

Revision of Mesozoic decapod crustaceans from Madagascar

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ABSTRACT

Decapod crustaceans from the Mesozoic of Madagascar have been studied by a number of authors during the last century. One of the largest sets of specimens was collected by the French General Maurice Collignon between 1930 and 1950; this was subsequently studied by Secrétan (1964) who described numerous species of macrurans, brachyurans, and axiideans. These crustaceans originate from the Upper Jurassic and the Upper Cretaceous of the Mahajanga Basin (NW Madagascar) and, especially, from the Morondava Basin (central-SW Madagascar). The purpose of the present study is twofold: to furnish an update of the stratigraphy and geology of the studied areas and, above all, to revise the Secrétan's species, employing current systematic nomenclature, supplying for each detailed geographic and stratigraphic data since such were either cursory or incomplete in previous papers. The present revision considers 13 species recorded by Secrétan as valid, namely: *Enoploclytia collignoni* Secrétan, 1964, *Eryma granuliferum* Secrétan, 1964, *Pustulina spinulata* (Secrétan, 1964) (all Erymidae Van Straelen, 1925); *Hoploparia collignoni* (Van Straelen, 1949), *H. pusilla* Secrétan, 1964 (both Nephropidae Dana, 1852 *sensu* Tshudy & Babcock 1997); *Ctenocheles madagascariensis* Secrétan, 1964 (Ctenocheleidae Manning & Felder, 1991); *Schlueteria menabensis* Secrétan, 1964 (Axiidae Huxley, 1879); *Linuparus bererensis* Secrétan, 1964 (Palinuridae Latreille, 1802); *Dromiopsis*

KEY WORDS

Crustacea,
Decapoda,
Macrura,
Brachyura,
Axiidea,
Jurassic,
Cretaceous,
Madagascar.

pulchella Secrétan, 1964 (Dynomenidae Ortmann, 1892); *Caloxanthus simplex* (Secrétan, 1964) (Etyidae Guinot & Tavares, 2001); “*Xanthosia*” *robertsi* Secrétan, 1982 (*nomen novum* pro *Xanthosia elegans* Secrétan, 1964, non Roberts, 1962), *Titanocarcinus mamillatus* Secrétan, 1964 (both Xanthoidea *incertae sedis*); and *Secretanella arcuata* (Secrétan, 1964) (indeterminate family). The three species described by Secrétan (1964) as belonging to the raninid genus *Notopocorystes* McCoy, 1849, *N. bituberculatus*, *N. australis* and *N. denisae* will be revised in a forthcoming paper. Our comparative studies have also revealed a number of synonymous taxa, as follows: *Eryma granuliferum* Secrétan, 1964 (junior synonym: *E. madagascariensis* Secrétan, 1964); *Linuparus bererensis* Secrétan, 1964 (junior synonym: *L. bererensis multispinosus* Secrétan, 1964); *Hoploparia collignoni* (Van Straelen, 1949) (junior synonym: *H. intermedia* Secrétan, 1964 and *H. sculpta* Secrétan, 1964); *Schlueteria menabensis* Secrétan, 1964 (junior synonym: *S. tuberculosa* Secrétan, 1964). Lastly, we have doubts about the systematic validity of *Enoploclytia armata* Secrétan, 1964, *Eryma australe* (Secrétan, 1964), and *Coleia incerta* Secrétan, 1964, because of the absence of main diagnostic features, useful for their systematic ascription.

RÉSUMÉ

Révision des crustacés décapodes mésozoïques de Madagascar.

Les crustacés décapodes du Mésozoïque de Madagascar ont été étudiés par plusieurs auteurs au cours du siècle dernier. L'une des plus grandes collections de crustacés décapodes a été récoltée par le Général français Maurice Collignon entre 1930 et 1950 et a été ensuite étudiée par Secrétan (1964) qui a décrit de nombreuses espèces de macroures, de brachyours et d'axiidés. Ces crustacés proviennent du Jurassique supérieur et du Crétacé supérieur du bassin de Mahajanga (NW Madagascar) et plus spécialement du bassin de Morondava (centre-SW Madagascar). Le but de cette étude est non seulement de fournir une mise à jour des données géologiques et stratigraphiques des secteurs étudiés, mais aussi et surtout de réviser les espèces décrites par Secrétan à la lumière des nouvelles données systématique et nomenclaturale, en donnant pour chacune d'entre elles une position géographique et stratigraphique précise, données toujours superficielles ou incomplètes chez les anciens auteurs. Cette révision traite de la validité systématique de treize espèces décrites par Secrétan : *Enoploclytia collignoni* Secrétan, 1964, *Eryma granuliferum* Secrétan, 1964 et *Pustulina spinulata* (Secrétan, 1964) (Erymidae Van Straelen, 1925); *Hoploparia collignoni* (Van Straelen, 1949) et *H. pusilla* Secrétan, 1964 (Nephropidae Dana, 1852 *sensu* Tshudy & Babcock 1997); *Ctenocheles madagascariensis* Secrétan, 1964 (Ctenochelidae Manning & Felder, 1991); *Schlueteria menabensis* Secrétan, 1964 (Axiidae Huxley, 1879); *Linuparus bererensis* Secrétan, 1964 (Palinuridae Latreille, 1802); *Dromiopsis pulchella* Secrétan, 1964 (Dynomenidae Ortmann, 1892); *Caloxanthus simplex* (Secrétan, 1964) (Etyidae Guinot & Tavares, 2001); «*Xanthosia*» *robertsi* Secrétan, 1982 (*nomen novum* pro *Xanthosia elegans* Secrétan, 1964 non Roberts, 1962) et *Titanocarcinus mamillatus* Secrétan, 1964 (Xanthoidea *incertae sedis*); *Secretanella arcuata* (Secrétan, 1964) (famille indéterminée). Les trois espèces décrites par Secrétan (1964) dans le genre *Notopocorystes* McCoy, 1849, à savoir *N. bituberculatus*, *N. australis* et *N. denisae* (Raninidae De Haan, 1849) seront le sujet d'une révision future. Nos études comparatives ont également révélé un certain nombre de synonymies telles que : *Eryma granuliferum* Secrétan, 1964 (synonyme plus récent : *E. madagascariensis* Secrétan,

MOTS CLÉS

Crustacea,
Decapoda,
Macrura,
Brachyura,
Axiidea,
Jurassique,
Crétacé,
Madagascar.

1964); *Linuparus bererensis* Secrétan, 1964 (synonyme plus récent: *L. bererensis multispinosus* Secrétan, 1964); *Hoploparia collignoni* (Van Straelen, 1949) (synonymes plus récents: *H. intermedia* Secrétan, 1964 et *H. sculpta* Secrétan, 1964); *Schlueteria menabensis* Secrétan, 1964 (synonyme plus récent: *S. tuberculosa* Secrétan, 1964). Enfin, en l'absence des principaux caractères diagnostiques utiles pour leur attribution systématique, nous nous interrogeons sur la validité systématique d'*Enoploclytia armata* Secrétan, 1964, d'*Eryma australe* (Secrétan, 1964) et de *Coleia incerta* Secrétan, 1964.

INTRODUCTION

GEOGRAPHIC DISTRIBUTION
AND GEOLOGICAL SETTING

Three principal sedimentary basins have been recognized in Madagascar: the Diégo Basin (in the north-northeast of the island), the Mahajanga Basin (along the northwestern coast), and the largest Morondava Basin, which extends from the central to the southwestern coast (Besairie 1972) (Fig. 1). All specimens studied for the present paper originate from the Mahajanga and Morondava basins.

Mahajanga Basin

This basin extends along the northwestern part of the island covering a crescent-shaped area around the town of Mahajanga and delimited by the Ampasindava peninsula in the north and the Cape Saint-André Anticline in the south (Fig. 2). Developed in the basin are sediments of Late Palaeozoic (Sakamena Formation) to Holocene age. We have divided the Mahajanga Basin into two geographic portions to simplify location of the fossiliferous levels, as follows: 1) the northern limb of the Mahajanga Basin, covering the area north of the town of Mahajanga, close to the delta of the Betsiboka River; and 2) the southern limb of the basin, including localities south of Mahajanga and to the west of the Mahavavy River (Mahajanga Province) (Fig. 2).

Morondava Basin

This basin covers a distance of about 1000 km on the western coast of the island, between Cape

Saint-André in the north and Cape Sainte-Marie in the south, forming a band running subparallel to the central-southern coast along the Mozambique Channel (Fig. 1). In view of its sheer size, it has been subdivided into geographic sectors, almost delimited from the north to south by the most important rivers which cross the basinal area more or less parallel from east to west (Besairie 1972; see Figure 3).

The most northerly part is situated between Cape Saint-André and the Manambao River (Fig. 1), the northern part between the Manambao and Manambolo rivers (northern Morondava Basin, Maintirano region) (Figs 3; 4). The central portion of the basin has been subdivided into two units: one between the Manambolo River and Parallel 590, crossing south of the port of Belo-sur-Mer (central Morondava Basin, including Belo-sur-Tsiribihina, Berere Plain, Menabe region), and another one extending between Parallel 590 and the Mangoky River in the south (Figs 3; 5). The southern part is located between the Mangoky and Onilahy Rivers (southern Morondava Basin, Tulear Province) (Figs 3; 6) and finally, the most southerly part of the basin, from the Onilahy River to Cape Sainte-Marie in the extreme south (Fig. 1). This basin also includes strata that range in age (from the west to the east) from the Holocene to the Late Palaeozoic (Sakoa Formation). Specimens studied come from different levels within the Mesozoic formations in these two basins. We here provide three simplified maps to show the location of the fossil-bearing outcrops, with particular regard to the type localities (Figs 2; 4-6).



FIG. 1. — Major sedimentary basins of Madagascar.

THE DECAPOD FAUNA

Below, we mostly follow the geological age assignment and the original species designations made by Secrétan (1964), but in a few cases these are updated here (see Systematic Palaeontology).

Species from the Mahajanga Basin

Northern Mahajanga Basin. As noted by Besairie (1972), Albian-Cenomanian (mid-Cretaceous) sandstones are exposed along the Berambo cliff at Antsatramahavelona, on the Radama Peninsula, situated north of the town of Analalava. The fauna comprises *Ctenocheles madagascariensis* Secrétan,

1964, *Xanthosia arcuata* Secrétan, 1964 and *Dromiopsis pulchella* Secrétan, 1964 (Fig. 2).

Southern Mahajanga Basin. About 100 km south of Mahajanga, in the Sitampiky Basin, west of the Mahavavy River, Lower to mid-Cretaceous strata outcrop (Besairie 1972). In the Soromaranina region (east of Sitampiky), Hauterivian (Lower Cretaceous) beds yield *Pustulina spinulata* (Secrétan, 1964). Some kilometres to the north, at Malandiandro, Befamoto, and Ambanjabe (the present-day Andrafiamanjara), Albian (Lower Cretaceous) beds in the so-called “Série de Ambarimaninga”, contain *Notopocorystes bituberculatus* Secrétan, 1964, *Hoploparia intermedia* Secrétan, 1964, *H. sculpta* Secrétan, 1964, and *H. collignoni* (Van Straelen, 1949), whereas Valanginian-Hauterivian strata (Secrétan 1964) contain *Pustulina spinulata* (Secrétan, 1964) (Fig. 2).

Species from the Morondava Basin

Northern Morondava Basin. Kimmeridgian-Tithonian (Lower Jurassic) marly sandstone strata, rich in ammonites, crop out south and east of Antsalova (southern Maintirano region; compare Besairie 1972). The fauna includes ?*Coleia incerta* Secrétan, 1964 (upper Tithonian), *Eryma madagascariensis* Secrétan, 1964 (middle Kimmeridgian) and *E. granuliferum* Secrétan, 1964 (upper Kimmeridgian) (Figs 3; 4).

Central Morondava Basin. The subbasin, between the Mananbolo (in the north) and the Tsiribihina (in the south) rivers (Belo-sur-Tsiribihina, Menabe region, Tulear Province) is highly fossiliferous and includes principally levels of Santonian to Campanian (Upper Cretaceous) age (Besairie 1972). In the outcrops to the east and northeast of Belo-sur-Tsiribihina (Berere Plain), the extraordinary abundance of cephalopods has permitted a detailed stratigraphic section and biozonation, in particular for the lower Campanian, strictly local and applicable only in the Menabe region (Collignon 1969: 4, 5). The fauna includes *Enoploclytia collignoni* Secrétan, 1964, *E. armata* Secrétan, 1964, *Linuparus bererensis* Secrétan, 1964, *Hoploparia pusilla* Secrétan, 1964, *Schlueteria menabensis* Secrétan, 1964, *Ctenocheles madagascariensis*,



FIG. 2. — The Mahajanga Basin (Mahajanga Province) with fossil-bearing outcrops. Type localities: 1, *Ctenocheles madagascariensis* Secrétan, 1964; 2, *Dromiopsis pulchella* Secrétan, 1964; 3, *Secretanella arcuata*; 4, *Hoploparia collignoni*; 5, *Notopocorystes bituberculatus*; 6, *Pustulina spinulata*. Note that we do not show the type localities of *H. sculpta* and *H. intermedia* because Secrétan (1964) failed to designate holotypes for both species. Full species name are indicated in Table 1.

Caloxanthus simplex (Secrétan, 1964), *Notopocorystes denisae* Secrétan, 1964, *N. australis* Secrétan, 1964, and “*Xanthosia*” *robertsi* Secrétan, 1982. These species have been recovered from numerous localities within this basin (Fig. 5).

Southern Morondava Basin. This subbasin, between the Mangoky and Onilahy rivers comprises strata of Late Jurassic age. In the region of the Sikily River, between the Mangoky and Fiherenana rivers, and north of the Analavelona Massif (north of Tulear),

discontinuous Tithonian (Upper Jurassic) sandstones crop out. The fauna includes *Erymastacus australis* Secrétan, 1964, from a small hill southwest of the village of Ankilivalo and from a locality close to the Marolalitra River, northern Analavelona Massif (lower Tithonian). In addition, *Titanocarcinus mamillatus* Secrétan, 1964 and other indeterminate xanthid remains have been collected from Maastrichtian levels (Upper Cretaceous) in the Sikily region, near the village of Soatana (northern Analavelona Massif, north of the Fiherenana River, Tulear Province) (Fig. 6).

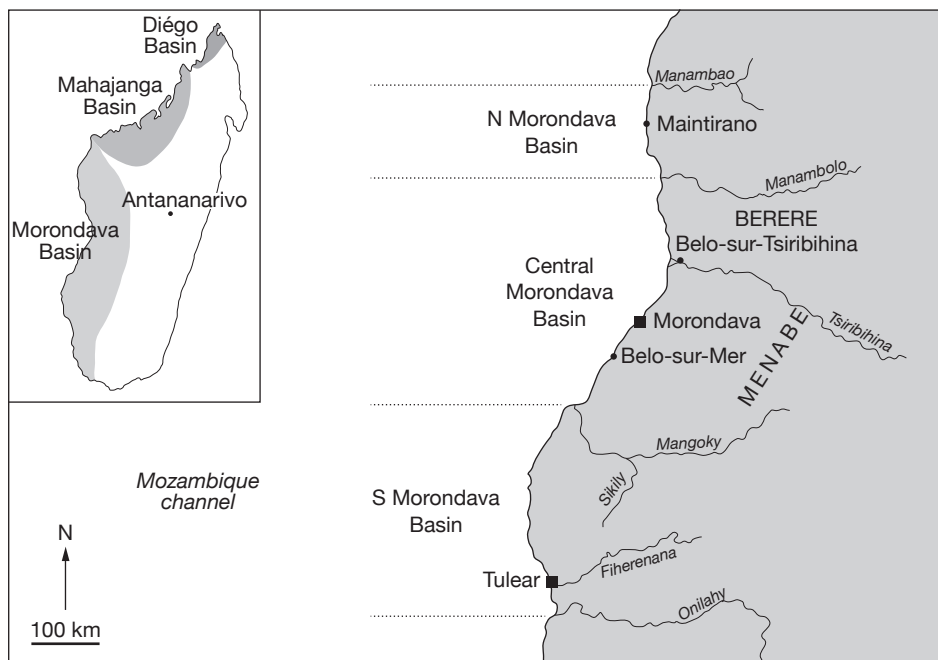


Fig. 3. — General map of the Morondava Basin (Tulear Province) subdivided into the three main sectors.

PREVIOUS STUDIES OF DECAPOD CRUSTACEANS FROM THE MESOZOIC AND CENOZOIC OF MADAGASCAR

Mesozoic and Cenozoic decapod crustaceans of Madagascar were studied by French, Belgian and Italian scholars during the twentieth century. Van Straelen (1931) was the first to record *Glyphea* sp. (MNHN.FR03935), *Enoplocyrtia* sp. (MNHN.FR03928), and *Notopocorystes* sp. (MNHN.FR03930) from the Cenomanian of Diégo Suarez Basin (northern Madagascar). These specimens, housed in the palaeontological collections of the Muséum national d'Histoire naturelle, Paris (MNHN.F), are very poorly preserved and preclude a detailed morphological description. Only the attribution to *Glyphea* von Meyer, 1835 is confirmed, on the basis of groove disposition on the carapace (MNHN.FR03935).

Later, Van Straelen (1933) described *Antrimpos madagascariensis* from the Permo-Triassic of the Ambilobe area (Diégo Suarez Province, northern Madagascar). Outcrops of Triassic strata in this region (Ankitokazo Basin) were studied by the Sezione

di Paleontologia, Museo di Storia Naturale, Milano (Italy), during two expeditions. During the first expedition (1999), extensive collections of vertebrates (fishes and amphibians) and invertebrates (worms, rare bivalves and gastropods, cephalopods, thylacoccephalans, a single xiphosuran, conchostraceans, cycloids and macruran decapod crustaceans) were made. The rich sample of decapod crustaceans (about 400 specimens) was the subject of a study by Garassino & Teruzzi (1995) who described *Ifasya*, with *I. madagascariensis* (new combination of *Antrimpos madagascariensis*) and *I. straeleni*. The second expedition (2000) yielded new decapod crustaceans which were described by Garassino & Pasini (2002) as the genus *Ambilobeia* (e.g., *A. karojoï*).

Decapod crustaceans from the Upper Jurassic to Upper Cretaceous of the Mahajanga and Morondava basins were the subject of several studies. Van Straelen (1949) described *Palaeohomarus collignoni*, from the Albian (Upper Cretaceous) of outcrops near Ambarimanga (Mahajanga Basin, north-western Madagascar). The most recent study on taxa

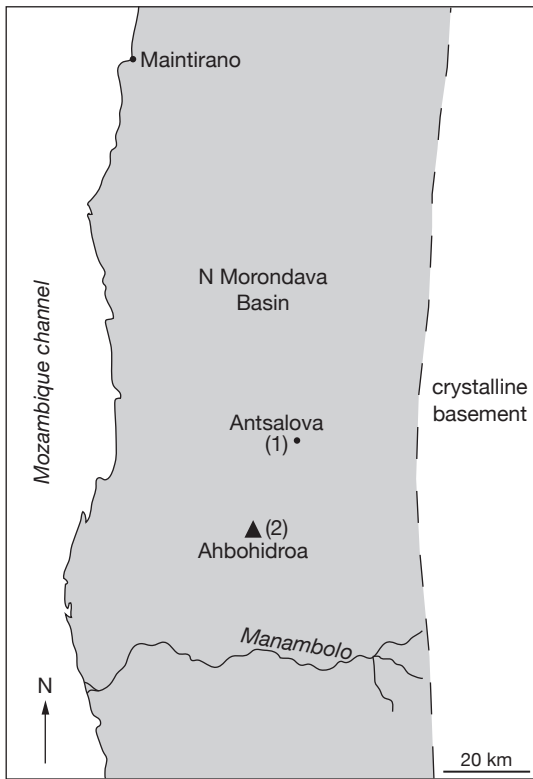


FIG. 4. — Detail of the northern Morondava Basin with fossil-bearing outcrops. Type localities: 1, *Eryma granuliferum* and ?*Coleia incerta*; 2, *Eryma madagascariensis*. Full species names are indicated in Table 1.

from the Mahajanga Basin was that by Garassino & Pasini (2003) who recorded incomplete chelae of brachyurans, assigned to calappaoids, dromioids and portunoids, from the upper Maastrichtian Berivotra Formation. Amongst the larger collections of decapod crustaceans from the Menabe region (Morondava Basin, Tulear Province, central-southwest Madagascar), is that amassed by the French General Maurice Collignon. This was later studied by Secrétan (1964) who described numerous macruran, brachyuran, and axiid species, which are revised in the present study.

To date, Cenozoic decapod faunas from Madagascar are poorly known. In fact, the sole study is that by Collignon & Cottreau (1927), who described a marine Miocene (Burdigalian-Aquitanian) assemblage from Mahakamby Island, in the Mozambique Channel, south of the town of Mahajanga (northwest

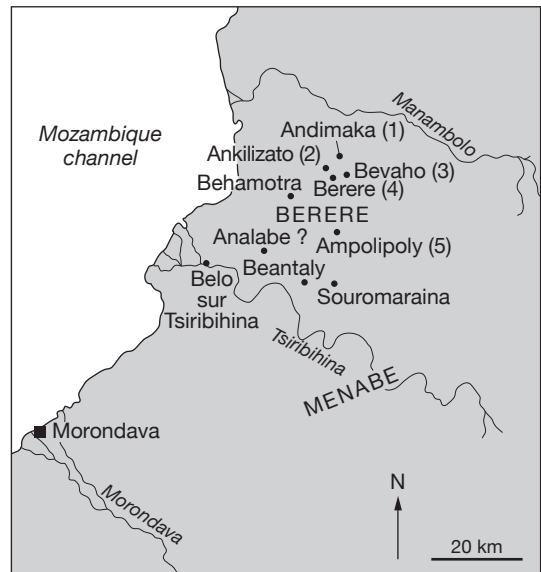


FIG. 5. — Detail of the Central Morondava Basin with fossil-bearing outcrops. Type localities: 1, *Ctenocheles madagascariensis*; 2, *C. madagascariensis* and *Caloxanthus simplex*; 3, *C. madagascariensis* and *Enoplocyrtia collignoni*; 4, *C. madagascariensis*, *Hoploparia pusilla*, *Notopocorystes australis*, *Schlueteria menabensis* and “*Xanthosia*” *robertsi*; 5, *C. madagascariensis*, *Linuparus bererensis* and *Notopocorystes denisae*. Full species names are indicated in Table 1.

Madagascar), comprising some incomplete brachyurans, referred to the portunoid *Achelous*. This fauna is currently the subject of review by Charbonnier *et al.* (in press). Finally, Rakotozafy & Goodman (2005) noted the presence of some indeterminate brachyuran chelipeds (“mangrove crabs”) in subfossil deposits in the extreme southwest of the island, associated with a terrestrial fauna and archaeological remains.

MATERIAL AND METHODS

All specimens studied are preserved three-dimensionally, slightly compressed, and partially exposed on the surface of subnodular, irregular calcareous concretions. They are rarely articulated, occurring mostly as incomplete parts, floating in sediment due to the natural erosion. The epicuticle generally is poorly preserved. Some samples are preserved as a three-dimensional casts inside nodules. The



FIG. 6. — Detail of the southern Morondava Basin with fossil-bearing outcrops. Type localities: 1, *?Eryma australe*; 2, *Titanocarcinus mamillatus*. Full species names are indicated in Table 1.

peculiar state of preservation and anatomical position of some macrurans suggests that these may represent moults. For a more detailed description some of the best-preserved specimens were partially prepared manually or, were the matrix proved too hard, with the help of mechanical engravers.

Secrétan (1964: 53) used unpublished stratigraphic data, supplied by General Collignon, who collected and studied cephalopod faunas from the Morondava and Mahajanga Basins. Subsequently, papers on these assemblages (Collignon 1966, 1969, 1970a, 1971) enabled some revised stratigraphic and geological interpretations, as summarized by Besairie (1972). Here, we follow the most recent stratigraphic data. The Belo-sur-Tsiribihina region (Berere, central Morondava Basin) (Figs 3; 5) in

particular has been prospected by different researchers for many years. Different cross-sections (“Coupes”), more or less directed east to west, between different villages and different ages were named, each including beds (“couches”), with numerous layers (“gisements”), all numbered and marked on specimens collected from them. The same “Coupe” may thus include layers of different age along the section. In the descriptions below, we report the age for the type species and for some certain specimens, listing in the discussion the stratigraphic range of the taxon. Many of the specimens recorded in the present paper were not included in the list supplied by Secrétan (1964).

For some specimens it is difficult to determine the exact provenance, because layer numbering occasionally results in double sets amongst the various scholars who collected and catalogued material over the years; for complete references we refer to Besairie (1972). Moreover, some small villages were deserted or displaced, leading to changes in the original tracks and names during recent years (G. Pasini, pers. comm. 2010). For each specimen, we list the registration number, locality or section (“coupe”), number of level (“gisement”), age and zonation (when known or recognized), region and provenance (basin). Biozonations are those of Collignon (1959, 1960, 1962, 1963, 1964, 1965a, b, 1966, 1969, 1970a, 1971), based on cephalopod (ammonite) faunas (see also Walaszczyk *et al.* 2004).

The collection studied by us comprises 1567 specimens, assigned to species as follows: *Enoploclytia collignoni* (60 specimens), *E. armata* (5), *Eryma granuliferum* (2), *E. australe* (Secrétan, 1964) (4), *Pustulina spinulata* (54), *Linuparus bererensis* (84), *?Coleia incerta* (1), *Hoploparia collignoni* (286), *H. pusilla* (3), *Schlueteria menabensis* (242), *Ctenocheles madagascariensis* (790), *Dromiopsis pulchella* (1), *Notopocorystes australis* Secrétan, 1964 (11), *N. bituberculatus* (1), *N. denisae* Secrétan, 1964 (8), *Caloxanthus simplex* (1), “*Xanthosia*” *robertsi* (1), *Titanocarcinus mamillatus* (1) and *Secretanella arcuata* (Secrétan, 1964) (12). For higher-level classification, we follow Ng *et al.* (2008), De Grave *et al.* (2009) and Schweitzer *et al.* (2010).

ABBREVIATIONS

- CH height of cephalothorax: linear distance measured perpendicular to the dorsal margin from its intersection with the branchiocardiac groove up to the ventral margin;
- CL length of cephalothorax, exclusive of rostrum: linear distance between the ocular incision and the dorsal posterior margin of the cephalothorax;
- CW width of cephalothorax: linear distance measured perpendicular to the dorsal margin between the lateral margins in the branchial region;
- P1-5 pereopods 1 to 5;
- s1-s6 somites 1 to 6;
- MNHN.F Muséum national d'Histoire naturelle, Paris, collection de Paléontologie.

SYSTEMATIC PALAEOONTOLOGY

Class MALACOSTRACA Latreille, 1802
 Order DECAPODA Latreille, 1802
 Infraorder GLYPHEIDEA von Zittel, 1885
 Superfamily ERYMOIDEA Van Straelen, 1925
 Family ERYMIDAE Van Straelen, 1925

Genus *Enoploclytia* McCoy, 1849

TYPE SPECIES. — *Astacus leachii* Mantell, 1822, by original designation.

Enoploclytia collignoni Secrétan, 1964
 (Figs 7; 8)

Enoploclytia [sic] *collignoni* Secrétan, 1964: 82-90, pl. 3, figs 10, 11; pl. 4, figs 4, 5; pl. 5, figs 1-8.

Enoploclytia [sic] sp. Secrétan, 1964: 93, 94, pl. 7, figs 3, 4; pl. 8, fig. 5.

Enoploclytia collignoni – Förster 1966: 151. — Schweitzer *et al.* 2010: 22.

HOLOTYPE. — MNHN.F.R03925, gisement 256.

PARATYPES. — From the “Coupe de Bevahô” (Lower Campanian): 14 specimens (MNHN.F.A33098, A33115, A33119, A33124, A33130, A33132, A33133, A33163, A33165, A33169, A33177, R03923, R03924, gisement 261, *Karapadites karapadensis* zone); 2 specimens (MNHN.F.A33116, A33195, gisement 260, *Karapadites*

karapadensis zone); 1 specimen (MNHN.F.A33203, gisement 255, *Anapachydiscus wittekindi* and *Eulophoceras jacobi* zone); 1 specimen (MNHN.F.A33200, gisement 251); 2 specimens (MNHN.F.A33194, gisement 254). From the “Coupe de Berere I” (Lower Campanian): 1 specimen (MNHN.F.A33170, gisement 161, *Anapachydiscus wittekindi* and *Eulophoceras jacobi* zone); 3 specimens (MNHN.F.A33074, A33155, A33337, gisement 163); 7 specimens (MNHN.F.A33046, A33077, A33083, A33149, gisement 165); 1 specimen (MNHN.F.A33198, gisement 166); 2 specimens (MNHN.F.A31655, A33053, gisement 167); 10 specimens (MNHN.F.A31656, A33081, A33118, A33131, A33153, A33173, A33174, A33191, A33471 gisement 171, *Karapadites karapadensis* zone).

From the “Coupe de Berere III” (Lower Campanian): 1 specimen (MNHN.F.R03914, gisement 192, *Anapachydiscus wittekindi* and *Eulophoceras jacobi* zone); 4 specimens (MNHN.F.A33062, A33112, A33161, A33183, gisement 190, *Anapachydiscus wittekindi* and *Eulophoceras jacobi* zone).

All specimens are from Belo-sur-Tsiribihina, Menabe region, central Morondava Basin, Tulear Province.

TYPE LOCALITY. — Coupe de Bevahô (gisement 256), Belo-sur-Tsiribihina, Menabe region, central Morondava Basin, Tulear Province.

TYPE AGE. — Early Campanian (*Anapachydiscus wittekindi* and *Eulophoceras jacobi* zone).

ADDITIONAL MATERIAL EXAMINED. — From the “Coupe d’Ampolypoly-Antsirasira-Behamotra” (Middle-Upper Santonian): 1 figured specimen (MNHN.F.R03919, gisement 280, *Texanites hourcqi* and *Pseudoschloenbachia umbulazi* zone).

From the “Coupe de Bevahô” (Lower Campanian): 3 specimens (MNHN.F.A33164, A33178, A33193, gisement 260, *Karapadites karapadensis* zone); 3 specimens (MNHN.F.A33362, gisement 261, *Karapadites karapadensis* zone).

From the “Coupe de Berere I” (Lower Campanian): 2 specimens (MNHN.F.A33079, A33469, gisement 165); 1 specimen (MNHN.F.A33187, gisement 162, *Anapachydiscus wittekindi* and *Eulophoceras jacobi* zone).

From the “Coupe de Berere III” (Lower Campanian): 1 specimen (MNHN.F.A33332, gisement 190, *Karapadites karapadensis* zone); 1 specimen (MNHN.F.A33137, gisement 192, *Anapachydiscus wittekindi* and *Eulophoceras jacobi* zone).

From unnamed outcrops: 2 specimens (MNHN.F.A33041, A33186, gisement 708).

From unknown outcrops: 6 specimens (MNHN.F.A33058, A33167, A33229). All specimens are from Belo-sur-Tsiribihina, Menabe region, central Morondava Basin, Tulear Province.



FIG. 7. — *Enoploclytia collignoni* Secrétan, 1964 from the lower Campanian of Belo-sur-Tsiribihina, Menabe region, central Morondava Basin: **A, B**, holotype (MNHN.FR03925, Coupe de Bevaho, gisement 256), isolated cephalothorax in dorsal and right lateral views, respectively; **C**, fragmentary chela of P1 (MNHN.FR03924, Coupe de Bevaho, gisement 261), lateral view, note the straight occlusal margins of dactylus and index, with a single row of strong teeth; **D, E**, globose propodus (MNHN.FR03914, Coupe de Berere III, gisement 192) covered by uniform pits and small tubercles on the outer surface (**D**) and by uniform pits with sparse, strong and aligned tubercles on the inner (**E**), note the articulation to the carpus; **F, G**, complete chela of P1 (MNHN.FR03923, Coupe de Bevaho, gisement 261) with globose propodus retaining index (**F**, outer surface) and dactylus (**G**, inner surface) very narrow, elongate and curved distally. Scale bars: 2 cm. Photographs by C. Lemzaouda (MNHN).

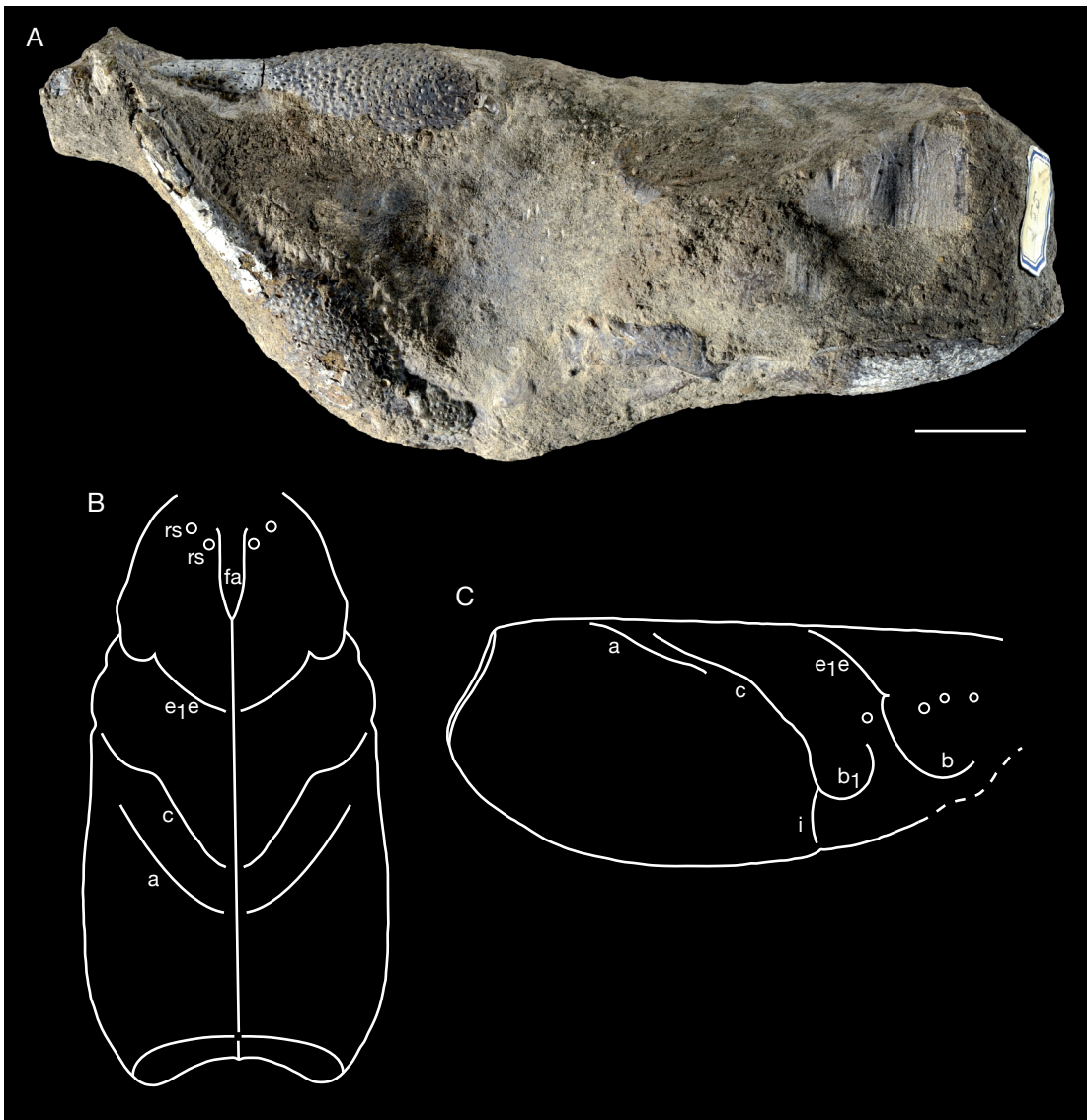


FIG. 8. — *Enoploclytia collignoni* Secrétan, 1964 from the lower Campanian of Belo-sur-Tsiribihina, Menabe region, central Morondava Basin: **A**, near-complete specimen in ventral view (MNHN.F.A33132, Coupe de Bevahlo, gisement 261) showing P1 with elongate chelae (note homochely), merus with strong spines on the ventral margin and a fragment of the cephalothorax; **B**, **C**, line drawings by F. Fogliazza, in dorsal and right lateral views, respectively. Abbreviations: **a**, branchiocardiac groove; **b**, antennal groove; **b₁**, hepatic groove; **c**, postcervical groove; **e+e**, cervical groove; **fa**, fusiform area; **i**, inferior groove; **rs**, rostral spine. Scale bar: 2 cm. Photographs by C. Lemzaouda (MNHN).

STRATIGRAPHIC RANGE. — Middle Santonian to Early Campanian.

DIAGNOSIS. — Cephalothorax with deep cervical groove; antennal groove elongate, weak; postcervical and branchiocardiac grooves parallel and well marked; branchio-

cardiac groove interrupted at $\frac{1}{3}$ of the carapace height; postcervical groove medially sinuous, joined to hepatic groove; inferior groove well marked; gastric region with one strong ventral spine; pterygostomial region prominent; antennal region with antennal carina bearing 3–4 strong, aligned spines, the last one stronger, directed forwards

(antennal spine); tuberculate fusiform area on the dorsal margin, flanked by two strong, basal rostral spines.

DESCRIPTION

Cephalothorax subrectangular (CL = 90 mm, CH = 32 mm); rostrum not preserved; tuberculate fusiform area on the dorsal margin, flanked by two strong, basal rostral spines; gastric and antennal region well defined between cervical and antennal grooves; antennal region slightly inflated with antennal carina bearing 3–4 strong, aligned spines, the last one strongest, directed forwards (antennal spine); wide cardiac region with one strong ventral spine; wide, rounded branchial region; cervical groove deep, slightly inclined and sinuous at mid-height, intercepting dorsal margin at an angle of *c.* 55°; postcervical and branchiocardiac grooves strongly inclined intercepting dorsal margin at an angle of *c.* 40°; branchiocardiac groove interrupted at 1/3 of the carapace height; postcervical groove medially sinuous joining the hepatic groove; well-marked hepatic and inferior grooves; prominent pterygostomial region; posterior margin with well-marked carina; differentiated ornament on cephalothoracic regions: branchial region uniformly covered by small pits, cardiac, pterygostomial, gastric and antennal covered by small pits and strong spiny tubercles.

Cephalic appendages and abdomen not preserved.

Only P1 and P2 are preserved of the thoracic appendages; P1 homochelous: chelae with globose propodus bearing very narrow, elongate dactylus and index incurved distally; propodus covered with uniform pits with sparse aligned strong tubercles on the inner surface and with uniform pits and small tubercles on the outer one; occlusal opening narrow; occlusal margins of dactylus and index straight, with one row of strong teeth; ventral margin of the merus bearing strong spines; P2 small chelae.

DISCUSSION

We concur with Förster's (1966) diagnosis of *Enoploclytia*. Based on our revision of the Malagasy material referred to *Enoploclytia* by Secrétan (1964), we subscribe to this generic attribution, but wish to note that the line drawings in Secrétan (1964: figs 43, 44) are incorrect in showing the postcervical groove to be joined by the hepatic one and not interrupted at 1/3 of carapace height.

?*Enoploclytia armata* Secrétan, 1964 (Fig. 9)

Enoploclytia [sic] *armata* Secrétan, 1964: 90–93, pl. 6, figs 2–6; pl. 7, figs 1, 2; pl. 8, fig. 3.

Enoploclytia armata – Förster 1966: 151. — Schweitzer *et al.* 2010: 22.

HOLOTYPE. — MNHN.F.R03913.

PARATYPES. — From the “Coupe de Ampolypoly-Antsirasia-Behamotra”: 3 specimens (MNHN.F.A33209, A33464, R03912, gisement 287).

TYPE LOCALITY. — Coupe de Ampolypoly-Antsirasia-Behamotra (gisement 287), Belo-sur-Tsiribihina, Menabe region, central Morondava Basin, Tulear Province.

TYPE AGE. — Early Campanian (*Anapachydiscus wittekindi* and *Eulophoceras jacobi* zone).

ADDITIONAL MATERIAL EXAMINED. — 1 specimen (MNHN.F.A33331), from an unknown outcrop. Belo-sur-Tsiribihina, Menabe region, central Morondava Basin, Tulear Province.

DISCUSSION

The type material included only fragmentary chelipeds that preclude a detailed characterisation of the species. The only features that can be recognized are: propodus massive, very large and compressed with inner and outer surfaces strongly tuberculate, dorsal margin finely tuberculate, ventral margin strongly tuberculate with two rows of more or less aligned strong tubercles; dactylus and index triangular in cross section; dactylus with two lateral strong basal spines. We question the attribution of this material to *Enoploclytia* in view of the fact that diagnostic characters of this genus are found mainly on the cephalothorax. Moreover, the chelae of *Enoploclytia* usually have a globose propodus with very elongate fingers, as seen in specimens of *E. collignoni*. Only the discovery of more complete specimens can resolve the systematic position of these specimens.

Genus *Eryma* von Meyer, 1840

TYPE SPECIES. — *Macrourites modestiformis* von Schlotheim, 1822, by subsequent designation of Glaessner (1929).

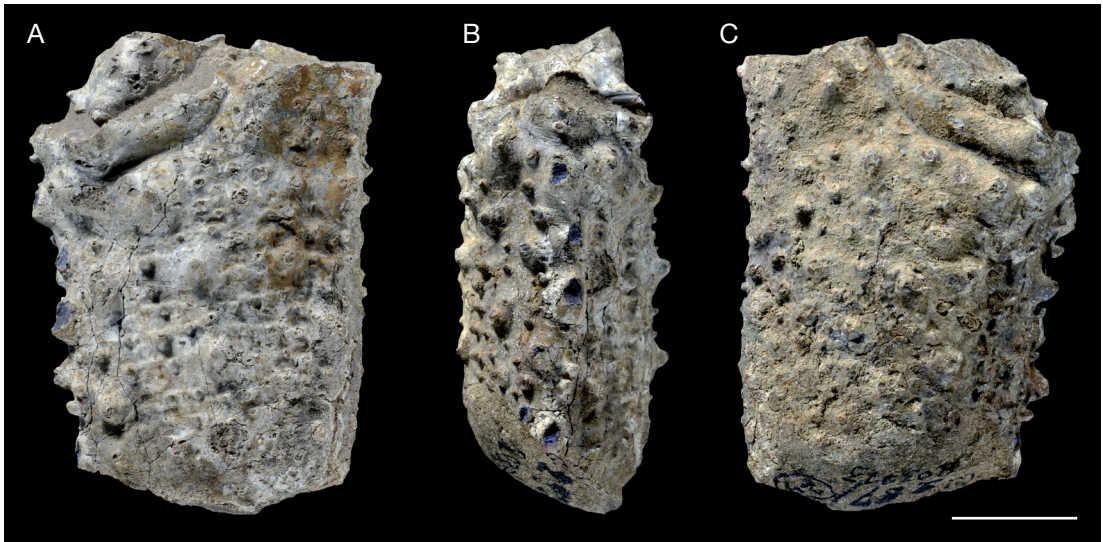


FIG. 9. — ?*Enoploclytia armata* Secrétan, 1964 from the Lower Campanian of Belo-sur-Thsiribihina, Menabe region, central Morondava Basin: A-C, holotype (MNHN.FR03913, Coupe de Ampolpoly-Antsirasira-Behamotra, gisement 287), very large, massive and compressed propodus, with inner (A) and outer (C) surfaces strongly tuberculate, dorsal margin finely tuberculate, ventral margin strongly tuberculate with two rows of more or less aligned strong tubercles (B). Scale bar: 2 cm. Photographs by C. Lemzaouda (MNHN).

Eryma granuliferum Secrétan, 1964
(Fig. 10)

Eryma granulifera Secrétan, 1964: 64-67, pl. 1, fig. 1; pl. 3, fig. 1.

Eryma madagascariensis Secrétan, 1964: 61-64, pl. 3, figs 2, 3. n. syn.

Eryma granulifera – Förster 1966: 125. — Feldmann & Titus 2006: 64.

Eryma granuliferum – Schweitzer *et al.* 2010: 24.

Eryma madagascariensis – Förster 1966: 116, 125, 162. — Feldmann & Titus 2006: 64. — Schweitzer *et al.* 2010: 24.

HOLOTYPE. — MNHN.FR03975.

TYPE LOCALITY. — Eastern Antsalova (gisement 236), south of the Maintirano region, northern Morondava Basin, Tulear Province.

TYPE AGE. — Middle Kimmeridgian (*Hibononticeras hibonotum* and *Aspidoceras acanthicum* zone).

ADDITIONAL MATERIAL EXAMINED. — Specimen MNHN.FR03974 (holotype of *Eryma madagascariensis*), Antsalova, east of Mount Ambohidroa (gisement 233)

Aspidoceras longispinum and *Torquatosphinctes alternepliacatus* zone, Lower Kimmeridgian, north of the Manambolo River, south of the Maintirano region, northern Morondava Basin, Tulear Province.

STRATIGRAPHIC RANGE. — Early to Middle Kimmeridgian.

DIAGNOSIS. — Cephalothorax with deep cervical and antennal grooves; postcervical and branchiocardiac grooves parallel and slightly marked; branchiocardiac groove connected with deep hepatic groove; postcervical groove not joined to branchiocardiac groove and interrupted prior to the junction with the hepatic groove; inferior groove not well marked.

DESCRIPTION

Cephalothorax subcylindrical (CL = 25 mm, CH = 17 mm); very small rostrum (length *c.* 2 mm) with rounded distal extremity and smooth margins; ocular incision rather shallow; gastric and antennal region well delimited between cervical and antennal grooves; inflated antennal region; very narrow cardiac region; wide, rounded branchial region; cervical groove near-right with a weak depression at mid-height, slightly inclined intercepting dorsal margin at an angle of *c.* 65°; postcervical and bran-

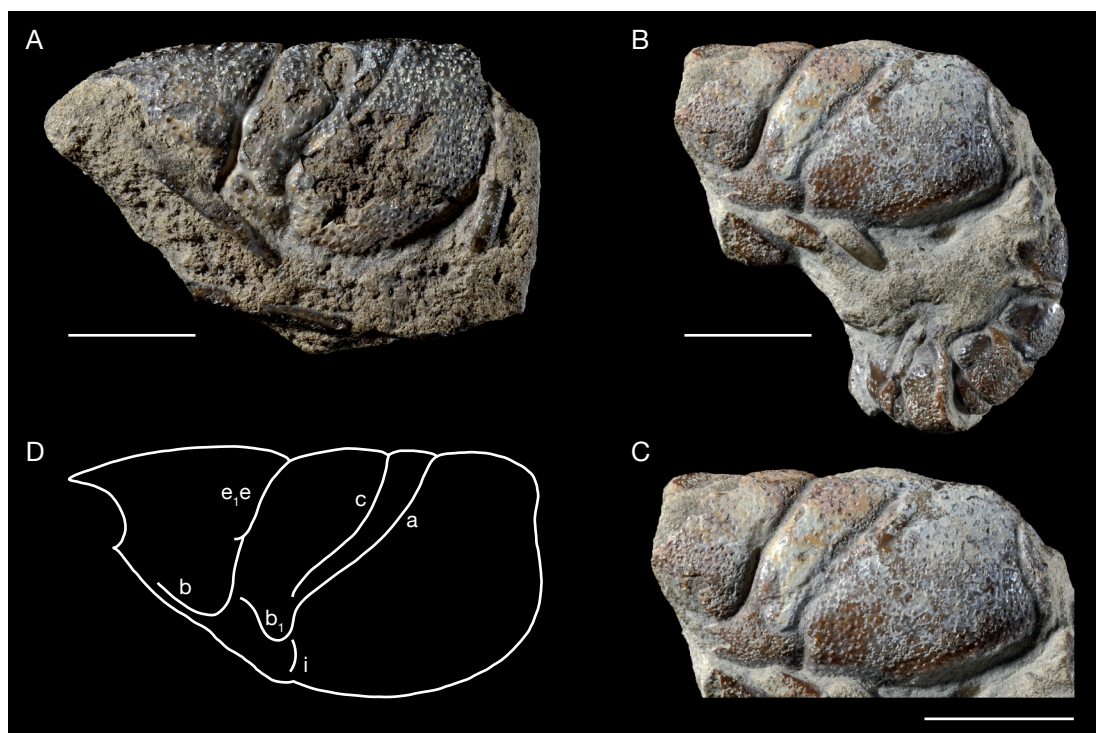


FIG. 10. — *Eryma granuliferum* Secrétan, 1964 from the lower to middle Kimmeridgian of Antsalova, south of the Maintirano region, northern Morondava Basin: **A**, holotype (MNHN.F.R03975, eastern Antsalova, gisement 236), complete cephalothorax in left lateral view; **B**, **C**, incomplete specimen (MNHN.F.R03974, holotype of *Eryma madagascariensis*, gisement 233, Antsalova, east of Mount Ambohdroa), right lateral view (**B**) and detail of cephalothorax (**C**); **D**, line drawings by F. Fogliazza in left lateral view. Abbreviations: **a**, branchiocardiac groove; **b**, antennal groove; **b₁**, hepatic groove; **c**, postcervical groove; **e₁e**, cervical groove; **i**, inferior groove. Scale bars: 2 cm. Photographs by C. Lemzaouda (MNHN).

chiodiac grooves strongly inclined intercepting dorsal margin at an angle of *c.* 40°; hepatic groove strongly rounded; inferior groove not well marked; posterior margin with small carina; ornament uniform with small tubercles.

Abdomen with subrectangular somites of uniform length; pleurae 1 and pleurae 4 and 5 with spiny ventral margin; tail fan not preserved; surface of somites smooth with sparse pits.

Pereiopods fragmentary (three different segments preserved, difficult to attribute to pereiopod).

DISCUSSION

We concur with Förster's (1966) diagnosis of *Eryma* as well as with Secrétan's (1964) reference of the Malagasy material to this genus. Secrétan (1964)

differentiated *Eryma granulifera* from *E. madagascariensis* on the presence of an anterior branch of the postcervical groove interrupted prior to joining the hepatic groove. Our re-examination of the type specimen of *E. granuliferum* has clearly shown that the postcervical groove is not divided into two branches. Moreover, the branchiocardiac groove is connected with the hepatic groove and not with the postcervical groove, as assumed by Secrétan (1964). Finally, the postcervical and branchiocardiac grooves are parallel, not fused. This configuration is similar in both *E. granuliferum* and *E. madagascariensis*, which is why we consider them to be conspecific, the name *E. granuliferum* being chosen as the valid name, on the basis of the Principle of the First Reviser (ICZN 1999: art. 24.2).

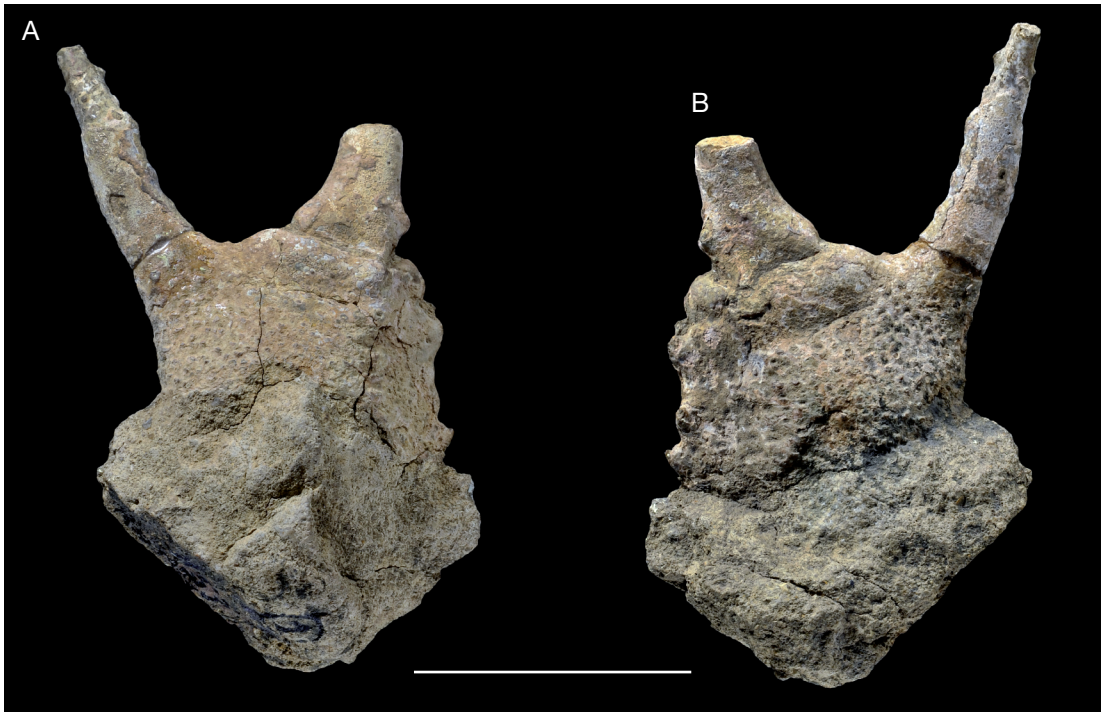


FIG. 11. — *?Eryma australe* (Secrétan, 1964) from the lower Tithonian of the northern Analavelona Massif, southern Morondava Basin: **A, B**, holotype (MNHN.FR03972, southwest of Ankilivalo, gisement 1153), fragmentary cheliped showing very large, compressed propodus with smooth outer margin (**A**), and strongly tuberculate inner margin (**B**); index and dactylus curved with occlusal opening very broad, note occlusal margin of index with one row of small rounded teeth and two strong basal tubercles of dactylus. Scale bars: 2 cm. Photographs by C. Lemzaouda (MNHN).

?Eryma australe (Secrétan, 1964)
(Fig. 11)

Erymastacus australis Secrétan, 1964: 72-74, pl. 1, fig. 2; pl. 2, figs 1-5.

Eryma australe – Schweitzer *et al.* 2010: 23.

HOLOTYPE. — MNHN.FR03972.

PARATYPES. — From Northern Analavelona Massif (Tulear Province): 2 specimens (MNHN.FR03971, A31660, hillock southwest of Ankilivalo, gisement 1153); 1 specimen (MNHN.FA33207, gisement 1205, Marolalitra River, Befandriana south). High Sikily region, northern Analavelona Massif, Tulear Province, southern Morondava Basin, Tulear Province.

TYPE LOCALITY. — Northern Analavelona Massif (Tulear Province), southwest Ankilivalo (gisement 1153), Tulear Province.

TYPE AGE. — Early Tithonian (*Hildoglochiceras kobelli* zone).

DISCUSSION

The type material comprises merely poorly preserved, fragmentary chelipeds and does not permit a detailed characterization of this species. The features that are recognizable include: very large and compressed propodus, with inner margin strongly tuberculate, outer margin smooth; index and dactylus curved; elongate and narrow index; outer margin smooth, occlusal margin with a single row of small, rounded teeth; dactylus fragmentary, with circular cross section, more thick-set than the index; two strong, basal tubercles, occlusal margin smooth; occlusal opening very broad and curved, with occlusal margins of dactylus and index not in contact. Comparing these specimens with the “classic type” of cheliped of *Eryma* von Meyer, 1840, we have doubts about the attribution of the Malagasy material to it. In *Eryma*, the

cheliped usually shows a stouter, shorter propodus with smooth inner and outer margins; index and dactylus straight, shorter, with occlusal margins tuberculate; occlusal opening narrower, with occlusal margins of dactylus and index in contact. Only the discovery of more complete specimens can resolve the systematic position of these specimens.

Genus *Pustulina* Quenstedt, 1857

TYPE SPECIES. — *Pustulina suevica* Quenstedt, 1857, by monotypy.

Pustulina spinulata (Secrétan, 1964) (Fig. 12)

Phlyctisoma spinulatum Secrétan, 1964: 75-81, pl. 2, figs 6-12; pl. 3, figs 4-9; pl. 4, figs 1-3.

Phlyctisoma spinulatum – Förster 1966: 145. — Garassino 1996: 341.

Pustulina spinulata – Garassino & Schweigert 2006: 12. — Schweitzer *et al.* 2010: 26.

HOLOTYPE. — MNHN.FR03961.

PARATYPES. — 46 specimens (MNHN.FA33176, A33185, R03939, R03949, R03956, R03958, R039589, R03960, R03962, R03963, R03964, R03965, R03966) from Soromaraina (gisement 43, upper Valanginian-Hauterivian); 5 specimens (MNHN.FA33189, A33190, R03957) from Soromaraina (gisement 44, Hauterivian). All specimens are from the Sitampiky area, southern Mahajanga Basin, Mahajanga Province.

TYPE LOCALITY. — Soromaraina (gisement 43), Sitampiky area, eastern Mahavavy River, southern Mahajanga Basin, Mahajanga Province.

TYPE AGE. — Late Valanginian-Hauterivian.

ADDITIONAL MATERIAL EXAMINED. — MNHN.FA33459 (gisement 43, Upper Valanginian-Hauterivian), MNHN.FA33470 (gisement 44), Sitampiky area, eastern Mahavavy River, southern Mahajanga Basin.

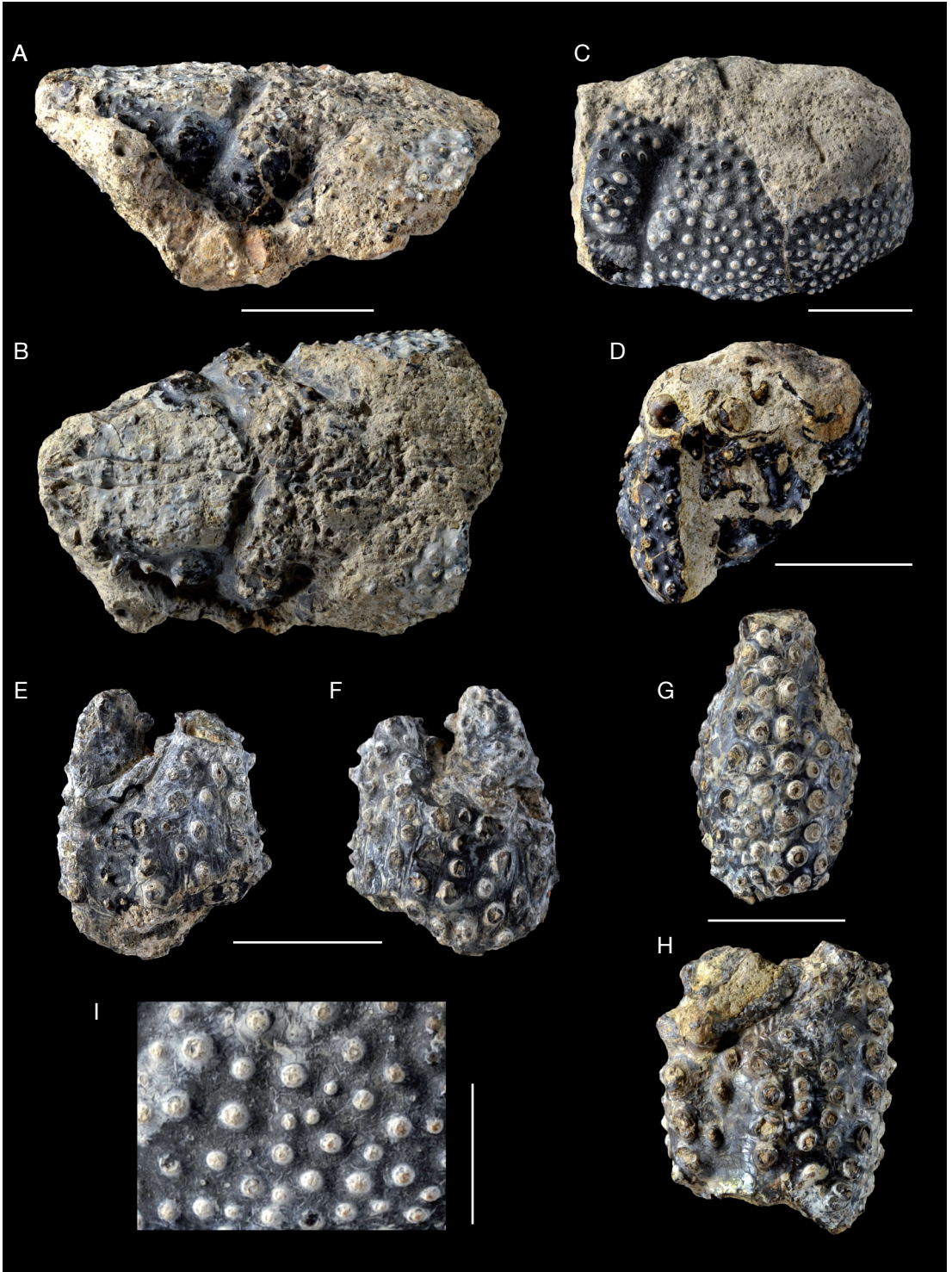
DIAGNOSIS. — Cephalothorax with deep cervical, antennal, postcervical and hepatic grooves; branchiocardiac groove almost absent; postcervical groove joined to hepatic groove; well-marked inferior groove; pterygostomial region strongly inflated; well-developed antennal spine; two strong spines in the antennal region aligned with the antennal spine; short rostrum with smooth margins; fusiform area on the dorsal margin, posteriorly closed to the rostrum.

DESCRIPTION

Cephalothorax subcylindrical (CL = *c.* 36 mm, CH = *c.* 25 mm); rostrum very small (length *c.* 2 mm) with rounded distal extremity and smooth margins; well-marked ocular incision, ventrally delineated by a strong antennal spine; eyestalk well developed with globose eye; gastric and antennal region well defined between cervical and antennal grooves, antennal region with two well-developed spines directed forwards and aligned with antennal spine; cardiac region wide, bounded by cervical and postcervical grooves; pterygostomial region strongly inflated and tuberculate; branchial region wide and flat; cervical groove almost straight, slightly inclined intercepting dorsal margin at an angle of *c.* 55°; postcervical groove markedly deep and inclined, intercepting dorsal margin at an angle of *c.* 65°; hepatic groove strongly curved; inferior groove well marked; ornament uniform with well-developed tubercles.

Pereiopods fragmentary (only two fragments of chelae, probably short); propodus globose with inner and outer margins tuberculate; index and dactylus with circular cross section, occlusal margin of a fragmentary dactylus with a small basal tooth, occlusal opening probably narrow.

FIG. 12. — *Pustulina spinulata* (Secrétan, 1964) from the Upper Valanginian-Hauterivian of the Sitampiky region, eastern Mahavavy River, southern Mahajanga Basin: **A, B**, holotype (MNHN.FR03961, Soromaraina, gisement 43), cephalothorax in left lateral and dorsal views, respectively; **C**, fragmentary cephalothorax (MNHN.FR03962, Soromaraina, gisement 43) showing uniform ornament of well-developed tubercles; **D**, fragment of cephalothorax (MNHN.FA33459), anterior dorsal view, note rostrum with rounded distal extremity and the eyestalks with globular eyes; **E, F**, fragment of small chela (MNHN.FR03965) with inner (**E**) and outer (**F**) margins tuberculate, note occlusal margin of fragmentary dactylus with a small basal tooth; **G, H**, fragment of chela (MNHN.FA33189), globose propodus with dorsal (**G**) and inner (**H**) margins tuberculate, note the circular cross section of index and dactylus; **I**, ornament of cephalothorax (detail of Figure 12C). Scale bars: A-H, 1 cm; I, 0.5 cm. Photographs by C. Lemzaouda (MNHN).



DISCUSSION

We here adopt Förster's (1966) diagnosis of *Pustulina* (= *Phlyctisoma*) and, after re-examination of the Malagasy material studied by Secrétan (1964), also agree with her generic attribution. However, we wish to point out that her reconstructions (Secrétan (1964: figs 37-39) are not correct in that: 1) the rostrum described in the text and illustrated as pointed and trifid is in fact rounded; 2) in the antennal region, only two spines (not three) are aligned, the first one is in fact the strong antennal spine; 3) the cervical groove does not show the small depression in the median portion; and 4) the groove "a", as shown in the line drawings is not the branchiocardiac groove, but the postcervical one, located not so close to the posterior margin of the cephalothorax; the short groove "c", as shown in the line drawings is the postcervical, which, in reality is more elongate, joining the hepatic groove.

Infraorder ASTACIDEA Latreille, 1802
 Superfamily NEPHROPOIDEA Dana, 1852
 Family NEPHROPIDAE Dana, 1852
sensu Tshudy & Babcock (1997)

Genus *Hoploparia* McCoy, 1849

TYPE SPECIES. — *Astacus longimanus* J. de C. Sowerby, 1826, by subsequent designation of Rathbun (1926).

Hoploparia collignoni (Van Straelen, 1949)
 (Figs 13-16)

Palaeohomarus collignoni Van Straelen *in* Collignon, 1949: 99, pl. 21, figs 8-10.

Hoploparia collignoni — Secrétan 1964: 98-102, pl. 6, fig. 1; pl. 8, figs 2-3; pl. 9, figs 5-10; pl. 10, fig. 1. — Bishop 1985: 613. — Aguirre Urreta 1989: 522, 524,

526. — Karasawa 2000: 235. — Tshudy & Sorhannus 2003: 709. — Kato & Karasawa 2006: 339. — Feldmann *et al.* 2007: 707. — Garassino *et al.* 2009: 89. — Schweitzer *et al.* 2010: 28.

Hoploparia intermedia Secrétan, 1964: 102-104, pl. 4, figs 6-10; pl. 9, fig. 11. n. syn. — Bishop 1985: 613. — Aguirre Urreta 1989: 526. — Tshudy & Sorhannus 2003: 709. — Feldmann *et al.* 2007: 707. — Karasawa *et al.* 2008: 105. — Garassino *et al.* 2009: 89. — Schweitzer *et al.* 2010: 29.

Hoploparia sculpta Secrétan, 1964: 105-109, pl. 4, fig. 11; pl. 9, figs 1-4, 12; pl. 10, figs 2, 5-9. n. syn. — Aguirre Urreta 1989: 524, 526, 529. — Tshudy & Sorhannus 2003: 709. — Feldmann *et al.* 2007: 707. — *Hoploparia sculpta* Secrétan *in* Garassino *et al.* 2009: 89. — Schweitzer *et al.* 2010: 30.

Hoploparia sculptata [sic] — Bishop 1985: 613.

HOLOTYPE. — A near-complete cephalothorax, see Van Straelen 1949: pl. 21, fig. 8.

PARATYPES. — Figured paratypes (2 complete propodi, pl. 21, figs 9, 10 *in* Van Straelen 1949).

Unfigured paratypes (1 small cephalothorax, 7 propodi, 1 dactylus, 1 fragment of pereopod). All type specimens were deposited in the collections of the École nationale supérieure des Mines de Paris and they are now housed in the collections of the Université Claude Bernard Lyon 1 (France). We did not examine these specimens.

TYPE LOCALITY. — Ambarimaninga, Sitampiky region, eastern Mahavavy River, southern Mahajanga Basin, Mahajanga Province.

TYPE AGE. — Middle Albian (*Lemuroceras spathi* and *Brancoeras besairiei* zone).

ADDITIONAL MATERIAL EXAMINED. — Type material of *Hoploparia sculpta*: 4 syntypes (MNHN.F.R03948, R03950, A31664, Befamonto, gisement 42, *Douvilleicerus inaequinodum* zone, Lower Albian); 24 syntypes (MNHN.F.R03947, R03952, R03953, R03954, R03955, A31665, Malandiandro, gisement 46, *Douvilleicerus inaequinodum* zone, Lower Albian).

FIG. 13. — *Hoploparia collignoni* (Van Straelen, 1949) from the lower to middle Albian of the Sitampiky region, eastern Mahavavy River, southern Mahajanga basin: **A**, complete cephalothorax (MNHN.F.R03946, Malandiandro, gisement 46), left lateral view, note well-preserved rostrum; **B**, incomplete cephalothorax (MNHN.F.A33462, Malandiandro, gisement 46), right lateral view, note cephalothoracic grooves; **C-D**, complete specimen (MNHN.F.A33152, Malandiandro, gisement 46) in dorsal and right lateral views, respectively, showing cephalothorax articulated with abdomen; **E-F**, complete cephalothorax (MNHN.F.R03954, syntype of *Hoploparia sculpta*, Malandiandro, gisement 46) in dorsal and right lateral views, respectively, note anterior cephalic region finely tuberculate and ocular incision rather shallow, delimited ventrally by antennal spine; **G**, incomplete cephalothorax (MNHN.F.R03947, syntype of *Hoploparia sculpta*, Malandiandro, gisement 46), left lateral view, note ornament; **H**, incomplete cephalothorax (MNHN.F.A31663), right lateral view, note well-developed cephalic grooves. Scale bars: 2 cm. Photographs by C. Lemzaouda (MNHN).

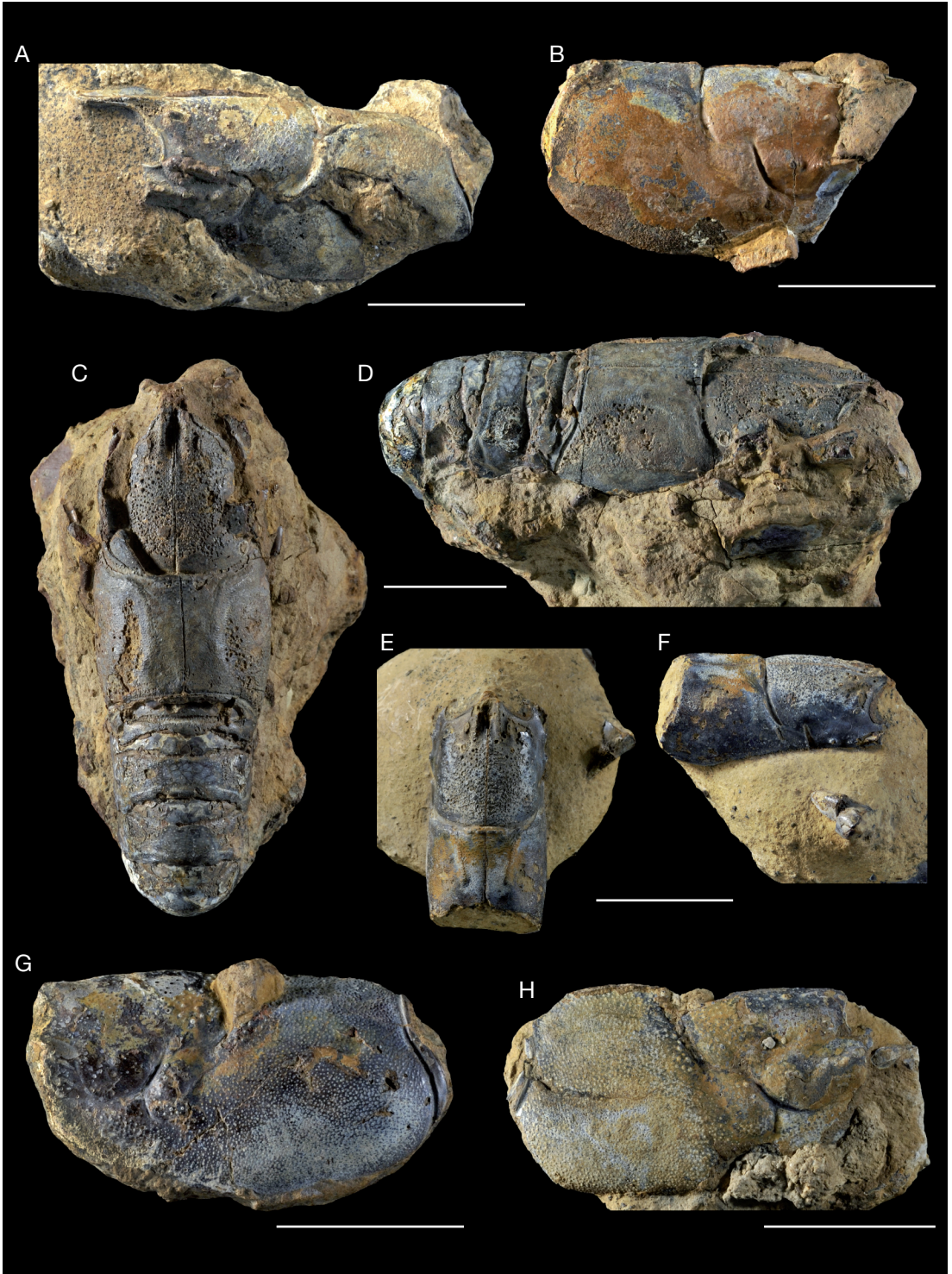




FIG. 14. — *Hoploparia collignoni* (Van Straelen, 1949) from the Albian of the Sitampiky region, eastern Mahavavy River, southern Mahajanga Basin: **A, B**, abdomen (MNHN.F.R03940, Malandiandro, gisement 46), in dorsal and right lateral views, respectively, note smooth somites; **C**, incomplete telson (MNHN.F.A33152, detail of Fig. 13C, D), note completely smooth dorsal surface; **D**, fragments of uropods (MNHN.F.R03943, Malandiandro, gisement 46), lateral view, exopod with distal diarsis bearing small spines on the upper margin; **E, G**, abdomen (MNHN.F.R03948, syntype of *Hoploparia sculpta*, Befamonto, gisement 42), dorsal (**E**), right lateral (**F**) and detailed (**G**) views, note ornament of somites: s1 completely smooth, s2-5 with two pairs of dorsal aligned tubercles, s6 with dorsal surface uniformly tuberculate (**E**); pleurae 2 and 3 with two proximal tubercles; pleurae 4 and 5 with a single proximal tubercle; pleurae 6 with one median tubercle (**F**); telson with two median tubercles (**G**); **H**, abdomen (MNHN.F.R03950, syntype of *H. sculpta*, Befamonto, gisement 42), dorsal view, detail of somites. Scale bars: A, B, E, F, H, 2 cm; C, D, G, 1 cm. Photographs by C. Lemzaouda (MNHN).

Type material of *Hoploparia intermedia*: 2 syntypes (MNHN.F.R03938, A31662, Befamonto, gisement 42, *Douvilleiceras inaequinodum* zone, Lower Albian); 17 syntypes (MNHN.F.R03936, R03937, A31663, Malandiandro, gisement 46, *Douvilleiceras inaequinodum* zone, lower Albian).

Figured material of *Hoploparia collignoni* by Secrétan (1964): 7 specimens (MNHN.F.R03940, R03941, R03942, R03943, R03944, R03945, R03946; Malandiandro, gisement 46, *Douvilleiceras inaequinodum* zone, Lower Albian). Unfigured material of *Hoploparia collignoni*: 194 specimens (MNHN.F.A33152, A33210, A33211, A33212, A33213, A33214, A33224, A33340, A33349, A33355,

A33357, A33462, Malandiandro, gisement 46, *Douvilleiceras inaequinodum* zone, Lower Albian); 2 specimens (MNHN.F.A33333, A33348, Befamonto, gisement 42, *Douvilleiceras inaequinodum* zone, Lower Albian); 10 specimens (MNHN.F.A33334, Ambarimaninga, gisement 38, *Lemuroceras spathi* and *Brancoceras besairiei* zone, Middle Albian); 10 specimens (MNHN.F.A33341, Ambanjabe, gisement 45); 16 specimens lacking locality data (MNHN.F.A33076, A33227, A33335, A33336, A33339, A33363, A33412, A33413, A33414, A33415, A33416). All material originates from the Sitampiky area, eastern Mahavavy River, southern Mahajanga Basin, Mahajanga Province.

STRATIGRAPHIC RANGE. — Early to Middle Albian.

EMENDED DIAGNOSIS. — Cephalothorax with postcervical groove very deep up to the mid-height and very weak ventrally not really joining the hepatic groove; cervical groove deep starting at mid-height and joining the antennal groove; hepatic groove weak; branchiocardiac and inferior grooves absent; weak longitudinal carina, parallel to the dorsal margin and located between the posterior margin and the postcervical groove; gastric region with one well-developed spine; antennal region with tuberculate antennal carina; rostrum dorsally flat with rounded distal extremity, flanked by two smooth lateral carinae; one strong well-developed basal spine; uropodal exopod with diarsis (modified after Van Straelen 1949).

DESCRIPTION

Cephalothorax subcylindrical (CL = *c.* 46 mm, CH = *c.* 26 mm); rostrum very elongate, dorsally flat with rounded distal extremity, smooth margins and flanked by two smooth lateral carinae; one strong, well-developed basal spine; ocular incision of slight depth, delimited ventrally by the antennal spine; gastric region not delimited by the cervical groove, bearing one spine located in the centre of the ocular incision; antennal region well delimited by the cervical and antennal grooves, bearing one single postantennal spine aligned with the tuberculate antennal carina distally prolonged by the antennal spine; deep cervical groove, starting at mid-height and joining the antennal groove; postcervical groove straight, intercepting dorsal margin at an angle of *c.* 90°: it starts very deep in the centre of the dorsal

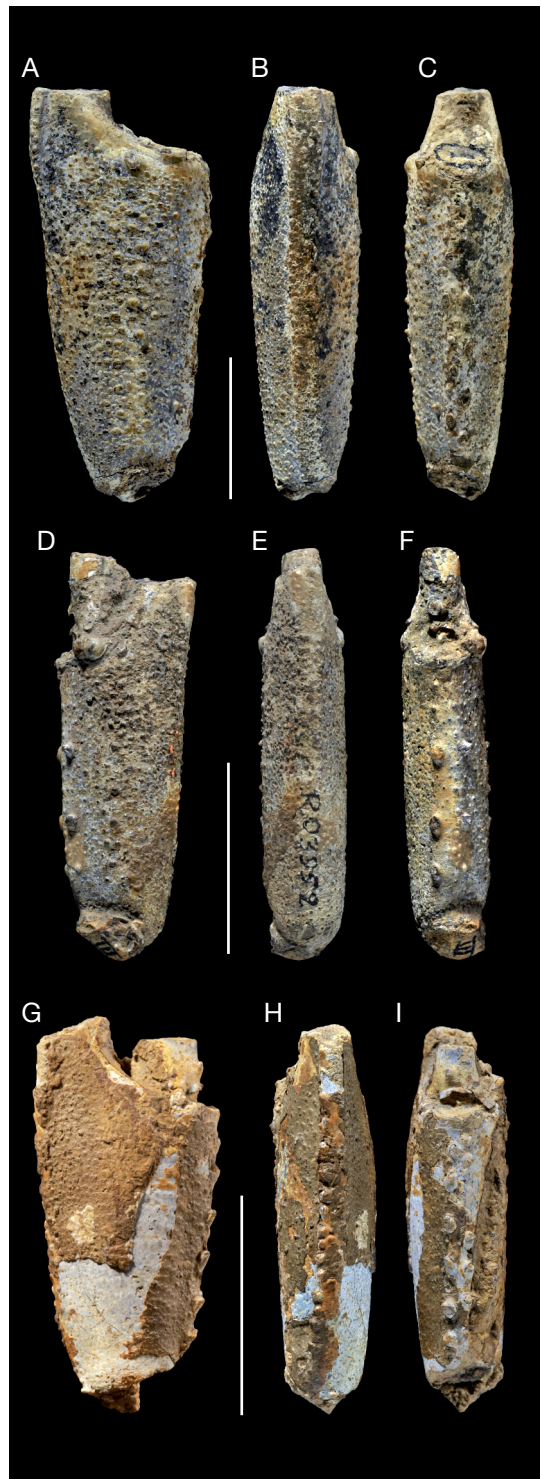


FIG. 15. — Pereiopods of *Hoploparia collignoni* (Van Straelen, 1949) from the Albian of the Sitampiky region, eastern Mahavavy River, southern Mahajanga Basin: **A-C**, fragmentary chela (MNHN.F.R03942, Malandiandro, gisement 46), in lateral, dorsal and ventral views, respectively, ornament of lateral margins: outer margin (**B**) reinforced by a slightly tuberculate carina, inner margin (**C**) by a carina of two rows of aligned, strong spines; **D-F**, fragmentary chela (MNHN.F.R03952, syntype of *Hoploparia sculpta*, Malandiandro, gisement 42), in lateral, dorsal and ventral views, respectively, ornament of lateral margins: outer margin (**E**) reinforced by a slightly tuberculate carina, inner margin (**F**) by a carina of two rows of aligned, strong spines; **G-I**, fragmentary chela (MNHN.F.A31662, syntype of *Hoploparia intermedia*, Befamonto, gisement 42), in lateral, dorsal and ventral views, respectively, ornament of lateral margins: outer margin (**H**) reinforced by a carina of two rows of aligned, small spines, inner margin (**I**) by a carina of two rows of aligned, strong spines. Scale bars: 2 cm. Photographs by C. Lemzaouda (MNHN).

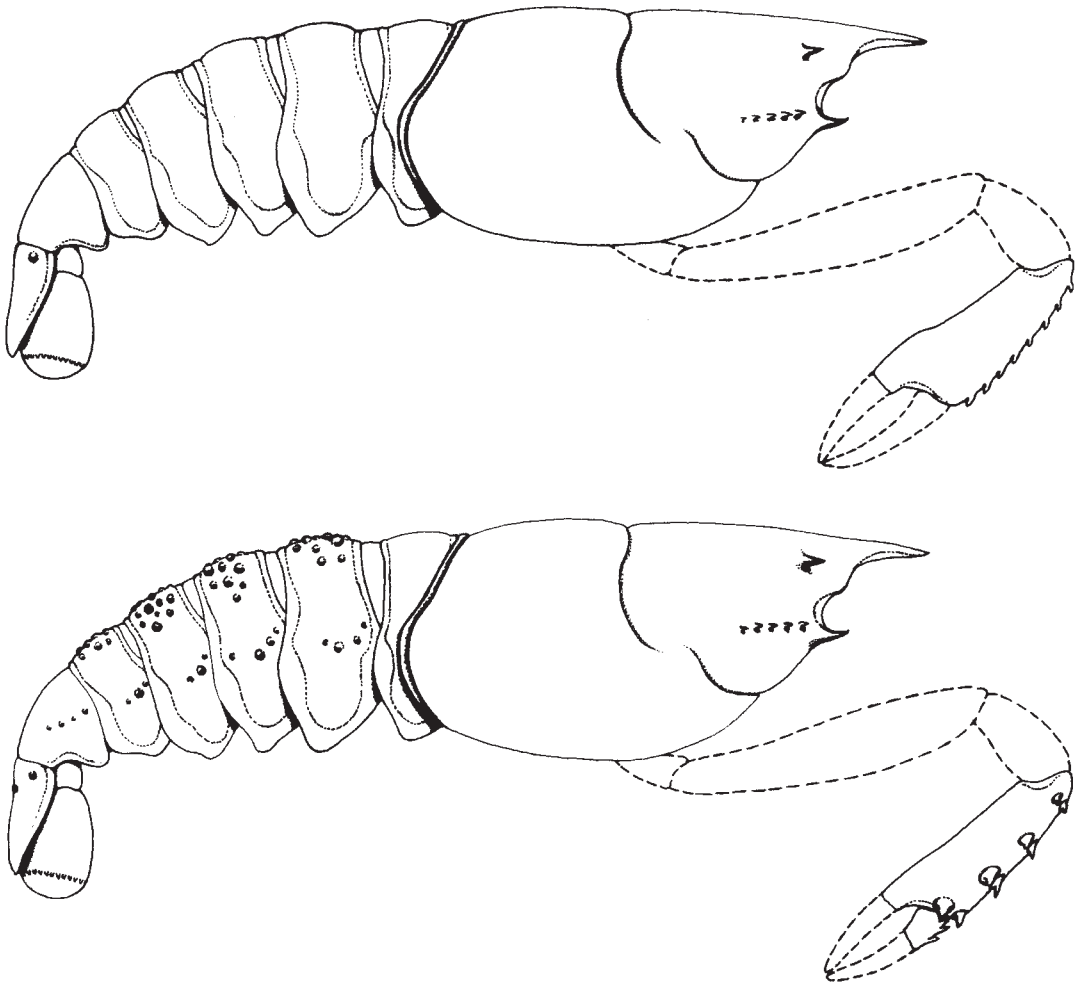


FIG. 16. — Line drawings of *Hoploparia collignoni* (Van Straelen, 1949), by F. Fogliazza, lateral views. Note differences in ornament of abdominal somites and first propodus that may be linked either to intraspecific variation or to sexual dimorphism.

margin up to mid-height, after becoming very weak, not really joining the weak and rounded hepatic groove; weak longitudinal branchial carina, parallel to the dorsal margin and located between the posterior margin and the postcervical groove; posterior margin slightly sinuous with a thin marginal carina; ornament: branchial region smooth, cardiac, gastric, and antennal regions finely tuberculate.

Abdomen with subrectangular somites; somites 1 and 6 smaller than others; somites 2-5 of uniform length; two different types of ornament on

abdomen: 1) somites 1-6 with terga and pleurae completely smooth; and 2) somite 1 completely smooth, somites 2-5 with two pairs of dorsally aligned tubercles, somite 6 with dorsal surface uniformly tuberculate; pleurae 2 and 3 with two proximal tubercles; pleurae 4 and 5 with a single proximal tubercle; pleura 6 with one median tubercle. Two different kinds of telson: one with dorsal surface completely smooth and the other with two median tubercles. Uropods fragmentary, exopod with distal diarsis bearing small spines on the upper margin.

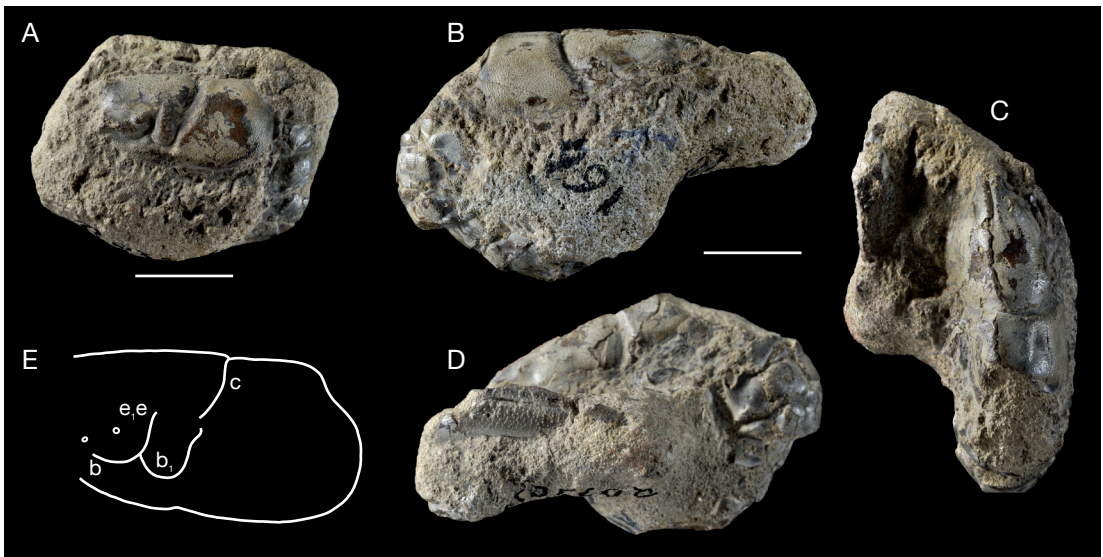


FIG. 17. — *Hoploparia pusilla* Secrétan, 1964 from the Lower Campanian of Belo-sur-Tsiribihina, Menabe region, central Morondava Basin: **A**, holotype (MNHN.F.R03904, Coupe de Berere, gisement 166), cephalothorax in left lateral view, note finely tuberculate ornament; **B-D**, paratype (MNHN.F.R03905, Coupe de Berere, gisement 166), incomplete specimen in right lateral, dorsal and left lateral views, respectively, showing articulated cephalothorax and abdomen, note left propodus of P1 with carinate outer margin; **E**, line drawing by F. Fogliazza, left lateral view. Abbreviations: **b**, antennal groove; **b₁**, hepatic groove; **c**, postcervical groove; **e₁e**, cervical groove. Scale bars: 1 cm. Photographs by C. Lemzaouda (MNHN).

Pereiopods fragmentary, only the propodi are well preserved; all are elongate, truncated conical, without apparent heterochely; specimen MNHN.F.R03941 shows ventrally two chelipedes associated with the carapace; two types of ornament occur on the lateral margins of chelipedes: 1) outer margin reinforced by a slightly tuberculate carina, inner margin by a carina of two rows of aligned strong spines; and 2) outer margin reinforced by a carina of two rows of aligned small spines, inner margin reinforced by a carina of two rows of aligned, strong spines; specimen MNHN.F.R03941 bears propodi of the first type.

DISCUSSION

We adopt the generic features outlined by Feldmann *et al.* (2007) for *Hoploparia*, and subscribe to Secrétan's (1964) assignment of the Malagasy material to it. Secrétan (1964) distinguished *Hoploparia collignoni* from *H. sculpta* and *H. intermedia* principally by: 1) the fact that cephalothoracic grooves were more or less well marked; and 2) the

occurrence of different ornament of the inner and outer margins of the propodus and of the abdominal somites. However, we question the validity of Secrétan's (1964) species for the following reasons: 1) all specimens of the three species come from the same outcrops; 2) the configuration of the cephalic grooves are quite similar in all three species, and also the location of the different spines on the gastric and antennal regions are similar; and 3) the propodus presents the same ornament of the inner and outer margins in these three species, irrespective of propodus size.

For these three reasons and also in view of the incomplete preservation of material of *H. sculpta* and *H. intermedia*, we here refer specimens assigned to those species to *H. collignoni*. Moreover, the differences observed in the ornament of the abdominal somites and of the propodus could either represent intraspecific variation and/or sexual dimorphism (Fig. 16). However, the specimens studied are not complete enough to be able to determine which of these interpretations is correct.

Hoploparia pusilla Secrétan, 1964
(Fig. 17)

Hoploparia pusilla Secrétan, 1964: 109-112, pl. 10, figs 3, 4. — Aguirre Urreta 1989: 519, 526. — Karasawa & Hayakawa 2000: 141. — Tshudy & Sorhannus 2003: 708, 709. — Garassino *et al.* 2009: 89. — Schweitzer *et al.* 2010: 30.

HOLOTYPE. — MNHN.F.R03904.

PARATYPES. — From the “Coupe de Berere”: 2 specimens (MNHN.F.R03905, A31657, gisement 166). Menabe region, central Morondava Basin, Tulear Province.

TYPE LOCALITY. — Coupe de Berere (gisement 166), Belo-sur-Thsiribihina, Menabe region, central Morondava Basin, Tulear Province.

TYPE AGE. — Early Campanian.

ADDITIONAL MATERIAL EXAMINED. — 1 specimen (MNHN.F.A33390, Coupe de Berere, gisement 166). Belo-sur-Thsiribihina, Menabe region, central Morondava Basin, Tulear Province.

DIAGNOSIS. — Cephalothorax with deep cervical groove starting at mid-height and joining the antennal groove; deep postcervical groove joining the well-marked hepatic groove; branchiocardiac and inferior grooves absent; gastric region with small spine; antennal region with tuberculate antennal carina; rostrum dorsally flat, flanked by two smooth lateral carinae, one strong, well-developed basal spine.

DESCRIPTION

Cephalothorax subcylindrical (CL = *c.* 19 mm, CH = *c.* 10 mm); rostrum dorsally flat with smooth margins and flanked by two smooth lateral carinae; one strong, well-developed basal spine; ocular incision shallow, delimited ventrally by

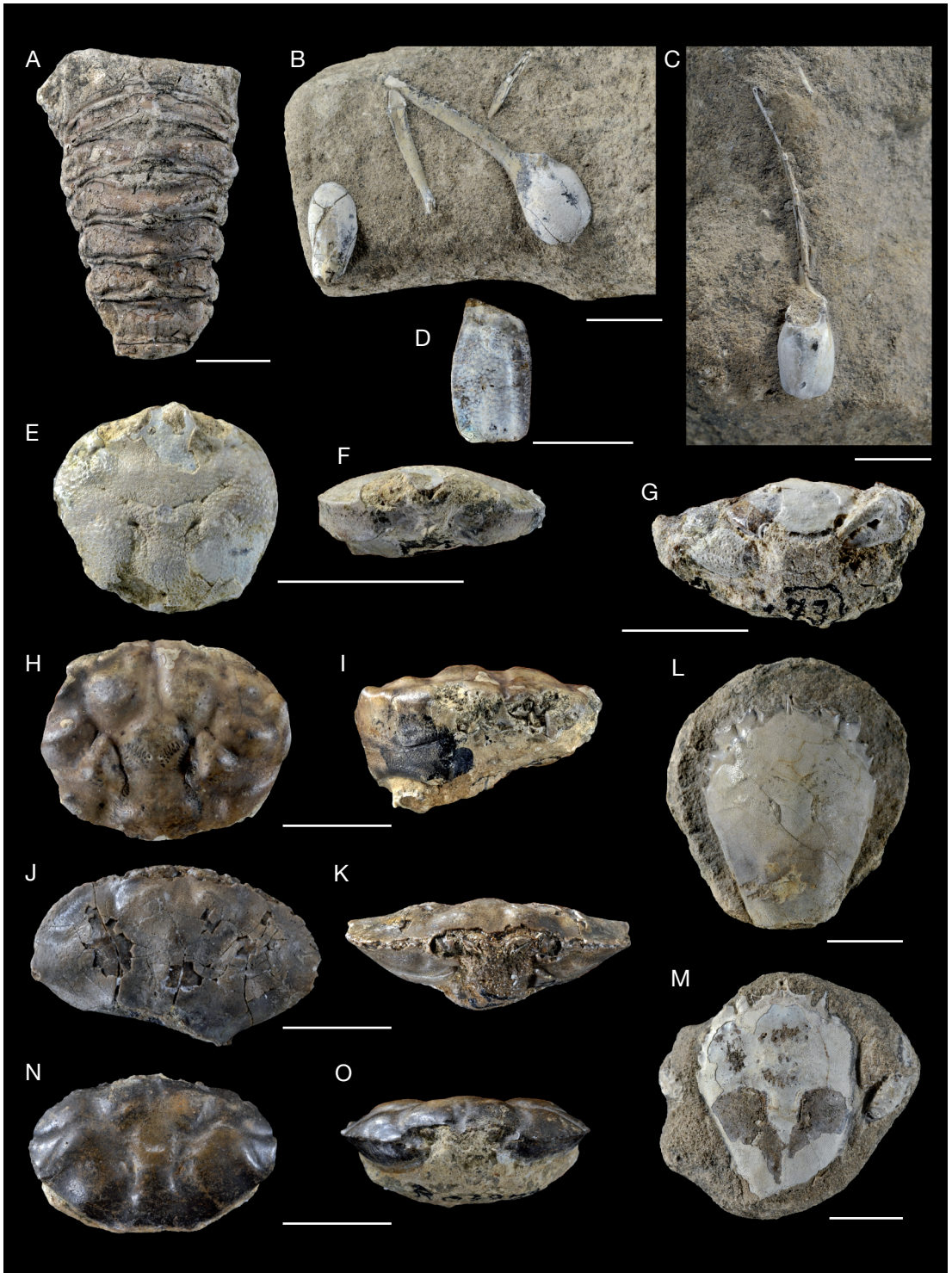
the antennal spine; gastric region not delimited by the cervical groove, bearing one small spine located in the centre of the ocular incision; antennal region well demarcated by the cervical and antennal grooves, bearing a single postantennal spine aligned with the tuberculate antennal carina distally prolonged by the antennal spine; deep cervical groove starting at mid-height and joining the antennal groove; postcervical groove deep, slightly inclined, intercepting dorsal margin at an angle of *c.* 70°, starting in the first posterior 1/3 of the dorsal margin and clearly joining the well-marked hepatic groove; pterygostomial region strongly inflated; posterior margin slightly sinuous with a thin marginal carina; ornament uniformly finely tuberculate.

Abdomen with subrectangular somites; somites 1 and 6 smaller than the others; somites 2-5 of uniform length; terga and pleurae uniformly tuberculate; pleurae with weak depression; telson subrectangular with two pairs of carinae converging distally, ornament similar to that of somites. Pereiopods fragmentary, only one propodus with carinate inner margin.

DISCUSSION

Upon re-examination of the Malagasy material studied by Secrétan (1964), we agree with her generic attribution and with the erection of a new species. As pointed out by Secrétan (1964) and confirmed by our new observations, *H. pusilla* differs from *H. collignoni* in having a deep postcervical groove joining an equally deep hepatic one. Moreover, there is a difference in stratigraphic age between the two species.

FIG. 18. — Mesozoic decapod crustaceans from Madagascar: **A**, ?*Coleia incerta* Secrétan, 1964 (holotype MNHN.F.R03969, Antsalova, gisement 217), dorsal view of a small fragment of posterior carapace and abdominal somites; **B-D**, *Ctenocheles madagascariensis* Secrétan, 1964: note two kinds of chelae (dactyli invariably are fragmentary): globose propodus with very elongate index (**B**, syntype MNHN.F.R03883, Coupe de Ankilizato, gisement 181; **C**, syntype MNHN.F.R03882, Coupe de Andimaka, gisement 203) and flat propodus with unknown index (**D**, syntype MNHN.F.R03931, Antsatramahavelona, gisement 117); **E, F**, *Dromiopsis pulchella* Secrétan, 1964 (holotype MNHN.F.R03929, Antsatramahavelona, gisement 117), in dorsal and frontal views, respectively; **G**, *Caloxanthus simplex* (Secrétan, 1964) (holotype MNHN.F.R03879, Coupe de Ankilizato, gisement 154), frontal view; **H-I**, *Titanocarcinus mamillatus* Secrétan, 1964 (holotype MNHN.F.R03871, Soatana, northern Mikoboka Creek, gisement 501), in dorsal and frontal views, respectively; **J, K**, “*Xanthosia*” *robertsi* Secrétan, 1982 (holotype, MNHN.F.R03979, Coupe de Berere I, gisement 161), in dorsal and frontal views, respectively; **L**, *Notopocorystes australis* Secrétan, 1964 (holotype MNHN.F.R03874, Coupe de Berere II, gisement 184), dorsal view; **M**, *Notopocorystes denisae* Secrétan, 1964 (holotype MNHN.F.R03875, Coupe de Ampolypoly-Antsirasira-Behamotra, gisement 317), dorsal view; **N, O**, *Secretanella arcuata* (Secrétan, 1964) (holotype MNHN.F.R03978, Antsatramahavelona, gisement 117), in dorsal and frontal views, respectively. Scale bars: 1 cm. Photographs by C. Lemzaouda (MNHN).



Infraorder POLYCHELIDA
Scholtz & Richter, 1995
Family COLEIIDAE Van Straelen, 1925

Genus *Coleia* Broderip, 1835

TYPE SPECIES. — *Coleia antiqua* Broderip, 1835, by monotypy.

?*Coleia incerta* Secrétan, 1964
(Fig. 18A)

Coleia incerta Secrétan, 1964: 115-119, pl. 18, figs 10, 11. — Schweitzer *et al.* 2010: 44.

HOLOTYPE. — MNHN.FR03969.

TYPE LOCALITY. — Antsalova (gisement 217), southern Maintirano region, northern Manambolo River, northern Morondava Basin, Tulcar Province.

TYPE AGE. — Late Tithonian (*Aulacosphinctes hollandi* zone).

DISCUSSION

Following the definition of ?*Coleia* by Van Straelen (1923, 1925), we doubt the generic attribution of the specimen studied by Secrétan (1964). In fact, the most important diagnostic characters of the genus are to be found on the cephalothorax and uropods. Since the single Malagasy specimen preserves only a small fragment of the posterior carapace and the abdominal somites, it is impossible to recognize the diagnostic generic characters. Although Secrétan (1964) pointed out that the three fragmentary carinae on the cephalothorax hint at ?*Coleia*, this feature can also be found in other palinuran taxa, such as *Linuparus*. The abdomen of the present specimen, considered typical of the eryonids by Secrétan (1964), can equally be assigned to other palinuran taxa. In conclusion, the characters displayed by the holotype are too general to ascribe it any fossil genus known to date.

Infraorder ACHELATA Scholtz & Richter, 1995
Family PALINURIDAE Latreille, 1802

Genus *Linuparus* White, 1847

TYPE SPECIES. — *Palinurus trigonus* von Siebold, 1824, by monotypy.

Linuparus bererensis Secrétan, 1964
(Figs 19-22)

Linuparus bererensis Secrétan, 1964: 122-128, pl. 8, fig. 1; pl. 11, figs 2-4; pl. 12, figs 1-5. — Collignon 1970b: 35. — Feldmann *et al.* 2007: 709, 710. — Schweitzer *et al.* 2010: 46.

Linuparus bererensis multispinosus Secrétan, 1964: 128-130, pl. 11, fig. 5. n. syn. — Collignon 1970b: 35.

HOLOTYPE. — MNHN.FR03916.

PARATYPES. — From the “Coupe de Ampolypoly-Antsirasira-Behamotra” (Lower Campanian): 2 specimens (gisement 324: MNHN.FA33148); 1 specimen (gisement 320: MNHN.FA33463, *Menabites boulei* and *Anapachydiscus arrialoorensis* zone); 1 specimen (gisement 315: MNHN.FA33075); 1 specimen (gisement 302: MNHN.FA33136, *Menabites boulei* and *Anapachydiscus arrialoorensis* zone); Middle Campanian: 11 specimens (gisement 317: MNHN.FA33168); 6 specimens (gisement 326: MNHN.FR03911, R03918, A33117, A33125, A33134, A33140, *Pachydiscus grossouvrei* zone); 2 specimens (gisement 327: MNHN.FR03915, A33147, *Pachydiscus grossouvrei* zone).

From the “Coupe de Berere II” (Lower Campanian): 1 specimen (gisement 165: MNHN.FA33199); 1 specimen (gisement 171: MNHN.FA33158, *Karapadites karapadensis* zone).

Paratypes from the “Coupe de Berere III” (Lower Campanian): 1 specimen (gisement 190: MNHN.FR03910, *Anapachydiscus wittekindi* and *Eulopoceras jacobii* zone); 1 specimen (gisement 206: MNHN.FA33146); 1 specimen (gisement 184: MNHN.FA33159).

From the “Coupe de Bevahô” (Lower Campanian): 3 specimens (gisement 261: MNHN.FA33120, A33157, *Karapadites karapadensis* zone).

FIG. 19. — *Linuparus bererensis* Secrétan, 1964 from the Campanian of the Coupe de Ampolypoly-Antsirasira-Behamotra, Belo-sur-Tsiribihina, Menabe region, central Morondava Basin: **A**, holotype (MNHN.FR03916, gisement 326), cephalothorax in dorsal view; note strong and spiny antennal articles. **B**, **C**, incomplete specimen (MNHN.FR03917, holotype of *L. b. multispinosus*, gisement 320), in dorsal and left lateral views, respectively; **D**, cephalothorax (MNHN.FA33532, gisement 328), dorsal view; note two strong supraorbital teeth directed upwards; **E**, cephalothorax (MNHN.FA33140, gisement 326), dorsal view; note two strong supraorbital teeth. Scale bars: 2 cm. Photographs by C. Lemzaouda (MNHN).



From the “Coupe de Ampamba-Antsirasira” (Middle Campanian): 1 specimen (gisement 709, *Karapadites karapadensis* zone: MNHN.F.A33204); 4 specimens (gisement 723: MNHN.F.A33082).

From the “Coupe de Andimaka” (Middle Campanian): 3 specimens (gisement 203: MNHN.F.A33202, A33122, *Pachydiscus grossouvrei* zone).

From the “Coupe de Beantaly-Soromaraina” (Lower Santonian): 1 specimen (gisement 340: MNHN.F.A33208, *Texanites oliveti* zone).

All specimens are from Belo-sur-Tsiribihina, Menabe region, central Morondava Basin, Tulear Province.

TYPE LOCALITY. — Coupe de Ampolypoly-Antsirasira-Behamotra (gisement 326), Belo-sur-Tsiribihina, Menabe region, central Morondava Basin, Tulear Province.

TYPE AGE. — Middle Campanian (*Pachydiscus grossouvrei* zone).

ADDITIONAL MATERIAL EXAMINED. — Type material of *Linuparus bererensis multispinosus*: holotype (MNHN.FR03917, Coupe de Ampolypoly-Antsirasira-Behamotra, gisement 320, *Menabites boulei* and *Anapachydiscus arrialoorensis* zone, Lower Campanian); 4 paratypes (MNHN.F.A33113, Coupe de Ampolypoly-Antsirasira-Behamotra, gisement 328, *Pachydiscus grossouvrei* zone, middle Campanian); 1 paratype (MNHN.F.A33206, Coupe de Andimaka, gisement 177, *Pachydiscus grossouvrei* zone, middle Campanian).

Unfigured material of *Linuparus bererensis*: 28 specimens from the Coupe de Ampolypoly-Antsirasira-Behamotra (gisement 326: MNHN.F.A33111, A33123, A33126, A33128, A33129, A33135, A33139, A33141, A33142, A33143, A33145, A33150, A33179, A33192, A33196, A33197, A33472, *Pachydiscus grossouvrei* zone, Middle Campanian); 1 specimen from the Coupe de Ankilizato (gisement 190: MNHN.F.A33127, Lower Campanian); 1 specimen from the Coupe de Ampamba-Antsirasira (gisement 709: MNHN.F.A33073, *Karapadites karapadensis* zone, middle Campanian); 1 specimen from the Coupe de Berere II (gisement 169: MNHN.F.A33172, *Karapadites karapadensis* zone, Lower Campanian); 5 specimens from uncertain outcrop (MNHN.F.A33144, A33154, A33465).

All specimens are from Belo-sur-Tsiribihina, Menabe region, central Morondava Basin, Tulear Province.

STRATIGRAPHIC RANGE. — Early Santonian to Middle Campanian.

DIAGNOSIS. — Cephalothorax with cephalic region smaller than branchial one. Cephalic region with: 1) two very strong supraorbital teeth directed upwards with two posterior basal spines; 2) wide frontal region without rostrum; 3) two dorsal carinae converging forwards into one strong spine; 4) two well-developed semicircular dorso-lateral carinae and strongly serrated; 5) straight lateral carina well developed, strongly serrated with very strong antennal spine delimiting the ocular incision; and 6) straight, smooth ocular incision; branchial region with: 1) three carinae well developed and strongly serrated; and 2) posterior margin of the cervical groove marked by small spines; posterior margin with submarginal groove of equal width both medially and laterally; abdominal somites with terga bearing two median spines; subrectangular, very strong somite 6 with two lateral depressions forming a rounded central part bearing two median spiny lines as well as two lateral parts slightly carinate with one small proximal spine and one very strong distal spine; subrectangular telson with two weakly curved lateral depressions forming a small rounded central part with two small median spines, lateral margins with strong distal spine, inferior margin near-straight and denticulate.

DESCRIPTION

Cephalothorax subrectangular (holotype: CL = c. 75 mm, CH = c. 18 mm), subdivided by a very deep cervical groove into two regions: cephalic region (length c. 33 mm) smaller than branchial region (length c. 38 mm).

Cephalic region with two very strong supraorbital teeth directed upwards with two posterior basal spines, wide frontal region without rostrum, two dorsal spiny carinae (c. 4–5 spines) converging forwards into one strong spine, two semicircular dorso-lateral carinae well developed and strongly serrate (c. 5–8 spines), straight lateral carina well developed, strongly serrate (c. 4–8 spines) ending by very strong antennal spine delimiting the straight, smooth ocular incision.

Branchial region with three well-developed, strongly serrated carinae: median carina (c. 7–9 spines, sometimes second proximal spines doubled) and lateral carinae (c. 14–15 spines); posterior margin of cervical groove marked by small spines; posterior margin with submarginal groove of equal width

FIG. 20. — *Linuparus bererensis* Secrétan (1964) from the Campanian of Belo-sur-Tsiribihina, Menabe region, central Morondava Basin: **A**, cephalothorax (MNHN.F.A33117, Coupe de Ampolypoly-Antsirasira-Behamotra, gisement 326), left dorso-lateral view; note two semicircular, serrated carinae; **B**, **C**, cephalothorax (MNHN.FR03918, Coupe de Ampolypoly-Antsirasira-Behamotra, gisement 326), in left lateral and ventral views, respectively, note lateral margin with possible stridulatory apparatus located just posterior to cervical groove (**B**), note also proepistome with two median, aligned tubercles and a slight median depression (**C**); **D**, cephalothorax



(MNHN.FR03911, Coupe de Ampolypoly-Antsirrasira-Behamotra, gisement 326), ventral view; note triangular mandibles; **E-H**, complete abdomen (MNHN.FA33146, Coupe de Berere III, gisement 206), in dorsal (**E**), right (**F**) and detailed (**G-H**) views; note terga of somites 2-5 with two transverse grooves (**E**), pleurae of somites 2-5 with trifid ventral margin (**G**), subrectangular somite 6 with two lateral depressions forming a rounded central portion with two spiny crests (**H**); **I-K**, tail fan (MNHN.FR03915, Coupe de Ampolypoly-Antsirrasira-Behamotra, gisement 327), in left lateral, dorsal and right lateral views, respectively, note subrectangular telson and uropods with rounded inferior margin. Scale bars: A-F, H-K, 2 cm; G, 1 cm. Photographs by C. Lemzaouda (MNHN).

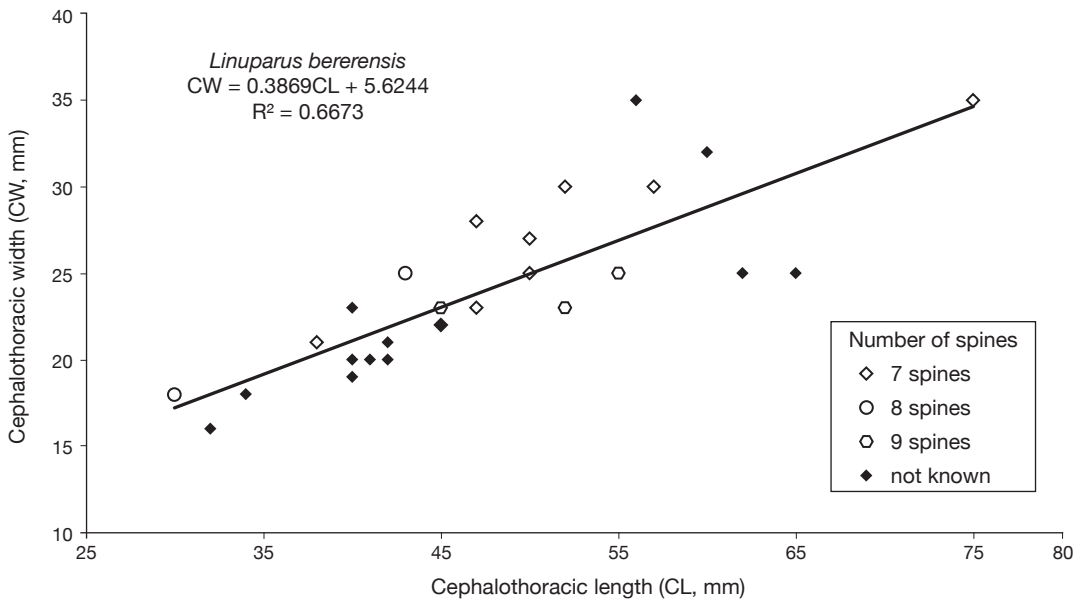


Fig. 21. — Biometric data for *Linuparus bererensis* Secrétan, 1964 from Madagascar: a linear relationship between cephalothoracic length (CL) and width (CW). The number of spines on the median dorsal carina is added, when known.

medially and laterally and with median dorsal spine; pleural region subdivided by one longitudinal groove extending from the posterior margin to the end of the cervical groove: inferior portion strongly tuberculate, superior portion near-smooth excepted for the proximal part which is mostly tuberculate; lateral margins with possible stridulatory apparatus (= appareil stridulant *sensu* Secrétan 1964), located just posterior to cervical groove; dorsal surface finely tuberculate.

Antennal articles very strong and spiny.

Proepistome with two median, aligned tubercles and one slight median depression.

Triangular mandibles well developed.

Abdomen slightly convergent distally, somite 1 highly reduced, somites 2-5 of equal size, somite 6 wider than others; terga of somites 2-5 with two transverse grooves: proximal groove slightly sinuous medially, distal groove triangular in shape anteriorly; one strong spine close to the median concavity of the proximal groove, one strong spine located at the top of the posterior margin; median spines of somites 1-4 directed forwards, median spines of somite 5 backwards; pleurae of somites 2-5 with

two aligned tubercles and trifold ventral margin: proximal spine slightly directed forwards, median spine larger than the others, distal spine slightly directed backwards; subrectangular somite 6 very strong, with two lateral depressions forming a rounded central part bearing two median spiny lines and two lateral, weakly carinate portions with a single small proximal spine and one very strong distal spine; subrectangular telson with two weakly curved lateral depressions forming a small rounded central portion with two small median spines, lateral margins with strong distal spine, inferior margin almost straight and denticulated; uropodal exopod and endopod equal in length with smooth lateral margins and rounded inferior margin, basipodite of uropods subrectangular.

Pereiopods 1-5 elongate, flattened, slightly tuberculate, with spiny ventral margin. Pereiopod 2 longer than the others.

DISCUSSION

We adopt the diagnosis of *Linuparus* given by Bruce (1965). After re-examination of the Malagasy material studied by Secrétan (1964), we subscribe

to her generic attribution. Secrétan (1964) erected the subspecies *Linuparus bererensis multispinosus*, based on the number (nine) of spines on the median carina and a more elongate cephalothorax. We question the validity of this subspecies for the following reasons: 1) in her description of *L. bererensis* (Secrétan 1964: 124), nine spines were recorded on the median carina, which fact leads to confusion in distinguishing these taxa; 2) the median carina in small and large specimens of *L. bererensis* shows a variable number of spines (ranging from 7 to 9); and 3) the ratio between cephalothoracic length (CL) and width (CW) measured on several specimens and the spine count on the median dorsal carina of *L. bererensis* and subspecies *multispinosus* do not show distinct values to confirm Secrétan's proposition. The CL/CW ratio of Malagasy specimens of *Linuparus* can be described as a linear model as has been observed for numerous fossil and extant crustaceans. Our plot diagram is relatively homogeneous and does not show any separate clusters that might be interpreted as distinct populations (Fig. 21). Moreover, we stress that the majority of the most complete specimens bear seven spines (68%) while only 18% and 14% have eight and nine spines respectively. In conclusion, with the number of spines of the median carina being so variable in the specimens studied and with cephalothorax proportions relatively homogeneous, these features are best considered to represent intraspecific variation and/or sexual dimorphism. Thus, they are not real diagnostic characters on which to erect a subspecies. In addition, all material stems from the same outcrops.

Infraorder AXIIDEA de Saint Laurent, 1979
Family CTENOCHELIDAE Manning & Felder, 1991

Genus *Ctenocheles* Kishinouye, 1926

TYPE SPECIES. — *Ctenocheles balssi* Kishinouye, 1926, by monotypy.

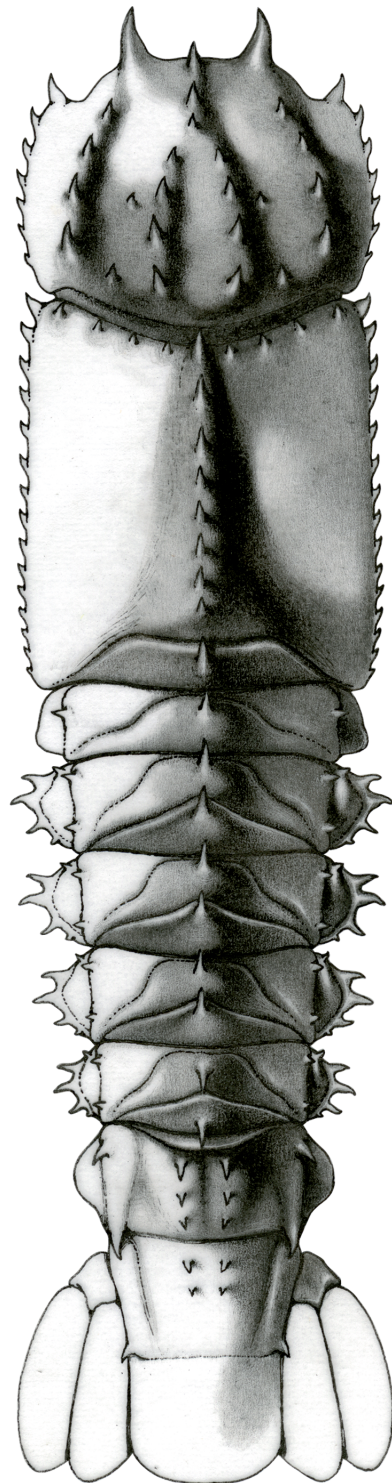


FIG. 22. — Reconstruction of *Linuparus bererensis* Secrétan, 1964 by F. Fogliazza, dorsal view.

Ctenocheles madagascariensis Secrétan, 1964
(Fig. 18B-D)

Ctenocheles madagascariensis Secrétan, 1964: 149-152, pl. 19, figs 1-4, 11-14; pl. 20, figs 9-16. — Collignon 1970b: 35. — Förster & Mundlos 1982: 154. — Feldmann *et al.* 1995: 8. — Feldmann *et al.* 2010: 340. — Schweitzer *et al.* 2010: 40.

TYPE MATERIAL. — Albian-Cenomanian of Antsaramahavelona: 8 syntypes (MNHN.F.A33425, R03931, R03932, R03933, gisement 117, grès à *Stoliczkaia*).

Middle Santonian of the “Coupe de Ampolypoly-Antsirrasira-Behamotra”: 5 syntypes (MNHN.F.A33427, A33429, gisement 280, *Texanites hourcqii* zone).

Lower Campanian of the “Coupe de Bevahô”: 11 syntypes (MNHN.F.A33437, R03881, gisement 251, *Anapachydiscus wittekindi* and *Eulopoceras jacobi* zone).

Lower Campanian of the “Coupe de Berere”: 5 syntypes (MNHN.F.A33421, gisement 163); 18 syntypes (MNHN.F.A33359, A33424, gisement 166); 4 syntypes (MNHN.F.A33423, A33424, gisement 167); 4 syntypes (MNHN.F.A33376, R03880, gisement 171, *Karapadites karapadensis* zone).

Lower Campanian of the “Coupe de Ampolypoly-Antsirrasira-Behamotra”: 82 syntypes (MNHN.F.A33398, A33399, A33400, A33401, gisement 302, *Menabites boulei* and *Anapachydiscus arrialoorensis* zone); 25 syntypes (MNHN.F.A33419, gisement 317).

Middle Campanian of the “Coupe de Ampolypoly-Antsirrasira-Behamotra”: 40 syntypes (MNHN.F.A33417, A33418, gisement 317).

Middle Campanian of the “Coupe de Andimaka”: 4 syntypes (MNHN.F.R03882, A33110, A33215, A33374, gisement 203, *Pachydiscus grossouvrei* zone).

Middle Campanian of the “Coupe de Ankilizato”: 43 syntypes (MNHN.F.A33407, A33408, A33409, gisements 153-155, *Pachydiscus grossouvrei* zone); 1 syntype (MNHN.F.A33433, gisement 181, *Pachydiscus grossouvrei* zone); 85 syntypes (MNHN.F.A33391, A33392, A33393, A33394, A33395, A33396, A33397, gisement 154, *Pachydiscus grossouvrei* zone); 32 syntypes (MNHN.F.A33330, A33406, A33381, gisement 155, *Pachydiscus grossouvrei* zone); 25 syntypes (MNHN.F.A33406, A33381, A33405, gisement 159, *Delawarella subdelawarensis* and *Australiella australis* zone); 25 syntypes (MNHN.F.A33358, gisement 177, *Pachydiscus grossouvrei* zone); 29 syntypes

(MNHN.F.A33410, A33411 gisement 179, *Pachydiscus grossouvrei* zone); 6 syntypes (MNHN.F.A 33344, R03883, gisement 181, *Pachydiscus grossouvrei* zone).

LOCALITIES. — Antsaramahavelona (northern Ananava, Peninsula of Radama, northern Mahajanga Basin, Mahajanga Province); Coupes de Bevahô, Ampolypoly-Antsirrasira-Behamotra, Berere Andimaka, Ankilizato (Belo-sur-Tsiriribihina, Menabe region, central Morondava Basin, Tulear Province).

AGES. — Albian-Cenomanian to Middle Campanian.

ADDITIONAL MATERIAL EXAMINED. — **Menabe region, central Morondava Basin.** From the middle Campanian of the “Coupe de Ankilizato”: 11 specimens [MNHN.F.A33353, A33354, A33388, A33436, gisements 176, 180 (*Pachydiscus grossouvrei* zone), 189].

“Coupe de Berere”: 156 specimens (MNHN.F.A33345, A33346, A33350, A33356, A33367, A33402, A33403, A33404, A33420, A33430, A33435, gisements 161, 162 [basal Lower Campanian, *Anapachydiscus wittekindi* and *Eulopoceras jacobi* zone], 184 [Lower Campanian, *Menabites boulei* and *Anapachydiscus arrialoorensis* zone], 200, 208 [Middle-Upper Santonian, *Texanites hourcqii* zone]).

From the Upper Turonian of the “Coupe de Berere”: 9 specimens (MNHN.F.A33428, gisement 246, [Masiaposa], *Coilopoceras requieni* and *Romaniceras deveriai* zone). From the Middle Campanian of the “Coupe de Andimaka”: 4 specimens (MNHN.F.A33175, A33351, A33380, gisements 201, 202, *Delawarella subdelawarella* and *Australiella australis* zone).

Lower Campanian of the “Coupe de Ampolypoly-Antsirrasira-Behamotra”: 21 specimens (MNHN.F.A33217, A33422, A33426, A33431, A33438, gisements 283, 285, 287 [*Anapachydiscus wittekindi* and *Eulopoceras jacobi* zone], 319, 322 [*Anapachydiscus wittekindi* and *Eulopoceras jacobi* zone]).

Middle Campanian of the “Coupe de Ampolypoly-Antsirrasira-Behamotra”: 5 specimens (MNHN.F.A33434, gisement 330).

Lower Campanian of the “Coupe de Bevahô”: 1 specimen (MNHN.F.A33377, gisement 261, *Karapadites karapadensis* zone).

From the Middle Coniacian of Analabe (Belo-sur-Tsiriribihina): 17 specimens (MNHN.F.A33432, gisement 344, *Kosmaticeras theobaldi* and *Barroisiceras onilayense* zone).

FIG. 23. — *Schlueteria menabensis* Secrétan, 1964 from the Santonian of Belo-sur-Tsiriribihina, Menabe region, central Morondava Basin: **A-C**, lectotype, designated herein (MNHN.F.R03920, Coupe de Berere, gisement 208), incomplete specimen in right lateral, left lateral and dorsal views, respectively, note very elongate rostrum and, in the gastric region, two dorsally curved, tuberculate carinae; **D-F**, incomplete specimen (MNHN.F.R03888, holotype of *Schlueteria tuberculosa*, Coupe de Bevahô, gisement 249), right lateral view (D) of articulated cephalothorax and abdomen, detail of cephalothorax (E) showing deep cervical groove delimiting very wide branchial region and very narrow gastric region, detail of abdomen (F) showing ornament: terga of somites 1 and 6 without dorsal carina, terga of somites 2-5 with dorsal carina, very wide subtriangular pleurae, with two carinae delimiting central depression. Scale bars: 2 cm. Photographs by C. Lemzaouda (MNHN).



Sikily region, Tulear Province, southern Morondava Basin. Lower Maastrichtian of Soatana (Manera): 1 specimen (MNHN.FA33225).

Northern Manambolo River, southern Maintirano region, northern Morondava Basin. Lower Campanian of Trangahy: 92 specimens (MNHN.FA33218, A33338, Antsalova, gisement 240, *Hoplitoplacentceras marroti* zone).

Uncertain localities and stratigraphic levels. 20 specimens (MNHN.FA33221).

STRATIGRAPHIC RANGE. — Albian, Cenomanian, Late Turonian, Middle Coniacian, Middle Santonian, Early to Middle Campanian and Early Maastrichtian.

DISCUSSION

Upon re-examination of the Malagasy material studied by Secrétan (1964), we agree with her generic attribution. As noted by Secrétan (1964), the preservational state of the specimens studied allows confirmation of the presence of two different propodus types: one globose with a very elongate index and the other flat with an unknown index. Dactyli invariably are always fragmentary. However, because two kinds of propodus are typical of *Ctenocheles*, the lack of diagnostic characters, such as the number of teeth along the occlusal margins of specimens studied precludes a detailed diagnosis of the Malagasy species and a comparison with other Cretaceous forms. Although *C. madagascariensis* is still considered to be the oldest fossil species known to date (Schweitzer & Feldmann 2002), only the discovery of more complete specimens can refine its morphological features.

Family AXIIDAE Huxley, 1879

Genus *Schlueteria* Fritsch in Fritsch & Kafka, 1887

TYPE SPECIES. — *Schlueteria tetracheles* Fritsch in Fritsch & Kafka, 1887, by monotypy.

Schlueteria menabensis Secrétan, 1964 (Figs 23–25)

Schuleria [sic] *menabensis* Secrétan, 1964: 138–143, pl. 13, fig. 1; pl. 14, figs 1–6; pl. 15, figs 1–6; pl. 16, figs 1–4; pl. 17, figs 3, 4.

Schlüteria tuberculosa Secrétan, 1964: 143–146, pl. 12, figs 6, 7; pl. 13, figs 2–5; pl. 15, fig. 7; pl. 16, figs 5, 6; pl. 17, figs 1, 2. n. syn.

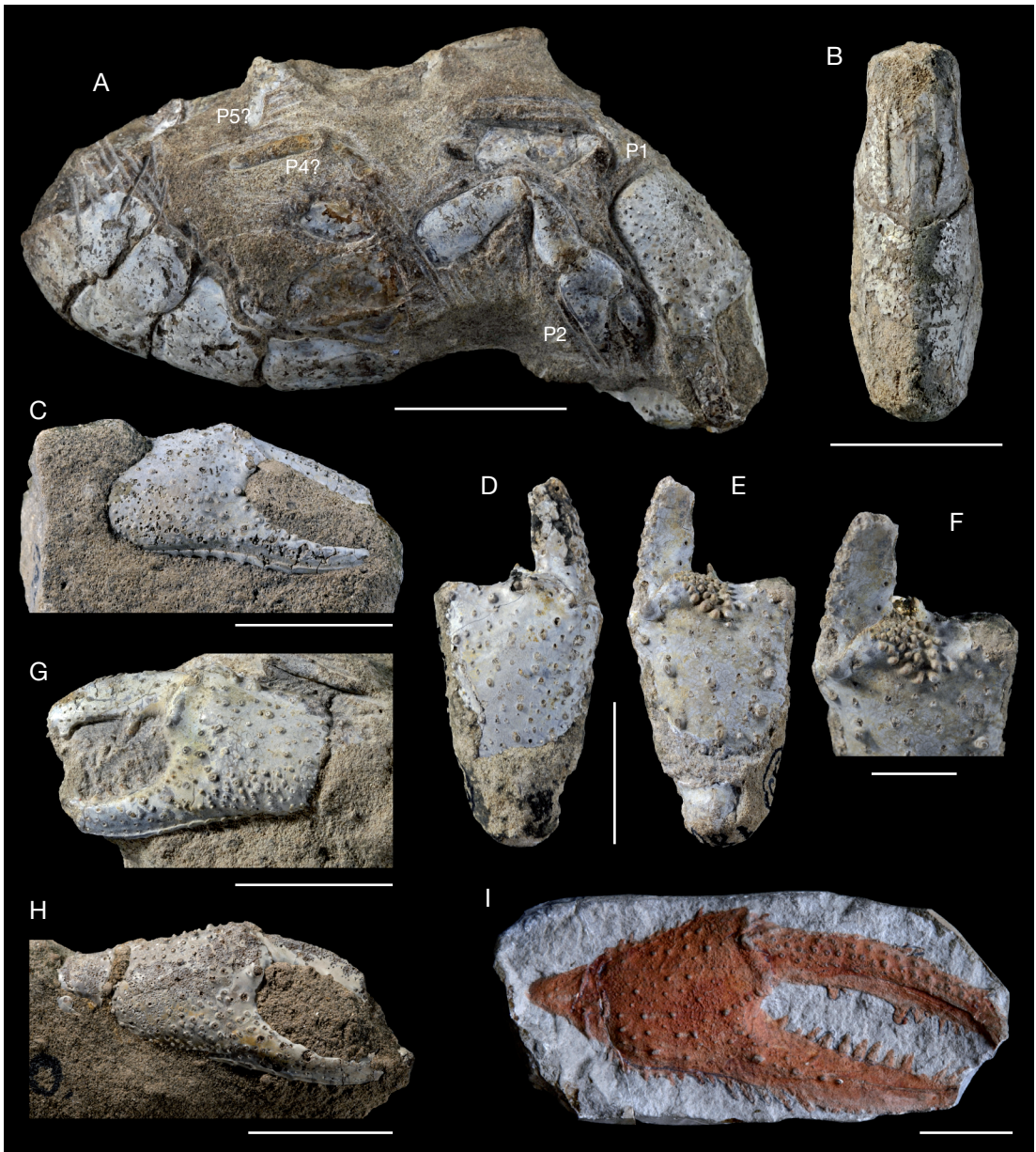
Schlueteria menabensis – Collignon 1970b: 35. — Taylor 1979: 24. — Schweitzer *et al.* 2010: 43.

Schlueteria tuberculosa – Schweitzer *et al.* 2010: 43.

LECTOTYPE. — MNHN.F.R03920.

PARALECTOTYPES. — From the middle Santonian of the “Coupe de Berere”: 2 specimens (MNHN.FA33084, R03920, gisement 208, *Texanites bourcqi* zone); 3 specimens (MNHN.FA33093, R03908, R03922, gisement 209); 1 specimen (MNHN.FA33045, gisement 210). From the lower Campanian of the “Coupe de Berere (I and II)”: 9 specimens (MNHN.FA33063, A33068, gisement 161, *Anapachydiscus wittekindi* and *Eulophoceras jacobi* zone); 2 specimens (MNHN.FA33072, gisement 162, *Anapachydiscus wittekindi* and *Eulophoceras jacobi* zone); 1 specimen (MNHN.FA33088, gisement 163); 3 specimens (MNHN.FA33370, gisement 166); 7 specimens (MNHN.FA33219, gisement 167); 3 specimens (MNHN.FA33085, gisement 169, *Karapadites karapadensis* zone); 10 specimens (MNHN.FA33382, gisement 171, *Karapadites karapadensis* zone); 1 specimen (MNHN.FA33069, gisement 172, *Karapadites karapadensis* zone); 13 specimens (MNHN.FA33220, A33347, A33369, gisement 184, *Menabites boulei* and *Anapachydiscus arrialoorensis* zone); 1 specimen (MNHN.FA33099, gisement 185, *Menabites boulei* and *Anapachydiscus arrialoorensis* zone); 5 specimens (MNHN.FA33089, A33102, A33223, A33364, R03891, gisement 191, *Karapadites karapadensis* zone); 2 specimens (MNHN.F.R03893, R03899, gisement 192, *Anapachydiscus wittekindi* and *Eulophoceras jacobi* zone); 1 specimen (MNHN.F.R03892, gisement 196, Upper Santonian); 1 specimen (MNHN.F.A33156, gisement 198, *Anapachydiscus wittekindi* and *Eulophoceras jacobi* zone); 1 specimen (MNHN.F.A33160, gisement 199); 1 specimen (MNHN.F.A33064, gisement 257).

FIG. 24. — *Schlueteria menabensis* Secrétan, 1964 from Belo-sur-Tsiribihina, Menabe region, central Morondava Basin (A–H) and *Schlueteria tetracheles* Fritsch in Fritsch & Kafka, 1887 (I): **A**, incomplete specimen (MNHN.F.R03894, paralectotype, Coupe de Andimaka, gisement 201), showing very massive P1 chela, P2 chela with short, inflated palm and smooth occlusal margins and achelate P4, P5 very elongate and thin, note ornament of abdomen: terga of somites 1–6 without dorsal carina, pleurae with one lateral carina inducing small ventral depression; **B**, isolated cephalothorax (MNHN.F.R03898, paralectotype, Coupe de Ankilizato, gisement 153), dorsal view, note deep cervical groove and cephalic carinae; **C**, P1 chela (MNHN.F.R03908, paralectotype, Coupe de Berere, gisement 209), outer surface of propodus with small and large tubercles in uniform distribution and ventral margin of index with a carina of strong, aligned spines directed forwards and decreasing in size anteriorly; **D–F**, incomplete propodus (MNHN.F.R03897, paralectotype,



Coupe de Ankilizato, gisement 180), outer surface (D) with uniformly distributed small and large tubercles, inner surface (E) with aligned, large tubercles alternating with small ones, detail of small area (F) covered by strong, rounded tubercles at level of propodus-dactylus articulation; G, P1 chela (MNHN.F.R03922, paralectotype, Coupe de Berere, gisement 209) showing occlusal margin of dactylus with one strong, very elongate proximal tooth and a strong median tooth; H, P1 chela (MNHN.F.A33045, paralectotype, Coupe de Berere, gisement 210) showing very strong spine located at base of articulation of dactylus (note very wide opening) and curved with occlusal margins of dactylus and index not in contact; I, P1 chela (O6905, National Museum, Prague) strongly tuberculata, showing occlusal margin of dactylus with two strong conical teeth located proximally and medially and with some strong pointed teeth distally, occlusal margin of index with a row of strong pointed, uniformly arranged teeth. Abbreviations: P1-P5, pereiopods 1 to 5. Scale bars: A-E, G-I, 2 cm; F, 1 cm. Photographs by C. Lemzaouda (MNHN).

From the lower Campanian of the “Coupe de Ampolypoly-Antsirasira-Behamotra”: 3 specimens (MNHN.FA33065, A33086, gisement 324); 2 specimens (MNHN.FA33138, R03895, gisement 327, *Pachydiscus grossouvrei* zone); 1 specimen (MNHN.FR03909, gisement 278, *Texanites hourcqi* zone); 2 specimens (MNHN.FA33383, gisement 284, *Anapachydiscus wittekindi* and *Eulophoceras jacobi* zone).

From the middle Campanian of the “Coupe de Ampolypoly-Antsirasira-Behamotra”: 2 specimens (MNHN.FA33071, R03900, gisement 317).

Paralectotypes from the lower Campanian of the “Coupe de Bevahô”: 1 specimen (MNHN.FA33096, gisement 253); 6 specimens (MNHN.FA33055, A33067, A33087, gisement 260, *Karapadites karapadensis* zone); 2 specimens (MNHN.FA33092, gisement 261, *Karapadites karapadensis* zone).

From the middle Campanian of the “Coupe de Andimaka”: 3 specimens (MNHN.FA33052, R03894, gisement 201, *Delawarella subdelawarensis* and *Australiella australis* zone); 3 specimens (MNHN.FA33372, gisement 189); 30 specimens (MNHN.FA33066, A33373, A33375, A33384, R03901, gisement 202, *Pachydiscus grossouvrei* zone); 53 specimens (MNHN.FA33047, A33049, A33051, A33060, A33090, A33101, A33387, R03896, gisement 203, *Pachydiscus grossouvrei* zone).

From the middle Campanian of the “Coupe de Ankilizato”: 1 specimen (MNHN.FR03898, gisement 153, *Pachydiscus grossouvrei* zone); 1 specimen (MNHN.FA33097, gisement 155, *Pachydiscus grossouvrei* zone); 5 specimens (MNHN.FA33043, gisement 176, *Pachydiscus grossouvrei* zone); 1 specimen (MNHN.FR03897, gisement 180, *Pachydiscus grossouvrei* zone); 1 specimen (MNHN.FA33121, gisement 182, *Pachydiscus grossouvrei* zone); 10 specimens (MNHN.FA33042, A33151, A33386, gisement 190); 2 specimens (MNHN.FA33366, gisement 199).

All type specimens are from Belo-sur-Tsiribihina, Menabe, central Morondava Basin, Tulear Province.

TYPE LOCALITY. — “Coupe de Berere” (gisement 208), Belo-sur-Tsiribihina, Menabe region, central Morondava Basin, Tulear Province (here designated).

TYPE AGE. — Middle Santonian (*Texanites hourcqi* zone).

ADDITIONAL MATERIAL EXAMINED. — Type material of *Schlueteria tuberculosa*: holotype (MNHN.FR03888, Coupe de Bevahô, gisement 249, *Pseudoschloenbachia* (*Pseudoschloenbachia*) *umbulazi* zone, Upper Santonian); 1 paratype (MNHN.FR03921, Coupe de Beantaly-Souromaraina, gisement 342, *Texanites hourcqi* zone, middle Santonian); 8 paratypes (MNHN.FA33091, A33378, R03886, R03889, R03890, Coupe Est de Bevahô, gisements 249 [*Pseudoschloenbachia* (*Pseudoschloenbachia*) *umbulazi* zone, Upper Santonian], 251 [*Anapachydiscus wittekindi* and *Eulopoceras jacobi* zone, Lower Campanian];

2 paratypes (MNHN.FA33365, R03887, Coupe de Ampolypoly-Antsirasira-Behamotra, gisements 281 [Upper Santonian], 287 [*Anapachydiscus wittekindi* and *Eulopoceras jacobi* zone, Lower Campanian]).

Unfigured material of *Schlueteria menabensis*: 8 specimens (MNHN.FA33061, A33100, A33171, A33343, A33385, Coupe de Berere, gisements 165, 166, 171, 188, 184, 205, *Menabites boulei* and *Anapachydiscus arrialoorensis* zone, Lower Campanian); 4 specimens (MNHN.FA33059, A33070, A33371, Coupe de Beantaly-Souromaraina, gisement 342, *Texanites hourcqi* zone, Middle Santonian); 4 specimens (MNHN.FA33108, A33389, A33467, Coupe Est de Bevahô, gisements 249 [*Pseudoschloenbachia* (*Pseudoschloenbachia*) *umbulazi* zone, Upper Santonian], 318, Lower Campanian); 1 specimen (MNHN.FA33103, Coupe de Andimaka, gisement 201, *Delawarella subdelawarensis* and *Australiella australis* zone, Middle Campanian); 2 specimens (MNHN.FA33095, Coupe de Ankilizato); 2 specimens (MNHN.FA33107, Coupe de Ampolypoly-Antsirasira-Behamotra, gisement 304, *Menabites boulei* and *Anapachydiscus arrialoorensis* zone, Lower Campanian); 3 specimens (MNHN.FA33057, A33180, Coupe de Ampamba-Antsirasira, gisements 701, 708, 710, *Karapadites karapadensis* zone, Middle Campanian).

From unnamed outcrops: 5 specimens (MNHN.FA33048, A33056, A33057, A33080, A33201, gisements 173 [Lower Campanian], 391).

From uncertain outcrops: 7 specimens (MNHN.FA33044, A33078, A33104, A33105, A33106, A33109).

All specimens are from Belo-sur-Tsiribihina, Menabe region, central Morondava Basin, Tulear Province.

STRATIGRAPHIC RANGE. — Middle Santonian to Middle Campanian.

DIAGNOSIS. — Cephalothorax with deep cervical groove delimiting a very wide branchial region and very narrow gastric region; markedly elongate rostrum, carinate dorsally; gastric region with two dorsally tuberculate carinae; P1 chela with short, stout palm and elongate dactylus and index incurved distally; small area covered by strong rounded tubercles at level of the propodus-dactylus articulation; occlusal margin of dactylus with one strong, very elongate proximal tooth, one strong median tooth, and a few pointed distal teeth in random arrangement; occlusal margin of index with a row of strong, pointed teeth in a uniform arrangement; P2 chela with short, inflated palm with smooth occlusal margin; uropodal exopod without diarsis.

DESCRIPTION

Cephalothorax subrectangular (CL = 36–56 mm, CH = 23–40 mm); very elongate rostrum with smooth median carina; weak ocular incision delimited only by rounded antennal margin; gastric region with two

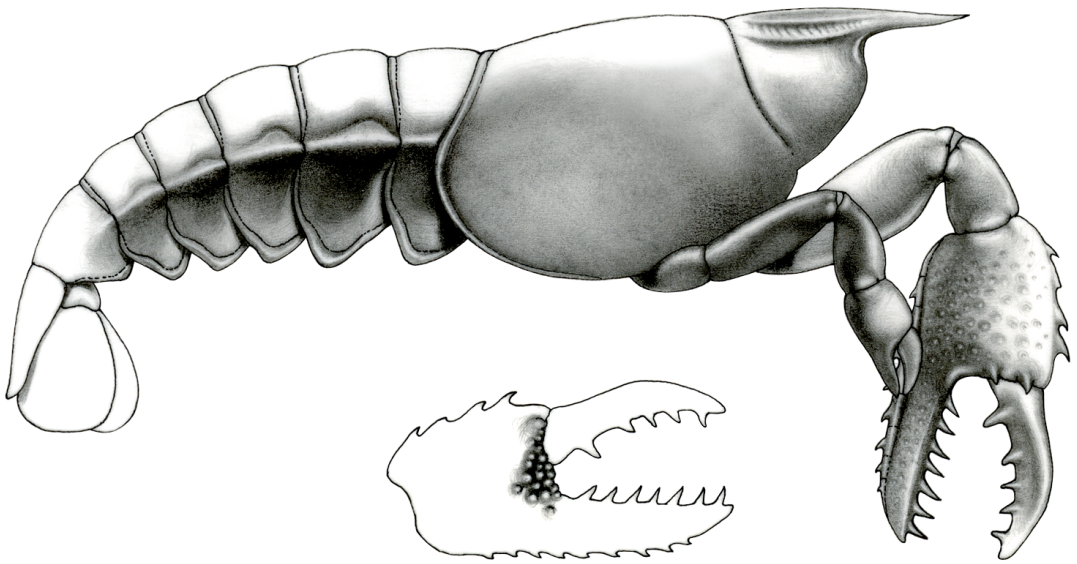


FIG. 25. — Reconstruction of *Schlueteria menabensis* Secrétan, 1964, by F. Fogliazza, right lateral view and detail of the inner surface of P1 chela.

dorsally tuberculate or smooth carinae curved, and converging to the base of the rostrum, the inferior one joining the lateral margin of the rostrum; area between the two curved carinae covered by aligned transverse small tuberculate lines; smooth antennal region; deep cervical groove arising in the first anterior quarter of the dorsal margin, strongly inclined, intercepting dorsal margin at an angle of *c.* 50°; cervical groove reaching the anterior ventral margin creating a strong inflection; cervical groove delimiting a very broad branchial region and very narrow gastric region; ornament of small pits uniformly distributed.

Abdomen with subrectangular somites; somite 1 smaller than others; somite 6 larger than preceding ones; somites 2-5 of equal length; pleurae with smooth inferior margins; two different types of ornament on the abdomen: 1) terga of somites 1-6 without dorsal carina, pleurae with one lateral carina inducing a small ventral depression; and 2) terga of somites 1 and 6 without dorsal carina, terga of somites 2-5 with dorsal carina, subtriangular, very wide subtriangular pleurae with two carinae delimiting central depression; subrectangular telson with slightly sinuous lateral margins bearing two small spines, dorsal margin with two aligned tubercles.

Uropods with subrectangular endopod and exopod, articulated to bilobed basipodite; inner margin reinforced by marginal carina.

P1 bearing very massive homochelous chelae; propodus with strongly tuberculate dorsal margin and ventral margin bearing a carina of strong aligned spines directed forwards and decreasing in size anteriorly; very strong spine located at the base of articulation of the dactylus; small area covered in strong, rounded tubercles at level of propodus-dactylus articulation; occlusal margin of dactylus with one strong, very elongate proximal tooth, one strong median tooth, and a few pointed distal teeth in random arrangement; occlusal margin of index with a row of strong, pointed teeth in uniform arrangement; opening very broad and curved with occlusal margins of dactylus and index not in contact; dorsal margin of dactylus bearing a median tuberculate carina; outer surface of propodus with uniformly distributed small and large tubercles; inner surface of propodus with aligned, large tubercles alternating with small ones; P2 chela well developed, with short, inflated palm; short dactylus and index with smooth occlusal margins; very elongate, thin P4-5 achelate.

DISCUSSION

Following re-examination of the Malagasy material studied by Secrétan (1964), we agree with her generic attribution. Secrétan (1964) distinguished *Schlueteria tuberculosa* from *S. menabensis* principally by (1) spiny carinae in the gastric region and (2) a dorsal carina on the terga of somites 2-5 in the former. We doubt the validity of *S. tuberculosa* for the following reasons: 1) all specimens of the two “species” originate from the same outcrops; 2) the configuration of the cephalic grooves is quite similar in both; and 3) P1 chelae are morphologically similar in both, irrespective of propodus size, as confirmed also by the type material of *S. tuberculosa* which has identical chelipeds to those of *S. menabensis*.

For these three reasons and in view of the incomplete state of preservation of material of *S. tuberculosa*, we synonymise both. Moreover, differences in ornament of carinae on the gastric region and on abdominal somites could be seen as reflecting intraspecific variation and/or sexual dimorphism. However, the material is not enough complete to determine which of these interpretations is correct. Because *S. carinata* Taylor, 1979, was described on the basis of a poorly preserved specimen, retaining only the P2 (Taylor 1979: 23, pl. IVa), *Schlueteria menabensis* represents, together with the type species *S. tetracheles*, the most complete member of the genus known to date. The original type of the latter, housed in the collections of the National Museum, Prague (Czech Republic), has allowed us to compare this with the Malagasy species, so as to outline features in common as well as different characteristics. The two share the following characters: two longitudinal, parallel ridges on the cephalic region of the carapace; deep cervical groove strongly inclined forwards, creating a cephalic region which is smaller than branchial region; P2 chela short, stout, with inflated palm; pleurae of abdominal somites ending in a point; smooth subrectangular telson; smooth uropods; uropodal exopod without diarsis. Although the original sample of *S. tetracheles* comprises a few more or less complete specimens we have been unable to observe the rostrum that could have been thin and elongate as in the Malagasy species. The main difference between the two species is the structure of P1 chela: in *S. tetracheles* (Fig. 24I),

it is strong with a short, stout palm and elongate dactylus and index; the dorsal margin of the chela has a few variably sized spines in a random arrangement, while the ventral margin has a row of strong spines in a uniform arrangement, disappearing prior to the distal extremity; the occlusal margin of the dactylus has two strong conical teeth located proximally and medially and some strong pointed teeth located distally; the occlusal margin of the index has a row of uniformly arranged strong, pointed teeth; the surface of the chela is strongly tuberculate, while that of the dactylus has two rows of aligned tubercles; 4-5 tubercles aligned at the level of propodus-dactylus articulation; in *S. menabensis* the chela is strong with short, stout palm and elongate dactylus and index; the dorsal margin of the chela is smooth, while the ventral margin has a carina of strong, aligned spines directed forwards and decreasing in size anteriorly; the occlusal margin of the dactylus has a single strong, very elongate proximal tooth, one strong median tooth, and a few pointed distal teeth randomly arranged; the occlusal margin of the index has a row of strong, pointed teeth in uniform arrangement; the surface of the chela is strongly tuberculate with a row of tubercles aligned along the occlusal margin of the index; a small area is covered by strong, rounded tubercles at the level of the propodus-dactylus articulation. The main features observed in both species confirm the reconstruction of *S. tetracheles* by Fristch *in* Fristch & Kafka (1887).

In view of the above, we consider it important to select a lectotype for *Schlueteria menabensis* because Secrétan (1964) did not designate a holotype for it. This is MNHN.F.R03920, from Berere (gisement 208, Middle Santonian) which shows almost all the diagnostic characters of both species and genus.

Infraorder BRACHYURA Latreille, 1802
Section DROMIACEA De Haan, 1833
Superfamily DROMIOIDEA De Haan, 1833
Family DYNOMENIDAE Ortmann, 1892

Genus *Dromiopsis* Reuss, 1859

TYPE SPECIES. — *Brachyurites rugosus* von Schlotheim, 1820, by subsequent designation of Beurlen (1928).

Dromiopsis pulchella Secrétan, 1964
(Fig. 18E, F)

Dromiopsis pulchella Secrétan, 1964: 169-172, pl. 19, fig. 7. — Schweitzer *et al.* 2010: 65.

HOLOTYPE. — MNHN.FR03929.

TYPE LOCALITY. — Antsatramahavelona (gisement 117), northern Analalava region, Peninsula of Radama, northern Mahajanga Basin, Mahajanga Province.

TYPE AGE. — Albian-Cenomanian.

DISCUSSION

Although this species is represented exclusively by the holotype, it does show the main characters of the genus. We point out that Van Bakel *et al.* (work in progress) consider *Dromiopsis pulchella* to be a necrocarcinid rather than a dynomenid. We have nothing to add to the diagnosis and description of Secrétan (1964: 169, text-figs 98-100, pl. 19, fig. 7).

Family ETYIDAE Guinot & Tavares, 2001

Genus *Caloxanthus* A. Milne-Edwards, 1863

TYPE SPECIES. — *Caloxanthus formosus* A. Milne-Edwards, 1863, by monotypy.

Caloxanthus simplex (Secrétan, 1964)
(Fig. 18G)

Carpiliopsis simplex Secrétan, 1964: 183-186, pl. 19, figs 8-10.

Caloxanthus simplex – Schweitzer *et al.* 2010: 67.

HOLOTYPE. — MNHN.FR03879.

TYPE LOCALITY. — Coupe de Ankilizato (gisement 154), Belo-sur-Tsiribihina, Menabe region, central Morondava Basin, Tulear Province.

TYPE AGE. — Middle Campanian (*Pachydiscus grossouvrei* zone).

DISCUSSION

Although the holotype is the sole specimen known to date, this does show the main characters of the

genus, and we have nothing to add to the diagnosis and description supplied by Secrétan (1964: 183, text-figs 108-109, pl. 19, figs 8-10).

Superfamily XANTHOIDEA *incertae sedis*

Genus *Titanocarcinus* A. Milne-Edwards, 1863

TYPE SPECIES. — *Titanocarcinus serratifrons* A. Milne-Edwards, 1863, by subsequent designation of Glaesner (1929).

Titanocarcinus mamillatus Secrétan, 1964
(Fig. 18H, I)

Titanocarcinus mamillatus Secrétan, 1964: 187-193, pl. 20, figs 1-3. — Schweitzer *et al.* 2007: 284.

HOLOTYPE. — MNHN.FR03871.

TYPE LOCALITY. — Soatana, northern Mikoboka Creek (gisement 501), Manera, Sikily region, southern Morondava Basin, Tulear Province.

TYPE AGE. — Early Maastrichtian (*Pachydiscus gollevilensis* and *P. neubergicus* zone).

DISCUSSION

Secrétan (1964: 187-191, text-figs 112, 114) described and illustrated a single incomplete specimen of this species. Judging from the original description and the line drawing (reconstruction), in comparison with the specimen itself, we noted inconsistencies such as the orbital area and the interpretation of the outline of the dorsal bosses. Recently Schweitzer *et al.* (2007) have discussed and reviewed *Titanocarcinus*, listing all species referred to this genus and their current status. Those authors pointed out that *T. mamillatus* showed a development of carapace regions which was similar not only to that of *Titanocarcinus*, but also to members of other Cretaceous xanthoid families, such as the Palaeoxanthopsidae. Concomitantly, they noted that the anterolateral margin in the Malagasy species was incomplete and that the fronto-orbital width was considerably less than the maximum width in other species of *Titanocarcinus*, which led those authors

to refer to *T. mamillatus* as *incertae sedis* within the Xanthoidea (see also Schweitzer *et al.* 2010).

Genus “*Xanthosia*” [*sensu lato*]

“*Xanthosia*” *robertsi* Secrétan, 1982
(Fig. 18J, K)

Xanthosia elegans Secrétan, 1964: 178-182, pl. 20, figs 4-6 [non Roberts, 1962]. — Bishop 1991: 311.

Xanthosia robertsi Secrétan, 1982: 927-933, 2 figs. — Schweitzer Hopkins *et al.* 1999: 80. — Guinot & Tavares 2001: 510, 512, 517. — Karasawa *et al.* 2008: 107. — Schweitzer *et al.* 2010: 131.

HOLOTYPE. — MNHN.FR03979.

TYPE LOCALITY. — Coupe de Berere I (gisement 161), Belo-sur-Tsirihibina, Menabe region, central Morondava Basin, Tulear Province.

TYPE AGE. — Early Campanian (*Anapachydiscus wittekindi* and *Eulophoceras jacobi* zone).

DISCUSSION

Secrétan (1964: 178) described a single fragmentary carapace, as a new species of *Xanthosia* Bell, 1863, *X. elegans*. As this name appeared to be preoccupied, the replacement name *X. robertsi* was later proposed by Secrétan (1982). However, as noted by Schweitzer Hopkins *et al.* (1999) despite superficial similarities of “*Xanthosia*” *robertsi* to the genus, numerous other features do not correspond to the diagnosis of *Xanthosia*, such as the single, large, lateral spine, carapace shape, and regions that differ from those of other species of *Xanthosia*. Schweitzer Hopkins *et al.* (1999) considered *X. robertsi* to be a portunid, rather than a species of *Xanthosia*. Currently, its systematic position is still uncertain. For now, in compliance with Schweitzer *et al.* (2010), we refer it to “*Xanthosia*” [*sensu lato*] until better-preserved specimens are available.

Section PODOTREMATA Guinot, 1977
Superfamily RANINOIDEA De Haan, 1839
Family RANINIDAE De Haan, 1839

Subfamily PALAEOCORYSTINAE
Lőrenthey *in* Lőrenthey & Beurlen, 1929

Genus *Notopocorystes* McCoy, 1849

TYPE SPECIES. — *Corystes stokesii* Mantell, 1844, by subsequent designation of Withers (1928).

Notopocorystes australis Secrétan, 1964
(Fig. 18L)

Notopocorystes australis Secrétan, 1964: 158-162, pl. 18, figs 1-3. — Collins 1996: table 1. — Schweitzer *et al.* 2010: 77.

Cretacoranina australis – Förster 1970: 140. — Jagt *et al.* 2003: 54.

Notopocorystes (Cretacoranina) australis – Collins 1996: 81.

HOLOTYPE. — MNHN.FR03874.

PARATYPES. — From the “Coupe de Ampolypoly-Ant-sirasira-Behamotra”: 1 specimen (MNHN.FR03903, gisement 280, *Texanites bourcqi* zone, Middle Santonian); 1 specimen (MNHN.FR03878, gisement 302, Lower Campanian). Belo-sur-Tsirihibina, Menabe region, central Morondava Basin, Tulear Province.

TYPE LOCALITY. — Coupe de Berere II (gisement 184), Belo-sur-Tsirihibina, Menabe region, central Morondava Basin, Tulear Province.

TYPE AGE. — Early Campanian (*Menabites boulei* and *Anapachydiscus arrialoorensis* zone).

ADDITIONAL MATERIAL EXAMINED. — From the “Coupe de Ampolypoly-Ant-sirasira-Behamotra”: 3 specimens (MNHN.FA33166, A33368, A33182, gisement 317, middle Campanian); 1 specimen (MNHN.FA33181, gisement 302, *Menabites boulei* and *Anapachydiscus arrialoorensis* zone, Lower Campanian); 1 specimen (MNHN.FA33184, gisement 339).

From the “Coupe de Ankilizato” (Middle Campanian): 2 specimens (MNHN.FA33188, A33468, gisement 179, *Pachydiscus grossouvrei* zone), 1 specimen (MNHN.FA33466, gisement 177, *Pachydiscus grossouvrei* zone).

All specimens are from Belo-sur-Tsirihibina, Menabe region, central Morondava Basin, Tulear Province.

STRATIGRAPHIC RANGE. — Middle Santonian to Middle Campanian.

TABLE 1. — List of Mesozoic decapod crustaceans of Madagascar from Mahajanga and Morondava basins.

Malagasy species	Age	Geography
Genus <i>Enoploclytia</i> McCoy, 1849 <i>Enoploclytia collignoni</i> Secrétan, 1964 <i>?Enoploclytia armata</i> Secrétan, 1964	Santonian-Campanian Campanian	Central Morondava Basin Central Morondava Basin
Genus <i>Eryma</i> von Meyer, 1840 <i>Eryma granuliferum</i> Secrétan, 1964 <i>?Eryma australe</i> (Secrétan, 1964)	Kimmeridgian Tithonian	Northern Morondava Basin Southern Morondava Basin
Genus <i>Pustulina</i> Quenstedt, 1857 <i>Pustulina spinulata</i> (Secrétan, 1964)	Valanginian-Hauterivian	Southern Mahajanga Basin
Genus <i>Hoploparia</i> McCoy, 1849 <i>Hoploparia collignoni</i> (Van Straelen, 1949) <i>Hoploparia pusilla</i> Secrétan, 1964	Albian Campanian	Southern Mahajanga Basin Central Morondava Basin
Genus <i>?Coleia</i> Broderip, 1835 <i>?Coleia incerta</i> Secrétan, 1964	Tithonian	Northern Morondava Basin
Genus <i>Linuparus</i> White, 1847 <i>Linuparus bererensis</i> Secrétan, 1964	Santonian-Campanian	Central Morondava Basin
Genus <i>Ctenocheles</i> Kishinouye, 1926 <i>Ctenocheles madagascariensis</i> Secrétan, 1964	Albian-Maastrichtian	Mahajanga & Morondava basins
Genus <i>Schlueteria</i> Fritsch in Fritsch & Kafka, 1887 <i>Schlueteria menabensis</i> Secrétan, 1964	Santonian-Campanian	Central Morondava Basin
Genus <i>Dromiopsis</i> Reuss, 1858 <i>Dromiopsis pulchella</i> Secrétan, 1964	Albian-Cenomanian	Northern Mahajanga Basin
Genus <i>Caloxanthus</i> A. Milne-Edwards, 1863 <i>Caloxanthus simplex</i> (Secrétan, 1964)	Campanian	Central Morondava Basin
Genus <i>Xanthosia</i> Bell, 1863 <i>"Xanthosia" robertsi</i> Secrétan, 1982	Campanian	Central Morondava Basin
Genus <i>Notopocorystes</i> McCoy, 1849 <i>Notopocorystes australis</i> Secrétan, 1964 <i>Notopocorystes bituberculatus</i> Secrétan, 1964 <i>Notopocorystes denisae</i> Secrétan, 1964	Santonian-Campanian Albian Campanian	Central Morondava Basin Southern Mahajanga Basin Central Morondava Basin
Genus <i>Secretanella</i> Guinot & Tavares, 2001 <i>Secretanella arcuata</i> (Secrétan, 1964)	Albian-Cenomanian	Northern Mahajanga Basin
Genus <i>Titanocarcinus</i> A. Milne-Edwards, 1863 <i>Titanocarcinus mamillatus</i> Secrétan, 1964	Maastrichtian	Southern Morondava Basin

Notopocorystes bituberculatus Secrétan, 1964TYPE AGE. — Early Albian (*Douvilleiceras inaequidum* zone).

Notopocorystes bituberculatus Secrétan, 1964: 155-158, pl. 18, figs 8, 9. — Collins 1996: table 1. — Schweitzer *et al.* 2010: 77.

Notopocorystes (*Notopocorystes*) *bituberculatus* – Collins 1996: 79, 83.

HOLOTYPE. — MNHN.FR03951.

TYPE LOCALITY. — Malandiandro (gisement 46), Sitampiky region, eastern Mahavavy River, southern Mahajanga Basin, Mahajanga Province.

Notopocorystes denisae Secrétan, 1964
(Fig. 18M)

Notopocorystes denisae Secrétan, 1964: 162-168, pl. 18, figs 4-7. — Collins 1996: table 1. — Schweitzer *et al.* 2010: 77.

Cretacorantina denisae – Förster 1970: 140. — Jagt *et al.* 2003: 54.

Notopocorystes (Cretacorantina) denisae – Collins 1996: 81.

HOLOTYPE. — MNHN.FR03875.

PARATYPES. — From the “Coupe de Ampolypoly-Antsirrasira-Behamotra”: 3 specimens (MNHN.FR03876, R03877, A31658, gisement 326, Middle Campanian); 1 specimen (MNHN.FA31659, gisement 325, Middle Campanian); 2 specimens (MNHN.FA31036, gisement 302, *Menabites boulei* and *Anapachydiscus arrialoovens* zone, Lower Campanian). All type specimens are from Belo-sur-Tsiribihina, Menabe region, central Morondava Basin, Tulear Province.

TYPE LOCALITY. — Coupe de Ampolypoly-Antsirrasira-Behamotra (gisement 317), Belo-sur-Tsiribihina, Menabe region, central Morondava Basin, Tulear Province.

TYPE AGE. — Middle Campanian.

STRATIGRAPHIC RANGE. — Early to Middle Campanian.

DISCUSSION

These three species of *Notopocorystes* McCoy, 1849, are not discussed any further in the present study because they will be revised in a forthcoming paper by Van Bakel *et al.* (work in progress).

Section HETEROTREMATA Guinot, 1977

Incertae sedis

Genus *Secretanella* Guinot & Tavares, 2001

TYPE SPECIES. — *Xanthosia arcuata* Secrétan, 1964, by monotypy.

Secretanella arcuata (Secrétan, 1964)

(Fig. 18N, O)

Xanthosia arcuata Secrétan, 1964: 173-178, pl. 19, figs 5, 6; pl. 20, figs 7, 8. — Karasawa *et al.* 2008: 107.

Secretanella arcuata – Guinot & Tavares 2001: 510, 517, 541, 542. — Schweitzer *et al.* 2010: 145.

HOLOTYPE. — MNHN.FR03978.

PARATYPES. — From Antsatramahavelona: 11 specimens (MNHN.FA31661, R03980, R03981, gisement 117). Northern Analalava, northern Mahajanga Basin, Mahajanga Province.

TYPE LOCALITY. — Antsatramahavelona (gisement 117), northern Analalava, Peninsula of Radama, northern Mahajanga Basin, Mahajanga Province.

TYPE AGE. — Albian-Cenomanian.

DISCUSSION

See Guinot & Tavares (2001).

Incertae sedis

Indeterminate xanthids

Propodes de Xanthidé Secrétan, 1964: 193, pl. 18, figs 12, 13.

MATERIAL. — A single isolated propodus (MNHN.FR03872).

LOCALITY. — Soatana, northern Mikoboka Creek (gisement 501), Manera, Sikily region, southern Morondava Basin, Tulear Province.

AGE. — Early Maastrichtian (*Pachydiscus gollevillensis* and *P. neubergicus* zone).

DISCUSSION

Although Secrétan (1964) gave a full description of this specimen, its state of preservation precludes systematic assignment, other than “xanthid”.

CONCLUSIONS

We have revised 13 species described by Secrétan (1964) on the basis of a collection of more than 1500 specimens and presented an updated systematic list of Malagasy decapod crustaceans (Table 1). It is apparent that assemblages of Mesozoic crustaceans from Madagascar are remarkable for their diversity and relative abundance. Unfortunately, these faunas are known exclusively from samples in relatively old collections; collection of new material appears highly rewarding in this respect.

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