

Review of the crabs (Crustacea, Decapoda, Brachyura) from the Miocene of the Mahakamby Island (Mahajanga, NW Madagascar) collected during the Waterlot's Mission (1922)

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Charbonnier S., Garassino A. & Pasini G. 2012. — Review of the crabs (Crustacea, Decapoda, Brachyura) from the Miocene of the Mahakamby Island (Mahajanga, NW Madagascar) collected during the Waterlot's Mission (1922). *Geodiversitas* 34 (4): 873-881. <http://dx.doi.org/10.5252/g2012n4a9>

ABSTRACT

The small Mahakamby Island (= Island of the Shrimp) is located in the Mozambique Channel (Indian Ocean) along the northwestern coast of the Mahajanga Province, (Soalala District, NW Madagascar). Miocene outcrops of Mahakamby were examined during the expeditions of two naturalists from the Muséum national d'Histoire naturelle, Paris: the first by Perrier de la Bâthie in 1915 and the second by Waterlot in 1922. Among the fossil invertebrates collected during the Waterlot's Mission, some decapod crustaceans were partially reported by Collignon & Cottreau (1927) but their specimens are nowadays almost completely lost. However, additional matériel collected by Waterlot was rediscovered in the palaeontological collections of the Paris Museum. It allows a review and a discussion of the crustacean samples previously studied on the basis of iconographic material. Moreover, new specimens of brachyurans, collected during the Waterlot mission, are here assigned for the first time to Portuninae Rafinesque, 1815.

KEY WORDS

Crustacea,
Decapoda,
Brachyura,
Portuninae,
Miocene,
Mahakamby,
Madagascar.

RÉSUMÉ

Révision des crabes (Crustacea, Decapoda, Brachyura) du Miocène de l'Île Mahakamby (Mahajanga, NW Madagascar) récoltés lors de la Mission Waterlot (1922). La petite île Mahakamby (= Île de la Crevette) est située dans le Canal du Mozambique (Océan Indien) le long des côtes nord-ouest de la Province de Mahajanga (District de Soalala, NW Madagascar). Sur l'île se trouvent des affleurements du Miocène qui ont été explorés lors des expéditions de deux naturalistes du Muséum national d'Histoire naturelle, Paris: celle de Perrier de la Bathie en 1915 et celle de Waterlot en 1922. Parmi les invertébrés fossiles récoltés lors de la Mission Waterlot, quelques crustacés décapodes ont été partiellement publiés par Collignon & Cottreau (1927) mais leurs spécimens sont aujourd'hui quasiment tous perdus. Néanmoins, du matériel additionnel collecté par Waterlot a été redécouvert dans les collections paléontologiques du Muséum de Paris. Il permet une révision et une discussion des échantillons de crustacés étudiés autrefois sur la base des photographies publiées. De plus, des spécimens inédits de brachyours, collectés durant la Mission Waterlot, sont assignés ici pour la première fois aux Portuninae Rafinesque, 1815.

MOTS CLÉS

Crustacea,
Decapoda,
Brachyura,
Portuninae,
Miocène,
Mahakamby,
Madagascar.

INTRODUCTION

The small Mahakamby Island also called Nosy Mahakamba (= Island of the Shrimp) is located in the Mozambique Channel (Indian Ocean) (Fig. 1). It covers an area of about 1.2 km² along the north-western coast of the Mahajanga Province, (Soalala District, NW Madagascar). Here a marine succession of Miocene layers crops out under the continental Pliocene sands. These outcrops were object of two expeditions by the Muséum national d'Histoire naturelle, Paris (France): the Perrier de la Bathie's Mission in 1915 and the Waterlot's Mission in 1922. Perrier de La Bathie (1921) provided the first stratigraphic section of the Mahakamby Island (Fig. 2A) and recognized the Cenozoic deposits. Later, the Waterlot's Mission, following this stratigraphic section, identified in the small bed n°7 (Fig. 2A; see Perrier de La Bathie 1921 for details) the presence of crab remains as reported in the field notes (Fig. 2B-D). Among the fossil invertebrates collected by the Waterlot's Mission, Collignon & Cottreau (1927) reported a sample of decapod brachyurans illustrated in the "Plate IV" of their monograph. Unfortunately, these first specimens are today almost completely lost and thus the original

figures are here reproduced in order to give to the specialists an instrument of comparison and reference (Fig. 3). Additional material collected during the Waterlot's Mission was recently discovered in the palaeontological collections of the Paris Museum, thus some brachyurans from the Miocene of Mahakamby Island are here reported for the first time. The description of some specimens made by Collignon & Cottreau (1927), collected during the same mission, and nowadays lost, is reviewed and discussed on the basis of iconographic material of their "plate IV" that is reported in the present Figure 3. Moreover, the original numeration of the material figured by these authors is reported between commas, both in the text and in Figure 3. The new studied sample includes 31 specimens divided as follows: 11 carapaces and 20 incomplete chelipeds. Six specimens are ascribed to *Portunus s. str.* (Portuninae Rafinesque, 1815). Nine specimens show morphological features of the Portuninae; they are not assigned to any genus or species known to date due to their incomplete preservation but only tentatively compared with some genera within this subfamily. The studied specimens are housed in the Muséum national d'Histoire naturelle, Paris (France), Collection de Paléontologie (MNHN.F).

GEOLOGICAL SETTING

In the central part of the Mahakamby Island the Miocene succession is covered by reddish clays and sands of the continental Pliocene. The studied specimens were collected, partially washed, from the natural erosion along the eastern side of the coast. They came from beds overlying directly the marno-calcareous layers dominated by tubes of *Cyphus arenarius* (Linnaeus, 1758) and echinoids. The marine assemblage includes some shark teeth and rich invertebrate fauna including mollusks, worms, and echinoids (for a complete list, see Besairie 1972: 185, 186). Collignon & Cottreau (1927) reported that the Mahakamby malacofauna belongs to beds younger than Aquitanian levels (Early Miocene) and ranges between Burdigalian and Helvetian. However, Lavocat *et al.* (1955) proposed a Late Miocene age by the foraminifera assemblage. The stratigraphy of the Mahakamby Island is not solved at present and therefore we assign by the previous data the studied specimens to the Miocene in generic terms.

PREVIOUS BRACHYURAN RECORD FROM THE MAHAKAMBY ISLAND

Collignon & Cottreau (1927) described and figured eight incomplete specimens (lacking of catalog number) of brachyurans from the Miocene of the Mahakamby Island (Soalala District, Mahajanga Province, NW Madagascar), collected during the Waterlot's Mission. Most of this material was lost or stolen and only two figured chelae are currently housed in the Collection de Paléontologie of the Paris Museum (specimens [MNHN.F.A33476](#), [A33477](#)). In synthesis, Collignon & Cottreau (1927) pointed out the following characters: "The carapace of the crabs ('pl. IV: figs 15, 16, 19'; see Fig. 3) is larger than long, slightly vaulted dorsally with regions poorly marked and granulate surface. The largest specimen measures 80 mm wide and 45 mm long ('pl. IV: fig. 19'; see Fig. 3). The adult specimens have nine subequal anterolateral spines, but with the last one larger and longer, projected outward in the juvenile specimens

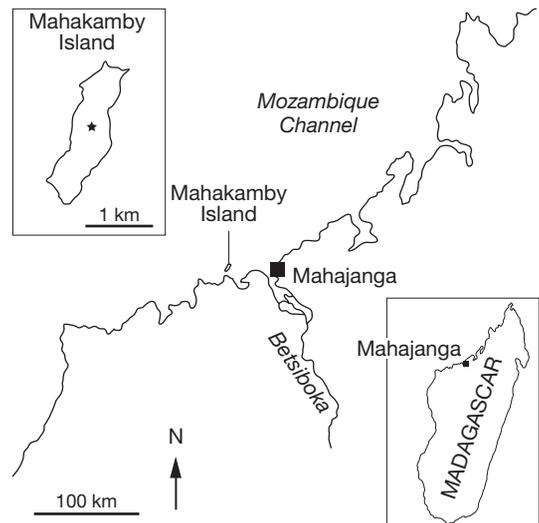


FIG. 1. — General map of Madagascar and location of the Mahakamby Island: the black star indicates the area of the small cliffs of Miocene deposits.

('pl. IV: figs 17, 18'; see Fig. 3). The fronto-orbital region is not preserved in all specimens, however almost a large orbit is observable. Elongate and prismatic chelae ('pl. IV: figs 20, 21'; see Fig. 3); finger with occlusal teeth increasing posteriorly, with the last one larger and molariform ('pl. IV: fig. 22'; see Fig. 3). The chelipeds bear three lateral spines, with short and large merus and with a single spine on the interior side ('pl. IV: figs 15, 19'; see Fig. 3). Flattened legs, laterally compressed in transverse section ('pl. IV: fig. 16'; see Fig. 3). Sternum longer than wide, curved distally; subtriangular abdomen with small triangular telson; episternites poorly preserved ('pl. IV: figs 15, 16'; see Fig. 3)."

All the specimens were ascribed to *Achelous* sp., and compared, especially for the elongated straight lateral spine, with *Achelous sindensis* Stoliczka, 1871 (*Neptunus*) and *A. delgadoi* Fontannes, 1884, that differs in the arrangement of the episternites. Unfortunately these specimens are today lost, so any direct comparison is possible. However in this review, some substantial observations are possible by the short description and figures proposed by Collignon & Cottreau (1927). In their "plate IV", reported partially here in Figure 3, we point out that:

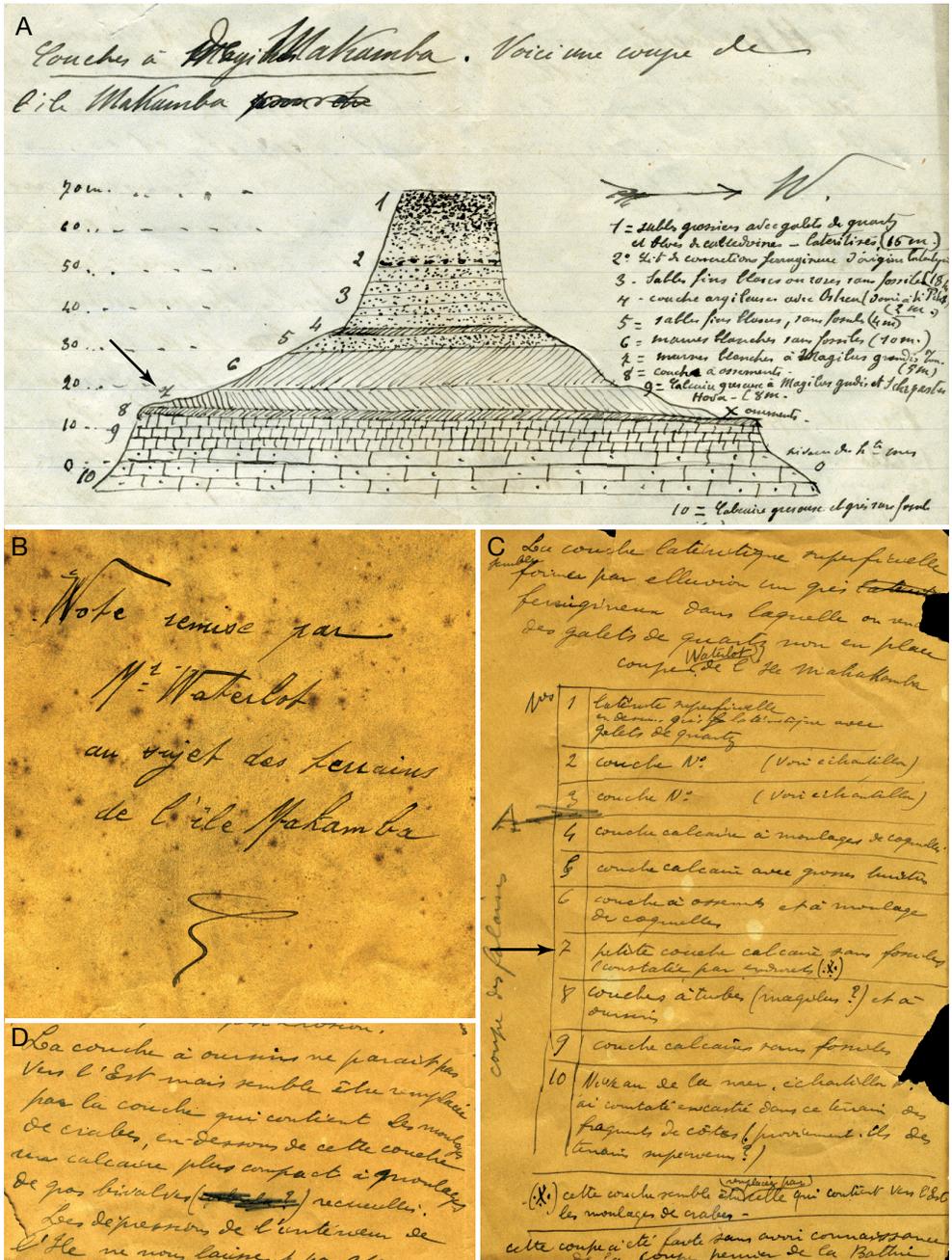


Fig. 2 — Reproduction of the original field notes on stratigraphy and faunal assemblage by the Perrier de la Bâthie's Mission and the Waterlot's Mission: **A**, Stratigraphic section of the Mahakamba Island (letter of Perrier de la Bâthie to the Professor Boule, April, 7th, 1921), the black arrow indicates the bed containing crab remains; **B-D**, Field notes of the Waterlot's Mission with comments on the cross section of the Mahakamba Island in which the bed containing fossil crabs is recognized (bed n° 7 of Perrier de la Bâthie's section, see black arrow), this field note arrived with the fossils in the Paris Museum in 1924. All these field notes are deposited in the Palaeontological Library of the Département Histoire de la Terre, Muséum national d'Histoire naturelle, Paris.

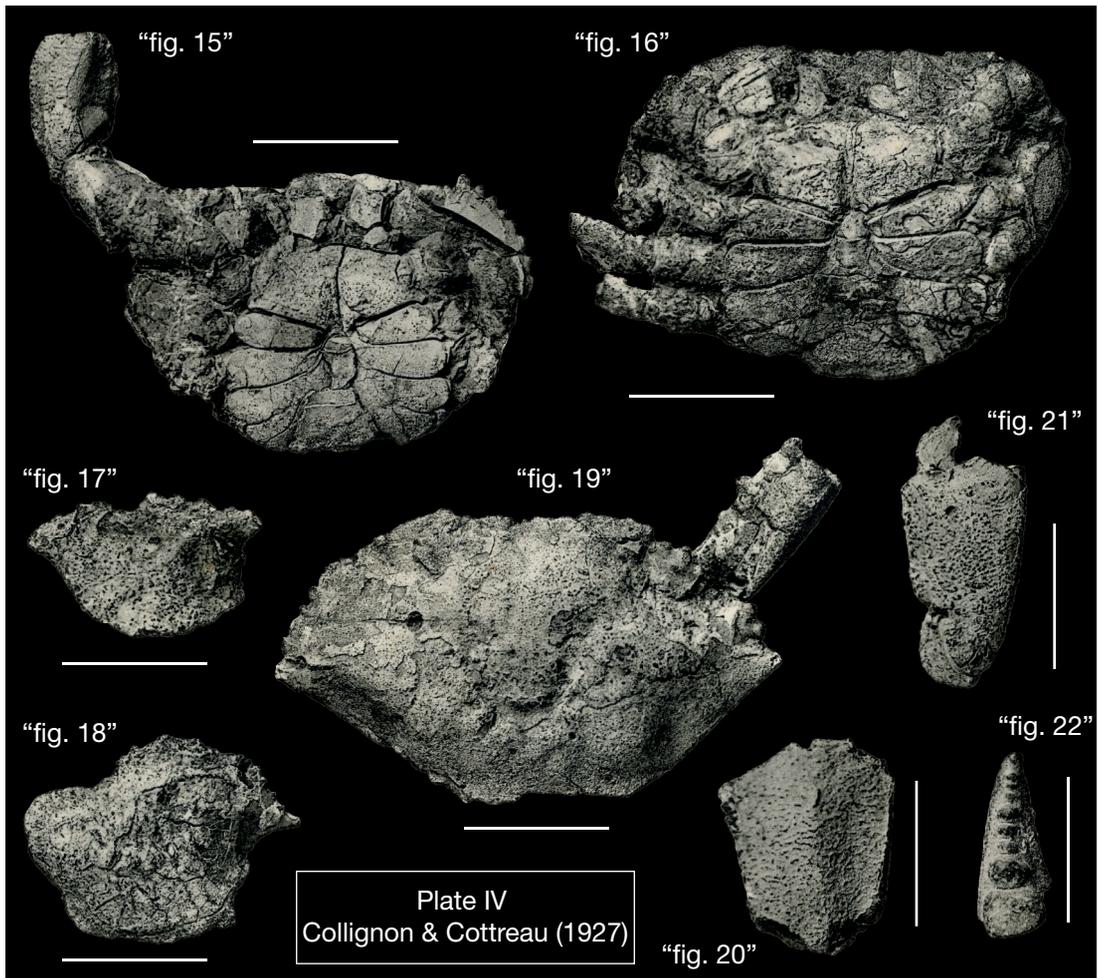


FIG. 3 — Reproduction of the original figures of *Achelous* sp. on the “plate IV” by Collignon & Cottreau (1927) with original numeration: specimens of “figs 15-19 and 22” are lost; specimens of “fig. 20” (MNHN.F.A33477) and “fig. 21” (MNHN.F.A33476) are still housed in the Paris Museum. Scale bars: 2 cm.

1) The general outline of the carapace (“pl. IV: fig. 19”; see Fig. 3) notably differs from the others two specimens in “plate VI, figs 15, 16” (see Fig. 3), showing a more elongate outline and the presence, although incomplete, of one last larger and outward directed lateral spine; moreover, the form and ornamentation of the merus, longer and with spines along the lateral margins in the first specimen (“pl. IV: fig. 19”; see Fig. 3), allow ascribing it to a separate genus (*Portunus s. str.*);

2) The two smaller and incomplete carapaces (“pl. IV: figs 17, 18”; see Fig. 3) belong to individuals at different grown stages. They are comparable with the first specimen (“pl. IV: fig. 19”; see Fig. 3) and included also in a separate genus (*Portunus s. str.*);

3) Other specimens (“pl. IV: figs 15, 16”; see Fig. 3) similar in shape and arrangement of the anterolateral spines and of the abdominal sternites, could be included in the genus *Achelous* as proposed by Collignon & Cottreau (1927);

4) The two incomplete chelae (“pl. IV: figs 20, 21”; see Fig. 3) ascribed by Collignon & Cottreau (1927) to *Achelous* sp., differ notably in general shape: in fact the first chela (“pl. IV: fig. 20”; see Fig. 3) has the palm higher distally, a median longitudinal ridge and a trapezoidal transverse section as in *Portunus s. str.*, whereas the second chela (“pl. IV: fig. 21”; see Fig. 3) is shorter and vaulted dorsally, similar to that preserved and articulated on the specimen referred to *Achelous* sp. (“pl. IV: fig. 15”; see Fig. 3);

5) The single strong dactylus, probably a left fixed finger, poorly preserved and in occlusal view (“pl. IV: fig. 22”; see Fig. 3) has strong molariform teeth. It does not show the typical characters of *Portunus s. str.* having denticulate and more elongate cutting finger with a single strong proximal molariform tooth. Therefore it could probably belong to another unrecognized genus.

ADDITIONAL MATERIAL

Recently, additional material collected during the Waterlot’s Mission, was discovered in the palaeontological collection of the Paris Museum. It includes eleven roughly complete carapaces, some of which preserving also the ventral parts, and twenty incomplete chelipeds. We can tentatively recognise three distinct groups with differentiated morphological characters.

GROUP 1

Three specimens (MNHN.F.A42028, A42029, A42042) have a carapace wider than long (MNHN.F.A42028, supposed width: *c.* 50 mm), slightly vaulted dorsally, with regions poorly marked; the anterolateral margin bears a number of small sharp spines comprised between 5 and 8, directed forward (Fig. 4A, B); one specimen (MNHN.F.A42028, Fig. 4A) preserved partially the last anterolateral longer spine directed outward. The incomplete left merus, preserved in specimen MNHN.F.A42029 (Fig. 4B), bears some alternate lateral spines. Other specimens (MNHN.F.A42030, A42043), consisting in a palm of the left cheliped, have an elongate and narrow

cheliped, prismatic in transverse section, with a single longitudinal median ridge on both inner and outer lateral margins and a short triangular carpus spinate anteriorly (Fig. 4C, D).

GROUP 2

Eight specimens (MNHN.F.A42031, A42032, A42033, A42034, A42035, A42036, A42037, A42041) have a carapace gently wider than long (MNHN.F.A42033, width: *c.* 60 mm, height: *c.* 42 mm; MNHN.F.A42036, width: *c.* 68 mm, height: *c.* 50 mm), slightly vaulted dorsally, with regions poorly marked; the anterolateral margin bears a number of small sharp similar spines comprised between 6 and 9 (Fig. 4E-K); the longer last anterolateral spine is absent and the posterolateral margin is gently convex. In ventral view, the abdominal sternites are well preserved in specimens MNHN.F.A42031, A42033, A42036, having similar sharp and form in all specimens (Fig. 4F, H, J).

GROUP 3

Eighteen specimens (MNHN.F.A42038, A42039, A42040, A42044) partially preserved, have vaulted transverse section of the palm of the chelae, very smooth inferior longitudinal ridge on both inner and outer sides and small, triangular and pointed teeth on the occlusal margin of the index (Fig. 4L-O).

DISCUSSION

Like the original sample studied by Collignon & Cottreau (1927), we can suppose that also the additional specimens could be related with the Portuninae Rafinesque, 1815. As reported by Williams (1984: 386), Poore (2004: 418), and Karasawa *et al.* (2008: 108), this subfamily include genera having carapaces always markedly wider than long, nine anterolateral spines but sometimes as few as four, last anterolateral spine usually notably longer or larger than the other ones. The specimens (MNHN.F.A42028, A42029) for the carapace wider than long and for the last anterolateral spine larger and probably longer than the previous ones, and for the elongate merus bearing lateral alternate spines, could be assigned to *Portunus s. str.* The

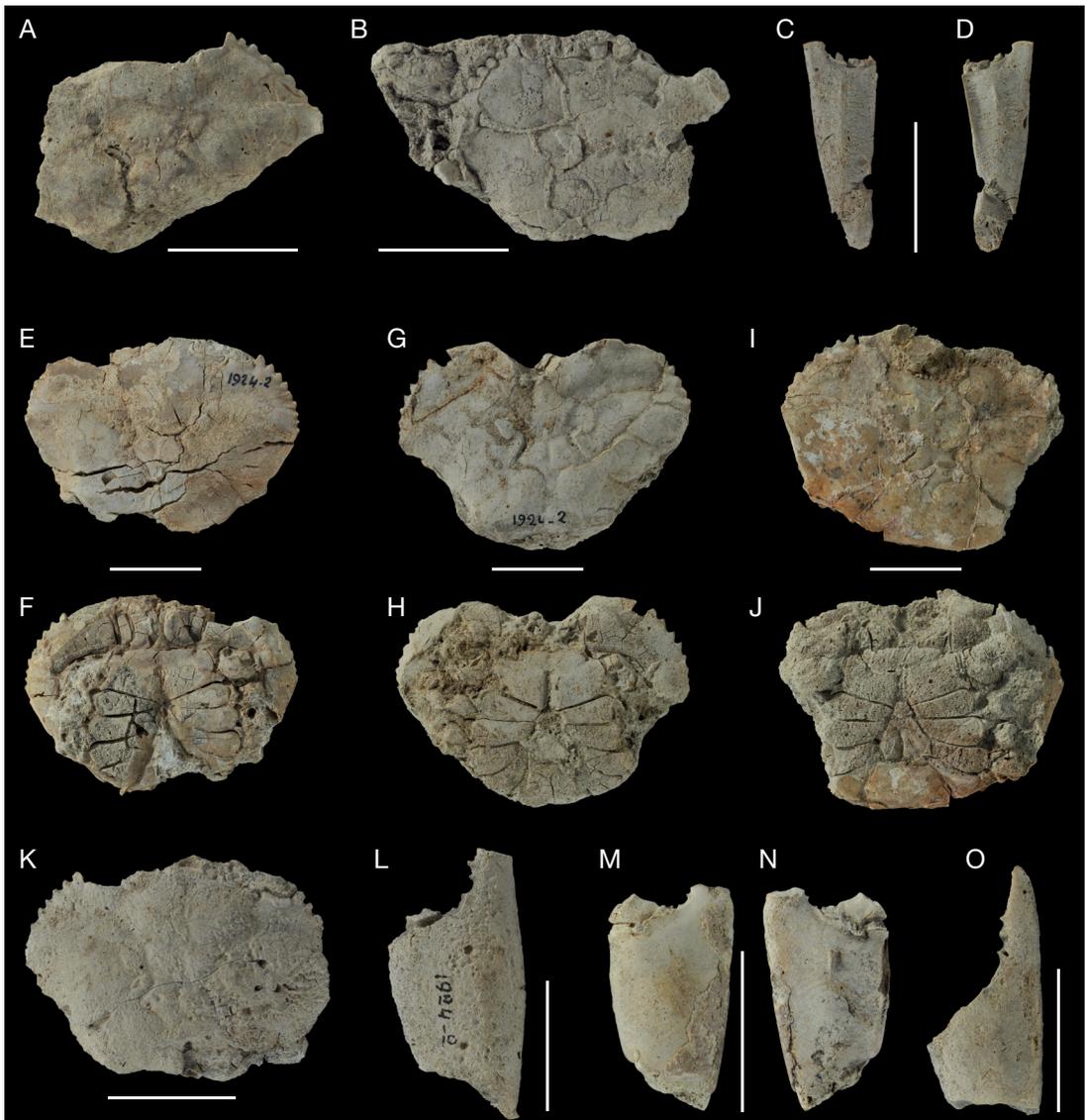


FIG. 4 — Portuninae, genus and species indeterminate, from the Miocene of Mahakamby Island: **A-D**, Group 1: **A**, [MNHN.FA42028](#), dorsal view; **B**, [MNHN.FA42029](#), dorsal view, preserving partially the left merus; **C**, [MNHN.FA42030](#), inner surface of the chela, showing the strong median longitudinal ridge; **D**, same, outer view; **E-K**, Group 2; **E**, [MNHN.FA42033](#), showing the well-preserved right anterolateral spines in dorsal view; **F**, same, ventral view; **G**, [MNHN.FA42036](#), showing the well-preserved anterolateral spines in both anterolateral margins in dorsal view; **H**, same, ventral view; **I**, [MNHN.FA42031](#), showing the well-preserved left anterolateral spines in dorsal view; **J**, same, ventral view; **K**, [MNHN.FA42035](#), showing the well-preserved left anterolateral spine in dorsal view; **L-O**, Group 3; **L**, [MNHN.FA42038](#), showing index with some proximal occlusal teeth in outer view; **M**, [MNHN.FA42039](#), showing the vaulted palm in outer view; **N**, same, inner view; **O**, [MNHN.FA42040](#), showing index with some proximal occlusal teeth in outer view. Scale bars: 2 cm. Photographs by C. Lemzaouda (MNHN).

single and isolate cheliped ([MNHN.FA42030](#)) having elongate palm, prismatic in cross section, with a single strong median longitudinal ridge on

both inner and outer lateral margins, and spinate carpus, could be also assigned to the same genus. The ascription to this genus could be also confirmed

for the original specimens studied by Collignon & Cottreau (1927: pl. IV, figs 17-20).

Instead, the studied specimens (MNHN.FA42031, A42033, A42035, A42038, A42039, A42040) and the original specimens by Collignon & Cottreau (1927: pl. IV, figs 15, 16, 21) having the carapace gently wider than long, the presence of some anterolateral small sharp similar spines, the anterolateral margin gently curved, the absence of the last anterolateral spine longer than the previous ones; the palm of cheliped having stout and globose propodus with smooth inner and outer lateral margins, and finally for the sharpness of the abdominal sternites, rise some problems with regard to their systematic ascription.

At first, we can suppose that they could be probably assigned to one of the extant subgenus of *Portunus*, although the real systematic validity of these subgenera is still the subject of controversy by different authors (Ng *et al.* 2008; De Grave *et al.* 2009; Schweitzer *et al.* 2010). Despite Ng *et al.* (2008: 151) reported five extant subgenera of *Portunus* (including *Achelous*), separated by the different number of anterolateral spines, it is difficult to try to assign the studied specimens to one of these since the front and the anterolateral margin are always incomplete not allowing to identify the real number of spines. Moreover, we point out that the ascription of the original specimens studied by Collignon & Cottreau (1927) to *Achelous* is probably incorrect because of, as reported by Nguyen & Ng (2010), this genus is mostly represented by Atlantic species. On the contrary the original and the additional specimens could be referred to *Cycloachelous* Ward, 1942, including only Indo-West Pacific species, as reported by Nguyen & Ng (2010). However the studied specimens differ in having anterolateral margins more curved (anterolateral margins almost parallel in *Cycloachelous*) and carapace slightly longer than wide (carapace as long as wide in *Cycloachelous*). At second, we can suppose that the original and additional specimens could be also referred as much as to *Scylla* De Haan, 1833, for the carapace slightly longer than wide, the anterolateral margins gently curved, the globose palm of chelipeds without transverse, parallel ridges and the occlusal margin of the robust index with strong posterior molar-

form teeth, decreasing anteriorly (see Collignon & Cottreau 1927: pl. IV, fig. 22). These characters are typical for example, of the common extant *Scylla serrata* (Forskål, 1755), today widespread in the Mozambique Channel, along all the western coast of Madagascar, inhabiting the mangrove environments (Cooke *et al.* 2003).

At third, the eighteen incomplete chelae (MNHN.FA42038, A42039, A42040, A42044) having vaulted palm in transverse cross section, very smooth inferior longitudinal ridge and small triangular and pointed teeth on the slender index, could be assigned to another different genus belonging to the Portuninae Rafinesque, 1815.

On the basis of the former discussion and the incompleteness of the studied sample, we assign generically the specimens of Collignon & Cottreau (1927) and the studied additional specimens to the Portuninae Rafinesque, 1815, genus and species indeterminate.

CONCLUSION

The extant marine brachyuran fauna of Madagascar amounts at 344 species, with 153 belonging to Portunidae, representing the largest fauna described to date from the western Indian Ocean (Cooke *et al.* 2003). Moreover, the Malagasy portunid fauna well “exemplifies the broad similarities between the W Pacific and Indian Ocean crab forms” (Cooke *et al.* 2003). Most of the Malagasy forms are present also in southern Africa, western Australia, Hawaii, and Japan (Crosnier 1962), bulk of species from the western Indian Ocean occurring at sites across the Pacific area. The discovery of different genus or morphotypes of portunids from the Miocene, allows dating to that time the first documented presence of Portuninae, with already different taxa, along the north western coast of Madagascar; enlarging the scarce knowledge on the paleo-distribution and relations among the portunids in the western Indian Ocean area. Finally, this faunal assemblage, excluding the note by Rakotozafy & Goodman (2005) about some indeterminate remains from the uppermost Pleistocene, is the only report of Cenozoic decapod brachyurans known to date from Madagascar.

Acknowledgements

We thank Annemarie Ohler (MNHN, Paris), Pedro Artal (Museo Geológico del Seminario de Barcelona, Spain) and an anonymous reviewer for their valuable reviews of this work. We wish to thank Peter Ng (Raffles Museum of Biodiversity Research, Singapore), for the useful advices of systematic problem concerning to the Portuninae. We also really thank Jean-Michel Pacaud (Département Histoire de la Terre, MNHN) for arranging all material for study and Christian Lemzaouda (Département Histoire de la Terre, MNHN) for assistance in photographic work. This paper is a contribution from the Museo di Storia Naturale di Milano (Paleontology Department), the Museo Civico dei Fossili di Besano (Varese, Italy) and the UMR CNRS 7207 Centre de Recherche sur la Paléobiodiversité et les Paléoenvironnements (CR2P) as well as the Département Histoire de la Terre (MNHN, Paris).

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Submitted on 16 May 2011;
accepted on 30 September 2011.