) P5 are unfortunately unknown in fossil palicids. Possible relationship between the three eubrachyuran families Retroplumidae, Palicidae and Hexapodidae, briefly evoked by Guinot & Quenette (2005: 334), needs further discussion (Guinot, Tavares & Castro unpublished).

LITHOPHYLACIDAE VS GONEPLACIDAE

MACLEAY, 1838

The family Goneplacidae is presently included within the Xanthoidea, by the neontologists (Martin & Davis 2001) as well as paleontologists (Schweitzer 2000; Schweitzer *et al.* 2002a; Karasawa & Kato 2003). The definition of the Goneplacidae, as recently given by Schweitzer (2000: 717) and Karasawa & Kato (2003: 137), shows the difficulty (also encountered by neontologists) to reconcile all the characters attributed to the members of this heterogeneous family: carapace angular, rectangular, trapezoidal or rounded; dorsal regions of carapace relatively flattened; areolation and ornamentation either indistinct, or weakly distinct or developed;

orbits wide and elongated; eyestalks short or elongated, cornea sometimes inflated; supra-orbital margin sometimes without fissures; supra-orbital angle sometimes present; outer-orbital spines attenuated or directed laterally; antero-lateral margins usually toothed; thoracic sternum broad; male abdomen with all segments free but segments may be fused in some; P2-P5 long, dactylus not modified, with or without corneous tip; G2 long or short.

The Late Cretaceous *Icriocarcinus* Bishop, 1988, differs from other goneplacid members in possessing well developed carapace regions. The thin exoskeleton is consistent with a burrowing mode of life as evidenced by a specimen of *I. xestos* found preserved in a simple, oblique burrow (Bishop 1988: 246, fig. 3D). *Icriocarcinus xestos* Bishop, 1988, species of *Ommatocarcinus* (as *O. corioensis* (Cresswell, 1886)), and of *Orbitoplax* Tucker & Feldmann, 1990 (as *O. weaveri* (Rathbun, 1926)) have deep grooves and inflations on the carapace, sometimes transverse ridges (Schweitzer 2000: 724). Fossil goneplacids as *Branchioplax* Rathbun, 1916 and *Orbitoplax* Tucker & Feldmann, 1990 exhibit a xanthid-like carapace (Schweitzer 2000: 718).

With respect to the recent revision of the Goneplacidae as divided into six subfamilies (Karasawa & Kato 2003), *Lithophylax* shares with the Goneplacinae *sensu stricto* (type genus: *Goneplax* Leach, 1814) the following characters: front straight and prolonging without notch to supra-orbital margin, orbital borders without fissures (only a tiny supra-orbital fissure in *Lithophylax*) nor angles, antero-lateral borders poorly toothed, thoracic sternum wide, sternal suture 7/8 interrupted, male abdomen wide, with all somites free, and long G2.

Lithophylax resembles *Goneplax sensu stricto* (type species: *G. rhomboides* (Linnaeus, 1758)) (see Guinot 1969b: 521, figs 64, 71, 72) and its allied genera (such as *Ommatocarcinus*) by having rectangular carapace that is much widened anteriorly; lateral margins strongly diverging anteriorly, with only one laterally directed tooth at the outer-orbital angle (Fig. 5A); usually developed orbits and eyes; wide thoracic sternum. The slanted and hollowed lateral margins of *Lithophylax* resemble those of the extant *Ommatocarcinus macgillivrayi* White, 1851 (type species of *Ommatocarcinus*) and fossil members.

The photographs and reconstruction of the dorsal surface carapace, mxp3 and abdomen of the well preserved *O. corioensis* by Jenkins (1975: fig. 1) allow a clear comparison with *L. trigeri*.

However, *Lithophylax* markedly differs from the Goneplacidae by several characters: rostrum extremely narrow and strongly downturned (wider and weakly inclined in *Goneplax*); front straight and continuous on the same line with orbital margin (sinuous in *Goneplax*); lobulation of dorsal surface of carapace marked (absent in *Goneplax*); G1 long, narrow and slightly tapering (rather stout and ending with a lobe in *Goneplax*); sternite 8 reduced, subdorsal and not exposed (more developed, not subdorsal and partly exposed in *Goneplax*); chelipeds short and stout (narrow and elongated in *Goneplax*); P2-P4 thick and massive (slender in *Goneplax*); P5 subdorsal and markedly reduced ("normal" position and size in *Goneplax*).

Goneplacidae *sensu lato* seems, however, the closest family to the Lithophylacidae. Both families share: sternal thoracic sutures 4/5 and 5/6 that are interrupted and with depressions; suture 6/7 complete or weakly interrupted, with its extremities ending together so that it is (presumably) complete in *Lithophylax*, interrupted medially in *Goneplax*; suture 7/8 either complete (for instance in the Mathildellinae Karasawa & Kato, 2003) or interrupted (for instance in the Goneplacinae) (for sketches of the "goneplacid" thoracic sternum see Guinot 1969a-c; Guinot & Richer de Forges 1981). An important feature shared by the Goneplacinae and the Lithophylacidae is the interrupted suture 7/8. The complete suture 5/6 of the Lithophylacidae indicates a less derived condition than that of the Goneplacidae. It should be noted that in the Mathildellinae the sternite 8 is (nearly) completely covered by the abdomen, as in the Lithophylacidae, a character that (with the complete suture 7/8) corroborates the basal place of the Mathildellinae (Karasawa & Kato 2003: 138). There is no close relationships, however, between the Lithophylacidae and the Mathildellinae, in which the sternite 8 is not subdorsal and the P5 are not reduced.

Lithophylax shows, like in the Recent goneplacid *Bathyplax*, a stridulating mechanism which roughly involves the same parts, i.e. the P1 merus and the

ventral surface of carapace. *Bathypylax* seems to be the only crab to possess a specialized and wide striated area on P1 merus similar to that of *Lithophylax*, with striae that are similarly oriented (Fig. 13). The subhepatic granules, however, are numerous and spaced in *Bathypylax*, instead of being aligned and few (only 8) in *L. trigeri* (Figs 8A, C; 13C). See Remarks on the stridulating apparatus.

Icriocarcinus xestos Bishop, 1988 (Bishop 1988: 250, figs 2, 3A-D, table 1) exhibits some characters similar to those of *L. trigeri*: carapace shape, dorsal surface with plateau-like areolations, slanted lateral margins, strong outer-orbital spine, narrow and downturned rostrum, long and flattened P2-P4, broad sternum with barely visible somite 8, all abdominal segments free. According to Bishop (1988) in *Icriocarcinus xestos* the broadly rounded antero-lateral margins bear “three spines, one at the outer angle of orbit?”. Another hypothesis may be that the supra-orbital margin itself is spined, the external spine being actually at the outer-orbital angle, and the antero-lateral margin is slanted and unarmed, as in some goneplacids and in *Lithophylax*. *L. trigeri* shows a stout, thick basophthalmite, and the podophthalmite (absent) is presumably long and club-shaped, with an inflated cornea. *Icriocarcinus xestos* is described with an “eyestalk long and slim, apparently folding back into long orbit extending beneath front from rostrum to first anterolateral spine” (Bishop 1988: 251, figs 2A, 3A), that might suggest a condition similar to that of *Lithophylax*. *Icriocarcinus* is perhaps the closest crab to *Lithophylax* by the preceding set of characters, but the two genera differ, however, by several features. *Icriocarcinus xestos* is characterized by: P5 being only smaller than preceding pereopods as usual, flattened and shaped similarly to preceding legs, with the merus as long as the broad carpus and propodus, with a straight dactylus (versus P5 subdorsal and much reduced in *L. trigeri*); chelipeds elongate and heterochelous (versus massive and only slightly heterochelous in *L. trigeri*).

Longusorbis Richards, 1975, considered close to *Icriocarcinus* (see Bishop 1988: 251) and with a similar burrowing mode of life (Richards 1975: fig. 6), was transferred into the Xanthidae (Vega *et al.* 1997: 619; Schweitzer *et al.* 2002a: 21), finally

into the Carcineretidae (Schweitzer *et al.* 2003a: 44), based upon a position justified by the paddle-like P5 in *Longusorbis cuniculosus*.

Jenkins (1975: fig. 7) suggested that *Ommatocarcinus corioensis* (Cresswell, 1886), a true goneplacid, was found in association with fossil burrow complexes which resembles the dwelling burrows of the extant *Goneplax rhomboides* (Pennant, 1777) (see Rice & Chapman 1971: figs 5-7). In *Ommatocarcinus* and *Goneplax*, as in *Icriocarcinus* and *Longusorbis*, the lateral extension and flattening of the body, the elongated pereopods, the developed orbits in which eyestalks may be folded are adaptive characters for burrowing. Conversely, *Lithophylax*, with its subdorsal and reduced P5, is not a burrower.

Placement of *Icriocarcinus* within the Goneplacidae has extended the geologic range of the Goneplacidae into the Late Cretaceous (Schweitzer *et al.* 2002a: 21, 28, 40). *Icriocarcinus* does not belong to the Lithophylacidae.

The components of the exclusively fossil subfamily recently erected within the Goneplacidae, the Icriocarcininae Štević, 2005, were unfortunately not quoted by the author (only mention of the type genus, *Icriocarcinus*), in a similar way that was used for all the new taxa established by this author (Štević 2005: 69).

CONCLUSION

It was unnecessary to compare *Lithophylax* with other fossil eubranchyuran groups already present in the Cretaceous, e.g., the Dorippoidea, from the Lower Cretaceous (Albian) with *Hillius* Bishop, 1983 (*H. youngi* Bishop, 1983, as type species) (Bishop 1983: 46, fig. 8C, pl. 1) and *Tepexicarcinus* Feldmann, Vega, Applegate & Bishop, 1998 (Larghi 2004; Vega *et al.* 2005a: 28, fig. 4, pl. 2, figs 2-12; Guinot, Tavares & Castro unpublished); the Hepatidae Stimpson, 1871, with the Albian *Prehepatius cretaceous* Rathbun, 1935 and *P. hodgesi* Bishop, 1983, only known by claw material (Schweitzer & Feldmann 2000a: 238). Because *Caloxanthus* was removed from the Xanthoidea and transferred to the Podotremata, questionably within the Dialucidae in the vicinity of the Dynomenidae, the Xanthoi-

dea *sensu* Schweitzer (2003: 277) remains without Lower Cretaceous representatives (see Schweitzer *et al.* 2002a: 39).

Within the Portunoidea Rafinesque, 1815, probably known only as post-Cretaceous, some genera possess a narrow, T-shaped rostrum, strongly converging lateral margins, developed outer-orbital spines, large orbits (e.g., in extant and fossil *Podophthalmus* Lamarck, 1801, subfamily Podophthalmiinae Dana, 1851; see Schweitzer *et al.* 2002b), but they are characterized by flattened and paddle-like terminal articles of P5. *Podophthalmus defrancii* Desmarest, 1822 (Desmarest 1822: 88, pl. 5, figs 6-8), from unknown origin and age, shows a thoracic sternum (with exposed sternite 8) and a male abdomen (somites 3-5 fused) apparently typical of the podophthalmine family. The well preserved *Proterocarcinus latus* (Glaessner, 1933), referred to the subfamily Polybiinae Ortmann, 1893 (Schweitzer & Feldmann 2000b; Casadío *et al.* 2005), has also a natatory P5, a condition not suspected in the Lithophylacidae. Because *P. latus* shows some similarities with *Longusorbis cuniculosus*, it may be suggested a strict comparison of these two species, both having a P5 with flattened, paddle-like propodus and oblancheolate dactylus. The placement of the type species of *Proterocarcinus* Feldmann, Casadío, Chirino-Gálvez & Aguirre-Urreta, 1995, *P. lophos* Feldmann, Casadío, Chirino-Gálvez & Aguirre-Urreta, 1995, is difficult owing to the absence of terminal articles on the "apparently subdorsal" P5 (Feldmann *et al.* 1995: 9, 11). The P5 shape is unknown in two other species of *Proterocarcinus*, *P. corsolini* Casadío, De Angeli, Feldmann, Garassino, Hetler, Parras & Schweitzer, 2004 and *P. navidad* Feldmann, Schweitzer & Encinas, 2005.

The genus *Lithophylax*, presently much better known than in the past, cannot be reasonably included in any existing families, since the combination of its characters precludes its placement within them. For this reason, its own family, Lithophylacidae Van Straelen, 1936, is recognized and redefined in the present paper. The family Lithophylacidae is extinct, with only one known genus, *Lithophylax*. Successive taxonomic transferrals of Cretaceous genera to different heterotreme families show the difficulty of determining its systematic position.

Besides the Hexapodidae, with vestigial P5, and the Dorippoidea, with reduced, dorsal P4 and P5, the only heterotreme families having a reduced and dorsally located P5 are the Lithophylacidae (extinct), the Retroplumidae, and the Palicidae.

Acknowledgements

We are greatly indebted to D. Decrouez (Muséum d'Histoire naturelle, Genève), A. Dhondt (IRSNB, Paléontologie des Invertébrés) (we were sorry to learn of her death in September 2006), N. Morel (Musée Vert, Le Mans), and A. Prieur (Université Claude Bernard, Lyon, Collections des sciences de la Terre) for their help in the search of *Lithophylax* material, and to R. Cousin for the thin sections and molds; A. De Angeli (Associazione Amici del Museo Civico "G. Zannato", Montecchio Maggiore, Italy) for providing paleontological data and valuable comments; F. J. Vega (Instituto de Geología, Coyoacan, Mexico) for providing information on *Mascaranada*; M. Tavares (Museu de Zoologia, Universidade de São Paulo) for providing information on *Araripecarcinus*; S. L. Jakobsen (Geological Museum, Copenhagen) for the gift of casts of *Camarcarcinus quinquetuberculatus*. We are grateful to J.-M. Pacaud (MNHN, Département Histoire de la Terre) who helped us in search of *Lithophylax* and *Palaeoplax* and provided documentation. Our deep appreciation to R. Roy (MNHN, Entomology) for his help in nomenclatural questions, to P. Castro (California State Polytechnic University, Pomona, USA) for kindly reviewing a first preliminary draft of the manuscript. Special thanks are due to R. M. Feldmann (Department of Geology, Kent State University) and H. Karasawa (Mizunami Fossil Museum, Mizunami, Japan) for their careful review of the manuscript and precious comments.

REFERENCES

- ABELE L. G., ROBINSON M. H. & ROBINSON H. 1973. — Observations on sound production by two species of crabs from Panama (Decapoda, Gecarcinidae, and Pseudothelphusidae). *Crustaceana* 25 (2): 147-152.
- ALCOCK A. 1899. — *An Account of the Deep-Sea Brachyura*

- Collected by the Royal Indian Marine Survey Ship "Investigator". Trustees of the Indian Museum, Calcutta, 85 p.
- ALCOCK A. 1900. — Materials for a carcinological fauna of India. No. 6. The Brachyura Catometopa, or Grapsoidea. *Journal of the Asiatic Society of Bengal* 69, pt 2 (3): 279-456.
- ALCOCK A. & ANDERSON A. R. J. 1894. — Natural history notes from H. M. Indian Marine Survey Steamer "Investigator", Commander C. F. Oldham, R. N., commanding. Series II. No. 14. An account of a recent collection of deep sea Crustacea from the Bay of Bengal and Laccadive Sea. *Journal of the Asiatic Society of Bengal* 63, pt 2 (3): 141-185.
- ALLISON P. A. 1988. — Taphonomy of the Eocene London Clay Biota. *Palaeontology* 31 (4): 1079-1100.
- BALSS H. 1957. — Decapoda. VIII. Systematik, in BRONNS H. G. (ed.), *Klassen und Ordnungen des Tierreichs*. Fünfter Band, I. Abteilung, 7. Buch, 12. Lieferung, Geest & Portig K.-G., Leipzig: 1505-1672.
- BELL T. 1858. — *A Monograph of the Fossil Malacostracous Crustacea of Great Britain*. Part I. *Crustacea of the London Clay*. Palaeontographical Society Monograph 10, London, viii + 44 p.
- BELL T. 1863. — A monograph of the fossil Malacostracous Crustacea of Great Britain. Part II. Crustacea of the Gault and Greensand. *Palaeontographical Society [Monogr.]* 14: 1-44.
- BELLWOOD O. 2002. — The occurrence, mechanics and significance of burying behaviour in crabs (Crustacea: Brachyura). *Journal of Natural History* (36) (10): 1223-1238.
- BENMORE R. A., COLEMAN M. L. & MCARTHUR J. M. 1983. — Origin of sedimentary francolite from its sulphur and carbon isotope composition. *Nature* 302: 516-518.
- BESCHIN C. & DE ANGELI A. 2003. — *Spinipalicus italicus*, nuovo genere e specie di Palicidae (Crustacea, Decapoda) dell'Eocene del Vicentino (Italia settentrionale). *Studi e Ricerche, Associazione Amici del Museo-Museo Civico "G. Zannato", Montecchio Maggiore, Vicenza*: 7-12.
- BESCHIN C., BUSULINI A., DE ANGELI A. & TESSIER G. 1994. — I Crostacei Eocenici della cava "Boschetto" di Nogarole Vicentino (Vicenza – Italia settentrionale). *Lavori Società Veneziana di Scienze Naturali* 19: 159-215.
- BESCHIN C., BUSULINI A., DE ANGELI A. & TESSIER G. 1996. — Retropiumoidae (Crustacea, Brachyura) nel Terziario del Vicentino (Italia settentrionale). *Lavori Società Veneziana di Scienze Naturali* 21: 83-102.
- BEURLEN K. 1930. — Vergleichende Stammesgeschichte. Grundlagen, Methoden, Probleme unter besonderer Berücksichtigung der höheren Krebse. *Fortschritte Geologie und Paläontologie* 8 (26): i-viii, 317-586.
- BEURLEN K. 1958. — Dois Crustáceos do Cretáceo superior do nordeste do Brasil (Decapoda, Brachyura). *Boletim do Museu Nacional Rio de Janeiro n.s. (Geologia)* 26: 1-23.
- BEURLEN K. 1965. — Crustáceos decápodes na Formação Riachuelo (Cretáceo-Sergipe). *Anais da Academia Brasileira de Ciências* 37 (2): 267-272.
- BISHOP G. A. 1972. — Moults of *Dakoticancer overanus*, an Upper Cretaceous crab from the Pierre Shale of South Dakota. *Palaeontology* 15 (4): 631-636.
- BISHOP G. A. 1983. — Fossil decapod crustaceans from the Lower Cretaceous, Glen Rose Limestone of Central Texas. *Transactions of the San Diego Society of Natural History* 20 (2): 27-55.
- BISHOP G. A. 1986. — Taphonomy of the North American Decapods. *Journal of Crustacean Biology* 6 (3): 326-355.
- BISHOP G. A. 1988. — Two crabs, *Xandaros sternbergi* (Rathbun, 1926) n. gen., and *Icriocarcinus xestos* n. gen., n. sp., from the Late Cretaceous of San Diego County, California, USA, and Baja California Norte, Mexico. *Transactions of the San Diego Society of Natural History* 21: 245-257.
- BISHOP G. A. & WILLIAMS A. B. 1991. — *Necrocarcinus olsonorum*, new species, a crab (Decapoda: Calappidae) from the Cretaceous Carlisle Shale (Turonian), Western Interior United States. *Journal of Crustacean Biology* 11 (3): 451-459.
- BORRADAILE L. A. 1907. — On the classification of the decapod crustaceans. *Annals and Magazine of Natural History* ser. 7, 19: 457-486.
- BOULE M. & PIVETEAU J. 1935. — *Éléments de paléontologie*. Masson, Paris, 899 p.
- BOURDILLON-CASANOVA L. 1960. — Les larves de crustacés décapodes, in Le méroplancton du golfe de Marseille. *Recueil des Travaux de la Station marine d'Endoume* 30 (18): 1-286.
- BOUVIER E.-L. 1897a. — Observations sur les crabes de la famille des dorippidés. *Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences* 125 (20): 784-787.
- BOUVIER E.-L. 1897b. — Sur la classification, les origines et la distribution des crabes de la famille des dorippidés. *Bulletin de la Société philomatique de Paris* (8) 9: 54-70 [sometimes quoted from 1898] (dated 1896, published 1897).
- BOUVIER E.-L. 1898. — Observations on the crabs of the family Dorippidae. *Annals and Magazine of Natural History* ser. 7, 1: 103-105.
- BOUVIER E.-L. 1940. — Décapodes marcheurs, in *Faune de France*. 37. Paris, Lechevalier, 404 p.
- BRETON G. 1996. — *Tethyaster guerangeri* sp. nov. (Astropectinidae, Asteroidea, Echinodermata): deux spécimens d'astérides d'une conservation exceptionnelle du Cénomani du Mans (Sarthe, France). *Bulletin trimestriel de la Société géologique de Normandie et des Amis du Muséum du Havre* 82 (4): 17-29 (dated

- 1995, published 1996).
- BRETON G. 2001. — La stratégie de protection du crabe *Inachus phalangium* (Fabricius, 1775): approche expérimentale. *Annales du Muséum d'Histoire naturelle de Perpignan* 11: 19-22.
- BRETON G. 2006. — Un cas de paléocoprofagie chez un crabe du Cénomaniien du Mans (Collection Boutillier, Université de Caen). *Bulletin de la Société linnéenne de Normandie* 119: 41-43.
- BRETON G., SYGUT A. & OMS R. 2004. — Approche expérimentale des stratégies de protection du crabe *Inachus phalangium* (Fabricius, 1775). *Bulletin trimestriel de la Société géologique de Normandie et des Amis du Muséum du Havre* 90 (2): 61-69 (dated 2003, published 2004).
- BROCCHI P. 1877. — Description de quelques crustacés fossiles appartenant à la tribu des raniniens. *Annales des Sciences géologiques* 8: 1-8.
- CANO G. 1891. — Sviluppo postembrionale dei Doripidei, Leucosiadi, Corystodei e Grapsidi. *Memorie della Società Italiana di Scienza Naturale* ser. 3, 8 (4): 1-14.
- CARTER J. A. 1898. — Contribution to the palaeontology of the decapod Crustacea of England. *Quarterly Journal of the Geological Society*, London 54: 15-44.
- CASADIO S., FELDMANN R. M., PARRAS A. & SCHWEITZER C. E. 2005. — Miocene fossil decapods (Crustacea: Brachyura) from Patagonia, Argentina, and their palaeoecological setting. *Annals of the Carnegie Museum* 74 (3): 151-188.
- CASTRO P. 2000. — Crustacea Decapoda: a revision of the Indo-west Pacific species of palicid crabs (Brachyura Palicidae), in CROSNIER A. (ed.), Résultats des campagnes MUSORSTOM, vol. 21. *Mémoires du Muséum national d'Histoire naturelle* 184: 437-610.
- COLLINS J. S. H. & JAKOBSEN S. L. 2003. — New crabs (Crustacea Decapoda) from the Eocene (Ypresian/Lutetian), Lillebælt Clay Formation of Jutland, Denmark. *Bulletin of the Mizunami Fossil Museum* (30): 63-96.
- COLLINS J. S. H. & MORRIS S. F. 1975. — A new crab, *Costacopluma concava*, from the upper Cretaceous of Nigeria. *Palaeontology* 18 (4): 823-829.
- COLLINS J. S. H. & RASMUSSEN H. W. 1992. — Upper Cretaceous-Lower Tertiary decapod crustaceans from West Greenland. *Bulletin of the Grønlands Geological Undersøgelse* 162: 1-46.
- COLLINS J. S. H. & WILLIAMS R. J. 2004. — A new genus and species of necrocarinid crab (Crustacea, Brachyura) from the Upper Cretaceous of England. *Bulletin of the Mizunami Fossil Museum* (31): 33-35.
- COLLINS J. S. H., KANIE Y. & KARASAWA H. 1993. — Late Cretaceous crabs from Japan. *Transactions and Proceedings of the Palaeontological Society of Japan* N. S. (172): 292-310.
- COLLINS J. S. H., HIGGS R. & CORTICULA B. 1994. — A new crab, *Costacopluma bifida* (Crustacea, Decapoda) from the Palaeocene of Venezuela. *Bulletin of the Mizunami Fossil Museum* (21): 29-34.
- COLLINS J. S. H., FRAAYE R. H. B. & JAGT J. W. M. 1995. — Late Cretaceous anomurans and brachyurans from the Maastrichtian type area. *Acta Palaeontologica Polonica* 40 (2): 165-210.
- COLLINS J. S. H., LEE C. & NOAD J. 2003. — Miocene and Pleistocene crabs (Crustacea, Decapoda) from Sabah and Sarawak. *Journal of Systematic Paleontology* 1 (3): 187-226.
- CRANE M. D. 1981. — Hexapod crabs of the genus *Goniocypoda* H. Woodward from the Upper Eocene of Hampshire. *Zoological Journal of the Linnean Society* 72: 1-19.
- DE ANGELI A. & GARASSINO A. 2006. — New reports of decapod crustaceans from the Mesozoic and Cenozoic of Friuli-Venezia Giulia (NE Italy). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia naturale Milano* 147 (II): 267-294.
- DELAUNAY P. 1937. — Galerie des naturalistes sarthois. Edouard Guéranger (1801-1895). *La Province du Maine*, Le Mans, 2^e sér., 17: 177-183, 229-236.
- DELAUNAY P. 1938. — Galerie des naturalistes sarthois. Edouard Guéranger (1801-1895) (fin). *La Province du Maine*, Le Mans, 2^e sér., 18: 8-15.
- DESMAREST A.-G. 1819. — Article "Crustacés fossiles". *Nouveau Dictionnaire d'Histoire naturelle...* Nouvelle éd. COR-CUN. Tome III. Deterville, Paris, 602 p.
- DESMAREST A.-G. 1822. — Les crustacés proprement dits, in *Histoire naturelle des crustacés fossiles, sous les rapports zoologiques et géologiques*. F. G. Levrault, Paris; Strasbourg: 67-154.
- DONOVAN S. K., PORTELL R. W. & COLLINS J. S. H. 2003. — Cretaceous and Cenozoic decapod crustaceans of Jamaica. *Contributions to Zoology* 72 (2/3): 105-109.
- FAXON W. 1895. — Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross" during 1891, Lieut.-Commander Z. L. Tanner, U.S.N., commanding. XV. The stalk-eyed Crustacea. *Memoirs of the Museum of Comparative Zoology at Harvard College* 18: 1-292.
- FELDMANN R. M. & GAZDZICKI A. 1998. — Cuticular ultrastructure of fossil and living homolodromiid crabs (Decapoda: Brachyura). *Acta Palaeontologica Polonica* 43 (1): 1-19.
- FELDMANN R. M. & MARTINS-NETO R. G. 1995. — *Costacopluma nordestina* n. sp. (Decapoda Retroplumidae) from the Maria Farinha Formation (Paleocene) of Brazil. *Journal of Paleontology* 69 (3): 601-611.
- FELDMANN R. M. & SCHWEITZER C. E. 2004. — Decapod crustaceans from the Lower Miocene of northwestern Venezuela (Cerro La Cruz, Castillo Formation).

- Special Papers in Paleontology* 71: 7-22.
- FELDMANN R. M. & THSUDY D. 1987. — Ultrastructure in cuticle from *Hoploparia stokesi* (Decapoda: Nephropidae) from the Lopez de Bertodano Formation (Late Cretaceous-Paleocene) of Seymour Island, Antarctica. *Journal of Paleontology* 61 (6): 1194-1203.
- FELDMANN R. M. & VILLAMIL T. 2002. — A new carcinereiid crab (Upper Turonian, Cretaceous) of Columbia. *Journal of Paleontology* 76 (4): 718-724.
- FELDMANN R. M., AWUOTA E. E. B. & WELSHENBAUGH J. 1976. — *Necrocarcinus siouxensis*, a new species of calappid crab (Crustacea: Decapoda) from the Fox Hills Formation (Cretaceous: Maastrichtian) of North Dakota. *Journal of Paleontology* 50 (5): 985-990.
- FELDMANN R. M., CASADÍO S., CHIRINO-GÁLVEZ L. & AGUIRRE-URRETA M. 1995. — Fossil decapod crustaceans from the Jagüel and Roca Formations (Maastrichtian-Danian) of the Neuquén-Basin, Argentina. *Memoir 43. Journal of Paleontology* 69, Suppl. to no. 5: 1-22.
- FELDMANN R. M., RODRIGUEZ M. F., MARTINEZ G. A. & AGUIRRE-URETTA M. 1997. — *Costacopluma salamanca* new species (Decapoda, Retroplumidae) from the Salamanca Formation (Danian) of Patagonia, Argentina. *Journal of Paleontology* 71 (1): 125-130.
- FELDMANN R. M., VEGA F. J. & VILLAMIL T. 1998. — Cretaceous extinction of the Tethyan crab family Carcineretidae: a victim of the impact? *Geological Society of America Abstracts with Program* 30: A-286.
- FÖRSTER R. 1968. — *Paranecrocarcinus libanoticus* n. sp. (Decapoda) und die Entwicklung der Calappidae in der Kreide. *Mitteilungen Bayerischen Staatsammlung für Paläontologische und historische Geologie* 8: 167-195.
- FRAAIJE R. H. B. 2002. — New calappid crabs (Crustacea, Decapoda, Brachyura) from the late Maastrichtian of the Netherlands. *Journal of Paleontology* 76 (5): 913-917.
- FRAAYE R. H. B. 1994. — Early Paleocene crabs (Crustacea, Decapoda) from the Middle Vistula Valley, Central Poland. *Acta Geologica Polonica* 44 (3-4): 261-266.
- FRAAYE R. H. B. 1996. — Late Cretaceous swimming crabs: radiation, migration, competition, and extinction. *Acta Geologica Polonica* 46 (3-4): 269-278.
- FRITSCH A. 1887. — *Die Crustaceen der böhmischen Kreideformation*, in FRITSCH A. & KAFKA J. Selbstverlag, Praha, 53 p.
- GLAESSNER M. F. 1929. — *Crustacea Decapoda. Fossilium Catalogus*, pars 41. W. Junk, Berlin, 464 p.
- GLAESSNER M. F. 1969. — Decapoda, in MOORE R. C. (ed.), *Treatise on Invertebrate Paleontology*, Part R, *Arthropoda*, 4 (2). University of Kansas Press; Geological Society of America, Lawrence, Kansas: R399-R533, R626-R628.
- GLAESSNER M. F. 1980. — New Cretaceous and Tertiary crabs (Crustacea: Brachyura) from Australia and New Zealand. *Transactions of the Royal Society of South Australia* 104 (6): 171-192.
- GLAESSNER M. F. & RAO V. R. 1960. — A new species of crab from the early Tertiary Fuller's earth deposits of Kapurdi, Rajasthan, Western India. *Records of the Geological Survey of India* 86 (4): 675-682.
- GLAESSNER M. F. & SECRETAN S. 1987. — Crabs (Crustacea Brachyura) de l'Éocène du Sulaiman Range (Pakistan). *Annales de Paléontologie (Vert.-Invert.)* 73 (4): 273-288.
- GUÉRANGER E. 1867a. — *Album paléontologique du département de la Sarthe représentant au moyen de la photographie les fossils recueillis dans cette circonscription*. Éd. normale. Beauvais et Vallienne, Le Mans, xii + 77 p., 21 pls.
- GUÉRANGER E. 1867b. — *Album paléontologique du département de la Sarthe représentant au moyen de la photographie les fossiles recueillis dans cette circonscription*. Éd. normale. Beauvais et Vallienne, Le Mans, 20 p., 25 pls.
- GUILLIER A. [1869]. — *Notice géologique et agricole [...] à l'appui des profils géologiques des routes impériales et départementales de la Sarthe, dressés avec le concours de feu M. Triger*. [Manuscrit imprimé] Broise & Thieffry, Paris, 55 p.
- GUILLIER A. 1886. — *Géologie du département de la Sarthe*. Monnoyer, Le Mans, 430 p.
- GUINOT D. 1969a. — Recherches préliminaires sur les groupements naturels chez les crustacés décapodes brachyours. VII. Les Goneplacidae. *Bulletin du Muséum national d'Histoire naturelle* 2^e sér., 41 (1): 241-265.
- GUINOT D. 1969b. — Recherches préliminaires sur les groupements naturels chez les crustacés décapodes brachyours. VII. Les Goneplacidae (suite). *Bulletin du Muséum national d'Histoire naturelle* 2^e sér., 41 (2): 507-528.
- GUINOT D. 1969c. — Recherches préliminaires sur les groupements naturels chez les crustacés décapodes brachyours. VII. Les Goneplacidae (suite et fin). *Bulletin du Muséum national d'Histoire naturelle* 2^e sér., 41 (3): 688-724.
- GUINOT D. 1977. — Proposition pour une nouvelle classification des crustacés décapodes brachyours. *Comptes Rendus de l'Académie des Sciences* sér. D, 285: 1049-1052.
- GUINOT D. 1978. — Principes d'une classification évolutive des crustacés décapodes. Brachyours. *Bulletin biologique de la France et de la Belgique* 112 (3): 211-292.
- GUINOT D. 1979. — Données nouvelles sur la morphologie, la phylogénèse et la taxonomie des crustacés décapodes brachyours. *Mémoires du Muséum national d'Histoire naturelle* sér. A, Zoologie, 112: 1-354.
- GUINOT D. 1990. — Crustacea Decapoda: le genre *Psopheticus* Wood-Mason, 1892 (Goneplacidae), in

- CROSNIER A. (ed.), Résultats des campagnes MUS-ORSTOM, vol. 6. *Mémoires du Muséum national d'Histoire naturelle* sér. A, 145: 331-367.
- GUINOT D. 2006. — Rediscovery of the holotype of *Paeduma cylindraceum* (Bell, 1859) and description of a new genus of Hexapodidae (Decapoda, Brachyura). *Zoosystema* 28 (2): 553-571.
- GUINOT D. & BOUCHARD J.-M. 1998. — Evolution of the abdominal holding systems of brachyuran crabs (Crustacea, Decapoda, Brachyura). *Zoosystema* 20 (4): 613-694.
- GUINOT D. & QUENETTE G. 2005. — The spermatheca in podotreme crabs (Crustacea, Decapoda, Brachyura, Podotremata) and its phylogenetic implications. *Zoosystema* 27 (2): 267-342.
- GUINOT D. & RICHER DE FORGES B. 1981. — Crabes de profondeur, nouveaux ou rares, de l'Indo-Pacifique (Crustacea, Decapoda, Brachyura) (Deuxième partie). *Bulletin du Muséum national d'Histoire naturelle* 4e sér., sect. A, 3 (1): 227-260.
- GUINOT D. & TAVARES M. 2001. — Une nouvelle famille de crabes du Crétacé, et la notion de Podotremata Guinot, 1977 (Crustacea, Decapoda, Brachyura). *Zoosystema* 23 (3): 507-546.
- GUINOT-DUMORTIER D. & DUMORTIER B. 1960. — La stridulation chez les crabes. *Crustaceana* 1 (2): 117-155.
- GURNEY R. 1942. — *Larvae of Decapod Crustacea*. The Ray Society, London, 306 p.
- HARTNOLL R. G. 1972. — The biology of the burrowing crab, *Corystes cassivelaunus*. *Bijdragen tot de Dierkunde* 42 (2): 139-155.
- ICZN 1999. — *International Code of Zoological Nomenclature*. Fourth Edition. The International Trust for Zoological Nomenclature, London, xxix + 306 p.
- JAGT J. W. M., FRAAYE R. H. B. & VAN BAKEL B. W. M. 2000. — Late Cretaceous decapod crustacean faunas of northeast Belgium and the southeast Netherlands. *Studi e Ricerche, Associazione Amici del Museo-Museo Civico "G. Zannato", Montecchio Maggiore, Vicenza*: 37-42.
- JAKOBSEN S. L. & COLLINS J. S. H. 1979. — Decapod Crustacea from the Palaeocene of Zealand, Denmark. *Proceedings of the Geologists' Association* 90 (2): 61-64.
- JENKINS R. F. J. 1975. — The fossil crab *Ommatocarcinus coriensis* (Cresswell) and a review of related Australasian species. *Memoirs of the National Museum of Victoria* (36): 33-62.
- JUIGNET P. 1974. — *La transgression crétacée sur la bordure orientale du Massif armoricain. Aptien, Albien, Cénomanién de Normandie et du Maine. Le stratotype du Cénomanién*. Thèse de Doctorat d'État, Université de Caen, France, 108 p.
- JUIGNET P. 1980. — Cénomanién, in MÉGNIEN C. & MÉGNIEN F. (eds), Synthèse géologique du Bassin de Paris. Vol. I. Stratigraphie et paléogéographie. *Mémoire BRGM* 101: 292-297.
- JUX U. 1971. — Ein Brachyuren-Rest aus der Oberkreide Afganistans. *Paläontologische Zeitschrift* 45 (3-4): 154-156.
- KARASAWA H. & KATO H. 2003. — The family Goneplacidae MacLeay, 1838 (Crustacea: Decapoda: Brachyura): systematics, phylogeny, and fossil records. *Paleontological Research* 7 (2): 129-151.
- LARGHI C. 2004. — Brachyuran decapod Crustacea from the Upper Cretaceous of Lebanon. *Journal of Paleontology* 78 (3): 528-541.
- LARGHI C. & GARASSINO A. 2000. — The brachyurans of the Cenomanian (Upper Cretaceous) of Lebanon, in First Workshop on Mesozoic and Tertiary Decapod Crustaceans, 6-8 October 2000. Extended abstracts. *Studi e Ricerche, Associazione Amici del Museo-Museo Civico "G. Zannato", Montecchio Maggiore, Vicenza*: 53-54.
- LEGENDRE R. 1908. — Traces fossiles d'autotomie. *Comptes rendus des Séances de la Société de Biologie* 65: 662-663.
- MANNING R. B. 1982. — A redescription of *Cancer sexpes* Fabricius, 1798 (Crustacea, Decapoda, Hexapodidae). *Steenstrupia* 8 (5): 157-161.
- MANNING R. B. & HOLTHUIS L. B. 1981. — West African brachyuran Crabs (Crustacea: Decapoda). *Smithsonian Contributions to Zoology* 306: i-xii + 1-379.
- MARTIN J. W. & DAVIS G. E. 2001. — An updated classification of the Recent Crustacea. *Natural History Museum, Los Angeles County, Science series* 39: 1-124.
- MARTINS-NETO R. G. 1987. — Primeiro registro de decápode na Formação Santana, bacia do Araripe (Crétáceo Inferior), Brasil. *Ciência e Cultura*, São Paulo 39 (4): 406-410.
- MCLAY C. L. 2006. — Retroplumidae (Crustacea: Decapoda) from the Indo-Malayan archipelago (Indonesia, Philippine) and the Melanesian arc islands (Solomon Islands, Fiji and New Caledonia) and paleogeographical comments, in RICHER DE FORGES B. & JUSTINE J.-L. (eds), Tropical Deep-Sea Benthos. Vol. 24. *Mémoires du Muséum national d'Histoire naturelle* 193: 375-391.
- MERTIN H. 1941. — Decapode Krebse aus dem subhercynen und Braunschweiger Emscher und Unterseenon sowie Bemerkungen über einige verwandte Formen in der Oberkreide. *Nova Acta Leopoldina* NF, 10 (68): 149-264.
- MILNE-EDWARDS A. 1862a. — Monographie des crustacés fossiles de la famille des cancériens. Première partie. *Annales de Sciences naturelles* (Zoologie) (4) 18: 31-85.
- MILNE-EDWARDS A. 1862b. — Sur l'existence de crustacés de la famille des raniniens pendant la période crétacée. *Comptes rendus hebdomadaires des Séances de*

- l'Académie des Sciences* 55: 492-494.
- MILNE-EDWARDS A. & BOUVIER E.-L. 1900. — Crustacés décapodes. Première partie. Brachyures et anomoures, in *Expéditions scientifiques du Travailleur et du Talisman pendant les années 1880, 1881, 1882, 1883*. Paris, Masson: 1-396.
- MILNE-EDWARDS A. & BOUVIER E.-L. 1902. — Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78), in the Caribbean Sea (1878-79), and along the Atlantic Coast of the United States (1880), by the U. S. Coast Survey Steamer "Blake". XXXIX. Les dromiacés et oxystomes. *Memoirs of the Museum of Comparative Zoology at Harvard College* 27 (1): 1-127.
- MILNE-EDWARDS A. & BROCCCHI P. 1879. — Note sur quelques crustacés fossiles appartenant au groupe des macrophthaliens. *Bulletin de la Société philomatique sér. 7*, 3: 113-117.
- MONOD T. 1956. — Hippidea et Brachyura ouest-africains. *Mémoires de l'Institut français d'Afrique Noire* (45): 1-674.
- MORRIS S. F. 1993. — The fossil arthropods of Jamaica, in WRIGHT R. M. & ROBINSON E. (eds), Biostratigraphy of Jamaica. *Memoirs of the Geological Society of America* 182: 115-124.
- MÜLLER P. 1984. — A bádeni emelet tízlábú rákjai [= Decapod Crustacea of the Badenian]. *Geologica Hungarica, ser. Palaeontologica* (42): 1-317 (in Hungarian).
- MÜLLER P. & GALIL B. 1998. — A note on a Miocene Matutine crab from Hungary (Decapoda, Brachyura, Calappidae). *Crustaceana* 71 (5): 583-587.
- QUAYLE W. J. & COLLINS J. S. H. 1981. — New Eocene crabs from the Hampshire Basin. *Paleontology* 24 (4): 733-758.
- RATHBUN M. J. 1908. — Descriptions of fossil crabs from California. *Proceedings of the Biological Society of Washington* 35 (1647): 341-349.
- RATHBUN M. J. 1918. — The grapsoid crabs of America. *Bulletin of the United States National Museum* (97): i-xxii + 1-461.
- RATHBUN M. J. 1935. — Fossil Crustacea of the Atlantic and Gulf Coastal Plain. *Geological Society of America Special Paper* (2): 1-160.
- RICE A. L. & CHAPMAN C. J. 1971. — Observations of the burrows and burrowing behaviour of two mud-dwelling decapod crustaceans, *Nephrops norvegicus* and *Goneplax rhomboides*. *Marine Biology* 10 (4): 330-342.
- RICHARDS B. C. 1975. — *Longusorbis cuniculosus*: a new genus and species of Upper Cretaceous crab; with comments on Spray Formation at Shelter Point, Vancouver Island, British Columbia. *Canadian Journal of Earth Sciences* 12 (11): 1850-1863.
- ROER R. & DILLAMAN R. 1984. — The structure and calcification of the crustacean cuticle. *American Zoologist* 24: 893-909.
- SAINT LAURENT M. DE 1989. — La nouvelle superfamille des Retroplumoidea Gill, 1894 (Decapoda, Brachyura): systématique, affinités et évolution, in FOREST J. (ed.), Résultats des campagnes MUSORSTOM, vol. 5. *Mémoires du Muséum national d'Histoire naturelle, sér. A*, 144: 103-179.
- SAKAI T. 1976. — *Crabs of Japan and the Adjacent Seas*. 3 vols. Kodansha, Tokyo, xxix + 773 p., 461 p., 16 p., 251 pls.
- SAVAZZI E. 1981. — Functional morphology of the cuticular terraces in *Ranina* (*Lophoranina*) (brachyuran decapods: Eocene of NE Italy). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 162 (2): 231-243.
- SAVAZZI E. 1982. — Burrowing habits and cuticular sculptures in Recent sand-dwelling brachyuran decapods from the Northern Adriatic Sea (Mediterranean). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 163 (3): 369-388.
- SCHÄFER W. 1951. — Fossilisations-Bedingungen brachyurer Krebse. *Senckenbergischen Naturforschenden Gesellschaft, Abhandlungen* 485: 221-238.
- SCHMALFUSS H. 1978. — Structure, patterns, and function of cuticular terraces in Recent and fossil Arthropods. I. Decapod crustaceans. *Zoomorphologie* 90: 19-40.
- SCHRAM F. R. 1986. — *Crustacea*. Oxford University Press, Oxford, 606 p.
- SCHWEITZER C. E. 2000. — Tertiary Xanthoidea (Crustacea: Decapoda: Brachyura) from the west coast of North America. *Journal of Crustacean Biology* 20 (4): 715-742.
- SCHWEITZER C. E. 2003. — Utility of proxy characters for classification of fossils: an example from the fossil Xanthoidea (Crustacea: Decapoda: Brachyura). *Journal of Paleontology* 77 (6): 1107-1128.
- SCHWEITZER C. E. & FELDMANN R. M. 2000a. — New species of calappid crabs from western North America and reconsideration of the Calappidae *sensu lato*. *Journal of Paleontology* 74 (2): 230-246.
- SCHWEITZER C. E. & FELDMANN R. M. 2000b. — New fossil portunids from Washington, USA, and Argentina and a reevaluation of generic and family relationships within the Portunoidea Rafinesque (Decapoda: Brachyura). *Journal of Paleontology* 74 (4): 636-653.
- SCHWEITZER C. E. & FELDMANN R. M. 2001a. — Differentiating fossil Hexapodidae Miers (Decapoda: Brachyura) from similar forms. *Journal of Paleontology* 75 (2): 330-345.
- SCHWEITZER C. E. & FELDMANN R. M. 2001b. — New Cretaceous and Tertiary decapod crustaceans from western North America. *Bulletin of the Mizunami Fossil Museum* (28): 173-210.
- SCHWEITZER C. E. & FELDMANN R. M. 2005. — Decapod crustaceans, the K/P event, and Palaeocene recovery, in KOENEMAN S. & JENNER R. A. (eds),

- Crustacea and Arthropods Relationships*. Taylor & Francis Group, Boca Raton; London; New York; Singapore: 17-53.
- SCHWEITZER C. E., FELDMANN R. M., GONZÁLES-BARBA G. & VEGA F. J. 2002a. — New crabs from the Eocene and Oligocene of Baja California Sur, México and an assessment of the evolutionary and paleobiogeographic implications of Mexican fossil decapods. *Journal of Paleontology* 76 (Supplement to no. 6): 1-43.
- SCHWEITZER C. E., SCOTT-SMITH P. R. & NG P. K. L. 2002b. — New occurrence of fossil decapod crustaceans (Thalassinidea, Brachyura) from late Pleistocene deposits, Guam, United States Territories. *Bulletin of the Mizunami Fossil Museum* (29): 25-49.
- SCHWEITZER C. E., FELDMANN R. M., FAM J., HESSIN W. A., HETRICKS S. W., NYBORG T. G. & ROSS R. M. L. 2003a. — *Cretaceous and Eocene Decapod Crustaceans from Southern Vancouver Island, British Columbia, Canada*. National Research Council Press, Ottawa, Ontario, 66 p.
- SCHWEITZER C. E., LACOVARA K. J., SMITH J. B., LAMANNA M. C., LYON M. A. & ATTIA Y. 2003b. — Mangrove-dwelling crabs (Decapoda: Brachyura: Necrocarcinidae) associated with dinosaurs from the Upper Cretaceous (Cenomanian) of Egypt. *Journal of Paleontology* 77 (6): 1107-1128.
- SERÈNE R. 1965. — *Guide for Curators of Brachyuran Collections in Southeast Asia*. Applied Scientific Research Corporation of Thailand, Bangkok, 65 p.
- SERÈNE R. 1968. — The Brachyura of the Indo-West Pacific region, in Prodrum for a check list of the non-planctonic marine fauna of South East Asia. *Singapore Academy of Science, Special Publication* 1: 33-112.
- SOLÉ J. & VÍA L. 1989. — Crustacis Decàpodes fòssils dels Països Catalans (Recopilació i actualització de dades des de 1855 a 1988). *Batalleria* (2): 23-42 (dated 1988, published 1989).
- STENZEL H. B. 1944. — A new Cretaceous crab, *Graptoarcinus muiri*, from Mexico. *Journal of Paleontology* 18: 550-552.
- STENZEL H. B. 1945. — Decapod crustaceans from the Cretaceous of Texas. *Texas University Publication* (4401): 401-416 (dated 1944, published 1945).
- STENZEL H. B. 1953. — Decapod Crustacea from the Woodbine Formation of Texas. *United States Geological Survey, Professional Paper* (242): 212-217 (dated 1952, published 1953).
- ŠTEVČIĆ Z. 2005. — The reclassification of brachyuran crabs (Crustacea, Decapoda: Brachyura). *Natura Croatica* 14 Suppl. 1: 1-159.
- TAVARES M. 1996. — Sur la validité de *Bathypylax typhlus oculiferus* Miers, 1886 (Decapoda, Brachyura). *Crustaceana* 69 (3): 413-423.
- TESCH J. J. 1918. — The Decapoda Brachyura of the *Siboga* Expedition. I. Hymenosomidae, Retroplumidae, Ocypodidae, Grapsidae and Gecarcinidae. *Siboga Expeditie* 39c, livr. 82: 1-148.
- VAN BAKEL B. W. M., JAGT J. W. M., FRAAIJE R. H. B. & COOLE Y. 2003. — New data on the crab *Binkhorstia ubaghsii* (Late Maastrichtian; NE Belgium, SE Netherlands). *Contributions to Zoology* 72 (2-3): 85-89.
- VAN STRAELEN V. 1934. — Contribution à l'étude des crustacés décapodes fossiles de la Catalogne, in *Géologie de la Méditerranée occidentale, Géologie des Pays Catalans* 3 (25): 1-6.
- VAN STRAELEN V. 1936. — Crustacés décapodes nouveaux ou peu connus de l'époque crétacique. *Bulletin du Musée royal d'Histoire naturelle de Belgique* 12 (45): 1-50.
- VAN STRAELEN V. 1938. — Crustacés décapodes cénozoïques des Indes orientales néerlandaises. *Leidsche Geologische Mededelingen* 10 (1): 90-103.
- VEGA F. J. & FELDMANN R. M. 1991. — Fossil crabs (Crustacea Decapoda) from the Maastrichtian Difunta Group, Northeastern Mexico. *Annals of Carnegie Museum* 60 (2): 163-177.
- VEGA F. J. & FELDMANN R. M. 1992. — Occurrence of *Costacopluma* (Decapoda: Brachyura: Retroplumidae) in the Maastrichtian of southern Mexico and its paleobiogeographic implications. *Annals of Carnegie Museum* 61 (2): 133-152.
- VEGA F. J., FELDMANN R. M. & DAVILA-ALCOCER V. M. 1994. — Cuticular structure in *Costacopluma mexicana* Vega and Perilliati, from the Difunta Group (Maastrichtian) of Northeastern Mexico, and its paleoenvironmental implications. *Journal of Paleontology* 68 (5): 1074-1081.
- VEGA F. J., FELDMANN R. M. & SOUR-TOVAR F. 1995. — Fossil crabs (Crustacea: Decapoda) from the Late Cretaceous Cardenas Formation, east-central Mexico. *Journal of Paleontology* 69 (2): 340-350.
- VEGA F. J. & FELDMANN R. M., OCAMPO A. C. & POPE K. O. 1997. — A new species of Late Cretaceous carcineretid crab (Brachyura: Carcineretidae) from Albion Island, Belize. *Journal of Paleontology* 71 (4): 615-620.
- VEGA F. J., FELDMANN R. M., GARCÍA-BARRERA P., FILKORN H., PIMENTEL F. & AVENDAÑO J. 2001. — Maastrichtian Crustacea (Brachyura: Decapoda) from the Ocozocuaula Formation in Chiapas, southeast Mexico. *Journal of Paleontology* 75 (2): 319-329.
- VEGA F. J., BRUCE N. L., SERRANO L., BISHOP G. A. & PERRILLIAT M. C. 2005a. — A review of the Lower Cretaceous (Tlayúa Formation: Albian) Crustacea from Tepexi de Rodríguez, Puebla, Central Mexico. *Bulletin of the Mizunami Fossil Museum* 32: 25-30.
- VEGA F. J., DAVILA-ALCOCER V. M. & FILKORN H. F. 2005b. — Characterization of cuticle structure in late Cretaceous and early Tertiary decapod Crustacea from Mexico. *Bulletin of the Mizunami Fossil Museum* 32: 37-43.

- VÍA L. 1957. — Contribution à l'étude paléontologique des Ocydopoda, Beurlen. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences (D)* 245 (5): 553-554.
- VÍA L. 1969. — Crustáceos Decápodos del Eoceno Español. *Pirineos* (91-94): 1-479.
- VÍA L. 1980. — Ocydopoda (crustacés décapodes) du Cénozoïque méditerranéen. Origine et évolution de cette superfamille. *Annales de Paléontologie (Invertébrés)* 66 (1): 51-66.
- VÍA L. 1982. — Nueva contribución al estudio paleontológico de la superfamilia Ocydopidea (Crustáceos Decápodos). *Boletín Geológico y Minero* 93-II: 115-119 [17-21].
- VÍA L. 1988. — Els decàpodes, in *Història natural dels Països Catalans*. Vol. 15 (Registre fòssil). Fundació Enciclopèdia Catalana, Barcelona: 343-352.
- VINCENT T. & BRETON G. 1999. — Présence du crabe *Hemigrapsus penicillatus* (de Haan, 1835) dans les bassins du port du Havre (Normandie, France). *Bulletin trimestriel de la Société géologique de Normandie et des Amis du Muséum du Havre* 86 (1): 19-23.
- WAUGH D. A. & FELDMANN R. M. 2002. — Analytical description of decapod cuticle morphology. *Geological Society of America, Abstracts Program* 34: 368.
- WAUGH D. A. & FELDMANN R. M. 2003. — Cuticle microstructure as a new tool in systematic paleontology. *Contributions to Zoology* 72 (2-3): 191-193.
- WITHERS T. H. 1922. — On a new brachyurous Crustacea from the Upper Cretaceous of Jamaica. *Annals and Magazine of Natural History* ser. 9, 59: 534-541.
- WITHERS T. H. 1928. — New Cretaceous crabs from England and Syria. *Annals and Magazine of Natural History* (10) 11: 456-460.
- WRIGHT C. W. 1997. — New information on Cretaceous crabs. *Bulletin of the Natural History Museum of London (Geology)* 53: 135-138.
- WRIGHT C. W. & COLLINS J. S. H. 1972. — British Cretaceous crabs. *Palaeontographical Society [Monographs]*, London: 1-114.

Submitted on 5 July 2006;
accepted on 18 October 2006.

ANNEXE

TABLE 1. — List of the material examined (Cenomanian of Le Mans and Lamnay, Sarthe, France), with indication of the best preserved and informative parts. Estimated measurements in square brackets. Abbreviations: **Abd**, abdomen; **A1-A3**, abdominal segments 1 to 3; **cx**, coxa; **Cx4-Cx5**, coxae of P4 and P5; **DS**, dorsal surface; **G1**, first male gonopod; **G2**, second male gonopod; **Md**, mandible; **Mxp3**, third maxilliped; **P1-P5**, first to fifth pereopods; **St**, sternum; **St1-8**, thoracic sternites 1-8; **VS**, ventral surface; **4/5-7/8**, thoracic sternal sutures 4/5 to 7/8. Type material not included, see Type material under *Lithophylax trigeri*.

Registration number	Sex	Length (L) × width (W) of carapace (mm)	W/L	Information	Figure
MHN LM 2005.1.1	♂: G1 visible	?	?	Two chelae; heterochely; left palm 25% narrower than right	
MHN LM 2005.1.2	?	?	?	Two chelae; fingers; heterochely; left palm 15% narrower than right	
MHN LM 2005.1.3	♀: vulva visible	[9.7 × 18.05]	[1.91]	Carapace; fronto-orbital margin; shutter; endostome	5
MHN LM 2005.1.4	?	[12.38 × 23.25]	[1.88]	Carapace; complete St; Abd; P2-P4 (merus); one chela with fingers	12A
MHN LM 2005.1.5	?	[8.75 × 16.25]	[1.86]	Carapace; fronto-orbital margin with the subfrontal lobe	
MHN LM 2005.1.6	♂: fragments of gonopods	[10.5] × 20.9	[2.0]	Fronto-orbital margin with 2 subfrontal lobes; 2 shutters; 2 buttons on St5; St; Abd with all segments; G2; relationships between P3, P4 and Abd	6 10B, C 13A
MHN LM 2005.1.7	?	[8.13 × 15.0]	[1.85]	Carapace DS only, with well preserved postero-lateral and posterior margins	
MHN LM 2005.1.14	?	?	?	Unprepared specimen. Both chelae, heterochely	3
MHNNH 9186	♀: vulva visible	[10.8 × 18.5]	[1.72]	Carapace; St with sterno-abdominal cavity; buttons on St5; Abd with 6 segments + telson; Mxp3 (proximal part); vulvae on St6; shutter and its fan; Cx4 reentrant; Cx5 reduced, subdorsal, reentrant; relationships between Abd, St, and cx of pereopods	9D 12C 13B
MHNNH 9187	?	[11.25] × 18.75	[1.67]	One very large Md; complete Abd with telson; cupules on St7 and St8	9A
MHNNH 9188	♂: both G1	[12.1] × 19.3	[1.60]	Eyestalks on each side of the complete rostrum; St7; removed P1 with pars stridens on merus; other P1 <i>in situ</i> with well visible pars stridens in contact with latero-ventral surface of the carapace	
MHNNH 9189	?	15.62 × [28.75]	[1.84]	Very distinct complete rostrum; wide orbits; removed chela with complete pars stridens on merus; compressed pereopods with a row of granules on the carina	
MHNNH 9190	♂: G1 visible	[10.62 × 17.5]	[1.65]	[carapace infilled with microcoprolites]	
MHNNH 9191	♀: both vulvae	[8.75 × 15.0]	[1.71]	Wide orbits; shutter; median line on St8; deep depressions at the extremity of sternal sutures; button of the press-button	9B

Registration number	Sex	Length (L) × width (W) of carapace (mm)	W/L	Information	Figure
MHNN 9192	♀: one vulva	[9.75 × 16.25]	[1.67]	Abd; both Cx5; pars stridens on P1 merus	
MHNN 9193	?	[10.75] × 17.75	[1.65]	Rostrum; Md; Abd; Cx4 covering St	
MHNN 9194	♂: G2 at the level of A2	? × 16.25	?	Abd segments 1-3 beneath the carapace	
MHNN 9196	♂: fragments of G1	?	?	Carapace; rostrum; fronto-orbital margin; outer-orbital tooth; orbits; sterno-abdominal cavity; well visible sternites; deep depressions at the extremity of sternal sutures; autotomy lines	8C
MHNN 9197	?	[8.12 × 13.13]	[1.62]	Dorsal carapace with “human face”; pereopods; heterochely; Cx4	
MHNN 9198	?	10.62 × 18.0	1.69	One eyestalk; Cx4	
MHNN 9199	probably ♀	0.5 × 17.75	1.69	Stridulating apparatus: pars stridens on P1 merus (29 striae) and plectrum = row of granules posterior to infra-orbital region; shutter on each side; Abd very wide	13C
MHNN 9201	?	[14.8 × 23.5]	[1.59]	Heterochely; buccal cavern wide; Mxp3 with most parts; 2 chelae; Cx4; Cx5 subdorsal with its articular condyle on St8; St6 and St7 with cupules	
MHNN 9202	♂: G1 prepared	[11.5 × 19.25]	[1.67]	Rostrum (broken); P5 (prepared) present with Cx, ischio-basis and merus with a row of tubercles; chelae (heterochely)	11B 12B
MHNN 9203	?	? × [13.0]	?	St; sutures 4/5 and 5/6 ending in two deep depressions	
MHNN 9204	♂: G1	?	?	Bipartite left orbit	
MHNN 9205	♀: left vulva	[11.5 × 20.5]	[1.78]	Sterno-abdominal cavity; P3 with large compressed merus with a carina;	
MHNN 9206	♂: fragments of gonopods	?	?	A1-A3 subdorsal	
MHNN 9207	♂: fragments of G1	12.25 × 21	1.71	Endophragma partly visible	
MHNN 9208	♀	13.5 × [22.5]	[1.67]	Carapace	
MHNN 9209	♂: G1 and G2	[16.25 × 27]	[1.66]	Heterochely; rostrum complete (developed length = 2.0 mm, width = 0.35 mm); both shutters; orbits bipartite	7B, C
				VS nearly complete; rostrum; infra-orbital rim with a row of granulations; both shutters; St1 and 2 complete; suture 7/8 very short; Abd wide; Cx5 present, with its articular condyle; removed merus of P1 with pars stridens; suborbital tubercles of plectrum	8A 11A
MHNN 9211	?	[11.0 × 18.0]	[1.64]	Orbits bipartite, with a small sulcus between the two parts; location of eyestalks; left shutter with part of its fan	8B

Registration number	Sex	Length (L) × width (W) of carapace (mm)	W/L	Information	Figure
MHNN 9212	♂: sections of G1	[11.0 × 18.0]	[1.64]	A row of dense granules on infra-orbital rim; Abd very wide; A1 beneath the carapace, A2 close to Cx4	
MHNN 9213	?	[11.12 × 19.0]	[1.7]		
MHNN 9214	♂: sections of G1	10.25 × 17.75	1.73	Carapace nearly complete: rostrum, posterior border; Abd rimmed; parts of the left Mxp3; button of the press-button	
MHNN 9215	?	11.87 × 20.0	1.68	Wide bipartite orbits with a slight sulcus between the two parts; left Md (broken); buttons of both press-buttons	
MHNN 9216	?	12.25 × [20.5]	[1.67]	Carapace (rostrum broken); pereopods; 2 chelipeds with fingers (heterochely, right palm 8% higher than left); A1 and A2 covered by carapace	
MHNN 9217	?	? × [16,25]	?	Both bipartite wide orbits; both eyestalks	
MNHN A 24793	♂: both G1, right G2	?	?	Bipartite orbits with a sulcus between the two parts; shutter; St8 exposed	
MNHN A 24794	?	14.37 × [24.0]	[1.67]	Mxp3 large, strongly diverging, with nearly all articles; thoracic sternites (St1 and part of St2 excepted); chelae (heterochely: right palm 25% higher than left)	8E
MNHN A 24795	♀	[11.75] × 19.38	[1.65]	Carapace well preserved; base of Mxp3; Md; thoracic sternum with St1 and St2; St7 joining the coxa, covered by Abd; sterno-abdominal cavity very wide; both buttons of the press-button; chelipeds with fingers; heterochely: right palm 23% higher than left	
MNHN A 24796	?	10.0 × 17.2	1.72	VS not prepared; well preserved and complete carapace with left outer-orbital tooth; rostrum; both eyestalks	7D
MNHN A 24797	♀?	9.12 × 15.25	1.67	Well preserved carapace with left outer-orbital tooth; base of both Mxp3, diverging, apart	

TABLE 2. — Measurements of coxae of specimen MHNN 9209, with ocular micrometre, second decimal figure not significant, due to the conversion of µm scale into mm. Abbreviations: **D**, maximum diameter in ventral view; **Lg**, length of the coxa, in ventral view, measured between the two condyles (sternal and basis-ischial); **P1-P5**, first to fifth pereopods.

	D mm	Left Lg mm	Right Lg mm
P1	3.60	1.50	1.80
P2	2.70	2.58	2.52
P3	2.58	2.58	2.76
P4	2.58	2.58	
P5	1.26	1.26	