

# The freshwater crabs of Madagascar (Crustacea, Decapoda, Potamoidea)

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## ABSTRACT

The taxonomy of the freshwater crabs of Madagascar is revised and the number of genera raised from five to six. Two new genera are erected and one genus is synonymised. *Hydrothelphusa* is revised with four species: *H. agilis* A. Milne-Edwards, 1872, *H. madagascariensis* (A. Milne-Edwards, 1872), *H. bombetokensis* (Rathbun, 1904) and *H. goudoti* (H. Milne Edwards, 1853) n. comb. *Malagasya* n. gen. is established to accommodate two species, *M. antongilensis* (Rathbun, 1905) and *M. goodmani* (Cumberlidge, Boyko & Harvey, 2002); *Marojejy* Cumberlidge, Boyko & Harvey, 2002 and *Madagapotamon* Bott, 1965 are recognised as monotypic genera, *Skelosophusa* remains unchanged, and *Boreas* n. gen. is established for one species *B. uglowi* n. sp. The genus *Gecarcinautes* Bott, 1960 is here synonymised with *Potamonautes* Macleay, 1838 and its former taxa are referred to other genera. All six genera of freshwater crabs found in Madagascar are endemic and all are here referred to the Potamonautidae. A new diagnosis for each of the 12 species is provided, many are redescribed, and most are figured from the type. Keys to the genera and species of the Madagascan freshwater crabs are provided, together with species distribution maps and a gazetteer.

## KEY WORDS

Crustacea,  
Decapoda,  
Brachyura,  
Potamoidea,  
freshwater crabs,  
Madagascar,  
identification keys,  
new genera,  
new species.

## RÉSUMÉ

*Les crabes d'eau douce de Madagascar (Crustacea, Decapoda, Potamoidea).*

La taxonomie des crabes d'eau douce de Madagascar est révisée et le nombre de genres passe de cinq à six. Deux nouveaux genres sont créés et un genre entre en synonymie. *Hydrothelphusa* est révisé, avec quatre espèces : *H. agilis* A. Milne-Edwards, 1872, *H. madagascariensis* (A. Milne-Edwards, 1872), *H. bombetokensis* (Rathbun, 1904) et *H. goudoti* (H. Milne Edwards, 1853) n. comb. *Malagasya* n. gen. est établi et comprend deux espèces *M. antongilensis* (Rathbun, 1905) et *M. goodmani* (Cumberlidge, Boyko & Harvey, 2002) ; *Marojejy* Cumberlidge, Boyko & Harvey, 2002 et *Madagapotamon* Bott, 1965 sont reconnus comme genres monotypiques ; *Skelosophusa* reste inchangé et *Boreas* n. gen. est établi pour une espèce *B. uglowi* n. sp. Le genre *Gecarcinautes* Bott, 1960 entre ici en synonymie avec *Potamonautes* Macleay, 1838 et ses taxons correspondants sont rapportés à d'autres genres. Les six genres de crabes d'eau douce trouvés à Madagascar sont tous endémiques et appartiennent à la famille des Potamonautidae. Une nouvelle diagnose pour chacune des 12 espèces est fournie, beaucoup de ces espèces sont redécrites et la plupart sont figurées d'après le type. Les clés des genres et des espèces des crabes d'eau douce malgaches sont données ainsi que des cartes de répartition et un répertoire géographique des espèces.

## MOTS CLÉS

Crustacea,  
Decapoda,  
Brachyura,  
Potamoidea,  
crabes d'eau douce,  
Madagascar,  
clés d'identification,  
nouveaux genres,  
nouvelle espèce.

## INTRODUCTION

The present work was prompted by an examination of a large previously unidentified collection of freshwater crabs from Madagascar in the MNHN, Paris, and by the acquisition of new specimens from the island deposited in the Field Museum, Chicago, and the AMNH, New York. The new material from Madagascar included three new taxa (Cumberlidge *et al.* 2002) and provided good series with excellent specimens of existing taxa.

The first three freshwater crabs to be described from Madagascar were *Thelphusa goudoti* H. Milne Edwards, 1853, *T. madagascariensis* A. Milne-Edwards, 1872, and *Hydrothelphusa agilis* A. Milne-Edwards, 1872. Rathbun's (1904, 1905, 1906) complete revision of the taxonomy of the freshwater crabs of the world recognised seven taxa from Madagascar. That author assigned one of these to *Hydrothelphusa* (*H. agilis*) and five to *Potamon* (*Potamon*): *P. (P.) madagascariensis*, *P. (P.) bombetokensis* Rathbun, 1904, *P. (P.) humbloti* Rathbun, 1904, *P. (P.) grandidieri* Rathbun, 1904, and *P. (P.) goudoti*, and one to *Potamon* (*Parathelphusa*): *P. (P.) antongilensis* Rathbun, 1905. Further additions included *P. (Potamon) pittarelli* Nobili, 1905, *P. (Geo-*

*thelphusa) ankaraharae* Nobili, 1905, and *P. (Geothelphusa) methueni* Calman, 1913. Later, Pretzmann (1961) recognised the genus *Bottia* Pretzmann, 1961 with one species, *H. madagascariensis*, and a new subspecies, *B. madagascariensis reticulata* Pretzmann, 1961.

Bott (1965) was the first to publish a treatment of the Madagascan freshwater crab fauna in its entirety. That work (Table 1) considered 13 taxa from the island (as seven species, two subspecies and four synonyms), but overlooked *P. (P.) pittarelli*. Bott (1965) placed the Madagascan freshwater crabs in three genera. Three taxa were assigned to *Hydrothelphusa*: *H. agilis agilis*, *H. a. madagascariensis*, and *H. humbloti*, three to *Gecarcinautes* Bott, 1960: *G. antongilensis antongilensis*, *G. antongilensis vondrozi* Bott, 1965 and *G. goudoti*, and three to *Madagapotamon* Bott, 1965: *M. humberti* Bott, 1965, *M. gollhardi* Bott, 1965 and *M. ankaraharae*. Bott (1965) treated the remaining taxa as follows: two (*P. [P.] bombetokensis* and *P. [P.] grandidieri*) were considered to be junior synonyms of *H. humbloti*, *Bottia* was viewed as a junior synonym of *Gecarcinautes*, and *B. madagascariensis reticulata* was treated as a junior synonym of *H. agilis madagascariensis*.

TABLE 1. — Summary of original names of taxa from Madagascar and the names of species recognised in the present work.

Original taxon name	Present work
<i>Thelphusa goudoti</i> H. Milne Edwards, 1853	<i>Hydrothelphusa goudoti</i> (H. Milne Edwards, 1853)
<i>Thelphusa madagascariensis</i> A. Milne-Edwards, 1872	<i>Hydrothelphusa madagascariensis</i> (A. Milne-Edwards, 1872)
<i>Hydrothelphusa agilis</i> A. Milne-Edwards, 1872	<i>Hydrothelphusa agilis</i> A. Milne-Edwards, 1872
<i>Potamon (Potamon) humbloti</i> Rathbun, 1904	<i>Hydrothelphusa madagascariensis</i> (A. Milne-Edwards, 1872)
<i>Potamon (Potamon) grandidieri</i> Rathbun, 1904	<i>Hydrothelphusa madagascariensis</i> (A. Milne-Edwards, 1872)
<i>Potamon (Potamon) bombetokensis</i> Rathbun, 1904	<i>Hydrothelphusa bombetokensis</i> (Rathbun, 1904)
<i>Potamon (Parathelphusa) antongilensis</i> Rathbun, 1905	<i>Malagasya antongilensis</i> (Rathbun, 1905) n. comb.
<i>Potamon (Geothelphusa) ankaraharae</i> Nobili, 1906	<i>incertae sedis</i>
<i>Potamon (Potamon) pittarrelli</i> Nobili, 1905	? <i>Malagasya antongilensis</i> (Rathbun, 1905) n. comb.
<i>Potamon (Geothelphusa) methueni</i> Calman, 1913	<i>Hydrothelphusa goudoti</i> (H. Milne Edwards, 1853)
<i>Bottia madagascariensis reticulata</i> Pretzmann, 1961	<i>Hydrothelphusa madagascariensis</i> (A. Milne-Edwards, 1872)
<i>Gecarcinautes antongilensis vondrozi</i> Bott, 1965	<i>Malagasya antongilensis</i> (Rathbun, 1905) n. comb.
<i>Madagapotamon humberti</i> Bott, 1965	<i>Madagapotamon humberti</i> Bott, 1965
<i>Madagapotamon gollhardi</i> Bott, 1965	<i>Skelosophusa gollhardi</i> (Bott, 1965)
<i>Skelosophusa prolixa</i> Ng & Takeda, 1994	<i>Skelosophusa prolixa</i> Ng & Takeda, 1994
<i>Skelosophusa eumeces</i> Ng & Takeda, 1994	<i>Skelosophusa eumeces</i> Ng & Takeda, 1994
<i>Marojejy longimerus</i> Cumberlidge <i>et al.</i> , 2002	<i>Marojejy longimerus</i> Cumberlidge <i>et al.</i> , 2002
<i>Gecarcinautes goodmani</i> Cumberlidge <i>et al.</i> , 2002	<i>Malagasya goodmani</i> (Cumberlidge <i>et al.</i> , 2002) n. comb.
<i>Boreas uglowi</i> n. gen. n. sp.	<i>Boreas uglowi</i> n. gen., n. sp.

Bott (1965) referred the three Madagascan genera to three different subfamilies, Hydrothelphusinae Bott, 1955, Gecarcinucinae Rathbun, 1904, and Potamoninae Bott, 1955, based primarily on differences in the form of the terminal segment of the mandibular palp. According to Bott (1965) *Madagapotamon* included those taxa with a mandibular palp with a simple terminal segment (i.e. with no anterior process of any kind at the junction between the two segments). *Hydrothelphusa* included those taxa possessing a mandibular palp with a terminal segment with a small basal thickening, and *Gecarcinautes* included those taxa possessing a mandibular palp with a deeply cleft, bilobed terminal segment.

Bott's (1965) work remains the most recent, and indeed, the only available, comprehensive classification of the Madagascan freshwater crabs. However, since that work was written, further contributions to the knowledge of Madagascan freshwater crab diversity have been made by Ng & Takeda (1994) and by Cumberlidge *et al.* (2002). Ng & Takeda (1994) established a new genus, *Skelosophusa* Ng & Takeda, 1994, with *Madagapotamon gollhardi* as type species, added two new species, *S. prolixa* Ng & Takeda, 1994

and *S. eumeces* Ng & Takeda, 1994, and revived discussion of the taxonomic position of *P. (P.) pittarrelli*. Recently, Cumberlidge *et al.* (2002) described *Marojejy* Cumberlidge, Boyko & Harvey, 2002 and added two new species: *Marojejy longimerus* Cumberlidge, Boyko & Harvey, 2002 and *Gecarcinautes goodmani* Cumberlidge, Boyko & Harvey, 2002. The present work aims at a synthesis of the current knowledge of the freshwater crabs of Madagascar, and includes a comprehensive revision of the taxonomy of these crabs (Tables 1; 2), together with species distribution maps (Fig. 11), a gazetteer (Table 4), and identification keys to the genera and species.

#### HIGHER TAXONOMY

Bott's (1970a, b) comprehensive revisions of the higher taxonomy of the freshwater crabs of the world recognised 11 families and three superfamilies, but unfortunately did not discuss the Madagascan crabs. Nevertheless, Bott's (1965) assignment of the island's crabs to three subfamilies (Gecarcinucinae for *Gecarcinautes*, Hydrothelphusinae for *Hydrothelphusa*, and Potamoninae for *Madagapotamon*) has been largely accepted by subsequent authors who interpreted Bott's

TABLE 2. — Summary of names of taxa from Madagascar listed in Bott (1965) and in the present work.

Bott (1965)	Present work
<i>Hydrothelphusa agilis agilis</i>	<i>Hydrothelphusa agilis</i> (A. Milne Edwards, 1872)
<i>Hydrothelphusa agilis madagascariensis</i>	<i>Hydrothelphusa madagascariensis</i> (A. Milne-Edwards, 1872)
<i>Hydrothelphusa humbloti</i>	<i>Hydrothelphusa madagascariensis</i> (A. Milne-Edwards, 1872)
<i>Potamon (Potamon) bombetokensis</i> (jun. synonym)	<i>Hydrothelphusa bombetokensis</i> (Rathbun, 1904)
<i>Gecarcinautes brincki</i>	<i>Potamonautes brincki</i> (Bott, 1960)
<i>Gecarcinautes goudoti</i>	<i>Hydrothelphusa goudoti</i> (H. Milne Edwards, 1853)
<i>Gecarcinautes antongilensis antongilensis</i>	<i>Malagasya antongilensis</i> (Rathbun, 1905) n. comb.
<i>Gecarcinautes antongilensis vondrozi</i>	<i>Malagasya antongilensis</i> (Rathbun, 1905) n. comb.
<i>Madagapotamon humberti</i>	<i>Madagapotamon humberti</i> Bott, 1965
<i>Madagapotamon gollhardi</i>	<i>Skelosophusa gollhardi</i> (Bott, 1965)
<i>Madagapotamon ankaraharae</i> (type)	<i>incertae sedis</i>
<i>Madagapotamon ankaraharae</i> (non-type)	<i>Boreas uglowi</i> n. gen., n. sp.

(1965) scheme in the light of Bott's (1970a, b) later revisions. For example, Ng & Takeda (1994) assigned *Gecarcinautes* to the Gecarcinucinae (Gecarcinucidae Rathbun, 1904), *Hydrothelphusa* to the Hydrothelphusinae (Potamonautidae Bott, 1970), and *Madagapotamon* to the Potamonautidae.

Recently, Bott's (1970a, b) recognition of 11 families of freshwater crabs has been fundamentally challenged by the results of phylogenetic studies (Holthuis 1979; Ng 1988; Ng & Sket 1996; Ng & Trontelj 1996; Cumberlidge 1999; Dai 1999; Sternberg *et al.* 1999) which are likely to impact the higher taxonomy of the freshwater crabs, including those from Madagascar. Cumberlidge (1999) and Cumberlidge *et al.* (2002) questioned Bott's (1965) and Ng & Takeda's (1994) assignment of the Madagascan freshwater crabs to two different families (and superfamilies), but deferred proposing formal taxonomic changes. In addition, there has also been a great deal of reorganisation at the genus level, with the recent description of a new genus (Cumberlidge *et al.* 2002), and the recognition of two new genera and the suppression of *Gecarcinautes* in the present study. In short, there is still a great deal of uncertainty surrounding the taxonomy of the Madagascan freshwater crabs and some of the literature accounts of their generic and higher taxonomic assignments remain questionable.

The present work is the first comprehensive revision of the entire Madagascan freshwater

crab fauna for 35 years. Wherever possible we have examined the types of all available described taxa, including those taxa previously considered to be synonyms by Bott (1965). Our findings support the recognition of 12 endemic species of freshwater crabs on Madagascar that belong to six endemic genera. All are provisionally assigned here to a single family, the Potamonautidae, on the basis of mandibular palp, gonopod, and carapace characters. The subfamily assignments of the Madagascan freshwater crabs are less clear, and it is likely that our cladistic studies of the relationships between the genera will lead to the recognition of more than one lineage within the crabs of the island.

We found no justification for assigning any of the 12 species of Madagascan freshwater crabs to more than one family as had been done by other authors (Bott 1965; Ng & Takeda 1994). Despite sometimes striking differences in aspects of their morphology, all six Madagascan genera share a number of characters with the African potamonautids (e.g., a two-segmented mandibular palp, a triangular or oval abdomen, and a medium length first gonopod terminal article, see Cumberlidge [1999]) and are considered here to belong to the Potamonautidae Bott, 1970 *sensu* Cumberlidge (1999). This view is supported by our preliminary findings of a cladistic analysis of the Madagascan freshwater crab fauna.

## MANDIBULAR PALP CHARACTERS

Bott (1965, 1970a, b) based his higher taxonomies of the freshwater crabs principally on characters of the mandibular palp, and afforded these characters great taxonomic weight. This approach was also followed by subsequent authors (Ng 1988; Ng & Takeda 1994; Ng *et al.* 1995). However, the comparative study of the mandibular palp structure of the African freshwater crabs by Cumberlidge (1999) argues for caution when dealing with these characters, particularly those that have been used to distinguish between genera and subfamilies (Bott 1965), and between families (Ng & Takeda 1994) of Madagascan freshwater crabs.

Bott (1965) recognised three different forms of the terminal segment of the mandibular palp: 1) simple ("Endglied des Mandibularpalpus weder gespalten noch verdickt"); 2) basally thickened, undivided ("Endglied des Mandibularpalpus basal verdickt, ungeteilt"); and 3) bilobed, deeply cleft ("Endglied des Mandibularpalpus tief gespalten"). These three forms of the mandible are also recognised in the present study, and our taxonomy takes this useful character into account, in combination with other characters. However, while the number of segments of the mandibular palp may be important, we can find no serious justification for using mandibular palp terminal segment characters to make family level and superfamily level assignments, as has been done in the past (Bott 1970a, b; Ng & Takeda 1994). Furthermore, our examination of all of the published taxa from Madagascar does not support some of Bott's (1965) and Ng & Takeda's (1994) conclusions at the family, subfamily, genus, species, and subspecies levels, and we found little support for Bott's (1965) assignments of some taxa to synonymy. Our findings show that the terminal segment of the mandibular palp is simple in *Madagapotamon*, basally thickened in *Skelosophsusa* and *Boreas* n. gen., and bilobed (with a medium-sized anterior lobe) and deeply cleft in *Malagasya* n. gen., *Marojejy* and *Hydrothelphusa*.

The medium-sized lobe-shaped anterior process on the terminal segment of the mandibular palp

of *Hydrothelphusa* is not seen in potamonautid and deckeniid African freshwater crabs (which have a simple terminal segment). Interestingly, a medium-sized bilobed mandibular palp terminal segment is also found in *Seychellum* Ng, Stevcic & Pretzmann, 1995 (Seychelles) and *Gecarcinucus* Rathbun, 1904 (Indian subcontinent) (see Cumberlidge 1999). Ng *et al.* (1995) assigned *Seychellum* and *Gecarcinucus* to the Gecarcinucinae (Gecarcinucidae), but assigned *Hydrothelphusa* to the Hydrothelphusinae (Potamonautidae). The validity of the assignment of the Madagascan freshwater crabs to two different families and superfamilies by Ng *et al.* (1995) based largely on a single mandibular palp character is questioned in the present work.

The bilobed mandibular palp found in the Madagascan freshwater crab genera may be morphologically homologous with the bilobed palp seen in pseudothelphusid, parathelphusid and globonautine freshwater crabs from elsewhere in the world (Rodriguez 1982; Ng 1988; Cumberlidge 1999). However, there are significant differences within those groups with a bilobed mandibular palp that should not be overlooked. For example, the anterior process of the terminal segment of the mandibular palp of *Malagasya* n. gen., *Marojejy* and *Hydrothelphusa* (where the ratio of the length of the terminal article to the subterminal segment is about 0.3-0.5) is distinctly smaller than the sub-equal, lobe-like anterior process of *Globonantes* Bott, 1959, *Afrithelphusa* Bott, 1969, *Parathelphusa* H. Milne Edwards, 1853 and *Pseudothelphusa* Ortmann, 1893 (where the ratio of the length of the terminal article to the subterminal segment is about 0.9).

## ABBREVIATIONS

AMNH	American Museum of Natural History, New York, NY;
FMNH	Field Museum of Natural History, Chicago, IL;
MNHN	Muséum national d'Histoire naturelle, Paris;
MRSN	Museo Regionale di Scienze Naturali, Torino;
NHM	The Natural History Museum, London;
NHMW	Naturhistorisches Museum, Wien;
NMU	Northern Michigan University, Marquette, MI;

NSMT	Natural Science Museum, Tokyo;	fw	front width, the width of the front measured along the anterior margin;
SMF	Senckenberg Museum, Frankfurt;	e	thoracic episternite;
USNM	The United States National Museum of National History, Smithsonian Institution, Washington DC;	s2/s3, s3/s4, s4/s5, s5/s6, s6/s7, s7/s8	thoracic sternal sutures between adjacent sternites;
ZIM	Zoological Institute and Museum, Hamburg;	s4/e4, s5/e5, s6/e6, s7/e7	thoracic episternal sutures between adjacent sternites and episternites;
ZMB	Museum für Naturkunde der Humboldt-Universität, Berlin;	a1-a6	abdominal segments 1-6;
ZSM	Zoologisches Staatssammlung, München;	a7	telson;
cw	distance across the carapace at the widest point;	p1-p5	pereiopods 1-5;
cl	carapace length measured along the median line, from the anterior to the posterior margin;	coll.	collected by;
ch	carapace height, the maximum height of the cephalothorax.	ad.	adult;
		subad.	subadult;
		juv.	juvenile.

The abbreviated date format is day.month.year.

## SYSTEMATICS

### KEY TO THE GENERA OF MADAGASCAN FRESHWATER CRABS

1. Walking legs p2-p5 normal length, not elongated and slender, ratio p5 merus length: cw 0.4-0.45 ..... 2
  - Walking legs p2-p5 elongated and slender, ratio p5 merus length: cw 0.5-0.6 ..... 3
2. Third maxilliped ischium with distinct vertical sulcus; sternal sulcus s3/s4 Y-shaped, completely crossing sternum; terminal segment of mandibular palp bilobed, with a medium-sized, lobe-shaped, anterior process ..... *Hydrothelphusa*
  - Third maxilliped ischium smooth, lacking vertical sulcus; sternal sulcus s3/s4 reduced to two short side notches; terminal segment of mandibular palp with small ledge at junction between segments ..... *Boreas* n. gen.
3. Exopod of third maxilliped lacking flagellum; ischium of third maxilliped wider than merus; adult male abdomen oval or egg-shaped ..... *Madagapotamon*
  - Exopod of third maxilliped with long flagellum; ischium of third maxilliped as wide as merus; adult male abdomen triangular ..... 4
4. Carapace distinctly elongated, outline heart-shaped (frontal, posterior margins very narrow, about 0.25 cw); anterolateral margin of carapace with row of sharp teeth .. ..... *Malagasya* n. gen.
  - Carapace transversely oval (frontal, posterior margins relatively wide, about 0.3 cw); anterolateral margin of carapace smooth or granular, lacking teeth ..... 5
5. Merus of cheliped extremely elongated; terminal segment of mandibular palp bilobed, with medium-sized, lobe-shaped, anterior process; eyestalks shortened, tapering ..... *Marojejy*
  - Merus of cheliped normal length (not elongated or shortened); terminal segment of mandibular palp with small ledge at junction between segments; eyestalks normal length, not tapering ..... *Skelosophusa*

Family POTAMONAUTIDAE Bott, 1970  
Subfamily HYDROTHELPHUSINAE Bott, 1955

Genus *Hydrothelphusa* A. Milne-Edwards, 1872

*Hydrothelphusa* A. Milne-Edwards, 1872: 2; 1887: 138. — Ortmann 1897: 299; 1903: 301. — Rathbun 1905: 266. — Balss 1929: 357. — Pretzmann 1961: 165. — Bott 1965: 339-340.

TYPE SPECIES. — *Hydrothelphusa agilis* A. Milne-Edwards, 1872, by original designation.

DISTRIBUTION. — Madagascar.

DIAGNOSIS. — Front distinctly indented. Anterolateral margin between orbital, epibranchial teeth lacking intermediate tooth. Postorbital crests not meeting anterolateral margins. Mandibular palp two-segmented, bilobed, with medium-sized anterior process (about one-third size of terminal segment). Frontal margin widened in center forming triangular shape. Ischium of third maxilliped with deep vertical sulcus, exopod of third maxilliped with long flagellum. Thoracic sternal sulcus s2/s3 deep, horizontal, thoracic sternal sulcus s3/s4 deep, Y-shaped. Episternal sulci s4/e4, s5/e5, s6/e6, s7/e7 not visible. Walking legs (p2-p5) normal length (neither shortened nor elongated). Male abdomen long, slim, triangular. Terminal article of gonopod 1 short (ratio of length terminal article to subterminal segment 0.3); broad dorsal membrane at segment junction. Ventral side of subterminal segment of gonopod 1 with lateral flap folded inward, long, reaching to basal margin of segment; medial part of ventral face flat with distinct distomedial triangular shoulder, and large rounded basolateral projection; opening of chamber for gonopod 2 positioned about one-third of segment length from basal margin. Gonopod 2 longer than gonopod 1; terminal article of gonopod 2 long flagellum, ratio of length terminal article to subterminal segment *c.* 0.8.

REMARKS

*Hydrothelphusa* has been recognised as a distinct genus by every author ever since its original description in 1872. Bott (1955, 1960) assigned *Hydrothelphusa* to the subfamily Hydrothelphusinae in the then recognised family Potamonidae, and included two species, *H. agilis* and *H. humbloti*. Ng & Takeda (1994) assigned *Hydrothelphusa* to the Hydrothelphusinae which

they included in the Potamonautidae, and these opinions are accepted here.

The present work recognises four species of *Hydrothelphusa*: *H. agilis*, *H. madagascariensis*, *H. bombetokensis* and *H. goudoti* n. comb. This represents a major departure from the concept of the genus by Bott (1965) which included only two species (Table 1). In that work, *H. agilis* was recognised but *H. madagascariensis* was treated as a subspecies of *H. agilis*, *H. bombetokensis* was treated as a junior synonym of *H. humbloti*, and *H. goudoti* n. comb. was assigned to *Gecarcinautes*.

COMPARISONS

*Hydrothelphusa* can be distinguished from the five other genera of Madagascan freshwater crabs as follows: the bilobed terminal segment of the mandibular palp of *Hydrothelphusa* is similar to that seen in *Malagasya* n. gen. and *Marojejy*, however, the walking legs of *Hydrothelphusa* are of normal length, while those of *Malagasya* n. gen. and *Marojejy* are slender and elongated. In addition, the frontal margin of *Hydrothelphusa* is horizontal or slightly deflexed, whereas that of *Malagasya* is strongly deflexed, and the meri of the chelipeds of *Hydrothelphusa* and *Malagasya* are of normal length whereas those of *Marojejy* are elongated.

The bilobed terminal segment of the mandibular palp of *Hydrothelphusa* distinguishes this genus from *Madagapotamon*, *Boreas* n. gen. and *Skelosophusa*, where the terminal segment is either simple, or has a small hard ledge (*Skelosophusa* and *Boreas* n. gen.). In addition, sternal suture s3/s4 in adults of *Hydrothelphusa* is Y-shaped and completely crosses the sternum, whereas s3/s4 in adults of *Boreas* n. gen. and *Skelosophusa* is incomplete, and consists only of two short notches in the sternal margins. Finally, the flagellum of the exopod of the third maxilliped is long in *Hydrothelphusa*, but virtually absent (a short stub) in *Madagapotamon*.

KEY TO THE SPECIES OF *HYDROTHELPUSA* A. Milne-Edwards, 1872

1. Inferior margins of merus of p1 with either large teeth or large granules; anterior carapace texture rough, antero-lateral regions of carapace distinctly granular with short carinae ..... 2
- Inferior margins of merus of p1 either smooth or faintly granular; anterior carapace texture smooth, antero-lateral regions of carapace with faint carinae ..... 3
2. Frontal margin deeply indented, clearly toothed; front horizontal (not deflexed); suborbital margin with large pointed teeth; anterior margins of ischia of p1 and p2 with large pointed teeth ..... *H. agilis*
- Frontal margin shallowly indented, granular (not toothed); front moderately deflexed; suborbital margin granular; suborbital region of carapace sidewall granular; anterior margins of ischia of p1 and p2 smooth, lacking teeth .....  
..... *H. madagascariensis*
3. Exorbital, epibranchial teeth both large, broad, outer margin of exorbital tooth long, clearly separating these teeth; epigastric, postorbital crests separated by distinct gap; cervical grooves very short; suborbital, pterygostomial regions of carapace sidewall both heavily granulated; carapace medium wide (cw/fw = 3.5), not highly arched (ch/fw = 1.3) ..... *H. bombetokensis*
- Exorbital, epibranchial teeth both low, blunt; outer margin of exorbital tooth short and teeth close together; epigastric, postorbital crests fused forming long horizontal postfrontal crest; cervical grooves very long; suborbital, pterygostomial regions of carapace sidewall both smooth; carapace very wide (cw/fw = 3.9), highly arched (ch/fw = 1.6) ..... *H. goudoti*

*Hydrothelphusa agilis* A. Milne-Edwards, 1872  
(Figs 1A; 3A; 4A; 5A; 6A; 7A, B; 8A; 9A-D; 11A)

*Hydrothelphusa agilis* A. Milne-Edwards, 1872:  
2. —Rathbun 1905: 266-268, fig. 72, pl. 15,  
fig. 7. — Balss 1929: 357. — Pretzmann 1961:  
165. — Cumberlidge 1997: 584, 585.

*Hydrothelphusa agilis agilis* – Bott 1965: 340, 341,  
fig. 4, pl. 2, figs 8, 9, pl. 4, fig. 18.

TYPE LOCALITY. — Madagascar, Sakaleone river.

MATERIAL EXAMINED. — **Madagascar.** Dry collection,  
coll. M. Grandidier, 1 ad. ♂ chosen as lectotype  
cw 50.2, cl 39.6 mm (MNHN-B 4383) (see Rathbun  
1904: 266 for more dimensions), 1 ♀ cw 46,  
cl 38.3 mm (MNHN-B 27931); in alcohol, coll.  
Grandidier, 1 ad. ♀ paratype cw 60.9, cl 47.1 mm,  
1 ad. ♀ paratype cw 54.5, cl 46.5 mm (MNHN-B

5010); coll. M. Grandidier (exchange with Paris  
Museum), 1 subad. ♂ paratype cw 30.1, cl 24.2,  
ch 11.3, fw 11.1 mm (NHM 1910.7.7.1). — Toa-  
masina (formerly Tamatave), Autumn 1922, coll.  
J. Millot, 1 ad. ♂ (MNHN-B 5009), 3 specimens  
(MNHN-B 5011), 6 specimens (MNHN-B 5013). —  
Andrafiavelo (Sakarava), 29.VIII.1930, coll.  
R. Decary, 1 juv. ♂ cw 21, cl 16.5 mm (MNHN-B  
5179). — Analamazastra river, Toamasina, Moramanga,  
7.IX.1963, 1 ♂, 1 juv. ♂, 1 ad. ♀ cw 50.5, cl 42,  
ch 18, fw 16.5 mm, 1 subad. ♀ cw 41, cl 33.5,  
ch 13.5, fw 13 mm (MNHN-B 25750); coll. J. Mil-  
lot, Autumn 1922, 1 ♂ (MNHN-B 15932). —  
Beforona, freshwater stream between Tananarive and  
Toamasina, 1897, coll. M. Bastard, 1 ad. ♂ (MNHN-  
B 15933). — Analamazastra river, forest streams,  
1926, coll. G. Petit, 1 ad. ♀, 1 ad. ♂ (MNHN-B  
15934), 2 subad. (MNHN-B 15935). — Anala-  
mazastra river, Moramanga, collected in a net,  
IX.1958, 1 ad. ♂ (MNHN-B 2625). — Ambodiriana,



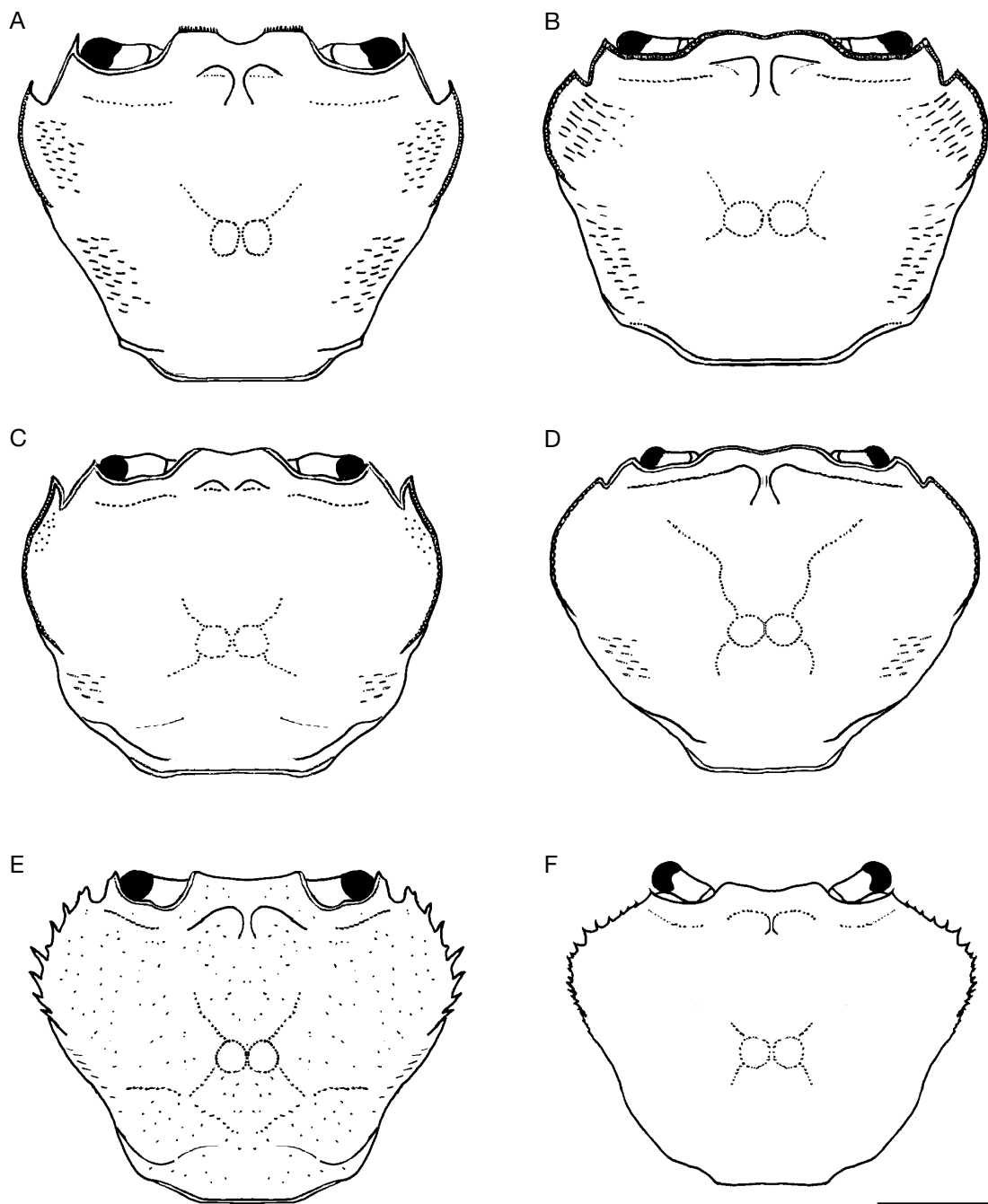


FIG. 1. — Dorsal view of the carapace of adult males of Madagascan freshwater crabs; **A**, *Hydrothelphusa agilis* A. Milne-Edwards, 1872; **B**, *H. madagascariensis* (A. Milne-Edwards, 1872); **C**, *H. bombetokensis* (Rathbun, 1904); **D**, *H. goudoti* (H. Milne Edwards, 1853) n. comb.; **E**, *Malagasya antongilensis* (Rathbun, 1905) n. comb.; **F**, *M. goodmani* (Cumberlidge, Boyko & Harvey, 2002) n. comb., holotype (FMNH 4651). Scale bar: A, 10.5 mm; B, 14.4 mm; C, 14.1 mm; D, 12.6 mm; E, 8.9 mm; F, 6.4 mm.

TABLE 3. — Carapace and other proportions of Madagascan freshwater crabs. Abbreviations: **cw**, carapace width; **cl**, carapace length; **ch**, carapace height; **fw**, front width; **p5m**, length of merus of right pereopod 5.

Taxon	cw/fw	cl/fw	ch/fw	p5m/cw
<i>Hydrothelphusa agilis</i> (A. Milne Edwards, 1872)	3.2	2.6	1.2	0.4
<i>H. bombetokensis</i> (Rathbun, 1904)	3.5	2.7	1.3	0.5
<i>H. madagascariensis</i> (A. Milne-Edwards, 1872)	3.4	2.7	1.2	0.5
<i>H. goudoti</i> (H. Milne Edwards, 1853) n. comb.	3.9	2.8	1.6	0.4
<i>Madagapotamon humberti</i> Bott, 1965	4.8	3.7	1.7	0.5
<i>Skelosophusa gollhardi</i> (Bott, 1965)	3.6	2.7	1.3	0.6
<i>S. proluxa</i> Ng & Takeda, 1994	3.6	2.8	1.4	0.5
<i>S. eumeces</i> Ng & Takeda, 1994	3.5	2.3	1.2	0.6
<i>Marojejy longimerus</i> Cumberlidge et al., 2002	3.8	2.6	1.3	0.4
<i>Malagasya antongilensis</i> (Rathbun, 1905) n. comb.	3.8	3.0	1.6	0.5
<i>M. goodmani</i> (Cumberlidge et al., 2002) n. comb.	4.9	3.8	1.5	0.5
<i>Boreas uglowi</i> n. gen., n. sp.	3.6	2.5	1.3	0.4

road to Lakato, Moramanga, coll. Thérézieu, 3 subad. (MNHN-B 25737). — Road to Toamasina, from lake near Mandrake dam, 28.V.1966, 1 ♂ (MNHN-B 25738). — Ambodiriana, road to Lakato, Moramanga, 5.VIII.1960, coll. Thérézieu, 2 ad. ♂♂ (MNHN-B 25748), 1 ad. ♂ (MNHN-B 25749). — Analamastra river, 1 ♂, 2 ad. ♀♀ cw 52, cl 43.5 mm and cw 49, cl 41.5 mm (MNHN-B 26619).

**DISTRIBUTION.** — Madagascar (Fig. 11A). This species is found in the streams and rivers between Tananarive and Toamasina, in the region between Bombetok and Tananarive, and in the Sakaleone river near Mahela. See Cumberlidge (1998) for more localities.

**DIAGNOSIS.** — Front horizontal (not deflexed); frontal margin deeply indented, toothed; exorbital, epi-branchial teeth large, tips pointed; suborbital margin with pointed teeth. Ischium of p1 and p2 with two large teeth with pointed tips; inferior margins of merus of p1 with several long teeth with pointed tips.

#### REDESCRIPTION

Carapace moderately wide (cw/fw = 3.2) moderately high (ch/fw = 1.2); anterolateral, posterolateral carapace regions distinctly granular, with short carinae; rest of carapace surface rough. Epigastric crests rounded; mid-groove between epigastric crests broad; distinct gap between epigastric, postorbital crests; postorbital crests not meeting anterolateral margins. Semi-circular groove deep; urogastric, cardiac grooves shallow; cervical grooves long. Front horizontal (not deflexed); frontal margin toothed, deeply indented;

frontal, posterior margins of carapace approximately one-third cw (0.3, 0.35). Exorbital, epi-branchial teeth large, directed forward, tips pointed. Anterolateral margin posterior to epi-branchial tooth raised, granular. Suborbital margin with pointed teeth, largest tooth at medial end. Anterior inferior margin of ischium of p1 and p2 with two large teeth with pointed tips, posterior inferior margin of pereopod 1 with one pointed tooth. Inferior margins of merus of p1 with large teeth with pointed tips; distal margin with single pointed tooth; superior surface of merus roughly granulated. Inner margin of carpus of cheliped with two large, pointed carpal teeth; second tooth half size of first, margin behind second tooth smooth.

#### Size

The adult size range is from cw 45-50 to 76 mm. The carapace proportions are given in Table 3.

#### REMARKS

The unique features of *H. agilis* have long been recognised, and the assignment of this species to a distinct genus has never been seriously questioned. The undeflexed front, the deeply-indented toothed frontal margin, the toothed suborbital margin, and toothed p1 ischium are all characters peculiar to *H. agilis*.

*Hydrothelphusa agilis* can be further distinguished from the other three species in the genus as follows. The carapace of *H. agilis* is narrower (cw/fw = 3.2) than that of *H. madagascariensis* (cw/fw = 3.4) and the subhepatic and pterygostomial regions of the carapace sidewall of *H. agilis* are both smooth, whereas those of *H. madagascariensis* are heavily granulated. *Hydrothelphusa agilis* can be distinguished from *H. bombetokenis* by comparing carapace proportions — the carapace of *H. agilis* is less wide (cw/fw = 3.2) than that of *H. bombetokenis* (cw/fw = 3.5). In addition, the inferior margins of the merus of p1 of *H. agilis* have several large and pointed teeth, while these margins in *H. bombetokenis* are granular; and the anterior carapace of *H. agilis* is coarse, whereas that of *H. bombetokenis* is smooth. *Hydrothelphusa agilis* can be distinguished from *H. goudoti* n. comb. as follows: the carapace of *H. agilis* is less wide (cw/fw = 3.2) and less arched (ch/fw = 1.2) than that of *H. goudoti* n. comb. (cw/fw = 3.9, ch/fw = 1.6). The exorbital and the epibranchial teeth of *H. agilis* are both large with pointed tips, whereas these teeth in *H. goudoti* n. comb. are small and the tips are blunt; the inferior margins of the merus of p1 of *H. agilis* are lined by several large, pointed teeth, whereas these margins in *H. goudoti* n. comb. are granular; the anterior carapace of *H. agilis* is heavily granulated whereas that of *H. goudoti* n. comb. is smooth; and the second carpal tooth of the carpus of p1 is large with a pointed tip in *H. agilis*, and a low granule in *H. goudoti* n. comb. The horizontal clearly indented and sharply toothed frontal margin of *H. agilis* are unusual characters in freshwater crabs in general, but are seen in African freshwater crab species such as the platythelphusid *Platythelphusa armata* A. Milne-Edwards, 1887, and the potamonautids *Erimetopus brazzae* A. Milne-Edwards, 1887 (particularly *E. b. frontospinulosa* Bott, 1955), and *Potamonautes* (*Longipotamonautes*) *vandenbrandenii* Balss, 1937. However, this similarity is only superficial and may be convergent, for there is no other supporting morphological evidence linking any of these taxa (see Bott 1955; Cumberlidge 1999). A detailed description of the arterial system of *H. agilis* was provided by Vuillemin (1964).

The present findings do not support Bott's (1965) characterization of the terminal segment of the mandibular palp of *H. agilis* as "basally thickened". In fact, this segment has a distinct bilobed terminal segment with a medium-sized anterior process. This point is important because *H. agilis* is the type species of the genus and subfamily, and so Bott's (1965) genus and subfamily assignments are substantially challenged.

### *Hydrothelphusa madagascariensis*

(A. Milne-Edwards, 1872)

(Figs 1B; 3B; 4B; 5B; 6B; 7C, D; 8B; 9E-I; 11B)

*Thelphusa madagascariensis* A. Milne-Edwards, 1872: 1.

*Potamon* (*Potamon*) *madagascariensis* Rathbun, 1904: 264, fig. 7, pl. 9, fig. 9. — Balss 1929: 254.

*Potamon* (*Potamon*) *humbloti* Rathbun, 1904: 297, 298, pl. 12, fig. 10.

*Potamon* (*Potamon*) *grandidieri* Rathbun, 1904: 298, fig. 29, pl. 12, fig. 11. — Balss 1929: 354.

*Bottia madagascariensis* Pretzmann, 1961: 163, fig. 2.

*Bottia madagascariensis reticulata* Pretzmann, 1961: 163, fig. 2.

*Hydrothelphusa agilis madagascariensis* Bott, 1965: 341, 342, pl. 3, figs 10, 11.

*Hydrothelphusa humbloti* Bott, 1965: 342-344, not pl. 3, figs 12, 13, not figs 5, 6. — Cumberlidge 1997: 585.

*Hydrothelphusa madagascariensis* — Cumberlidge 1997: 585; 1998: 209.

MATERIAL EXAMINED. — **Madagascar.** Sakaleone river, 4 dried paralectotypes of *Potamon* (*Potamon*) *madagascariensis*, 1903, coll. M. Grandidier, auct. det., Mary J. Rathbun, 1 ♂ (MNHN-B 4352). — Near Bombetok, other paratypes in alcohol, coll. M. Grandidier, 1 juv. ♂, 1 ♀ (MNHN-B 5289). — Near Bombetok, 1 subad. ♀ lectotype of *Potamon* (*Potamon*) *grandidieri* Rathbun, 1904, cw 28.1, cl 20.5, ch 10.5, fw 9 mm, coll. M. Grandidier, photographed and figured in Rathbun (1904) (MNHN-B 5168). — Forest, 1904, coll. Humblot, 1 subad. ♀, lectotype of *Potamon* (*Potamon*) *humbloti* Rathbun, cw 29, cl 21.5, ch 11, fw 9 mm, broken up, photographed and figured in Rathbun (1904) (MNHN-B 5176), 1 subad. ♀, paratype, cw 28 mm (USNM 29987). — Androkabe Bach, NW of Fort-Dauphin (Straße F. Dauphin-Ranomafan du Sud), 40 ♂ ♂, 10.IX.1958, coll. F. Starmühlner, 1 ♂ holotype of

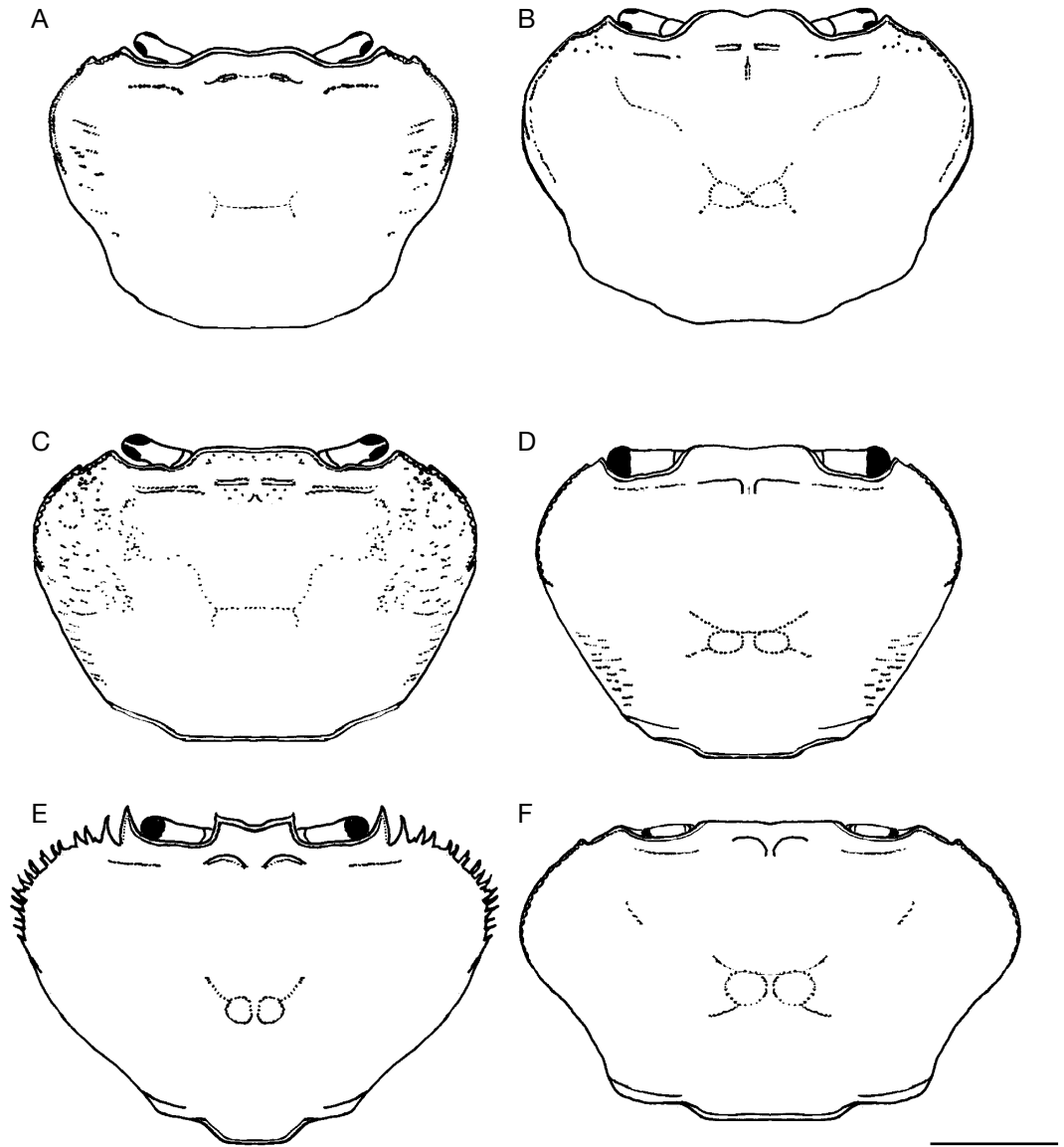


FIG. 2. — Dorsal view of the carapace of adult males of Madagascan freshwater crabs (A-C based on Ng & Takeda 1994); **A**, *Skeleosophusa gollhardi* (Bott, 1965), holotype (MNHN B-5165); **B**, *S. prolixa* Ng & Takeda, 1994, holotype, (MRSN); **C**, *S. eumeces* Ng & Takeda, 1994, holotype, (MRSN); **D**, *Boreas uglowi* n. gen., n. sp., holotype (MNHN B- 11292); **E**, *Madagapotamon humberti* Bott, 1965; **F**, *Marojejy longimerus* Cumberlidge, Boyko & Harvey, 2002, holotype, (AMNH 17833). Scale bar: A, 7.2 mm; B, 7.1 mm; C, 6.5 mm; D, 9 mm; E, 9.4 mm; F, 6 mm.

*Bottia madagascariensis reticulata* Pretzmann, 1961 (Österr. Madagascar Exp. FM 216) cw 23, cl 17 mm (NHMW 2731). — Réserve naturelle de Betampona Est, 1 ad. ♀ cw 55.5 mm, 1 subad. ♂ cw 30 mm, 1 juv. ♂ cw 26 mm (MNHN-B 5014). — Diego-Suarez (now Antsiranana), Montagne d'Ambre, 1896,

coll. Ch. Alluaud, 1 subad. ♀ cw 40.5, cl 24.5, ch 12, fw 20.5 mm (MNHN-B 5015), 2 subad. ♂ cw 33.5, cl 25, ch 30, fw 22 mm (MNHN-B 5150). — Fort-Dauphin, banks of stream, under stomes, 22.VI.1932, coll. R. Decary, 1 juv. ♂ cw 23.5, cl 18.5 mm, 1 subad. ♀ cw 29, cl 22.5 mm (MNHN-

B 5175). — Andrafiavelo (Sakalava), 29.VIII.1930, coll. R. Decary, 1 juv. ♂ cw 25, cl 20 mm (MNHN-B 5179). — Tananarive, 1 juv. ♂ (MNHN-B 5280). — Vallée d'Isaka, mountain stream, 1901, coll. Ch. Alluaud, 4 specimens, all subad. and juv. (MNHN-B 5284). — East of Sakavalana, 1901, coll. Ch. Alluaud, 4 specimens, 3 subad. ♀ ♀ cw 29, 31, 24.5 mm, 1 juv. ♂ cw 22 mm (MNHN-B 5285). — Toamasina, 1923, coll. Millot, 3 specimens, 1 subad. ♂ cw 29, cl 23.5 mm, 1 subad. ♀ cw 30, cl 23.5 mm, 1 juv. ♀ cw 27, cl 21 mm (MNHN-B 5286). — Toamasina, 1923, 1 subad. ♂ cw 34 mm (MNHN-B 5288). — Bezofo, Autumn 1922, coll. Millot, 1 ad. ♀, ovig. cw 48.5, cl 39, ch 18, fw 15 mm, 1 subad. ♂ cw 33, cl 26.5, ch 12, fw 11.5 mm (MNHN-B 5338). — Forest, 1880, coll. Humblot, seven to eight specimens (MNHN-B 17718). — 1905, coll. F. Geay, 1 juv. ♀ cw 18, cl 14.5, ch 7, fw 6 mm, (MNHN-B 17719), 1 juv. ♂ cw 26, cl 18.5 mm (MNHN-B 25733). — Nosy-Bé, rivière de la route des lacs, 23.XI.1972, coll. A. Crosnier, 1 ad. ♂ cw 25.5, cl 18.6, ch 9.2, fw 7.7 mm (MNHN-B 25734). — Ambodirano, road to Lakato, Moramanga, 1 specimen (MNHN-B 25737). — Marozohy river, 8.XII.1965, 1 juv. ♂ cw 15, cl 11 mm (MNHN-B 25745). — Ambodirano, road to Lakato, Moramanga, 1 specimen (MNHN-B 25748). — Analamazastra river, Toamasina, Moramanga, 1 specimen (MNHN-B 25750). — Tapimbato, 1 juv. cw 15, cl 11.5 mm (MNHN-B 25761). — Near Cuidongy, road to Farafangana, from rapids in forest, 26.VIII.1926, coll. R. Decary, 1 ♂ cw 44, cl 34, ch 16, fw 13 mm, 1 juv. cw 19, cl 16.5 mm, 1 juv. cw 13.5, cl 11.5 mm (MNHN-B 27556). — Nosy-Bé, coll. J. Millot, Autumn 1922, 1 subad. ♂ cw 30.5, cl 24.5, ch 11, fw 9 mm, 1 subad. ♂ cw 36, cl 28.5, 12.5, fw 11.5 mm (MNHN-B 27557). — Diego-Suarez (now Antsiranana), Montagne d'Ambre, coll. Ch. Alluaud, 1 ♂ cw 28.5 mm (MNHN-B 27558). — Col de Sakavalana, 1901, coll. Ch. Alluaud, 1 subad. ♂ cw 31, cl 24.5, ch 12, fw 10.5 mm (MNHN-B 27559), 1 subad. ♂ cw 40 mm, 1 ♀ cw 38.5 mm, 1 juv. ♂ cw 14 mm (MNHN-B 27560). — Isandra river at Ankodobé, east of Béfotaké, 500 m, road to Farafangana, 13.VIII.1926, coll. R. Decary, 1 juv. ♀ cw 30.5, cl 22.5, ch 11.5, fw 9 mm (MNHN-B 27561). — Bijofo, Diego-Suarez (now Antsiranana), II.1923, coll. R. Decary (Bijofo) and Dr J. Millot, 9 specimens (MNHN-B 27562). — Toamasina, coll. Dr J. Millot, 1 ad. ♀ cw 61.7 mm (ZSM 1533/1). — Betaur, Pora-Ost (SMF 2617). — Tsingalapaky, Fetoky, Fandiarano (= Fandriana?), Tsimantsy, Marotsy river, 13.XII.1965, 1 specimen. — Lily river, Ampéfy, Soavinandriana, 16.I.1963, 2 subad. ♂ ♂ cw 36, 26 mm, 2 subad. ♀ ♀ cw 25.1, 23.1 mm (MNHN). — Marotsy river, Farafangana, 13.XII.1965, 1 juv. ♂ cw 14.6 mm (MNHN), 1 ad. ♂ cw 41.9 mm (ZSM 1534/1).

TYPE LOCALITY. — Madagascar. *Potamon (Potamon) madagascariensis*: Sakaleone river, near Bombetok, Madagascar. *Potamon (Potamon) grandidieri*: close to Bombetok, Madagascar. *Potamon (Potamon) humbloti*: forest, Madagascar.

DISTRIBUTION. — Madagascar (Fig. 11B). See Cumberlidge (1998) for more localities.

DIAGNOSIS. — Front slightly deflexed, neither perfectly horizontal nor vertically deflexed; frontal margin distinctly granulated; exorbital, epibranchial teeth both large, pointed; suborbital margin distinctly granular; ischium of p1 distinctly granular; inferior margins of merus of p1 distinctly granular; subhepatic region of carapace sidewall heavily granulated.

#### REDESCRIPTION

Carapace wide (cw/fw = 3.4), moderately high (ch/fw = 1.2); fields of short carinae on anterolateral, posterolateral carapace; epigastric crests distinct, located anterior to postorbital crests; postorbital crests not meeting anterolateral margins; mid-groove between epigastric crests broad. Semi-circular, urogastric grooves deep; cervical grooves short. Front slightly deflexed; frontal margin granulated, indented. Exorbital, epibranchial teeth both large, forward-directed, teeth with blunt tips. Anterolateral margin posterior to epibranchial tooth heavily granulated. Suborbital margin distinctly granulated. Suborbital, subhepatic, pterygostomial regions of carapace sidewall all heavily granulated. Anterior inferior margin of ischium of p1 distinctly granulated. Inferior margins of merus distinctly granulated, distal margin with single pointed tooth; superior surface of merus granulated. Inner margin of carpus of cheliped with two pointed carpal teeth; first carpal tooth large, with pointed tip; second carpal tooth one-third size of first, margin behind second tooth sometimes with several small teeth.

#### Size

The adult size range is from cw 40-44 to 61.7 mm. The carapace proportions are given in Table 3.

#### REMARKS

*Hydrothelphusa madagascariensis* has long been recognised as a distinct species and is one of the most common and largest freshwater crabs on the island.

Bott's (1965) assignment of this taxon as a subspecies of *H. agilis* is not accepted here, and *H. madagascariensis* is recognised as a valid species (Cumberlidge 1997, 1998). The differences between *H. madagascariensis* and *H. agilis* are provided above. *Hydrothelphusa madagascariensis* can be distinguished from *H. bombetokensis* by differences in the carapace dimensions: the carapace of *H. madagascariensis* is less wide (cw/fw = 3.4) and less arched (ch/fw = 1.2) than that of *H. bombetokensis* (cw/fw = 3.5, ch/fw = 1.3), and in carapace texture: the anterior carapace of *H. madagascariensis* is coarse, whereas that of *H. bombetokensis* is smooth.

*Hydrothelphusa madagascariensis* can be distinguished from *H. goudoti* n. comb. as follows: the carapace of *H. madagascariensis* is less wide (cw/fw = 3.4) and less arched (ch/fw = 1.2) than that of *H. goudoti* n. comb. (cw/fw = 3.9, ch/fw = 1.6); the exorbital and epibranchial teeth of *H. madagascariensis* are both large teeth each with a pointed tip, whereas in *H. goudoti* these teeth are small and low, with blunt tips; the subhepatic region of the carapace sidewall of *H. madagascariensis* is heavily granulated, whereas in *H. goudoti* n. comb. this region of the sidewall is smooth; the anterior carapace of *H. madagascariensis* is heavily granulated, whereas that of *H. goudoti* n. comb. is smooth; and the cervical grooves of *H. madagascariensis* are short, whereas those of *H. goudoti* n. comb. are long.

We have examined the lectotype and a female paralectotype of *P. (P.) humbloti* (USNM 29987), cw 28 mm, and found that the characters of the mandible, third maxilliped, carapace, sidewall, and chelipeds correspond well with those described above for *H. madagascariensis*. We therefore regard *P. (P.) humbloti* as a junior objective synonym of *H. madagascariensis*. It should be noted that the specimen SMF 2618 labeled *H. humbloti* in Bott (1965: figs 5, 6, pl. 3, figs 12, 13) from Sakalava was not from the type series of this taxon. We consider it likely that this specimen (SMF 2618) was misidentified, and that it may not actually belong to the same species as *H. humbloti* sensu Rathbun, 1904. For example, the illustration of the mandibular palp in Bott (1965: fig. 5a, b) indicates that the palp of Bott's specimen (SMF 2618) is only basally

thickened rather than deeply cleft and bilobed, as is the case for the paralectotype of *P. (P.) humbloti*. Further, Bott (1965) considered *Potamon (P.) bombetokensis* to be a junior synonym of *H. humbloti*. We could find no support for this view in the present work, and *P. (P.) bombetokensis* is here recognised as a valid species of *Hydrothelphusa*. Rathbun (1904) described *P. (P.) grandidieri* as a separate species based on a female syntype, while Bott (1965) treated *P. (P.) grandidieri* as a junior synonym of *H. humbloti*. We have examined the lectotype specimen of *P. (P.) grandidieri*, a subadult female (cw 28.1, cl 20.8 mm) (MNHN-B 5168), and found the mandibular palp terminal segment to be deeply cleft and bilobed, corresponding to that described above for *Hydrothelphusa*. Other characters of the carapace, third maxilliped, chelipeds and walking legs place this taxon close to *H. madagascariensis*. Therefore, *P. (P.) grandidieri* is treated here as a junior objective synonym of *H. madagascariensis*.

Bott (1965) reassigned the type of *Bottia madagascariensis reticulata* Pretzmann, 1961 (NHMW 2731) to *H. agilis madagascariensis* (A. Milne-Edwards, 1872); *B. m. reticulata* is here recognised as *H. madagascariensis*.

A detailed description of the arterial system of *H. madagascariensis* is provided by Vuillemin (1963).

*Hydrothelphusa bombetokensis* (Rathbun, 1904) (Figs 1C; 3C; 4C; 5C; 6C; 7E, F; 8C; 9N-Q; 11C)

*Potamon (Potamon) bombetokensis* Rathbun, 1904: 298-299, pl. 12, fig. 6. — Bals 1929: 354.

*Bottia bombetokensis* – Pretzmann 1961: 164, fig. 4.

*Hydrothelphusa humbloti* – Bott 1965: 342-344.

**MATERIAL EXAMINED.** — **Madagascar.** Close to Bombetok, coll. M. Grandidier, 1 ad. ♂, lectotype of *Potamon (Potamon) bombetokensis* Rathbun, 1904, cw 50.1, cl 38, ch 17, fw 15.5 mm (MNHN-B 5062). — Bombetok, Province Faranfangana, 6 specimens (MNHN-B 5063), 1 specimen (MNHN-BP 5150). — Andrafiavelo (Sakalava), 1 subad. ♂ cw 39.5, cl 30.5 mm (MNHN-B 5177). — 29.VIII.1930, coll. R. Decary, 2 subad. ♀ ♀ cw 36, cl 29, ch 25, fw 20 mm and cw 35, cl 29 mm (MNHN-B 27563), collected together with *Hydrothelphusa humbloti* (MNHN-B 5179). — Forest, 1700 m, Ambo-

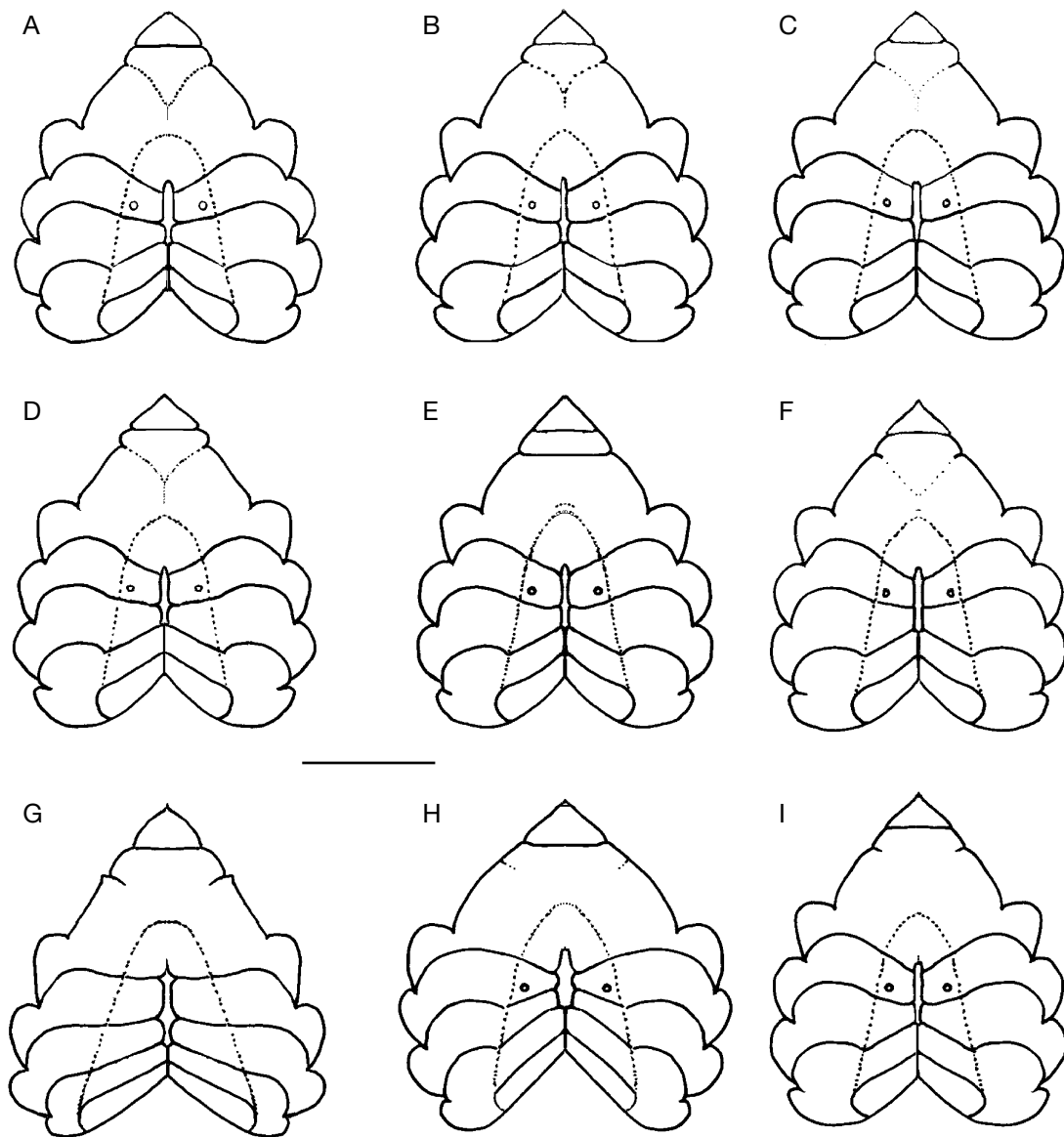


FIG. 3. — Inferior view of the sternum of adult males of Madagascan freshwater crabs; **A**, *Hydrothelphusa agilis* A. Milne-Edwards, 1872; **B**, *H. madagascariensis* (A. Milne-Edwards, 1872); **C**, *H. bombetokensis* (Rathbun, 1904); **D**, *H. goudoti* (H. Milne Edwards, 1853) n. comb.; **E**, *Malagasya antongilensis* (Rathbun, 1905) n. comb.; **F**, *M. goodmani* (Cumberlidge, Boyko & Harvey, 2002) n. comb.; **G**, *Madagapotamon humberti* Bott, 1965; **H**, *Marojejy longimerus* Cumberlidge, Boyko & Harvey, 2002; **I**, *Boreas uglowi* n. gen., n. sp. Scale bar: A, 11.7 mm; B, 17.2 mm; C, 15.9 mm; D, 14.5 mm; E, 10.2 mm; F, 7 mm; G, 9.6 mm; H, 6.4 mm; I, 9.1 mm.

hitantely, 10.IV.1939, coll. R. Decary, 6 specimens, all juv. or subad., largest subad. ♀ ♀ cw 35.5, cl 27.5 mm (MNHN-B 5180). — Lily River-Ampefy, Department of Soavinandriana, 16.I.1963, 2 subad. ♀ ♀ cw 23.5, cl 20 mm and cw 25.5, cl 19.5 mm (MNHN-B 25751). — Province d'Antananarivo,

Réserve spéciale d'Ambohitantely, 24 km NE Ankazobe, 1450 m, 18°10.1'S, 47°16.6'E, 15.XII.1997, coll. S. M. Goodman, 5 ad. ♀ ♀ cw 52.5, 53.1, 53.4, 54.2, 59.4 mm, 2 subad. ♀ ♀ cw 45.3, 49 mm, 1 ad. ♂ cw 61.9 mm, 1 subad. ♂ cw 41.5 mm, 2 juv ♂ ♂ cw 31, 25.7 mm (FMNH 5471).

TYPE LOCALITY. — Madagascar, close to Bombetok.

DISTRIBUTION. — Madagascar (Fig. 11C).

DIAGNOSIS. — Exorbital, epibranchial teeth both large, broad, triangular. Fingers of right, left propodi of chelipeds each with characteristic large molariform cluster of three or four fused teeth; second carpal tooth on carpus of p1 extremely short.

#### REDESCRIPTION

Carapace wide (cw/fw = 3.5), high (ch/fw = 1.3). Anterior carapace surface completely smooth, except for faint carinae in the anterolateral corners; posterolateral regions with short carinae; distinct gap between epigastric, postorbital crests; mid-groove between epigastric crests broad; postorbital crests not meeting anterolateral margins. Semi-circular, urogastric grooves deep; cervical grooves short. Front moderately deflexed; frontal margin indented, slightly granulated. Exorbital, epibranchial teeth both large, directed forward; anterolateral margin posterior to epibranchial tooth granulated; suborbital, pterygostomial regions of carapace sidewall both heavily granulated, subhepatic region smooth; suborbital margin distinctly granulated. Fingers of right, left propodi of chelipeds each with characteristic large molariform cluster of three or four fused teeth, dactylus with two large fused proximal teeth, one large tooth at midpoint. Anterior inferior margin of ischium of p1 lined by small teeth, posterior margin smooth. Inferior margins of merus of p1 granular, distal margin with single, large pointed distal meral tooth; superior surface of merus of p1 smooth. Inner margin of carpus of cheliped with two teeth; first carpal tooth long, triangular, tip pointed; second carpal tooth small, one-quarter size of first; margin behind second tooth with small tooth.

#### Size

The adult size range is from cw 50 to 61.9 mm. The carapace proportions are given in Table 3.

#### REMARKS

Rathbun (1904) described *P. (P.) bombetokensis* from an adult male specimen (cw 50.1 mm), which is here designated the lectotype. The new material reported on here includes a good series

of adult specimens (up to cw 61.9 mm), making these the largest representatives of the species yet known. *Hydrothelphusa bombetokensis* is a widely distributed species found in most regions of the island. *Hydrothelphusa bombetokensis* is recognised here as a valid species, and we can find no support for Bott's (1965) opinion that this species is a junior synonym of *H. humbloti*.

Although Pretzmann (1961) recognised *P. (P.) bombetokensis* as a distinct species, he assigned this taxon to *Bottia* Pretzmann, 1961 (type species *Potamon (Potamon) bombetokensis* Rathbun, 1904), a genus that was subsequently synonymised by Bott (1965) with *Hydrothelphusa*.

The distinguishing differences between *H. bombetokensis*, *H. madagascariensis* and *H. agilis* are provided above. *Hydrothelphusa bombetokensis* can be distinguished from *H. goudoti* n. comb. as follows: the carapace of *H. bombetokensis* is less wide (cw/fw = 3.5) and less arched (ch/fw = 1.3) than that of *H. goudoti* n. comb. (cw/fw = 3.9, ch/fw = 1.6); the exorbital angle tooth and the epibranchial tooth of *H. bombetokensis* are both large and triangular, whereas these teeth in *H. goudoti* n. comb. are small and blunt; the suborbital and pterygostomial regions of the carapace sidewall of *H. bombetokensis* are both heavily granulated, whereas those of *H. goudoti* n. comb. are smooth; the cervical grooves of *H. bombetokensis* are very short, whereas those of *H. goudoti* n. comb. are very long.

#### *Hydrothelphusa goudoti*

(H. Milne Edwards, 1853) n. comb.

(Figs 1D; 3D; 4D; 5D; 6D; 7G, H; 8D; 9J-M; 11D)

*Thelphusa goudoti* H. Milne Edwards, 1853: 212. — A. Milne-Edwards 1869: 172, pl. 8, fig. 4a-b; 1887: 135.

*Telphusa goudoti* – De Man 1892: 235.

*Potamon goudoti* – De Man 1898: 434.

*Potamon (Potamon) goudoti* Rathbun, 1904: 305, 306, fig. 34, pl. 13, fig. 10. — Balss 1929: 355.

*Potamon (Geothelphusa) methueni* Calman, 1913: 920.

*Bottia goudoti* – Pretzmann 1961: 164, fig. 3.

*Gecarcinautes goudoti* — Bott 1965: 338, 339, pl. 2, figs 6, 7. — Cumberlidge 1997: 585; 1998: 209.



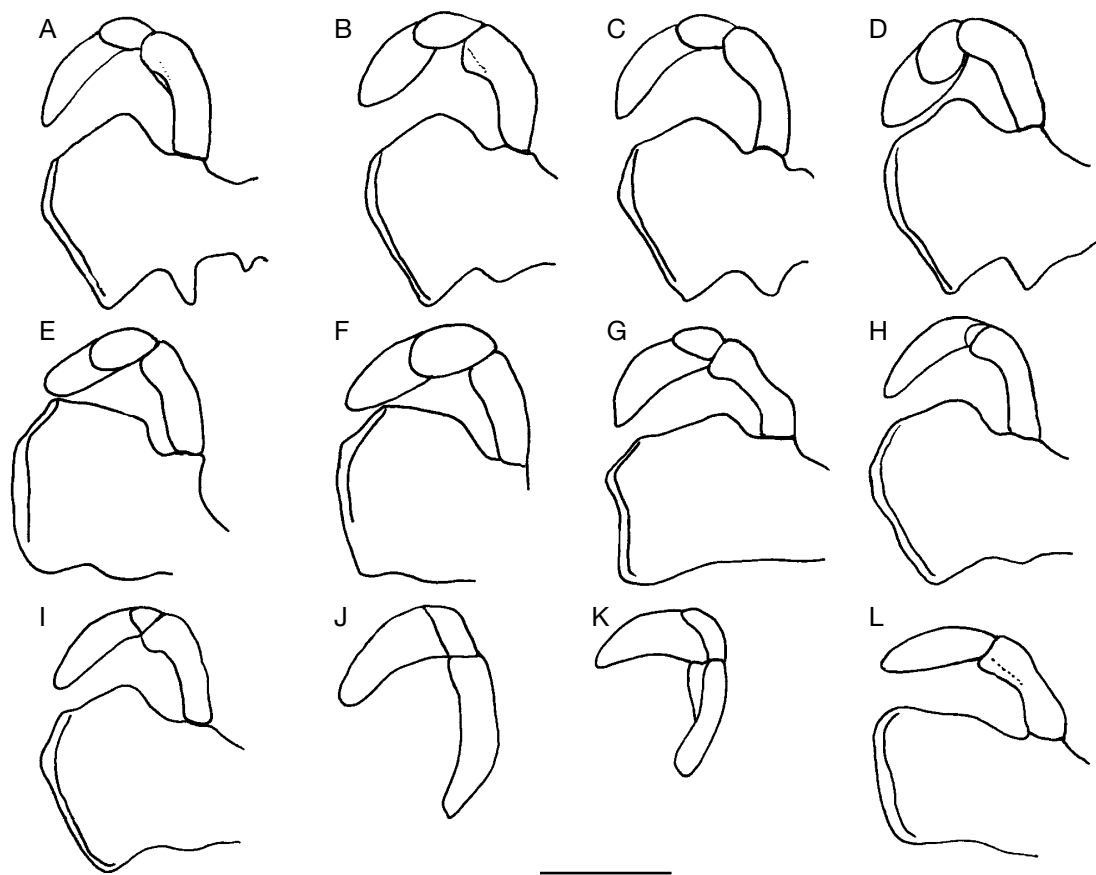


FIG. 4. — Left mandible of Madagascan freshwater crabs, frontal view showing the palp (J, K based on Ng & Takeda 1994); **A**, *Hydrothelphusa agilis* A. Milne-Edwards, 1872; **B**, *H. madagascariensis* (A. Milne-Edwards, 1872); **C**, *H. bombetokensis* (Rathbun, 1904); **D**, *H. goudoti* (H. Milne Edwards, 1853) n. comb.; **E**, *Malagasya antongilensis* (Rathbun, 1905) n. comb.; **F**, *M. goodmani* (Cumberlidge, Boyko & Harvey, 2000) n. comb.; **G**, *Marojejy longimerus* Cumberlidge, Boyko & Harvey, 2000; **H**, *Boreas uglowi* n. gen., n. sp.; **I**, *Skeleosophusa gollhardi* (Bott, 1965); **J**, *S. proluxa* Ng & Takeda, 1994; **K**, *S. eumeces* Ng & Takeda, 1994; **L**, *Madagapotamon humberti* Bott, 1965. Scale bar: A-I, K, L, 1.0 mm; J, 1.25 mm.

**MATERIAL EXAMINED.** — **Madagascar.** Road between Bombetok and Tananarive, coll. Goudot, lectotype of *Thelphusa goudoti*: 1 ad. ♂ cw 46, cl 33.5 mm, dried specimen (MNHN-B 3817). — 2 dried paralectotypes, 1 ad. ♂ cw 41, cl 30.7 mm, second specimen broken, presumed syntype, described by A. Milne-Edwards (1869) in *Arch. Mus. Hist. Nat.* V: 172 (MNHN-B 3818). — Imerimandrosa, type of *P. (G.) methueni* (NHM 1914.6.11.3). — Tananarive, 1 subad. ♀ cw 37 mm (MNHN-B 5166). — Tananarive, coll. M. Catat, 3 subad. ♂ cw 29, 29.5, 40 mm (MNHN-B 167). — 20.IV.1897, coll. Ct. Dorr, 1 subad. ♀ cw 23, cl 17 mm (MNHN-B 26642). — Forest, Manambato Valley, 1927, coll. G. Petit, 1 subad. ♀ cw 23, cl 17 mm (MNHN-B 26643). — Forest, Manambato Valley, North of Tsaratanana Mountains, 1 subad. ♂ cw 23.6 mm (ZSM

1532/1). — 1911, coll. J. de Joannis, 1 ad. ♀, ovig. cw 30 mm (MNHN-B 26644), 1 subad. ♂ cw 26, cl 18.5 mm (MNHN-B 25733). — Lake Alaotra, North of Antananarivo (formerly Tananarive), coll. Voeltzkow, 3 ad. ♂ cw 46.8, 41.4, 32.8 mm, 1 ad. ♀ cw 31.2 (ZSM 1532/2). — Toamasina, coll. J. Millot, 1 subad. ♀ cw 20.9 mm (ZSM 1532/3). — Chambendiana river, 1 specimen (ZIM K3543). — Lake Alaotra, 1 specimen (SMF 4486). — Lake Alaotra, 1 specimen (ZMB 13912). — Tananarive, 1 specimen (ZMB 13911).

**TYPE LOCALITY.** — Madagascar. *Thelphusa goudoti*: Madagascar, road between Bombetok and Tananarive. *Potamon (Geothelphusa) methueni*: Imerimandrosa.

**DISTRIBUTION.** — Madagascar (Fig. 11D). See Cumberlidge (1998) for more localities.

DIAGNOSIS. — Carapace very wide (cw/fw = 3.9), very long (cl/fw = 2.8), highly arched (ch/fw = 1.6); epigastric, postorbital crests fused forming distinct postfrontal crest, ending just before meeting anterolateral margins. Front distinctly deflexed (but not vertical); exorbital, epibranchial teeth broad, low, blunt, continuous with curve of anterolateral margin; cervical grooves long, p5 merus very short (ratio length p5 merus/cw = 0.4). Midpoint of medial fold of terminal article of gonopod 1 widened by rounded, raised lobe.

#### REDESCRIPTION

Carapace very wide (cw/fw = 3.9), very long (cl/fw = 2.8), highly arched (ch/fw = 1.6). Suborbital margin with faint granules. Anterior carapace regions smooth, posterolateral regions with short, faint, carinae. Semi-circular, urogastric, cardiac grooves deep; cervical grooves deep, long, not meeting postorbital crest. Epigastric, postorbital crests fused, forming distinct postfrontal crest, ending just before meeting anterolateral margins (i.e. postfrontal crest incomplete). Front distinctly deflexed (but not vertical); front with shallow indentation, margin raised, smooth. Exorbital, epibranchial teeth broad, low, blunt, continuous with curve of anterolateral margin. Anterolateral margin posterior to epibranchial tooth raised, granular. Suborbital margin faintly granulated. Suborbital, pterygostomial regions of carapace sidewall granular, subhepatic region either smooth or with faint granules.

Finger of propodus of p1 (cheliped) with three medium-sized pointed proximal teeth, one large tooth, several small teeth; dactylus with small teeth interspersed by three medium teeth. Anterior inferior margin of ischium of p1 granular, posterior inferior margin smooth. Inferior margins of merus of p1 distinctly granulated, distal margin with single large pointed tooth; superior surface of merus granular. Inner margin of carpus of cheliped with two teeth; first carpal tooth large, pointed; second tooth small, low; margin behind second tooth raised, smooth. Midpoint of medial fold of terminal article of gonopod 1 with distinct, rounded, raised lobe.

#### Size

The adult size range is from cw 40 to 46.8 mm. The carapace proportions are given in Table 3.

#### REMARKS

*Hydrothelphusa goudoti* n. comb. was the first freshwater crab to be described from Madagascar (in 1853), and it has long been recognised as a distinct species. However, the generic assignment of this species has been less stable and has been revised a number of times (Rathbun 1904; Colosi 1920; Pretzmann 1961; Bott 1965), and is revised once again in the present study. The present reassignment of *H. goudoti* n. comb. to *Hydrothelphusa* (Hydrothelphusinae, Potamonautidae) is made on the basis of similarities of characters of the mandibular palp, carapace, thoracic sternum, third maxilliped, and gonopods 1 and 2 of *H. goudoti* n. comb., which unite this species with *H. bombetokensis*, *H. agilis* and *H. madagascariensis*. The distinguishing differences between *H. goudoti* n. comb., *H. bombetokensis*, *H. madagascariensis* and *H. agilis* are provided above. *Hydrothelphusa goudoti* n. comb. is characterized by its unusual carapace proportions: it has the widest, longest and most arched carapace of any species in this genus, and the p5 merus length/cw ratio is the shortest of any species in this genus (Table 3).

Bott (1965) regarded *P. (G.) methueni* as a junior synonym of *Madagapotamon ankaraharae* (Nobili, 1906), but we can find no support for that opinion here. For example, the type of *P. (G.) methueni* was examined in this study and the mandibular palp is bilobed, of the kind seen in *Hydrothelphusa* (and is not simple, as has been reported for *M. ankaraharae* by Bott [1965], but see below for a different opinion). In addition, the type of *P. (G.) methueni* compares well with type of *H. goudoti* n. comb. in all important characters of the carapace, chelipeds, mouthparts, sternum and gonopods. For these reasons, *P. (G.) methueni* is regarded here as a junior objective synonym of *H. goudoti* n. comb.

Bott (1965) considered *P. (G.) ankaraharae* to be a species of *Madagapotamon*, but we do not follow this view here. The illustration of the carapace, third maxilliped, sternum and abdomen of the type of *Potamon (Geothelphusa) ankaraharae* provided by Nobili (1906) and reproduced in Bott (1965: fig. 9a-c) conform with characters described above for *H. goudoti* n. comb., and we sus-

pect that *P. (G.) ankaraharae* should be regarded as a junior subjective synonym of *H. goudoti*. However, without examining the type specimen of *P. (G.) ankaraharae* (which has proved difficult to obtain) we have no first-hand knowledge of the characters of the mandibular palp and first gonopod of this taxon. It should be noted that the male specimen cw 28 mm (MNHN Paris, no number provided) labeled *M. ankaraharae* in Bott (1965: fig. 9d, e, pl. 5, figs 23-25) from Diego-Suarez (now Antsiranana) was not part of the type series, and we consider it likely that his specimen was actually misidentified, and that it may not actually be *P. (G.) ankaraharae* Nobili, 1906. As such, the illustrations of gonopods 1 and 2 in Bott 1965 (fig. 9d, e) and this text description of the mandibular palp as simple, should not be regarded as those of *P. (G.) ankaraharae* sensu Nobili, 1906.

#### *The taxonomic position of Gecarcinautes Bott, 1960*

The genus *Gecarcinautes* Bott, 1960 is here synonymised with *Potamonautes* Macleay, 1838. *Gecarcinautes* was erected by Bott (1960) to accommodate *G. brincki* Bott, 1960, from South Africa, which he referred to the Gecarcinucinae in the then recognised family Potamonidae. In his revision of the Madagascar freshwater crabs, Bott (1965) assigned *Thelphusa goudoti* to *Gecarcinautes* (together with *P. [P.] antongilensis* and *P. [P.] a. vondrozi*). Although Bott (1969, 1970a, b) later included the African and Indian species of Gecarcinucinae in the Gecarcinucidae, he made no mention of the Madagascar species he had previously assigned to this subfamily. Later authors (Ng & Takeda 1994) simply assumed that all of the Madagascar species of *Gecarcinautes* assigned to the Gecarcinucinae belonged there.

The Madagascar Gecarcinucinae of Bott (1965) included crabs with a bilobed terminal segment of the mandibular palp, and the photograph of the palp of *G. a. antongilensis* (Bott 1965: fig. 3a, b) clearly shows a bilobed palp with a medium-sized anterior process. However, Bott (1965) failed to recognise that this type of mandibular

palp is also found in *Hydrothelphusa*, and this confusion may have led to his erroneous assignment of *H. goudoti* n. comb. to *Gecarcinautes*. The fact that Ng & Takeda (1994) followed Bott in classifying *Hydrothelphusa* in the Hydrothelphusinae (Potamonautidae) and *Gecarcinautes* in the Gecarcinucinae (Gecarcinucidae) on the basis of mandibular palp characters described by Bott (1965) only compounded this confusion.

The uncertain taxonomic status of *Gecarcinautes* is further complicated by our examination of *G. brincki*, the type species of *Gecarcinautes* from South Africa. This taxon has a mandibular palp terminal segment with only a small ledge-like anterior process (the basal thickening of Bott 1965) which is definitely not bilobed (Cumberlidge 1996a, b, 1999; Stewart 1997). Those authors found no justification for the family assignment of this taxon to a separate family, the Gecarcinucidae, and transferred *G. brincki* to *Potamonautes* (Potamonautidae). The transfer of the type species of the genus *Gecarcinautes* (Gecarcinucinae, Gecarcinucidae) to *Potamonautes* (Potamonautidae) effectively synonymising both genera, creates a few problems. This unfortunate situation raises questions about the proper generic assignment of other taxa that have been referred to *Gecarcinautes*, such as *G. goudoti*, *G. a. antongilensis*, *G. a. vondrozi*, and *G. goodmani*. The taxonomic status of all of these taxa is revised in the present work: *G. goudoti* is reassigned to *Hydrothelphusa*, while *G. a. antongilensis*, *G. a. vondrozi* and *G. goodmani* are all referred to *Malagasya* n. gen.

#### Genus *Malagasya* n. gen.

*Potamon (Parathelphusa)* Rathbun, 1905: 265, 266, fig. 21, pl. 12, fig. 5. — Cumberlidge 1998: 210 [non *Parathelphusa* H. Milne Edwards, 1853].

*Hydrothelphusa (Acanthothelphusa)* Bouvier, 1921: 52 [non *Acanthothelphusa* Ortmann, 1893].

*Potamon (Geothelphusa)* Balss, 1929: 355, fig. 21, fig. 2 [non *Geothelphusa* Stimpson, 1858].

*Gecarcinautes* Bott, 1960: 337, 338, figs 1-3, pl. 1, figs 1-3; 338, pl. 1, fig. 45. — Vuillemin 1972: 135-166. — Ng & Takeda 1994: 163 [non *Gecarcinautes* Bott, 1965 = *Potamonautes* Macleay, 1838].

TYPE SPECIES. — *Potamon* (*Parathelphusa*) *antongilensis* Rathbun, 1905, by present designation.

ETYMOLOGY. — *Malagasya* is a noun in apposition derived from Malagasy, for the Malagasy Republic. Gender feminine.

DIAGNOSIS. — Carapace outline heart-shaped, elongated (cl/fw = 3), high (ch/fw = 1.6), very wide anteriorly (cw/fw = 3.8), frontal, posterior margins narrow (cw 0.3 mm); distinct gap between epigastric, postorbital crests; front sharply deflexed, almost vertical; exorbital tooth pointed; epibranchial tooth pointed, smaller; anterolateral margin between exorbital, epibranchial teeth lacking intermediate tooth; anterolateral margin behind epibranchial tooth with five or more large pointed teeth. Mandibular palp two-segmented, terminal segment with enlarged anterior process (about 0.5 as big as terminal segment) at junction between segments; third maxilliped exopod with long flagellum, ischium with deep vertical sulcus. Thoracic sternal sulcus s2/s3 horizontal, completely crossing sternum, s3/s4 either horizontal or V-shaped. Episternal sulci s4/e4, s5/e5, s6/e6, s7/e7 smooth, all lacking visible groove. Walking legs (p2-p5) extremely long, slender (ratio length merus p5 to cw 0.52). Adult male abdomen slim, triangular. Deep suture between terminal article and subterminal segment of gonopod 1 visible dorsally, ventrally; dorsal membrane broad. Long medial flap on ventral side of subterminal segment of gonopod 1, flap reaching to basal margin of segment; lateral flap on ventral face of subterminal segment of gonopod 1 with distinct disto-medial shoulder; opening of chamber for gonopod 2 on subterminal segment of gonopod 1 positioned about one-quarter of segment length from basal margin. Gonopod 2 terminal article flagellum medium length, ratio length terminal article to subterminal segment 0.6.

#### REMARKS

*Malagasya* n. gen. is the commonest and most widely distributed of the long-legged freshwater crabs of Madagascar. The bilobed mandibular palp terminal segment of *Malagasya* n. gen. is similar to that seen in *Hydrothelphusa* and *Marojejy*, but *Malagasya* n. gen. is easily distinguished from both by its heart-shaped carapace outline. Other distinguishing characters are the walking legs of *Hydrothelphusa* (which are not elongated), and the chelipeds of *Marojejy* (which are strikingly elongated). *Malagasya* n. gen. is established to accommodate two species: *M. antongilensis* and *M. goodmani* previously assigned to *Gecarcinautes* (see above).

*Malagasya* n. gen. superficially resembles *Globonautes macropus* (Rathbun, 1898) from West Africa in the heart-shaped carapace outline, the highly deflexed almost vertical front, and the extremely elongated walking legs (Cumberland 1991, 1999). The two genera can be distinguished as follows: the anterolateral margins of the carapace of *Malagasya* n. gen. are clearly toothed, whereas these margins in *Globonautes* are smooth; the anterior process on the terminal segment of the mandibular palp of *Malagasya* n. gen. is about half as large as the posterior lobe, whereas this process is large and subequal in *Globonautes*; and the exopod of the third maxilliped of *Malagasya* n. gen. has a long flagellum, whereas in *Globonautes* the exopod lacks a flagellum.

*Malagasya* n. gen. can be distinguished from *Hydrothelphusa* and *Boreas* n. gen. by the length of the walking legs, which are of normal length in *Hydrothelphusa* and *Boreas* n. gen. and slender and elongated in *Malagasya* n. gen. *Malagasya* n. gen. can be distinguished from the other Madagascan genera with slender, elongated walking legs (e.g., *Madagapotamon*, *Skelosophusa* and *Marojejy*) as follows. *Malagasya* n. gen. is close to *Madagapotamon* because both share the following suite of characters: an elongated, heart-shaped carapace outline, very narrow anterior and posterior margins of the carapace, sharply-pointed exorbital and epibranchial teeth, a row of small teeth on the anterolateral margin, a sharply deflexed, and an almost vertical front. The two taxa can be easily distinguished by differences in the terminal article of the mandibular palp (which in *Malagasya* n. gen. is bilobed with a medium-sized anterior process whereas that of *Madagapotamon* is simple and lacks an anterior process), by the exopod of the third maxilliped (which in *Malagasya* n. gen. is a long flagellum, whereas in *Madagapotamon* the flagellum is lacking), and by the shape of the adult male abdomen (which is triangular in *Malagasya* n. gen. but oval and egg-shaped in *Madagapotamon*).

*Malagasya* n. gen. can be distinguished from *Marojejy* by the length of the eyestalks (which taper sharply, and have a reduced cornea in

*Marojejy*, and are of normal length with a large cornea in *Malagasya* n. gen.); by the length of the merus of the chelipeds (which is extremely elongated in *Marojejy* and of normal length in *Malagasya* n. gen.); by the exorbital and epibranchial teeth (which are low and blunt in *Marojejy*, and relatively large and pointed in *Malagasya* n. gen.); by the anterolateral margins of the carapace (which are granular in *Marojejy*, but conspicuously toothed in *Malagasya* n. gen.); and by the frontal region (which is wide and moderately deflexed in *Marojejy*, but narrow and sharply deflexed in *Malagasya* n. gen.).

*Malagasya* n. gen. can be distinguished from *Skelosophusa* as follows: *Malagasya* n. gen. has an elongated, heart-shaped carapace outline, narrow frontal and posterior carapace margins, a sharply pointed epibranchial tooth, several small teeth on the anterolateral margin, and a sharply deflexed vertical front. In contrast, *Skelosophusa* has a transversely oval carapace, relatively wide frontal and posterior margins of the carapace, a blunt and low epibranchial tooth, smooth or granular (never toothed) anterolateral margins, and a moderately deflexed (not vertical) front.

### *Malagasya antongilensis*

(Rathbun, 1905) n. comb.

(Fig 1E; 3E; 4E; 5E; 6E; 7I, J; 8I; 10C, D; 11F)

*Potamon (Parathelphusa) antongilensis* Rathbun, 1905: 265, 266, fig. 21, pl. 12, fig. 5. — Cumberlidge 1998: 210.

*Hydrothelphusa (Acanthothelphusa) antongilensis* — Bouvier 1921: 52.

*Potamon (Geothelphusa) antongilensis* — Balss 1929: 355, fig. 21.

*Thelphusa madagascariensis* — Balss 1929: 254 — Balss 1934: 520, pl. 1, fig. 1 [non *madagascariensis* H. Milne Edwards, 1872].

*Gecarcinautes antongilensis antongilensis* Bott, 1965: 337, figs 1-3, figs 1-3; 338, pl. 1. — Vuillemin 1972: 135-166. — Ng & Takeda 1994: 163.

*Gecarcinautes antongilensis vondrozi* — Bott 1965: 338, pl. 1, figs 4, 5. — Cumberlidge *et al.* 2002: 75.

MATERIAL EXAMINED. — Madagascar. Antongil Bay, coll. M. Mocquerys, 1 ♂ holotype of *Potamon (Parathelphusa) antongilensis* Rathbun, 1905, cw 22.3,

cl 17.5 mm (MNHN-B 5033). — Forest, Manambato Valley, 1927, coll. G. Petit, 1 subad. ♀ cw 19, cl 14.5 mm, 1 ad. ♀ cw 34, cl 25 mm (MNHN-B 5035). — Ambilobé, coll. J. Millot, 1 ad. ♀ cw 34, cl 25 mm (MNHN-B 5036). — Tamatave, coll. J. Millot, several specimens (MNHN-B 5037). — Tamatave, 1924, coll. J. Millot, more than 10 specimens (MNHN-B 5041). — Toamasina, Autumn 1922, coll. J. Millot, 2 ad. ♀ ♀ cw 32, cl 23.5, ch 12.5, fw 7.5 mm and cw 29.5, cl 23, ch 12, fw 7.5 mm, 1 subad. ♀ cw 27.5 mm, 1 ad. ♀ cw 32 mm, 1 ad. ♀ ovig. cw 29.5 mm, 1 subad. ♀ cw 22.5, cl 17.2 mm (MNHN-B 5063). — Tsingalapaky, Fetoky, Fandiarano, Marotsy river, Tsimantsy (another label indicates Forêt de Périnet, Moramanga), 13.XII.1965, 5 specimens (MNHN-B 25752). — Forêt de Périnet, I.1966, 1 specimen, 3 subad. ♂ ♂ cw 20.8, 19.8, 16 mm, 2 subad. ♀ ♀ cw 23.5, 21 mm, 1 juv. cw 14.3 mm (MNHN-B 25764). — Grotte de la Mananjiba, Nosy-Bé, Ambilobe, 1924, coll. Waterlott, 2 juv. cw 12.8, 11.6 mm (ZSM 1163/1). — Toamasina, coll. J. Millot, 2 ad. ♂ ♂ cw 30.7, 30.4 mm, 2 juv. ♂ ♂ cw 18.9, 15.8 mm, 3 ad. ♀ ♀ cw 31.2, ovig., 29.0, ovig., 30.1 mm, 1 subad. ♀ cw 23.5 mm (ZSM 1531/1). — Toamasina, 1 ad. ♂ cw 30, cl 22.5, ch 11.5, fw 8 mm (SMF 2615).

TYPE LOCALITY. — *Potamon (Parathelphusa) antongilensis*: Antongil Bay, Madagascar. *Gecarcinautes antongilensis vondrozi*: Vondrozo, crab in a hole in an old tree, in the forest.

DISTRIBUTION. — Madagascar (Fig. 11F).

DIAGNOSIS. — Pterygostomial region of carapace sidewall with small sparse hairs; suborbital, subhepatic regions of carapace sidewall finely granulated; ischium of third maxilliped with deep vertical sulcus. Third sternal sulcus s3/s4 straight, horizontal, completely crossing sternum; s6/s7 meeting a5/a6 junction; inner margin of propodus of p5 with distinct spines.

### REDESCRIPTION

Carapace outline heart-shaped, elongated (cl/fw = 3), high (ch/fw = 1.6), very wide anteriorly (cw/fw = 3.8), tapering sharply, frontal, posterior margins narrow (cw 0.3 mm); entire dorsal carapace finely granulated, sculpted by grooves; branchial groove deep; semi-circular, urogastric, cardiac grooves deep; cervical grooves short; distinct gap between epigastric, postorbital crests; front sharply deflexed, almost vertical. Exorbital, epibranchial teeth equal, large, curved, pointed; anterolateral margin behind epibranchial tooth with five or

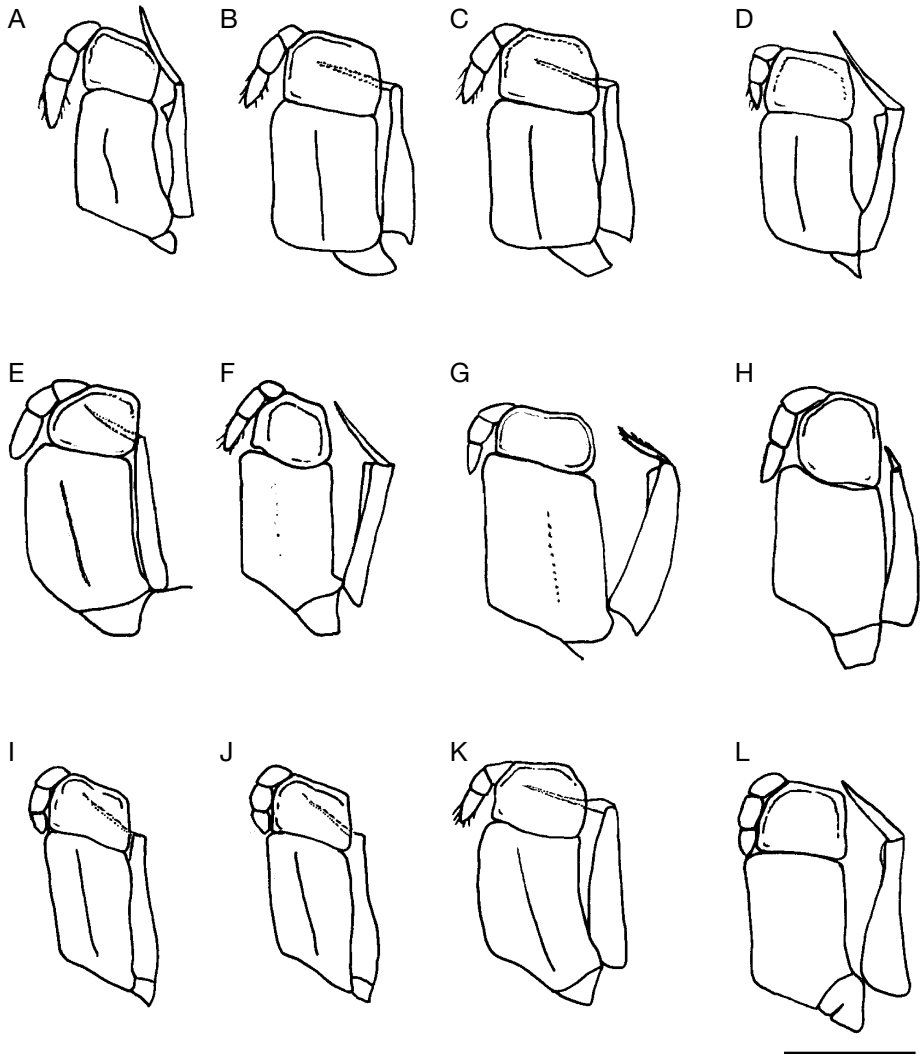


FIG. 5. — Left third maxilliped of Madagascan freshwater crabs, frontal view (J, K based on Ng & Takeda 1994); **A**, *Hydrothelphusa agilis* A. Milne-Edwards, 1872; **B**, *H. madagascariensis* (A. Milne-Edwards, 1872); **C**, *H. bombetokensis* (Rathbun, 1904); **D**, *H. goudoti* (H. Milne Edwards, 1853) n. comb.; **E**, *Malagasya antongilensis* (Rathbun, 1905) n. comb.; **F**, *M. goodmani* (Cumberlidge, Boyko & Harvey, 2002) n. comb.; **G**, *Marojejy longimerus* Cumberlidge, Boyko & Harvey, 2002; **H**, *Madagapotamon humberti* Bott, 1965; **I**, *Skelosophusa gollhardi* (Bott, 1965); **J**, *S. proluxa* Ng & Takeda, 1994; **K**, *S. eumeces* Ng & Takeda, 1994; **L**, *Boreas uglowi* n. gen., n. sp. Scale bar: A-D, 5.0 mm; E-L, 3.5 mm.

more large pointed teeth; anterolateral margin curving inward, not continuous with posterolateral margin. Vertical sulcus on carapace sidewall running from base of epibranchial tooth to epimeral sulcus, dividing suborbital region from hepatic region, sidewall divided into three regions; suborbital, subhepatic regions of cara-

pace sidewall finely granulated, pterygostomial region near third maxilliped with short, sparse hairs. Suborbital margin raised, smooth. Mandibular palp two-segmented, terminal segment with enlarged lobe-shaped anterior process (about 0.5 as big as terminal segment) at junction between segments. Third maxilliped exopod

medium length, reaching to mid-point of merus, with long flagellum; ischium with deep vertical sulcus. Thoracic sternal sulcus s1/s2 not visible; sternal sulcus s2/s3 deep, horizontal; sternal sulcus s3/s4 horizontal, completely crossing sternum, meeting anterior margin of sterno-abdominal cavity on sternite s4. Anterior sternum with conspicuous setae.

Adult male abdomen slim, triangular; a6 short, only as long as width of distal margin of a6; telson sides indented, bell-shaped. Gonopod 1 terminal article short, ratio length terminal article to subterminal segment 0.25, longitudinal groove on terminal article clearly visible on ventral, superior sides, not visible on dorsal side; lateral, medial folds of ventral side of terminal article equal in height, width; terminal article almost straight, directed slightly outward; slim tapering to upcurved tip with clear apical opening; subterminal segment of gonopod 1 with distinct triangular shoulder on external margin near junction with terminal article. Gonopod 1 terminal article/subterminal segment junction marked by deep sulcus; dorsal membrane broad. Gonopod 2 longer than gonopod 1; gonopod 2 terminal article long, flagellum-like, shorter than subterminal segment, ratio length terminal article to subterminal segment 0.62.

Dactylus of right, left chelipeds relatively narrow, straight (one-quarter height of palm); upper margin of dactylus smooth; finger of propodus slim (one-third height of palm) lower margin of propodus of cheliped slightly indented. Fingers of propodus, dactylus with series of small teeth, no interspace when closed. Anterior, posterior inferior margins of ischium of p1 smooth. Inferior margins of merus of p1 toothed, distal margin with single pointed distal meral tooth; superior surface of merus granular. First carpal tooth on inner margin of carpus of p1 large, pointed, second carpal tooth smaller, pointed, followed by several smaller teeth. Anterior, posterior margins of propodus of p5 slightly serrated. Merus, carpus, propodus, dactylus of p2-p5 all conspicuously elongated, walking legs elongated, slender, ratio length merus p5/cw = 0.52.

#### Size

The adult size range is from cw 27.5-29 to 34 mm. The carapace proportions are given in Table 3.

#### REMARKS

Bott (1965) recognised one subspecies of *M. antongilensis* n. comb., which he called *Gecarcinautes antongilensis vondrozi*. We have examined the types of both taxa and we conclude that *G. a. vondrozi* should properly be viewed as a junior objective synonym of *M. antongilensis*, in agreement with the opinion of Cumberlidge *et al.* (2002).

*Potamon (Potamon) pittarrelli* Nobili, 1905 from Madagascar was overlooked in the study by Bott (1965) and its current taxonomic status is still uncertain. Ng & Takeda (1994) considered *P. (P.) pittarrelli* to resemble members of *Skelosophusa*. The type specimen of *P. (P.) pittarrelli* that was described and figured by Nobili (1905: 2, fig. 1) is unavailable, despite our best efforts to locate it. Ng & Takeda (1994) did not directly examine *P. (P.) pittarrelli* but nevertheless referred this taxon to *Gecarcinautes* based on a quote from Colosi (1920: 25): "Il palpo mandibolare è bilobo...". However the next part of the same sentence in Colosi (1920: 25) continues "il lobo accessorio è piuttosto piccolo" which implies that the anterior lobe/process is distinctly smaller than the posterior segment: but this is also the case for *Malagasya* n. gen., *Hydrothelphusa* and *Marojejy*. The heart-shaped carapace outline and elongated, slender walking legs of *P. (P.) pittarrelli* place it closest to *Malagasya* n. gen. However, it has proved difficult to locate and borrow the type material of *P. (P.) pittarrelli*, and our opinion is based only on photographs and illustrations in Nobili (1905). In our opinion, *P. (P.) pittarrelli* is most likely *M. antongilensis* n. comb., however, without first-hand knowledge of the specimens in question, it is difficult to be more certain.

Vuillemin (1972) provided excellent ecological notes and a detailed description of the habitat of *M. antongilensis* n. comb. It is possible that some of her specimens may belong to *Madagapotamon*

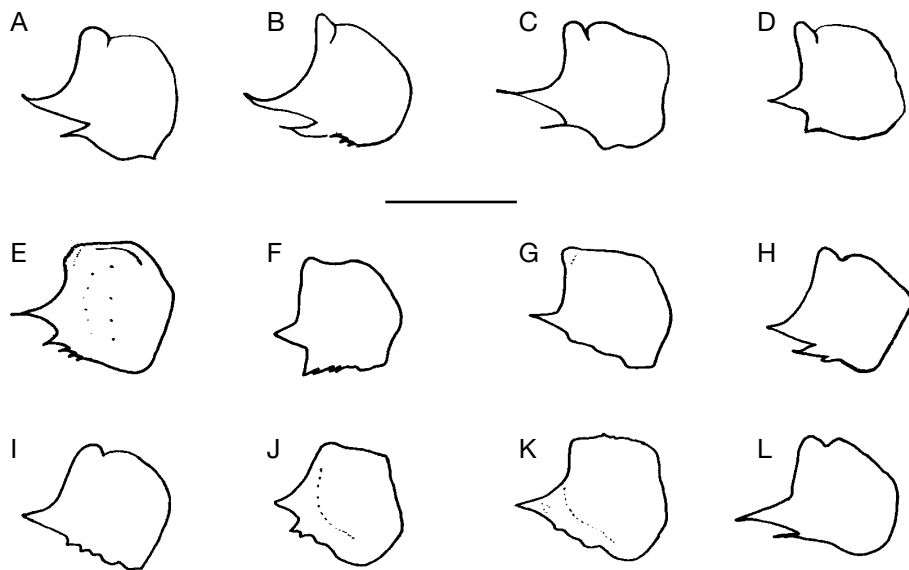


FIG. 6. — Superior view of the carpus of the cheliped (pereopod 1) of adult males of Madagascar freshwater crabs (J, K based on Ng & Takeda 1994); **A** *Hydrothelphusa agilis* A. Milne-Edwards, 1872; **B**, *H. madagascariensis* (A. Milne-Edwards, 1872); **C**, *H. bombetokensis* (Rathbun, 1904); **D**, *H. goudoti* (H. Milne Edwards, 1853) n. comb.; **E**, *Malagasya antongilensis* (Rathbun, 1905) n. comb.; **F**, *M. goodmani* (Cumberlidge, Boyko & Harvey, 2002) n. comb.; **G**, *Madagapotamus humberti* Bott, 1965; **H**, *Marojejy longimerus* Cumberlidge, Boyko & Harvey, 2002; **I**, *Skeleosopha gollhardi* (Bott, 1965); **J**, *S. proluxa* Ng & Takeda, 1994; **K**, *S. eumeces* Ng & Takeda, 1994; **L**, *Boreas uglowi* n. gen., n. sp. Scale bar: A-D, 5.5 mm; E-L, 3.5 mm.

*humberti* which is similar in many respects, but an exact identification is difficult to make from the photographs supplied in that publication.

#### *Malagasya goodmani*

(Cumberlidge, Boyko & Harvey, 2002) n. comb.  
(Figs 1F; 3F; 4F; 5F; 6F; 7E, F; 8J; 11G)

*Gecarcinautes* cf. *antongilensis antongilensis* — Harvey & Boyko 1998: 145, 146.

*Gecarcinautes goodmani* Cumberlidge, Boyko & Harvey, 2002: 71-76, figs 4-6.

TYPE MATERIAL. — Madagascar. Station forestière de Tampolo, Province de Toamasina, Madagascar, 17°17'2"S, 49°24'5"E, 1 ad./subad. ♂ holotype of *Gecarcinautes goodmani* Cumberlidge, Boyko & Harvey, 2002 cw 23.0, cl 17.6, ch 6.8, fw 4.7 mm (FMNH 4651). — 1 ad./subad. ♀, paratype cw 23.5, cl 18.4, ch 8.0, fw 5.4 mm, 1 juv. ♂, paratype cw 12.6, cl 10.6, ch 4.2, fw 3.1 mm (FMNH 4651). — 1 subad. ♂, paratype cl 16.5 mm (AMNH 17530). — 4.IV.1997, coll. S. M. Goodman, 1 ad. ovigerous ♀, paratype cl 18.1 mm (AMNH 17530a).

TYPE LOCALITY. — Madagascar. Station forestière de Tampolo, Province de Toamasina, 17°17'2"S, 49°24'5"E, 10 m elevation, in leaf axils of *Pandanus*.

DISTRIBUTION. — Madagascar (Fig. 11G). Known only from the Station forestière de Tampolo, Province de Toamasina. *Malagasya goodmani* n. comb. is found at different elevations, always in association with *Pandanus* leaf axils.

DIAGNOSIS. — Suborbital, pterygostomial regions of carapace sidewall smooth; subhepatic region finely granulated; ischium of third maxilliped smooth (vertical sulcus either faint or absent). Third sternal sulcus s3/s4 deep at edges, sides angled backward, middle horizontal, completely crossing sternum; outer margins of dactylus, propodus of p2 to p5 with thick covering of velvet-like hair.

#### DESCRIPTION

See Cumberlidge *et al.* (2002).

#### Size

The adult size range is from cw 24 mm. The carapace proportions are given in Table 3.

#### REMARKS

This taxon is referred to *Malagasya* n. gen. due to the synonymy of the genus *Gecarcinautes* (see above).



*Malagasya goodmani* n. comb. can be distinguished from *M. antongilensis* n. comb. as follows: the epigastric crests of *M. goodmani* n. comb. are separated by a narrow midgroove, whereas the midgroove of *M. antongilensis* n. comb. is wide; the inner margin of the propodus of pereopods p2 to p5 of *G. goodmani* is smooth (with tufts of hair), whereas these margins in *M. antongilensis* n. comb. are distinctly toothed; and the outer margins of the dactylus and propodus of p2 to p5 of *M. goodmani* n. comb. have a thick covering of velvet-like hair, whereas this hair is lacking in *M. antongilensis* n. comb. In addition, the propodus of pereopod p5 of *G. goodmani* is short and broad, whereas that of *M. antongilensis* n. comb. is elongated and slim; the suborbital and pterygostomial regions of the carapace sidewall of *M. goodmani* n. comb. are smooth, whereas those of *M. antongilensis* n. comb. are finely granulated with a field of sparse hairs; the ischium of the third maxilliped of *M. goodmani* n. comb. is smooth, whereas in *M. antongilensis* n. comb. the vertical sulcus of the ischium is deep; and the sternal sulcus s3/s4 of *M. goodmani* n. comb. is V-shaped, whereas in *M. antongilensis* n. comb. this sulcus is horizontal.

#### Genus *Madagapotamon* Bott, 1965

*Madagapotamon* Bott, 1965: 344-346, fig. 7, pl. 4, figs 14-17. — Vuillemin 1970: 245-265. — Ng & Takeda 1994: 162, 163, table 1.

TYPE SPECIES. — *Madagapotamon humberti* Bott, 1965.

DIAGNOSIS. — Carapace outline heart-shaped, elongated (cl/fw = 3.7), highly arched (ch/fw = 1.7), very wide (cw/fw = 4.9), frontal, posterior margins very narrow (cw 0.25 mm); front sharply deflexed, almost vertical; exorbital tooth large, pointed; epibranchial tooth pointed, smaller; anterolateral margin with four to five pointed teeth behind epibranchial tooth; suborbital, subhepatic, pterygostomial regions of carapace sidewall smooth. Mandibular palp two-segmented, terminal segment simple, no anterior process of any kind at junction between segments; third maxilliped exopod short, just reaching ischium/merus junction; flagellum extremely reduced, stub-like; ischium smooth, vertical sulcus shallow, barely visible. Male sternite s5 smooth, lacking pair of sternal knobs ("bouton-

pressions" of Guinot 1977, 1978, 1979). Walking legs (p2-p5) extremely long, slender (ratio length merus p5 to cw 0.54). Adult male abdomen oval, egg-shaped. Gonopod 1 terminal article straight, tube-like, tip broad. Terminal article of gonopod 2 a short flagellum, much shorter than the subterminal segment (ratio length terminal article to subterminal segment 0.5).

#### REMARKS

*Madagapotamon* is one of the most distinctive genera of all of the Madagascan freshwater crabs and this pale-coloured long-legged, rock-crevice and cave-dwelling species stands apart from all other freshwater crabs on the island. *Madagapotamon* can be distinguished from all other genera of Madagascan freshwater crabs by the absence of a flagellum on the exopod of the third maxilliped, and by the egg-shaped outline of the adult male abdomen.

Bott (1965) assigned three very different taxa to *Madagapotamon*: *M. humberti*, *M. gollhardi* and *M. ankaraharae*, apparently because he perceived that all had a mandibular palp with a simple terminal segment. However, the findings of the present work do not support Bott's (1965) opinion. *Madagapotamon ankaraharae* bears little resemblance to *M. humberti*: for example, *M. ankaraharae* has normal length walking legs, a flagellum on the exopod of the third maxilliped, and a transversely-oval carapace outline. Similarly, the terminal segment of the mandibular palp of *M. gollhardi* is not truly simple, but actually has a small hard ledge on the terminal segment. The present findings support the removal of *M. gollhardi* and *M. ankaraharae* from *Madagapotamon*, and the recognition of this genus as monotypic for *M. humberti*, as was suggested by Ng & Takeda (1994).

#### *Madagapotamon humberti* Bott, 1965

(Figs 2E; 3G; 4L; 5H; 6G; 7K, L; 8G; 10G, H; 11H)

*Madagapotamon humberti* Bott, 1965: 344-346, fig. 7, pl. 4, figs 14-17. — Vuillemin 1970: 245-265. — Ng & Takeda 1994: 162, 163, table 1.

MATERIAL EXAMINED. — Madagascar. Forest of Ankara and of Analamera in northern Madagascar,

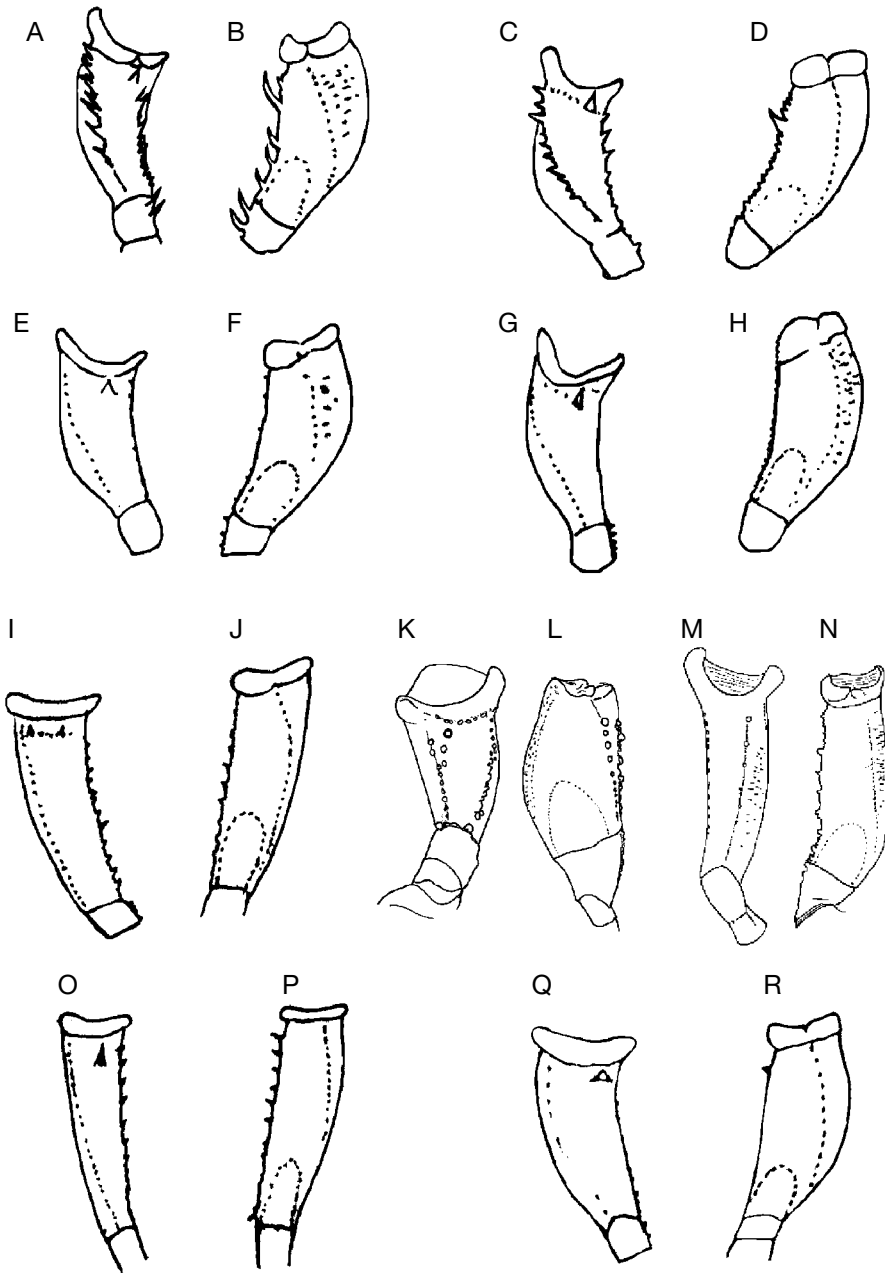


FIG. 7. — Superior and inferior views of the merus of the cheliped (pereopod 1) of adult males of Madagascan freshwater crabs; **A, B**, *Hydrothelphusa agilis* A. Milne-Edwards, 1872; **C, D**, *H. madagascariensis* (A. Milne-Edwards, 1872); **E, F**, *H. bombetokensis* (Rathbun, 1904); **G, H**, *H. goudoti* (H. Milne Edwards, 1853) n. comb.; **I, J**, *Malagasya antongilensis* (Rathbun, 1905) n. comb.; **K, L**, *Madagapotamon humberti* Bott, 1965; **M, N**, *Skelosophusa gollhardi* (Bott, 1965); **O, P**, *Marojejy longimerus* Cumberlidge, Boyko & Harvey, 2002; **Q, R**, *Boreas uglowi* n. gen., n. sp. Scale bar: A-H, 5.0 mm; I-T, 3.0 mm.

coll. H. Humblot, 1 ad. ♂, holotype of *Madagapotamon humberti* Bott, 1965 cw 33, cl 24.5, ch 11.5, fw 6 mm (MNHN-B 5182). — Analamera, northern Madagascar, 1 ad. ♂, paratype cw 24.8, cl 18.8, ch 9, fw 5.2 mm (SMF 2614). — Forest of Ankara and Analamera, 1937/1938, coll. Prof. H. Humbert, 1 ♀ paratype, broken up specimen (MNHN-BP 5174). Handwritten note, probably by Prof. Humbert: "Forêts à feuilles caduques, sur calcaire (lapias) de l'Ankara et de l'Analamera. Crabe arboricole en saison des pluies. Passe probablement la saison sèche dans les fissures très profondes, les avens et les cours d'eau souterrains de ces lapias. XII.1937 et I.1938". — Baie de Diego, Diego-Suarez (now Antsiranana), Antsirana, 230 m altitude, V.1899, coll. R. Decary, 1 ♂, dried specimen, 1 ♀, dried specimen (broken) (MNHN-B 5034). Note from M. Decary: "Ces crabes corps et pinces blanc opaque ne sont pas rares sur les rochers, dans la forêt qui recouvre les pentes ouest de la Montagne des Français. Ils sont extrêmement vifs, à la saison sèche, vivent dans les trous des rochers et sortent dès que la pluie commence". — Nosy-Bé, 2 juv. ♂ cw 12.8, 11.6 mm (ZSM 1163/1), 1 ♂ cw 15.8 mm (SMF 4487).

TYPE LOCALITY. — Northern Madagascar, between Ankara and Analamera.

DISTRIBUTION. — Northern Madagascar, between Ankara and Analamera (Fig. 11H).

DIAGNOSIS. — As for genus.

#### REDESCRIPTION

Carapace outline heart-shaped, elongated (cl/fw = 3.7), highly arched (ch/fw = 1.7), very wide anteriorly (cw/fw 4.9), sides tapering sharply; frontal, posterior margins both very narrow (cw 0.2 mm); distinct gap between epigastric, postorbital crests; latter not meeting anterolateral margins; all carapace grooves faint; anterior, posterolateral carapace regions smooth, no granules or carinae; front indented, margin raised, smooth; front sharply deflexed, almost vertical; exorbital tooth large, pointed, epibranchial tooth smaller, pointed, conspicuous; anterolateral margin between exorbital, epibranchial teeth lacking intermediate tooth; anterolateral margin with four to five pointed teeth behind epibranchial tooth; anterolateral margin continuous with posterolateral margin; vertical sulcus on carapace sidewall running from base of epibranchial tooth to epimeral sulcus, dividing suborbital from hepatic region, carapace sidewall clearly divided into three

regions (suborbital, subhepatic, pterygostomial), all smooth. Mandibular palp two-segmented, terminal segment simple, completely lacking anterior process of any kind at junction between segments; third maxilliped exopod short, just reaching ischium/merus junction; flagellum extremely reduced, stub-like, ischium smooth, vertical sulcus shallow, barely visible.

Thoracic sternal sulcus s1/s2 not visible, sternal sulci s2/s3, s3/s4 completely crossing sternum, s3/s4 deep at edges, angling backward, middle horizontal, close to anterior margin of sterno-abdominal cavity on sternite s4. Male sternite s5 smooth, lacking pair of sternal knobs ("boutonpressions" of Guinot 1977, 1978, 1979). Episternal sulci s4/e4, s5/e5, s6/e6, s7/e7 smooth, no groove visible. Merus, carpus, propodus, dactylus of walking legs (p2-p5) extremely long, slender (ratio length merus p5 to cw 0.54). Dactylus of right, left chelipeds narrow (one-quarter height of palm), upper margin smooth, dactylus straight, finger of propodus slim (one-third height of palm) lower margin of propodus of cheliped slightly indented. Fingers of propodus, dactylus with series of small teeth interspersed with three medium teeth; closed fingers enclosing long interspace. Anterior inferior margin of ischium of p1 granular, posterior inferior margin smooth. Inferior margins of merus toothed, distal margin with single pointed distal meral tooth; superior surface of merus smooth. First carpal tooth on inner margin of carpus of cheliped large, pointed; second carpal tooth small, pointed, followed by several smaller teeth. Anterior, posterior margins of propodi of p5 slightly serrated.

Adult male abdomen oval, egg-shaped, not triangular, a6 short, as long as width of distal margin of a6; lateral margins of a2-a7 distinctly convex; telson rounded, dome-shaped. Gonopod 1 terminal article straight, tube-like, tip broad; terminal article short, ratio terminal article to subterminal segment length 0.25; longitudinal groove on terminal article clearly visible on ventral, superior sides, not visible on dorsal side; lateral, medial folds of ventral side of terminal article equal in height, width, medial

fold overlapping lateral fold. Subterminal segment of gonopod 1 with rounded disto-medial shoulder-like projection at junction of segments and a rounded baso-medial projection. Lateral flap on ventral side of subterminal segment not reaching basal margin of segment, so opening of chamber for gonopod 2 positioned about one-third of segment length from basal margin. Suture marking junction between terminal article and subterminal segment of gonopod 1 visible dorsally, ventrally; narrow dorsal membrane on dorsal side at junction between segments. Gonopod 2 longer than gonopod 1; terminal article of gonopod 2 a short flagellum, much shorter than subterminal segment of gonopod 2 (ratio length terminal article to subterminal segment 0.5).

#### Size

The adult size range is from cw 24 to 33 mm. The carapace proportions are given in Table 3.

#### REMARKS

This genus is closest to *Malagasya* n. gen., which shares the heart-shaped carapace outline, distinct teeth on the anterolateral margins, and slender elongated walking legs. The two genera can be easily told apart by examination of the mandible and third maxilliped (see above).

There are a number of errors in the characterisation of *Madagapotamon* by Ng & Takeda (1994), because those authors relied entirely on Bott's (1965) figures and descriptions rather than on direct examination of specimens. For example, Ng & Takeda (1994: table 1) described the epibranchial tooth of *M. humberti* as "not visible" when in fact, although small, this tooth is nevertheless visibly distinct without magnification. In addition, their description of the terminal article and subterminal segment of gonopod 1 of *M. humberti* as not separated by a suture (i.e. fused) is incorrect: the segments are separated by a suture that is clearly visible from the ventral, superior and dorsal views.

Vuillemin (1970) provided excellent ecological notes and a detailed description of the habitat of *M. humberti*.

#### Genus *Skelosophusa* Ng & Takeda, 1994

*Skelosophusa* Ng & Takeda, 1994: 162, 163.

TYPE SPECIES. — *Madagapotamon gollhardi* Bott, 1965, by original designation.

DIAGNOSIS. — Carapace transversely oval (cw/fw = 3.5-3.6, cl/fw = 2.3-2.8); medium height (ch/fw 1.2-1.36); exorbital tooth broad, small; epibranchial tooth distinct, rounded, low, continuous with anterolateral margin; anterolateral margin granulated, posterior end curving inward, not continuous with posterolateral margin. Mandibular palp two-segmented, terminal segment simple, not bilobed, with small hard ledge-like process at terminal article ♀ subterminal segment junction. Third maxilliped ischium with deep vertical sulcus. Sternal suture s3/s4 reduced to two short notches at edges of sternum. Gonopod 1 terminal article short, tube-shaped, tip broad; gonopod 1 terminal article / subterminal segment junction marked by deep sulcus both ventrally, dorsally. Lateral flap on ventral side of subterminal segment long, reaching to basal margin of segment; medial flap on ventral face with distinct disto-medial shoulder; opening of chamber for gonopod 2 positioned about one-third of segment length from basal margin. Gonopod 2 terminal article flagellum medium length, ratio length terminal article to subterminal segment 0.5. Walking legs (p2-p5) elongated, slender, ratio length merus p5 to cw 0.5-0.6.

#### REMARKS

Ng & Takeda (1994) assigned three species to *Skelosophusa*: *S. gollhardi*, *S. prolixa* and *S. eumeces*. These authors described the terminal segment of the mandibular palp of *Skelosophusa* as simple (i.e. not bilobed). In fact, the mandibular palp of *Skelosophusa* is not strictly simple because there is a small hard ledge-like anterior process at the junction between the two segments which these authors clearly illustrated for *S. prolixa* and *S. eumeces* (Ng & Takeda 1994: fig. 6j, k). The type material of *S. prolixa* and *S. eumeces* are not in Turin, but are apparently still in the Tokyo National Museum with M. Takeda (P. K. L. Ng pers. comm.). It has proved difficult for us to borrow the specimens in question, and the following account of these two species is, therefore, based only on the photographs and illustrations provided by Ng & Takeda (1994). Without first-hand knowledge of these specimens, it is difficult to elaborate on our doubts concerning the validity of the species assignments of *Skelosophusa*.

*Skelosophusa* can be distinguished from all other genera of Madagascan freshwater crabs (except *Boreas* n. gen.) by the small ledge-like anterior process of the terminal segment of the mandibular palp. *Skelosophusa* can be distinguished from *Boreas* n. gen. as follows. The ischium of the third maxilliped of *Skelosophusa* has a deep vertical sulcus, whereas in *Boreas* n. gen. the ischium is smooth, and the walking legs of *Boreas* n. gen. are of normal length, whereas those of *Skelosophusa* are slender and remarkably elongated.

*Skelosophusa gollhardi* (Bott, 1965)

(Figs 2A; 4I; 5I; 6I; 7M, N; 10E, F; 11I)

*Madagapotamon gollhardi* Bott, 1965: 346, fig. 8, pl. 5, figs 19-22.

*Skelosophusa gollhardi* – Ng & Takeda 1994: 164, 165, fig. 1a-f, table 3.

MATERIAL EXAMINED. — **Madagascar.** Grotte de l'Ankara, 23.VII.1939, coll. R. Decary, 1 ad. ♂, holotype of *Madagapotamon gollhardi* Bott, 1965, cw 23, cl 16, ch 7.5, fw 6 mm (MNHN-B 5165).

TYPE LOCALITY. — Grotte de l'Ankara, Madagascar.

DISTRIBUTION. — Madagascar (Fig. 11I). This species is known only from the type locality.

DIAGNOSIS. — Epigastric, postorbital crests weak, rugose, not joined. Cervical groove very short, shallow. Field of dense, short hair on carapace sidewall in pterygostomial region. Ratio length p5 merus to cw 0.63, ratio length p5 merus cl 0.91, ratio length first gonopod terminal article to subterminal segment 0.35.

DESCRIPTION

See Ng & Takeda (1994).

*Size*

The adult size range is from cw 23 mm. The carapace proportions are given in Table 3.

REMARKS

*Skelosophusa gollhardi* is known only from the holotype collected from a cave near Ankara. Ng & Takeda (1994) considered *S. gollhardi* to be closest to *S. prolixa* based on carapace characters but cited "significant" differences in the form of the first gonopod and in the relative

length of the merus of p5. It is difficult to discern significant differences between gonopod 1 of the two species as illustrated by Ng & Takeda (1994: fig. 1a, c-f, 2a-f, h, i), and the proposed species boundaries defined by the relative length of the merus of p5 may not be robust (Ng & Takeda 1994: table 3). For example, although the ratio of the length of the merus of p5 to cl of *S. prolixa* is 0.75 (which is close to 0.73, 0.74 of Ng & Takeda 1994) the ratio of the length of the merus of p5 to cw of *S. gollhardi* is 0.51 (not 0.73, 0.74).

*Skelosophusa prolixa* Ng & Takeda, 1994

(Figs 2B; 4J; 5J; 6J; 8H; 11J)

*Skelosophusa prolixa* Ng & Takeda, 1994: 166, table 3, figs 2a-c, 3a, 5a-i, 6 k-n.

MATERIAL EXAMINED. — **Madagascar.** Nosy-Bé, rivière de la route des lacs, 23.XI.1972, coll. A. Crosnier, 1 ad. ♂ cw 25.6, cl 18.8, ch 9.3, fw 7.1 mm (MNHN-B 25734).

TYPE LOCALITY. — Grotte nord de l'Ankara, Berges Sable, Madagascar.

DISTRIBUTION. — Madagascar (Fig. 11J). This species is known only from the type locality.

DIAGNOSIS. — Epigastric crests, postorbital crests weak, low, smooth. Cervical groove long, shallow. Dense field of hairs on carapace sidewall in pterygostomial region. Ratio length merus p5 to cw 0.51, ratio length p5 merus cl 0.75, ratio length first gonopod terminal article to subterminal segment 0.38.

DESCRIPTION

See Ng & Takeda (1994).

*Size*

The adult size range is from cw 24 mm. The carapace proportions are given in Table 3.

REMARKS

Our recalculations of the length of the merus of p5 relative to the carapace dimensions based on diagrams and photographs of *S. prolixa* in Ng & Takeda (1994) (see above) indicate different values for these diagnostic dimensions from those reported by Ng & Takeda (1994: table 3).

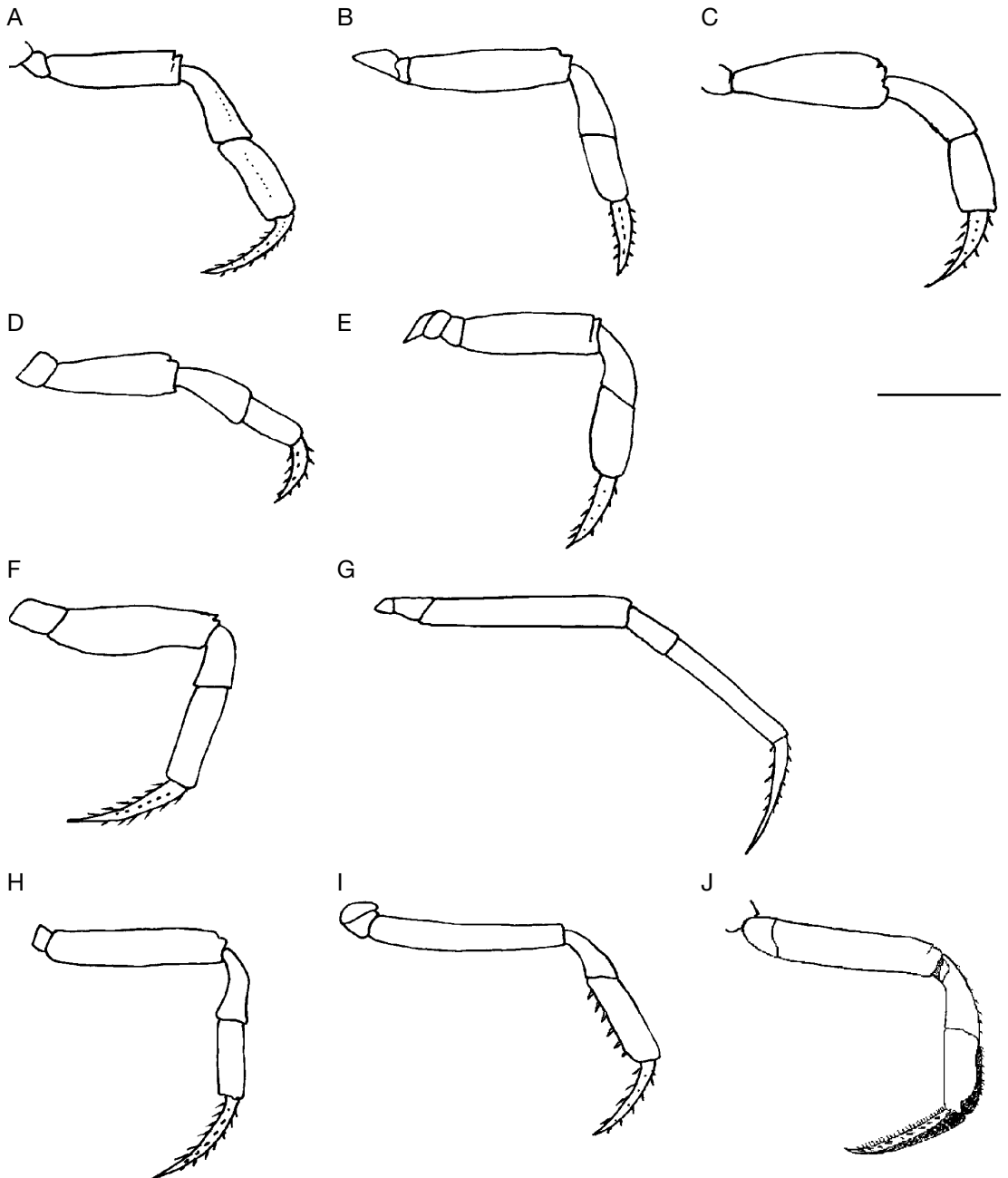


FIG. 8. — Last walking leg (pereiopod 5) of adult males of Madagascan freshwater crabs (H based on Ng & Takeda 1994); **A**, *Hydrothelphusa agilis* A. Milne-Edwards, 1872; **B**, *H. madagascariensis* (A. Milne-Edwards, 1872); **C**, *H. bombetokensis* (Rathbun, 1904); **D**, *H. goudoti* (H. Milne Edwards, 1853) n. comb.; **E**, *Boreas uglowi* n. gen., n. sp.; **F**, *Marojejy longimerus* Cumberlidge, Boyko & Harvey, 2002; **G**, *Madagapotamon humberti* Bott, 1965; **H**, *Skelosophusa prolixa* Ng & Takeda, 1994; **I**, *Malagasya antongilensis* (Rathbun, 1905) n. comb.; **J**, *M. goodmani* (Cumberlidge, Boyko & Harvey, 2002) n. comb. Scale bar: A-D, 5.0 mm; E-L, 2.6 mm.

*Skelosophusa eumeces* Ng & Takeda, 1994  
(Figs 2C; 4K; 5K; 6K; 11K)

*Skelosophusa eumeces* Ng & Takeda, 1994: 166, 169, 171, table 3, figs 3b, 4, 6a-g, j, o.

MATERIAL EXAMINED. — Madagascar. Andrafiabe, 1 ad. ♂, holotype of *Skelosophusa eumeces* Ng & Takeda, 1994 cw 22.7, cl 15.8 mm (MRSN).

TYPE LOCALITY. — Andrafiabe, Madagascar.

DISTRIBUTION. — Madagascar (Fig. 11K). This species is known only from the type locality.

DIAGNOSIS. — Epigastric, postorbital crests distinct, rugose. Cervical groove broad, distinct, short. Ratio length p5 merus to cw 0.56, ratio length p5 merus to cl 0.82, ratio length first gonopod terminal article to subterminal segment 0.35.

*Size*

The adult size range is from cw 24 mm. The carapace proportions are given in Table 3.

REMARKS

Our recalculations of the length of the merus of p5 relative to the carapace dimensions based on the diagrams and photographs of *S. eumeces* in Ng & Takeda (1994) indicate different values for these diagnostic dimensions from those reported by Ng & Takeda (1994: table 3). For example, the ratio of the length of the merus of p5 to cw in *S. eumeces* is 0.56 (not 0.82) and the ratio of the terminal article to subterminal segment length of gonopod 1 in *S. eumeces* is 0.35 (not 0.43).

Genus *Marojejy*

Cumberlidge, Boyko & Harvey, 2002

TYPE SPECIES. — *Marojejy longichela* Cumberlidge, Boyko & Harvey, 2002.

DIAGNOSIS. — Eyestalks tapering distally, corneas very reduced; merus, carpus, propodus of both chelipeds extremely elongated, ratio total length cheliped p1 (from ischium to dactylus) to cw 2.6 (right), 2.3 (left).

REMARKS

*Marojejy* can be distinguished from all other genera of Madagascan freshwater crabs by the tapering eyestalk with a reduced cornea, and by the

extremely elongated merus of the cheliped. In addition, *Marojejy* can be further distinguished from the other small long-legged crabs found in Madagascar (*Madagapotamon*, *Skelosophusa*, and *Malagasya* n. gen.) as follows. The anterior process of the terminal segment of the mandibular palp is bilobed in *Marojejy* but this process is completely lacking in *Madagapotamon*, and the flagellum of the exopod of the third maxilliped while reduced (i.e. of medium length) in *Marojejy*, is virtually absent (a short stub) in *Madagapotamon*. The terminal segment of the mandibular palp of *Skelosophusa* is simple, with a small ledge-like anterior process, whereas the terminal segment of the mandibular palp of *Marojejy* is bilobed with a medium sized, lobe-like anterior process. The exorbital and epi-branchial teeth are low and blunt in *Marojejy*, but relatively large and pointed in *Malagasya* n. gen.; the anterolateral margins of the carapace are granular in *Marojejy*, but conspicuously toothed in *Malagasya* n. gen., and the front is wide and moderately deflexed in *Marojejy*, but narrow and sharply deflexed in *Malagasya* n. gen. The long, slender walking legs of *Marojejy* set this genus apart from *Hydrothelphusa* and *Boreas* n. gen., which both have walking legs of normal length.

*Marojejy longimerus*

Cumberlidge, Boyko & Harvey, 2002  
(Figs 2F; 3H; 4G; 5G; 6H; 7O, P; 8F; 10I, J; 11E)

*Marojejy longimerus* Cumberlidge, Boyko & Harvey, 2002: 67-71, figs 1-3.

MATERIAL EXAMINED. — Madagascar. Province d'Antsiranana, Réserve naturelle intégrale de Marojejy, Andranomifototra river, 14°26'8"S, 49°44'1"E, 1875 m, 11 km northwest of Manantenina, 1 ad. ♂, holotype cw 23, cl 15.1, ch 7.45, fw 5.9 mm (AMNH 17833), 1 subad. ♀, paratype cw 15.1, cl 11.3, ch 5.4, fw 4.5 mm, 1 juv. ♂, paratype cw 11.1, cl 8.4, ch 4.5, fw 3.1 mm (AMNH 17833). — 11 km northwest of Manantenina, Province d'Antsiranana, Réserve naturelle intégrale de Marojejy, 14°26'8"S, 49°44'1"E, source of Andranomifototra river, under rocks, 1875 m, 13-19.XI.1996, coll. E. Quinter, 4 ♂ ♂, paratypes cl 13.0-14.7 mm, 5 ♀ ♀, paratypes cl 12.2-14.2 mm (FMNH 4656).

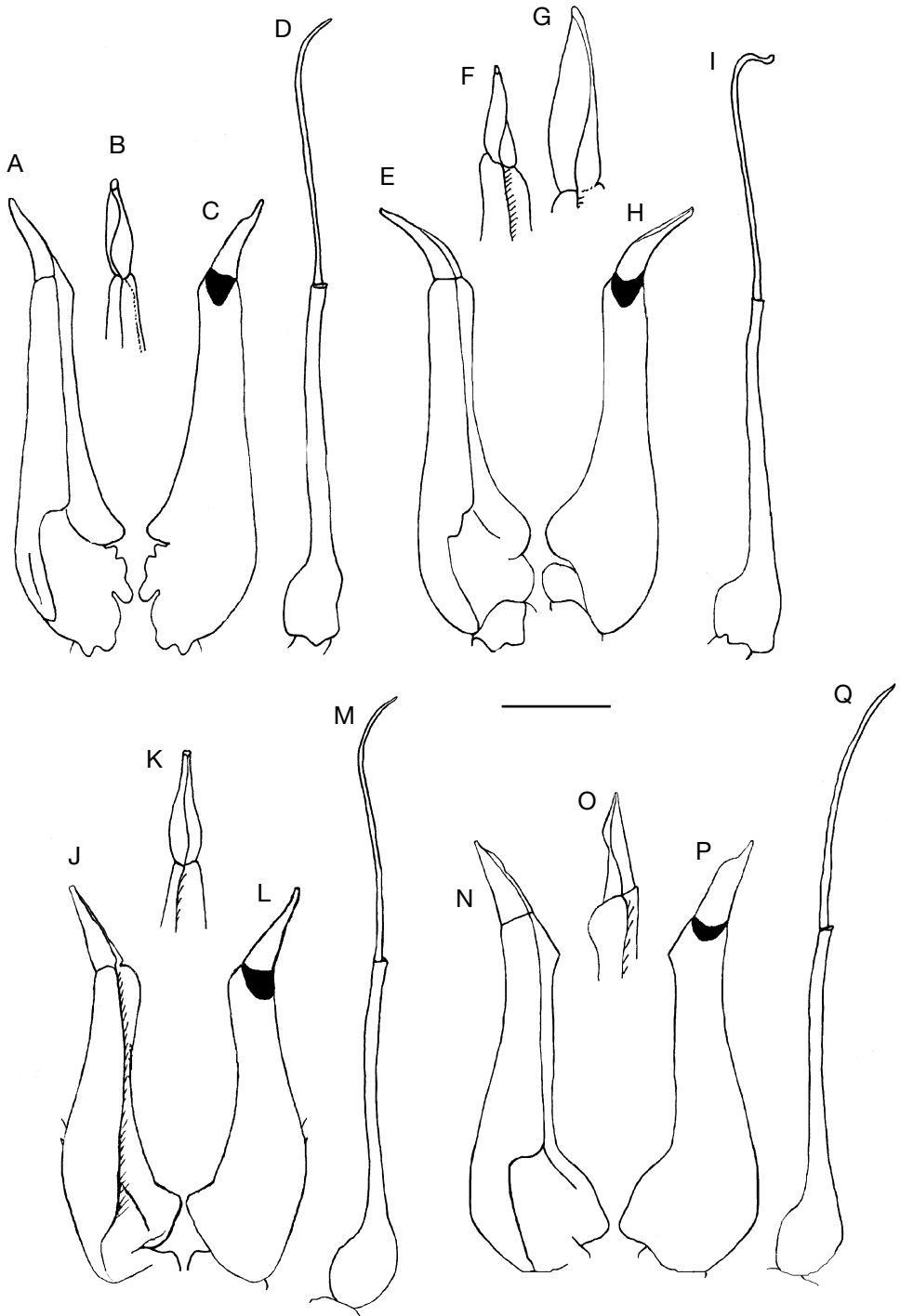


FIG. 9. — Right first gonopod (dorsal view; superior view; ventral view) and right second gonopod (dorsal view) of adult males of species of *Hydrothelphusa* A. Milne-Edwards, 1872; **A-D**, *H. agilis* A. Milne-Edwards, 1872; **E-I**, *H. madagascariensis* (A. Milne-Edwards, 1872); **J-M**, *H. bombetokensis* (Rathbun, 1904); **N-Q**, *H. goudoti* (H. Milne Edwards, 1853) n. comb. Scale bar: 4.5 mm.



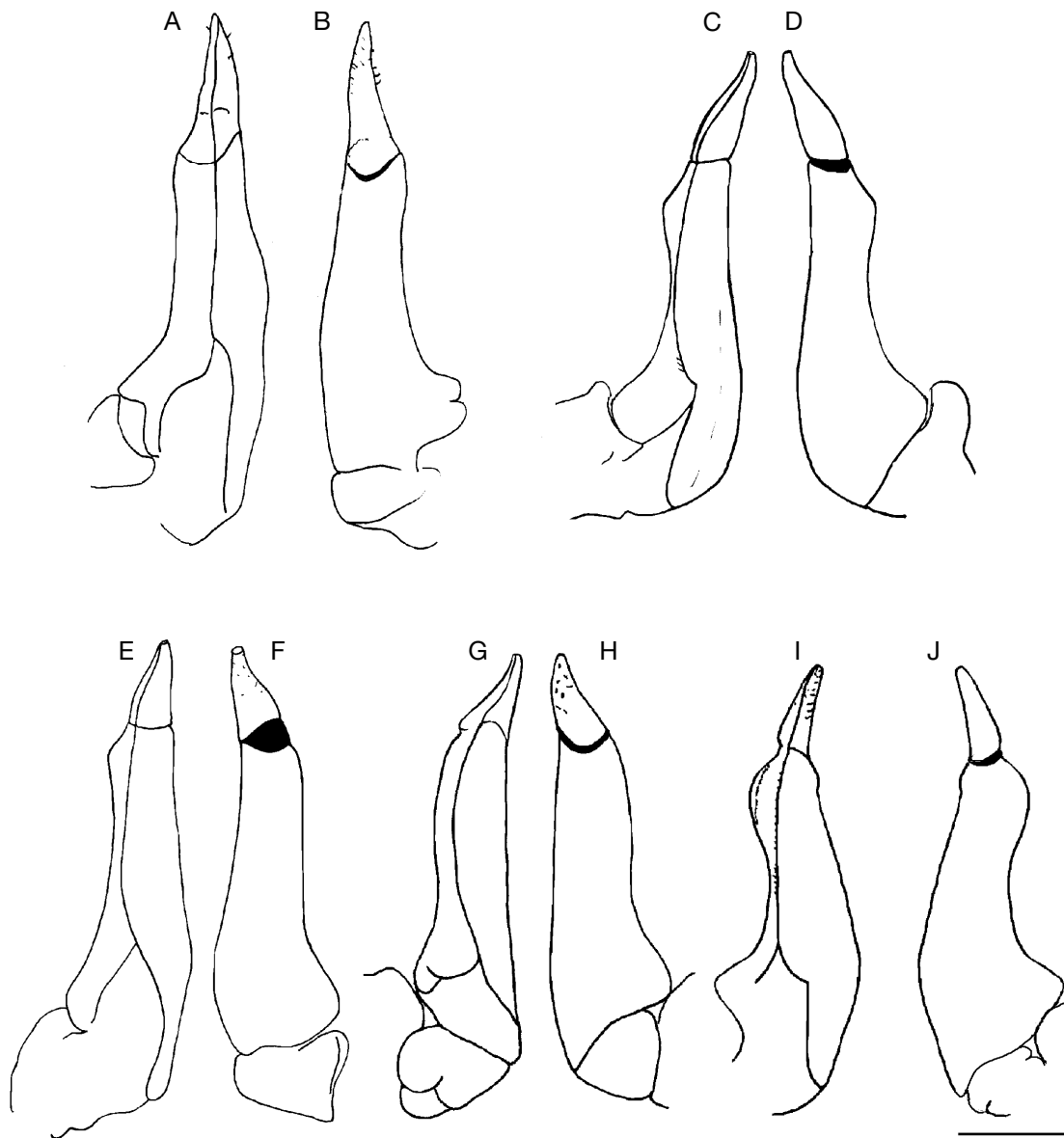


FIG. 10. — Right first gonopod (dorsal and ventral views) of adult males of Madagascan freshwater crabs; **A, B**, *Boreas ugloi* n. gen., n. sp.; **C, D**, *Malagasya antongilensis* (Rathbun, 1905) n. comb.; **E, F**, *Skeleosophusa gollhardi* (Bott, 1965); **G, H**, *Madagapotamon humberti* Bott, 1965; **I, J**, *Marojejy longimerus* Cumberlidge, Boyko & Harvey, 2002. Scale bar: 4.0 mm.

**TYPE LOCALITY.** — Andranomifototra river, 14°26'8"S, 49°44'1"E, 1875 m, 11 km northwest of Manantenina, Province d'Antsiranana, Réserve naturelle intégrale de Marojejy, Madagascar.

**DISTRIBUTION.** — Madagascar (Fig. 11E). Known only from the Réserve naturelle intégrale de Marojejy.

**DIAGNOSIS.** — As for genus.

#### DESCRIPTION

See Cumberlidge *et al.* (2002).

#### Size

The adult size range is from cw 24 mm. The carapace proportions are given in Table 3.

TABLE 4. — Madagascar gazetteer. Taxa: **1**, *Hydrothelphusa agilis* (A. Milne Edwards, 1872); **2**, *H. madagascariensis* (A. Milne Edwards, 1872); **3**, *H. bombetokensis* (Rathbun, 1904); **4**, *H. goudoti* (H. Milne Edwards, 1853) n. comb.; **5**, *Malagasya antongilensis* (Rathbun, 1905) n. comb.; **6**, *M. goodmani* (Cumberlidge, Boyko & Harvey, 2002) n. comb.; **7**, *Madagapotamon humberti* Bott, 1965; **8**, *Skelosophusa gollhardi* (Bott, 1965); **9**, *S. prolixa* Ng & Takeda, 1994; **10**, *S. eumeces* Ng & Takeda, 1994; **11**, *Marojejy longimerus* Cumberlidge, Boyko & Harvey, 2002; **12**, *Boreas uglowi* n. gen., n. sp.

Locality	Coordinates	Taxon
Alaotra Lake	17°30'S, 48°30'E	4
Ambilobé	15°40'S, 46°20'E	5
Ambodiriana	17°55'S, 49°18'E	1, 2
Ambohitantely Forest	18°10'S, 47°17'E	2, 3
Andranomifototra river, RNI Marojejy	14°26'S, 49°44'E	11
Ambositra	20°30'S, 47°15'E	1
Ampefy	19°09'S, 46°43'E	2, 3
Analamazastra river	18°56'S, 48°25'E	1, 2
Andrafi(a)be	17°27'S, 44°44'E	10
Androkabe	24°41'S, 47°12'E	2
Ankara	12°57'S, 49°00'E	2, 7, 8, 9
Ankarana district	12°40'S, 47°00'E	1, 2, 3, 5
Ankarana Plateau	12°44'S, 48°59'E	7
Antananarivo (formerly Tananarive)	18°52'S, 47°30'E	1, 4
Antongil Bay	15°26'S, 49°51'E	5
Antsampsandrano	19°31'S, 47°42'E	2, 3
Antsiranana (formerly Diégo-Suarez)	13°20'S, 48°15'E	2, 5, 7, 12
Beforona	18°58'S, 48°35'E	1, 4
Bombetok	15°50'S, 46°17'E	2, 3
Diégo-Suarez (now Antsiranana)	12°17'S, 46°17'E	2, 5, 7, 12
Fandiarano	20°14'S, 47°23'E	2, 5
Farafangana	24°37'S, 46°54'E	2, 5
Fort Dauphin	25°02'S, 47°00'E	2
Ifanadiana	21°15'S, 47°35'E	1, 2
Isandra river	23°56'S, 47°15'E	2, 5
Itasy Lake	19°04'S, 46°17'E	1
Kinkony lake	12°27'S, 49°16'E	5
Lakato	19°10'S, 48°26'E	1, 2
Lily River	18°54'S, 46°31'E	1, 2
Majunga	15°40'S, 46°20'E	2
Majunga	22°18'S, 47°10'E	5
Manambato	22°53'S, 47°34'E	4, 5
Mananjiba (Mananjeba?)	18°57'S, 48°13'E	1, 2, 5
Manankazo	18°09'S, 47°12'E	2
Manjakatampo	18°58'S, 47°17'E	4
Maroheza	18°57'S, 48°13'E	2, 5
Marotsy river	24°41'S, 47°12'E	2, 12
Mont D'Ambre (Diego Suarez)	12°39'S, 49°02'E	2
Montagne des Francais	12°12'S, 46°20'E	7
Moramanga	18°56'S, 48°25'E	1, 2, 5
Namorona	21°39'S, 48°12'E	1
Nosy Be	13°25'S, 48°19'E	2, 5, 8, 12
Nosy Komba	13°24'S, 48°20'E	12
Périnet	18°56'S, 48°52'E	2, 5
Ranomafana	21°14'S, 47°26'E	1, 4, 5
Sakalava	19°50'S, 48°20'E	1, 2, 3, 5
Sakaleone River	20°34'S, 47°49'E	2
Sisaony	18°51'S, 47°23'E	1
Soavinadriana	19°31'S, 47°42'E	2
Tamatave (now Toamasina)	18°10'S, 49°23'E	1, 2, 4, 5, 6
Station Forestière de Tampolo	17°17'S, 49°24'E	6
Tananarive (now Antananarivo)	18°52'S, 47°30'E	2, 4
Toamasina (formerly Tamatave)	18°09'S, 49°25'E	1, 2, 4, 5, 6
Vert Lake	13°21'S, 49°59'E	1
Vondrozo	22°49'S, 47°19'E	5

Genus *Boreas* n. gen.

*Potamon* (*Geothelphusa*) – Nobili 1906: 1-4, fig. a. — Balss 1929: 356 [non *Geothelphusa* Stimpson, 1858].

*Madagapotamon* – Bott 1965: 347, 348 (part), fig. 9, pl. 5, figs 23-25 [non *Madagapotamon* Bott, 1965 s. str.].

TYPE SPECIES. — *Boreas uglowi* n. gen., n. sp.

ETYMOLOGY. — The genus name *Boreas* is taken from the Latin and Greek words for north, in reference to the distribution of this genus in the north of the island of Madagascar. Gender masculine.

DIAGNOSIS. — Carapace outline transversely oval (wider than long, cw/fw = 3.2, cl/fw = 2.3), moderately arched (ch/fw = 1.1); exorbital, epibranchial teeth both low, blunt, continuous with anterolateral margin; anterior carapace surface smooth, with faint granules in anterolateral corners, carinae in posterolateral regions; epigastric and postorbital crests both faint; frontal margin straight, front highly deflexed; mandibular palp two-segmented, terminal article with flat basal thickening at junction between segments; ischium of third maxilliped smooth (vertical sulcus either faint or absent); sternal sulcus s3/s4 reduced to two short side notches; walking legs (p2-p5) normal length, neither elongated nor shortened, ratio length merus p5 to cw 0.34-0.4.

## REMARKS

The postfrontal crest, carapace outline shape, thoracic sternum, and mandible of *Boreas* n. gen. are similar to those of *Skelosophusa*. *Boreas* n. gen. can be distinguished from *Skelosophusa*, and indeed from all other genera of Madagascar freshwater crabs, by the following combination of characters: legs of normal length, a faint or completely absent vertical sulcus on the ischium of the third maxilliped, and a slim (rather than broad) terminal article of gonopod 1.

*Boreas uglowi* n. sp.

(Fig 2D; 3G; 4L; 5H; 6L; 7Q, R; 8E; 10A, B; 11L)

*Madagapotamon ankarabarae* – Bott 1965 (part): 347, 348, fig. 9d, e, pl. 5, figs 23-25 (non fig. 9a-c).

MATERIAL EXAMINED. — Madagascar. Nosy-Bé, Madagascar, 1 ad. ♂, holotype cw 29.3, cl 21.3, ch 10, fw 8.5 mm (MNHN-B 12292). — Diego-Suarez (now Antsiranana), coll. J. Millot, 1 ad. ♂ cw 24.3, cl 18.8, ch 8.6, fw 7.6 mm (MNHN-B 5028). — Nosy-Bé, Autumn 1927, coll. J. Millot, 1 ad. ♂,

cw 19.8 mm, broken in pieces (MNHN-B 5029). — Nosy-Bé, X.1922, coll. J. Millot, 1 ad. ♂ cw 25 mm, carapace damaged (MNHN-B 26147). — Nosy Komba, 500 m altitude, on a path, XII.1922, coll. J. Millot, 1 ♀ subadult cw 22, cl 16, ch 8, fw 6.5 mm, 1 ♂, broken cw 28.5, cl 19.5 mm, 1 juv. cw 18, cl 13.5, ch 6, fw 5 mm (MNHN-B 12293).

TYPE LOCALITY. — Nosy-Bé, Madagascar.

ETYMOLOGY. — The species is named for Dr. Roger Frederick Uglow, Department of Applied Biology, University of Hull, U.K., in recognition of his prolific contributions to decapod crustacean physiology.

DISTRIBUTION. — Madagascar, Nosy-Bé (Fig. 11L).

DIAGNOSIS. — As for genus.

## DESCRIPTION

Carapace outline transversely oval (wider than long, cw/fw = 3.2, cl/fw = 2.3), moderately arched (ch/fw = 1.1); epigastric, postorbital crests faint, not fused; postorbital crests not meeting anterolateral margins; exorbital, epibranchial teeth similar, both low, blunt, continuous with anterolateral margin; anterior regions of carapace surface smooth; anterolateral, posterolateral regions with short carinae; semi-circular, urogastric grooves deep; cervical grooves very short. Suborbital margin raised, faintly granulated. Front highly deflexed; frontal margin smooth, straight; frontal, posterior margins of carapace wide (cw 0.3 mm). Suborbital, subhepatic, regions of carapace sidewall smooth or with faint granules; pterygostomial region smooth with sparse short setae or a few small granules near third maxilliped. Carapace sidewall in three parts; distinct vertical sulcus on sidewall running from epibranchial tooth to longitudinal (epimeral) groove, dividing suborbital, hepatic regions. Mandibular palp two-segmented, terminal segment with flat basal thickening at junction between segments; ischium of third maxilliped smooth, vertical sulcus either faint or completely absent; exopod of third maxilliped medium length, reaching only proximal part of merus, exopod with long flagellum. Thoracic sternal sulcus s1/s2 not visible; sternal sulcus s2/s3 deep, horizontal; sternal sulcus s3/s4 reduced to two short side notches; anterior sternum

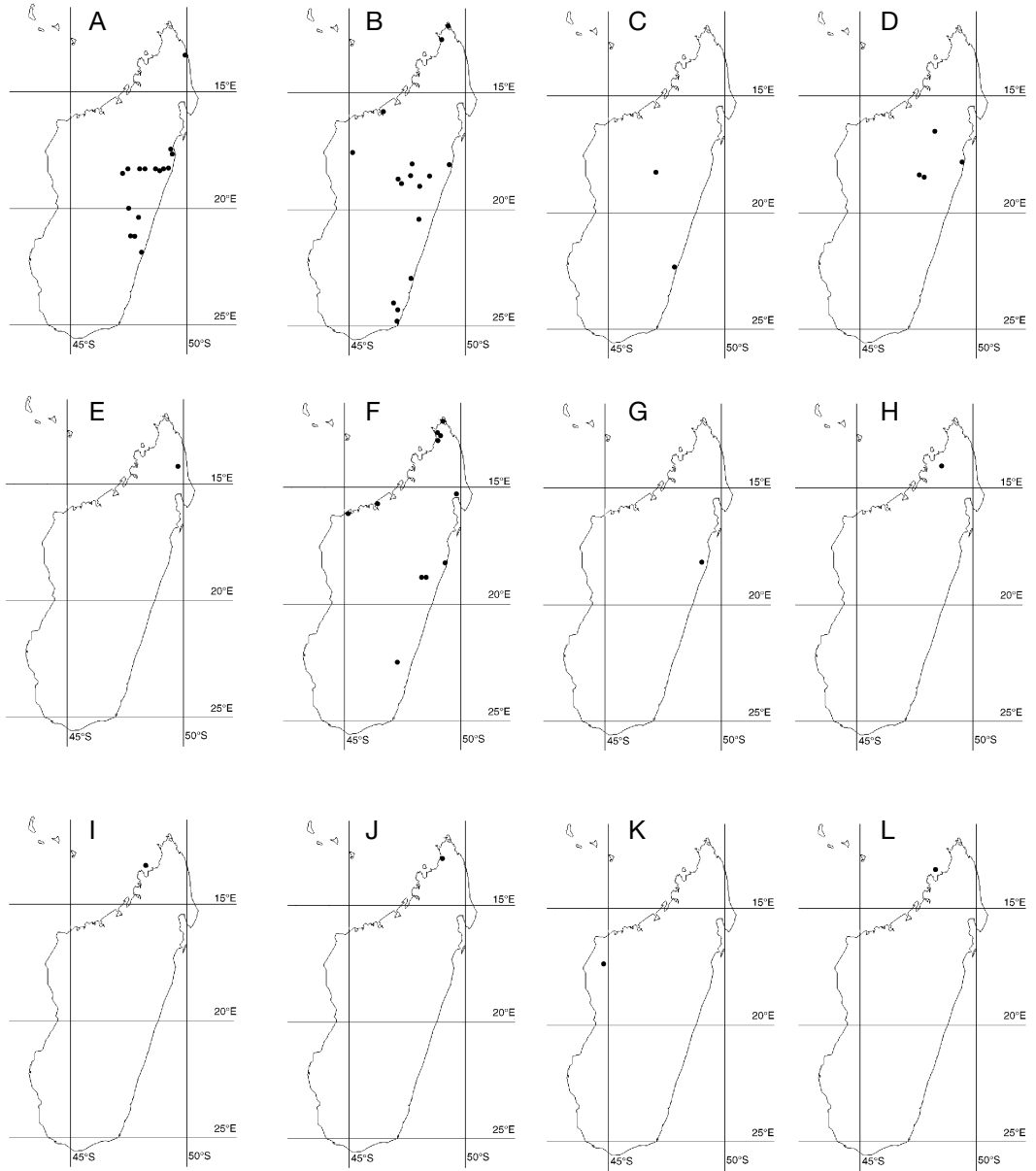


FIG. 11. — Summaries of the known distribution of the Madagascan freshwater crabs; **A**, *Hydrothelphusa agilis* A. Milne-Edwards, 1872; **B**, *H. madagascariensis* (A. Milne-Edwards, 1872); **C**, *H. bombetokensis* (Rathbun, 1904); **D**, *H. goudoti* (H. Milne Edwards, 1853); **E**, *Marojejy longimerus* Cumberlidge, Boyko & Harvey, 2002; **F**, *Malagasya antongliensis* (Rathbun, 1905) n. comb.; **G**, *M. goodmani* (Cumberlidge, Boyko & Harvey, 2002) n. comb.; **H**, *Madagapotamon humberti* Bott, 1965; **I**, *Skelosophusa gollhardi* (Bott, 1965); **J**, *S. prolixa* Ng & Takeda, 1994; **K**, *S. eumeces* Ng & Takeda, 1994; **L**, *Boreas uglowi* n. gen., n. sp.

smooth; episternal sulci  $s4/e4$ ,  $s5/e5$ ,  $s6/e6$ ,  $s7/e7$  smooth, no groove visible. Male abdomen slim, triangular.

Gonopod 1 terminal article straight, slim, short (ratio length terminal article to subterminal segment 0.25), tip directed weakly outward, longi-

tudinal groove clearly visible on ventral, superior sides, not visible on dorsal side; terminal article/subterminal segment junction distinct, with narrow dorsal membrane; lateral, medial folds of ventral side of terminal article equal in height, width. Gonopod 2 longer than gonopod 1; gonopod 2 terminal article medium flagellum, ratio length gonopod 2 terminal article to subterminal segment 0.6.

Dactylus of right, left chelipeds relatively narrow (one-quarter height of palm), upper margin smooth, finger of dactylus curved; slim interspace between closed fingers; finger of propodus one-third height of palm lower margin of propodus of cheliped slightly indented. Dactylus with series of small teeth interspersed by larger teeth; finger of propodus of right cheliped with large fused molar tooth. Anterior, posterior inferior margins of ischium of p1 smooth. Inferior margins of merus faintly granulated, distal margin with single low distal meral tooth; superior margin of merus with row of granules. First carpal tooth of carpus of cheliped large, wide, with pointed tip; second carpal tooth small. With pointed tip, followed by small granules. Anterior, posterior margins of propodi of p5 slightly serrated. Walking legs (p2-p5) normal length, neither elongated nor shortened, ratio length merus p5 to cw 0.3. P5 propodus short, broad, margins serrated; dactylus of p5 short, half length of dactylus of p2-p4.

#### REMARKS

The generic assignment and validity of *Potamon* (*Geothelphusa*) *ankaraharae* remains uncertain. Nobili's (1906) type is unavailable and the figures of the type in Bott (1965: fig. 9a-c) do not show the mandible or first gonopod. It should be noted that the male specimen cw 28 mm (MNHN Paris, no number provided) labeled *M. ankaraharae* in Bott (1965: fig. 9d, e, pl. 5 figs 23-25) from Diego-Suarez (now Antsiranana) was not part of the type series from Ankarahara, and probably does not represent this taxon. We consider it likely that this specimen was misidentified, and that it may not actually belong to the same species as *P. (G.) ankaraharae* sensu Nobili, 1906. Although Bott (1965) did not provide a

catalogue number, it is likely that the specimen from Diego-Suarez (MNHN-B 28) is the same one that was used (in part) in the redescription of *M. ankaraharae* by Bott (1965: pl. V, figs 23-25, fig. 9e, f). For this reason, the illustrations of gonopods 1 and 2 in Bott 1965 (fig. 9d, e), the photographs of the whole animal (pl. V, figs 23-25), and the text description of the mandibular palp as simple, may describe these structures in *B. uglowi* n. gen, n. sp., rather than *P. (G.) ankaraharae* sensu Nobili, 1906. This means that the gonopods and mandible of *P. (G.) ankaraharae* sensu Nobili, 1906, still await description.

Characters of the carapace, thoracic sternum and walking legs of *B. uglowi* n. gen, n. sp. are similar to those shown in the figures of the type of *P. (G.) ankaraharae* provided by Bott (1965). The two taxa have a similar carapace outline and texture and walking legs of similar proportions. The two taxa can be distinguished by examination of the ischium of the third maxilliped, which has a deep vertical groove in *P. (G.) ankaraharae*, but which is characteristically faint or lacking in *B. uglowi* n. gen, n. sp. The specimens from northern Madagascar from Diego-Suarez (MNHN-B 5028), Nosy-Bé (MNHN-B 5029) and (MNHN-B 26147), and Nosy Komba (MNHN-B 12293) that were formerly identified as *P. (G.) ankaraharae* are included here in the new taxon, because they resemble *B. uglowi* n. gen, n. sp. very closely. These specimens differ from *B. uglowi* n. gen, n. sp. in the texture of the pterygostomial region of the carapace sidewall, which is smooth in *B. uglowi* n. gen, n. sp. and distinctly setose in these other specimens.

#### Acknowledgements

Professor Danièle Guinot (MNHN, Paris) is thanked for hosting several visits to the MNHN by one of the authors (NC) and for loaning the type specimens used in this study. We also thank Steven M. Goodman (FMNH, Chicago), Christopher B. Boyko (AMNH, New York), Michael Türkay (SMF, Frankfurt), Ludwig Tiefenbacher (ZSM, Munich), and Paul Clark (NHM, London) for making specimens available to us.

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