

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/345822791>

New lineages within the Malagasy freshwater crab fauna: Agora n. gen. for Thelphusa goudoti H. Milne Edwards, 1853, and a phytotelmic new species of Malagasya Cumberlidge & Sternbe...

Article in *Journal of Crustacean Biology* · September 2020

DOI: 10.1093/jcobi/ruaa050

CITATIONS

7

4 authors, including:



Neil Cumberlidge

Northern Michigan University

179 PUBLICATIONS 5,018 CITATIONS

[SEE PROFILE](#)

READS

277



Savel R Daniels

Stellenbosch University

385 PUBLICATIONS 3,427 CITATIONS

[SEE PROFILE](#)



The Crustacean Society

Journal of Crustacean Biology

Journal of Crustacean Biology 40(5), 584–599, 2020. doi:10.1093/jcbiol/ruaa050

New lineages within the Malagasy freshwater crab fauna: *Agora* n. gen. for *Thelphusa goudoti* H. Milne Edwards, 1853, and a phytotelmic new species of *Malagasya* Cumberlidge & Sternberg, 2002 (Brachyura: Potamonautesidae: Deckeniinae)

Neil Cumberlidge^{1,✉}, Julia B. Soma^{1,✉}, Ellen M. Leever^{1,✉} and Savel R. Daniels^{2,✉}

¹Department of Biology, Northern Michigan University, Marquette, MI, USA; and

²Department of Botany and Zoology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa

Correspondence: N. Cumberlidge; e-mail: ncumberl@nmu.edu

(Received 6 March 2020; accepted 30 June 2020)

ABSTRACT

New molecular and morphological analyses of the relationships of 77 specimens of potamonautesid freshwater crabs collected from all parts of Madagascar support the monophly of the island's freshwater crab fauna and verify most of the existing taxa. The phylogenetic tree identified several new lineages that represent four new genera and 10 new species, and found *Foza* Reed & Cumberlidge, 2006 to be paraphyletic. The present work is the first of a series of articles reporting on these discoveries that provide an improved understanding of the relationships between the endemic potamonautesid species found on this tropical island. We describe a new species of *Malagasya* Cumberlidge & Sternberg, 2002 from a phytotelmic habitat in northeast Madagascar, and establish *Agora* gen. nov. to accommodate *Thelphusa goudoti* H. Milne Edwards, 1853. Both of these new taxa are recognized based on combinations of morphological characters and molecular data. The new species of *Malagasya* is distinguished from the other two species of this genus, which are illustrated here for comparative purposes. *Agora goudoti* n. comb. is endemic to Madagascar, and is compared with and distinguished from the eight other genera of freshwater crabs occurring in that country.

Key Words: freshwater brachyurans, mtDNA COI, new combination, taxonomy

INTRODUCTION

Madagascar freshwater crabs are found in lakes, streams, and rivers and in adjacent terrestrial habitats such as rocky crevices and phytotelmata in evergreen moist forests, savannas, and forested highlands, and are particularly species-rich in the northern parts of the island (Cumberlidge *et al.*, 2002a, 2004, 2005). All 17 species and eight genera of Malagasy (Madagascar) freshwater crabs form a monophyletic group (Daniels *et al.*, 2006, 2015) that is included in the Afrotropical subfamily Deckeniinae in the family Potamonautesidae Bott, 1970 (Bott, 1960, 1965; Ng & Takeda, 1994; Cumberlidge, 1999, 2014; Cumberlidge *et al.*, 2002a, 2007, 2015; Cumberlidge & Sternberg, 2002; Reed & Cumberlidge, 2006; Cumberlidge & Meyer, 2009; Meyer *et al.*, 2014). The Malagasy freshwater crabs are completely endemic, a characteristic which is shared by several other faunal groups (e.g.,

lemurs, reptiles, amphibians, baobabs) that have evolved on this long-isolated tropical island (Goodman & Benstead, 2005; Vences *et al.*, 2009).

The present work arises from a molecular analysis of the largest taxonomic sample of Malagasy freshwater crabs assembled to date and includes 77 specimens representing seven of the eight described genera and 16 of 17 known species. Specimens are compiled from museum collections and from freshly sampled material. Our analysis of the relationships of the Malagasy freshwater fauna focuses only on the subfamily Deckeniinae, but we also took into account the results of two earlier molecular phylogenetic studies of the entire Afrotropical freshwater crab fauna that included representative species of Malagasy freshwater crabs (Daniels *et al.*, 2006, 2015). Our taxonomic conclusions are guided by the present detailed morphological and molecular studies, taken together with the results of two earlier phylogenetic works (Daniels *et al.*, 2006, 2015) that raise

questions about the current taxonomic assignments of several of the Malagasy freshwater crabs.

Here we focus on the proper generic assignment of the taxonomically difficult *Thelphusa goudotii* H. Milne Edwards, 1853 that has already been assigned to several different genera over the years. In the light of the new evidence we here reassign it to *Agora* **n. gen.** and provide a redescription. We also describe a new species of *Malagasya* Cumberlidge & Sternberg, 2002 from the Diana Region in northern Madagascar, based on fresh material obtained by Dr. Stephen M. Goodman of the Field Museum of Natural History, Chicago, USA. We also provide photographs of the habitus of adult male specimens of the two new taxa being described, *Agora goudotii* **n. comb.** and *Malagasya elvisi* **n. sp.**

MATERIALS AND METHODS

Taxonomically important characters such as first and second gonopods, carapace, sternum, chelipeds, third maxilliped, and mandible were examined in detail and photographed with a digital camera and a Keyence VHX 5000 digital microscope (Keyence, Itasca, IL, USA), and post processing was undertaken using Adobe Photoshop CC5. Measurements were made with callipers and are given in millimetres (mm). Measurements of the subterminal segments (SS) of gonopods 1 and 2 (G1, G2) were made along a straight line beginning at the midpoint of the basal margin and ending at the midpoint of the distal margin (at the junction between the two parts). Measurements of the terminal articles (TA) of G1 and G2 were made on the ventral face along the midline beginning at the midpoint of the basal margin that forms the SS/TA junction and ending at the TA tip. The length of the TA of G1 and G2 relative to the length of the SS of each of these structures is presented as the ratio of the terminal article/subterminal segment (TA/SS). The terminology used follows Cumberlidge (1999) and the classification follows Ng *et al.* (2008). The following abbreviations are used: A1–6, plemomes 1–6 respectively); ASL, altitude above sea level in metres; CW, carapace width measured at widest point; CL, carapace length measured along median line from anterior to posterior margin; CH, carapace height measured at maximum height of cephalothorax; FW, front width measured along anterior frontal margin between inner angles of orbits; G1, first gonopod; G2, second gonopod; mya, millions of years ago; P2–5, pereiopods 2–5 (ambulatory legs 1–4, respectively); TA, terminal article of G1 or G2; TS, terminal segment of mandibular palp; SS, subterminal segment of G1 or G2; AMNH = American Museum of Natural History, New York, USA; FMNH = Field Museum of Natural History, Chicago, USA; NHMW = Natural History Museum, Vienna, Austria; NMU = Northern Michigan University, Marquette, Michigan, USA; ZIM = Zoological Institute and Museum, Hamburg, Germany.

Samples

A total of 77 specimens of Malagasy freshwater crabs were obtained from three museums (AMNH, FMNH, and NMU) (Table 1). Recently collected whole specimens were preserved in either absolute (96%) or 70% ethanol. The adult male voucher specimen of *Agora* **n. gen.** (NMU NC1987) from Antananarivo is illustrated here (Figs. 3–5), as is the adult male holotype of *M. elvisi* **n. sp.** from Bobankora forest, Sava Region (FMNH 12646; Figs. 6–9).

DNA extraction, PCR, and sequencing

Tissue was harvested from either the gills or the ambulatory legs and subjected to DNA extraction using a DNEasy kit (Qiagen, Hilden, Germany) following the manufacturer's protocol. Extracted DNA was stored in a refrigerator until required for

PCR. Generally, a 1 µl DNA in 19 µl water dilution was performed prior to use. We used the barcoding mitochondrial locus cytochrome oxidase subunit one (COI) to examine the taxonomic diversity among the Malagasy freshwater crabs because this locus has been used successfully by a number of authors to reconstruct evolutionary relationships among African freshwater crabs (Daniels *et al.*, 2002, 2006, 2015; Daniels & Klaus, 2018; Gouws *et al.*, 2015; Klaus *et al.*, 2006; Phiri & Daniels, 2013, 2014, 2016). Primer pairs are outlined in Daniels *et al.* (2006) and standard PCR conditions for amplification and DNA sequencing protocols were followed (Daniels *et al.*, 2006, 2015).

Phylogenetic analyses

Sequence Navigator (Applied Biosystems, Foster City, CA, USA) was used to compute a consensus sequence from forward and reverse strands. No insertions or deletions were evident for the protein-coding COI locus and sequences were aligned manually. Novel sequences were deposited in GenBank (see Supplementary material Table S1). We used maximum likelihood (ML) and Bayesian approaches to estimate evolutionary relationships and jModelTest (Posada, 2008) to obtain the best-fit substitution model for the locus (results not shown). The substitution model was used in the partitioned Bayesian analyses. The best-fit maximum likelihood score was chosen using the Akaike Information Criteria (AIC) (Akaike, 1973), because this reduces the number of parameters that contribute little to describing the data by penalizing more complex models (Nylander *et al.*, 2004; Posada & Buckley, 2004). Maximum likelihood analysis was conducted on the concatenated data set in RAxML version 7.2.7 (Stamatakis, 2006). The robustness of branches of the best ML tree was assessed with 1,000 bootstrap replicates using the CAT algorithm for fast bootstrapping, whereas the final tree search was conducted under the GTR+Γ model for both partitions as less complicated models are not implemented in RAxML. Only bootstrap values > 75% were regarded as statistically supported.

Bayesian inferences were used to investigate optimal tree spaces using the program MRBAYES version 3.2.6 (Ronquist *et al.*, 2012). Four Markov chains were run for each analysis, with each chain starting from a random tree and running for 50 million generations, sampling each chain every 10,000th tree. This process was repeated four times to ensure that trees converged on the same topology. A 50% majority rule consensus tree was generated from the trees retained (after the burn-in trees were discarded using likelihood plots) with posterior probabilities (*pP*) for each node estimated by the percentage of time the node was recovered. Posterior probability values < 0.95 *pP* were regarded as poorly resolved.

Divergence-time estimations

We estimated divergence times for the Malagasy freshwater crabs by applying a Yule tree prior to initial test runs, and an uncorrelated lognormal relaxed molecular clock after the test runs (investigating whether the standard deviation of the uncorrelated lognormal clock approaches zero). We used potamonaustid substitution rates (and their standard deviations) as priors that originate from a fossil calibrated phylogeny of the whole Potamonautilidae (Daniels *et al.*, 2015; Daniels & Klaus, 2018): 2.85% per Ma (SD 0.005) for the COI locus. The maximum clade credibility tree was determined and annotated in TreeAnnotator version 2.4.1 (part of the Beast package) (Rambaut *et al.*, 2013) after removal of 10% of the trees as burn-in.

Outgroup selection

We selected outgroup taxa from the subfamily Deckeniinae: two *Deckenia* species (East Africa), three *Seychellum* species (Seychelles Archipelago), and one *Afrithelphusa* species (West Africa), because

these three genera have been demonstrated to be sister to the monophyletic Malagasy freshwater crab clade (Daniels *et al.*, 2006, 2015).

Distance calculations for genera and species

Our preliminary analyses for the Malagasy COI data revealed the presence of several novel genera and species (Fig. 1). Because some of the currently recognized Malagasy genera appear to be paraphyletic, we calculated the uncorrected p-distances (%) in PAUP* 4b10 (Swofford, 2001) and compared these with those based on representative COI sequence data from morphologically well-defined Afrotropical genera from Daniels *et al.* (2006, 2015). The uncorrected p-distances based on COI sequence data were used as a guide (along with morphological data) to distinguish existing and novel genera and species of Malagasy crabs.

RESULTS

Phylogenetic analysis

Both the BI and ML analyses retrieved a near identical tree topology, hence only the BI topology is shown (Fig. 1). The tree topology revealed the Malagasy freshwater-crab fauna to be monophyletic, diverging from the continental Afrotropical freshwater crab fauna about 10.58 mya (95% HDP 8.39–13.22 mya) (Fig. 1). The divergence time estimations indicate that most of the divergence within the monophyletic Malagasy freshwater-crab genera occurred during the Middle to Late Miocene epochs. We retrieved a major clade with two deep lineages representing sister taxa (new genera B and C) in the early branching portion of the tree topology. The latter two genera diverged 8.74 mya (6.35–11.38 mya) from a common ancestor. New genus C is characterized by very shallow terminal branches, suggesting the genus is possibly monotypic. In contrast, new genus B has several deeply divergent nested lineages, implying the presence of a number of distinct operational taxonomic units.

The second large clade diverged 8.23 mya (95% HDP, 6.52–10.18 mya) into two major divisions. One of these is taxonomically unstable, and contains several divergent described genera, some of which may prove to be paraphyletic. For example, within this clade there are multiple distinct, deeply divergent, statistically highly-supported lineages suggesting the presence of a number of distinct genera and species. These lineages are currently represented by five genera (*Boreothelphusa* Cumberlidge, 2010, Foza Reed & Cumberlidge, 2006, *Madagapotamon* Bott, 1965, *Marojejy* Cumberlidge, Boyko & Harvey, 2002 (Cumberlidge *et al.*, 2002a), and *Skelosophsa* Ng & Takeda, 1994), but the exact taxonomic status of these taxa needs to be reexamined in the light of the present findings given that taxonomic systems should reflect natural evolutionary groups.

The second major division of this large clade diverged 8.29 mya (95% HDP, 6.55–10.05 mya), and one branch includes the genus *Hydrothelphusa* A. Milne-Edwards, 1872, which is early branching and monophyletic, with a divergence time of 3.26 mya (95% 2.47–4.14 mya). There are five deeply divergent lineages within *Hydrothelphusa*, suggesting the presence of five distinct species. The other branch from this common ancestor diverged 7.33 mya (95% HDP, 5.71–9.08 mya) and this resulted in a clade that includes *Malagasya* and two new genera (*Agora* n. gen. and new genus A (N. Cumberlidge *et al.*, unpublished data), each of which is monophyletic. Divergence within *Malagasya* occurred 3.56 mya (95% HDP, 2.57–4.63 mya), with *M. antongilensis* (Rathbun, 1905) representing an early branch that is sister to the clade shared by *M. goodmani* (Cumberlidge, Boyko & Harvey, 2002) (Cumberlidge *et al.*, 2002a), and *M. elvsi* n. sp. Divergence within the other two clades (new genus A and *Agora* n. gen.) was initiated 5.60 mya

(95% HDP 4.22–7.08 mya), where one of these clades (new genus A) has at least four deeply divergent lineages that each corresponds to a new species, while *Agora* n. gen. appears to be monotypic.

Uncorrected p-distances based on COI sequence data among representatives of six Afrotropical genera of Potamonautesidae Bott, 1970 (*Afrithelphusa* Bott, 1969, *Deckenia* Hilgendorf, 1869, *Platythelphusa* A. Milne-Edwards, 1887, *Potamonautes* Cumberlidge & Clark, 1992, *Seychellum* Ng, Števčić & Pretzmann, 1995, and *Sudanonautes* Bott, 1955) ranged from a minimum of 15.34% to a maximum of 22.31%. Similarly, uncorrected p-distances based on COI sequence data among the known Malagasy genera ranged from a minimum of 14.77% (between new genera A and C) to a maximum of 16.85% (between the two new genera B and C) that all fall within the range observed among the Afrotropical genera as a whole.

Uncorrected p-distances based on COI sequence data among species of Afrotropical freshwater crabs were highly variable. For example, the two *Deckenia* species have an uncorrected p-distance of 3.75%, whereas this value ranged from 3.44% to 9.13% among species of *Liberonautes* Bott, 1955 (between *L. lugbe* Cumberlidge, 1999 and *L. rubigimanus* Cumberlidge & Sachs, 1989, two morphologically distinct species) to 15.66% (between *L. nimba* (Cumberlidge, 1999) and *L. rubigimanus*). Within *Potamonautes*, the most widespread continental genus, uncorrected p-distances based on COI sequence data ranged from as low as 0.02% (between *P. perlatus* (H. Milne Edwards, 1837) and *P. barbarai* Phiri & Daniels, 2014) to as high as 18.99% (between *P. principe* Cumberlidge, Clark & Baillie, 2002 (Cumberlidge *et al.*, 2000b) and *P. obsesus* (A. Milne-Edwards, 1868)).

Similarly, within the recognised Malagasy genera, the uncorrected p-distances based on COI sequence data between species of *Malagasya* was 9.02% (between *M. goodmani* and *M. antongilensis*) and 8.97% (between *M. goodmani* and *M. elvsi* n. sp.). Within *Hydrothelphusa*, the uncorrected p-distances between species was 8.07% (between *H. agilis* A. Milne-Edwards, 1872 and *H. madagascariensis* A. Milne-Edwards, 1872). While we do not advocate for the use of uncorrected p-distance values alone to define genera and species, the values we have observed for the Malagasy genera and species both fall well within the range reported for the equivalent Afrotropical taxonomic levels used to corroborate their distinct evolutionary status.

SYSTEMATICS

Infraorder Brachyura Latreille, 1802

Superfamily Potamoidea Ortmann, 1896

Family Potamonautesidae Bott, 1970

Subfamily Deckeniinae Ortmann, 1897

Tribes Hydrothelphusini Colosi, 1920

***Agora* gen. nov.**

(Figs. 2–5)

Bottia Pretzmann, 1961 (partim): 164, fig. 3.

Gecarcinautes Bott, 1965 (partim): 336, 338–339, pl. 2, figs. 6, 7.

Hydrothelphusa Cumberlidge & Sternberg 2002 (partim): figs. 1D; 3D; 4D; 5D; 6D; 7G, H; 8D; 9J–M; 11D.

Foza Reed & Cumberlidge, 2006 (partim): 59–60, figs. 1, 2.

Type species: *Thelphusa goudotii* H. Milne Edwards, 1853, by present designation.

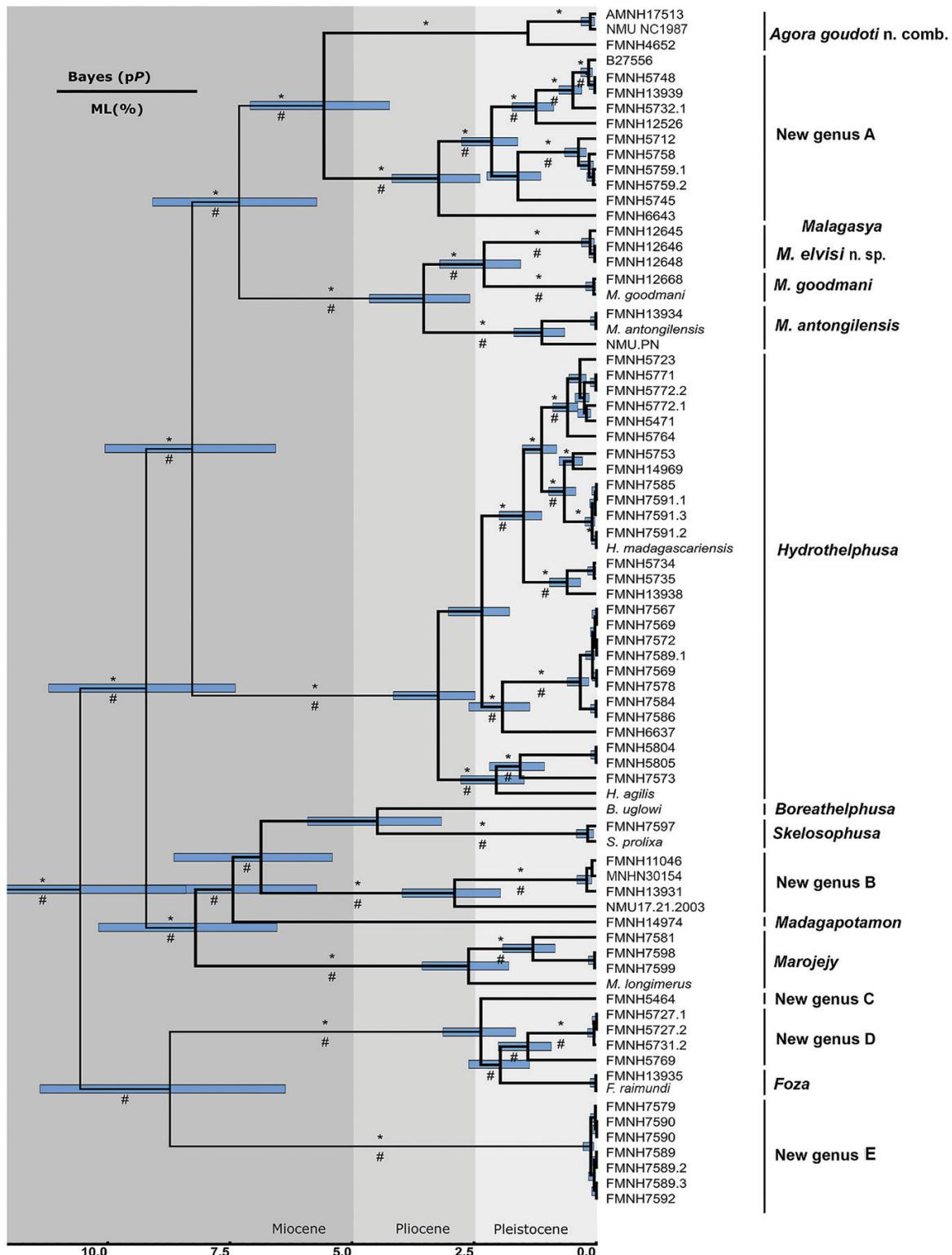


Figure 1. Maximum clade credibility tree of the Malagasy freshwater crab fauna based on mt COI with support values (posterior probabilities and bootstrap values of the ML analyses) with a geological time scale below the tree topology. Posterior probabilities > 0.95 pP (*) and bootstrap values > 75% (#) were regarded as statistically supported and are shown on the tree topology.

Diagnosis (male): Carapace noticeably wide (CW/FW 4.2), highly arched (CH/FW 1.9), dorsal surface smooth, urogastric groove deep, distinct; cervical groove distinct, long, ending just before meeting postfrontal crest; semicircular groove, cervical grooves S-shaped each curving distinctly outward meeting postorbital

crest behind orbits; postfrontal crest distinct, prominent, completely crossing carapace, meeting anterolateral margins of carapace at epibranchial teeth (Figs. 2A, 3A); exorbital tooth faint, low; epibranchial tooth small but distinct, low (Figs. 2A, 3A). Subhepatic region of branchiostegal wall smooth, suborbital

region smooth except for rows of large granules along longitudinal groove, inferior part of pterygostomial region smooth (lacking granules or setae), superior part with rows of large granules along longitudinal suture. Mandibular palp 2-segmented; terminal segment (TS) bilobed, with small distinct anterior lobe ($0.44 \times$ TS length; Fig. 5F, G). Third maxilliped exopod with long flagellum; ischium with distinct vertical groove (Fig. 3B). Thoracic sternal sulcus S3/4 V-shaped, distinct, completely crossing sternum, ending just before meeting anterior margin of subpleonal cavity (Fig. 3B). G1 TA short (TA/SS 0.26), directed outwards at 35° angle to longitudinal axis of G1 SS; dorsal face G1 SS with broad dorsal membrane (maximum length $0.13 \times$ SS length) at TA/SS junction (Fig. 5B, D). G2 TA long, flagellum-like (TA/SS 0.65), almost as long as G2 SS (Fig. 5E), tip straight, in line with longitudinal axis of G2 TA. Adult CW 45.3 mm.

Colour in life: Carapace dark maroon-brown, underside pale yellow brown.

Type locality: Madagascar. The exact place for the type locality of *T. goudoti* is vague because the original label only records that it was collected somewhere along the road (RN4) between Antananarivo and Bombetoka Bay in northwest Madagascar. The voucher specimen illustrated here (NMU NC1987, Figs. 3–5) was purchased

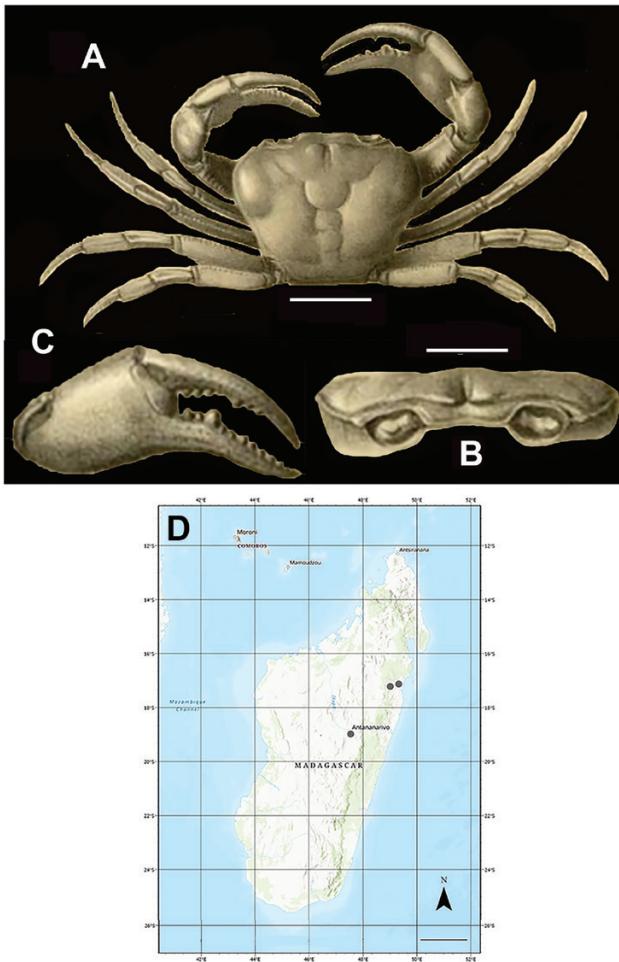


Figure 2. *Thelphusa goudoti* H. Milne Edwards, 1853, lectotype, male CW 46.2 mm from road between Bombetoka Bay and Antananarivo, Madagascar (MNHN B3817). Dorsal view of entire animal (A), frontal view (B), right (major) cheliped (C), map showing revised distribution of *A. goudoti* n. comb. (D). Figures A–C based on H. Milne Edwards (1853: 8). Scale bars: A = 16.7 mm, B = 9.8 mm, D = 190 mm.

live by the first author as part of a string of crabs on sale in the Analakely Market in Antananarivo, Madagascar ($-18.907448S$, $47.526232E$). This specimen was presumably collected in a nearby locality in Analamanga region and was transported to the market for sale as a food item. The collection locality of the other specimens examined here (ZRC 2000.2303) is also from the vicinity of Antananarivo, recorded simply as from a lake near Antananarivo (possibly Lac Anosy ($-18.915482S$, $47.520799E$)). The other specimens (FMNH 4652, AMNH 17531) were caught in pitfall traps set in lowland forest 10 m ASL in the Station Forestière de Tampolo in Atsinanana region ($-17.286667S$, $49.408333E$).

Etymology: The genus name is masculine and is derived from the Greek *agora* for “market” or “public area.” This refers to the purchase of the voucher specimens described here by the first author that were part of a string of crabs offered for sale as a food item in the Analakely Market in Antananarivo. The name is used as a Latin noun in apposition and treated as neuter.

Remarks: The family name Potamonautidae Bott 1970 is recognised herein (despite being junior to Deckeniidae Ortmann, 1897 and Hydrothelphusinae Colosi, 1920) according to Article 35.5 of the ICBN code (Cumberlidge et al., 2008; Ng et al., 2008). The subfamily name Deckeniinae Ortmann, 1897 is senior to Hydrothelphusinae Colosi, 1920 and follows priority (Cumberlidge et al., 2008).

The generic status of *Thelphusa goudoti* H. Milne Edwards, 1853 has long been controversial despite being the first species of freshwater

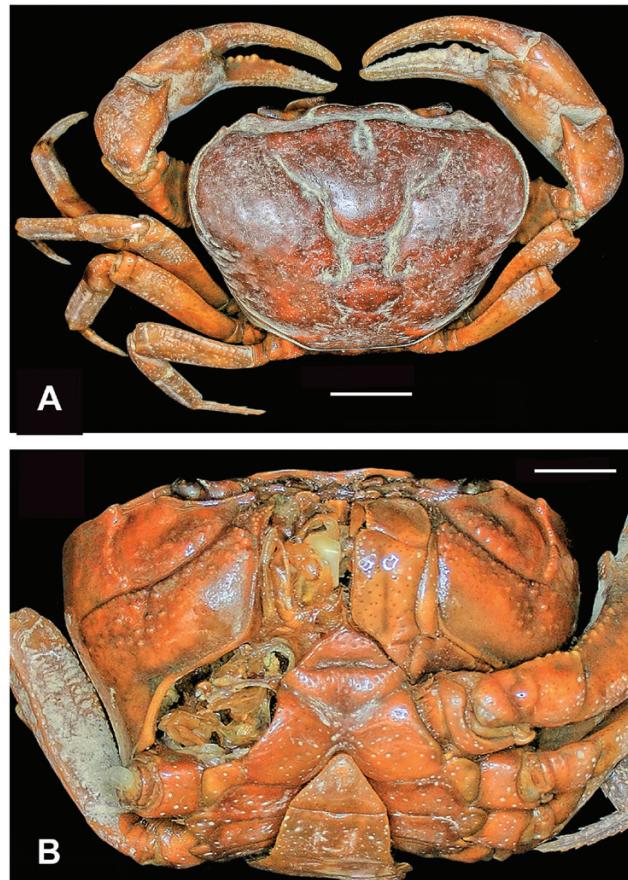


Figure 3. *Agora goudoti* (H. Milne Edwards, 1853, n. comb.), voucher specimen, male CW 45.3 mm from Analakely Market in Antananarivo, Madagascar (NMU NC1987). Whole animal, dorsal view (A), whole animal, ventral view (B). Scale bars: A = 10 mm, B = 6.7 mm. This figure is available in colour at *Journal of Crustacean Biology* online.

crab to be described from Madagascar. The taxonomic confusion surrounding this taxon has resulted in *T. goudoti* being included by different authors in several different genera over the years, as classification systems have evolved. For example, *T. goudoti* was transferred to *Telphusa* Latreille, 1819 (by De Man, 1892), to *Potamon* Savigny, 1816 (by De Man, 1898), and to *Potamon* (*Potamon*) by Rathbun, 1904 and Calman, 1913. Since then, *T. goudoti* has been assigned to four other genera: *Bottia* Pretzmann, 1961 (by Pretzmann, 1961), *Gecarcinautes* Bott, 1965 (by Bott, 1965), *Hydrothelphusa* (by Cumberlidge & Sternberg, 2002), and *Foza* (by Cumberlidge & Meyer, 2009). *Thelphusa goudoti* is transferred herein to *Agora n. gen.* based on independent morphological and molecular datasets.

The classifications of Bott (1960, 1965) and Pretzmann (1961) that included *T. goudoti* are inconsistent and raise doubts about their validity. For example, Bott (1960) established *Gecarcinautes* (type species *G. brincki* Bott, 1960 from South Africa, by original designation) and included three Madagascan taxa (*Thelphusa goudoti*, *Potamon* (*Potamon*) *bombetokensis* Rathbun, 1904 and *Thelphusa madagascariensis*). Bott (1965) subsequently reorganized *Gecarcinautes* to include *G. brincki*, *T. goudoti*, *G. antilongensis antongilensis* Rathbun, 1905, and *G. a. vondrozi* Bott, 1965 (and reassigned *Potamon* (*P.*) *bombetokensis* Rathbun, 1904 as a junior synonym of *Hydrothelphusa humbloti* (Rathbun, 1904), and *T. madagascariensis* as a subspecies of *H. agilis*). The description of *G. goudoti* by Bott (1965: pl. 2, figs. 6, 7), however, relied on a female specimen (ZIM 3551) from Ivolina River, Atsinanana region near Tamatave ($-18.058728S$, $49.366585E$). Bott (1965) provided photographs of the dorsal and ventral views of the whole animal (ZIM 3551), but relied for the G1 and G2 on the description of a different specimen in Pretzmann (1961: figs. 3a, b). There is reason to doubt that the Madagascan specimens identified by Bott (1965) as *G. goudoti* were accurately identified. For example, the carapace characters of the female from the Ivolina River (Bott, 1965: pl. 2, figs. 6, 7) differ from the lectotype of *T. goudoti* in a number of ways. The specimen from the Ivolina River has a postfrontal crest that is faint and incomplete (whereas that of the type of *T. goudoti* and in NMU NC1987 is very distinct and completely crosses the carapace), its cervical grooves are short and barely discernible (grooves are long, deep and clear in the type of *T. goudoti* and in NMU NC1987), the epibranchial teeth are weak but pointed (teeth are blunt but not pointed in the type of *T. goudoti* and in NMU NC1987), and the distal third of its G2 TA is widened and then sharply bent like a bird's beak (Pretzmann, 1961: fig. 3b; Bott, 1965) (distal third is not straight and not bent in NMU NC1987).

Pretzmann (1961) established *Bottia* with *P. (P.) bombetokensis* Rathbun, 1904 as the type species and included *Thelphusa goudoti* together with *T. madagascariensis* and *Bottia m. reticulata* Pretzmann, 1961 based mainly on a shared bilobed mandibular palp. Pretzmann (1961: fig. 3A, B) identified two male specimens in NHMW from 'Madagascar' (CL 32–44 mm) collected by Steindachner in 1883 as *B. goudoti* and illustrated them with only a brief sketch of the G1 and part of the G2. The sketches by Pretzmann (1961: figs. 3A, B), however, differ from the G1 and G2 of the voucher specimens of *T. goudoti* provided here (Fig. 5A–E). It is likely, therefore, that Pretzmann's (1961) specimens belong to a different taxon.

Bott (1965) did not recognize *Bottia* because this genus was based on a character that is widely distributed among several other Madagascan species, and he assigned *Potamon* (*Potamon*) *bombetokensis*, *Thelphusa madagascariensis*, and *Bottia madagascariensis reticulata* to *Hydrothelphusa*, and *T. goudoti* to *Gecarcinautes*. Cumberlidge & Sternberg (2002) did not recognize *Gecarcinautes* and referred *G. brincki*, the type species, to *Potamonautes*, *T. goudoti* to *Hydrothelphusa*, and *G. a. antongilensis* and *G. a. vondrozi* to *Malagasya* (Cumberlidge & Sternberg, 2002). Cumberlidge & Meyer (2009) subsequently transferred *T. goudoti* to *Foza* Reed & Cumberlidge, 2006. None of the above opinions are accepted here in the light of the new morphological and molecular evidence presented.

Distribution: Madagascar. *Agora gen. nov.* is known from the region around the capital city of Antananarivo and from Atsinanana region along the east coast of the island (Fig. 5D).

Comparisons: *Agora n. gen.* is assigned to the Potamonautidae because of the common possession of a suite of diagnostic familial characters, including a 2-segmented mandibular palp (Fig. 5B, C), a triangular abdomen (Fig. 3B), and a G1 with a medium-length terminal article (Fig. 5A–D) (Cumberlidge, 1999). Although all potamonautid crabs possess a 2-segmented mandibular palp, other characters of the mandible vary a great deal, especially among Madagascar crabs (Cumberlidge, 1999; Cumberlidge & Sternberg, 2002). Cumberlidge *et al.* (2015), for example, recognized four different forms of the mandibular palp among the Malagasy freshwater crabs. Of these, *Agora n. gen.* groups with those genera whose palp has a clearly bilobed terminal segment with a substantial medium-sized anterior lobe about 0.3–0.5 times as long as the terminal segment (*Hydrothelphusa*, *Marojejy*, *Malagasya*, *Foza*, and *Glabrithelphusa* Meyer, Cumberlidge & Koppin, 2014).

Other important taxonomic characters that set *Agora n. gen.* apart from the eight other genera of Malagasy freshwater crabs include its completely smooth dorsal carapace surface (Figs. 2A, 3A; Cumberlidge & Sternberg, 2002: fig. 2A–F). *Agora n. gen.* can also be distinguished from *Foza* and *Malagasya* by the smooth anterolateral margin of the carapace (Figs. 2A, 3A), which has small teeth in *Foza* (Reed & Cumberlidge, 2006: fig. 1), and conspicuous teeth in *Malagasya* (Fig. 11A, B). The new genus can be distinguished from *Hydrothelphusa* and *Marojejy* by the small notch-like space between the exorbital and epibranchial teeth (Figs. 2A, 3A) (wide space or cleft between these teeth in both *Hydrothelphusa* and *Marojejy* (Cumberlidge & Sternberg, 2002: figs. 1A–C, 2F)). The ambulatory legs (P2–5) (not elongated or slim) and eyestalks and corneas (normal length and size) of *Agora n. gen.* (Figs. 1A, 3A) further distinguish the new genus from *Marojejy* whose walking legs are long, slender, and elongated, and whose eyestalks taper distally and have reduced corneas (Cumberlidge & Sternberg, 2002: figs. 2F, 8F). *Agora n. gen.* is distinguished from *Madagapotamon* by the length of the flagellum of the exopod of the third maxilliped, which is long and well developed in *Agora n. gen.* (Fig. 1C), but almost absent, and reduced to a short stub in *Madagapotamon* (Cumberlidge & Sternberg, 2002: fig. 5H). *Agora n. gen.* is distinguished from *Boreathelphusa* and *Skelosophusa* by the size of the flap on the mandibular palp, that of *Agora n. gen.* is large (0.3× TS length), whereas that of *Boreathelphusa* and *Skelosophusa* is noticeably small, reduced to a small ledge (0.1× TS length) (Cumberlidge & Sternberg, 2002: fig. 4H–K). *Agora n. gen.* is distinguished from *Glabrithelphusa* by the postfrontal crest, which is distinct and completely crosses the carapace in *Agora n. gen.* (Figs. 2A, 3A) and faint and interrupted in *Glabrithelphusa* (Meyer *et al.*, 2014: figs. 1A, 3A).

Nomenclatural statement: A life science identifier (LSID) number was obtained for the new genus: urn:lsid:zoobank.org:pub: 97D882FC-2789-45A4-9070-3ED88C46023A.

Agora goudoti (H. Milne Edwards, 1853) **n. comb.**

(Figs. 2–5, Supplementary material Table S1)

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, pl. xiii., fig. 10 — Bals, 1929: 355.

Potamon (*Potamon*) *methueni* – Calman, 1913: 920–921, pl. XCI.

Hydrothelphusa goudoti – Cumberlidge & Sternberg, 2002: 56–59.

— Daniels *et al.*, 2006, table 1, fig. 1. — Ng *et al.*, 2008: 169.

Foza goudotii – Cumberlidge & Meyer, 2009: 85–86, table 1. — Daniels et al., 2015, table 1, fig. 2.

Type locality: As for genus.

Type material: Lectotype of *Thelphusa goudotii* (MNHN B3817) (Figs. 2A–C): dried adult male (CW 46, CL 33.5 mm) coll. Jules Prosper Goudot, exact date unknown (probably between 1828 and 1839 based on Goudot's travel records (Beolens et al., 2013), from the road between Bombetok and Tananarive, Madagascar. Two dried adult paralectotypes (MNHN B3818) (CW 41, CL 30.7 mm, second specimen broken), described by A. Milne-Edwards (1869) (MNHN B3818). The lectotype and paralectotypes of *T. goudotii* are dried and in poor condition and cannot supply important adult male taxonomic characters (such as the gonopods) or DNA sequences. It was necessary to select voucher specimens whose carapace and cheliped characters closely resemble the lectotype (Figs. 2, 3, 4); these specimens made available the full range of morphological characters used in the rediagnosis and redescription as well as DNA sequence data.

Other material: Adult male (CW 45.1, CL 32.8, CH 18.55, FW 13.3) voucher for DNA sequence data; adult female (CW 39.7, CL 30.8, CH 16.5, FW 12.2 mm), 1987, purchased live by NC as part of a string of crabs on sale in the Analakely Market, Antananarivo, Madagascar (NMU NC1987).

Two adult males (CW 38.0, CL 28.1, CH 15.1, FW 10.2; CW 34.4, CL 27.5, CH 14.5, FW 8.4), 2 adult females (CW 38.2, CL 33.1, CH 17.0, FW 9.5; CW 32.0, CL 25.1, CH 13.6, FW 8.2), from a lake near Antananarivo, coll. H. Morioka (ZRC 2000.2303); 3 subadult males (CW 30.3, CL 23.2, CH 13.5, FW 8.6; CW 23.8, CL 19.4, CH 10.3, FW 7.4; CW 23, CL 19, CH 10.6, FW 6.8 mm) Station Forestière de Tampolo in Atsinanana region ($-17.286667S, 49.408333E$), 10 m ASL, in pitfall traps, coll. S.M. Goodman, April 1997 (FMNH 4652); 2 subadult males (CW 31.8, CL 27.7, CH 15.2, FW 10.3; CW 23.8, CL 19.4, CH 10.7, FW 6.7 mm) Station Forestière de Tampolo in Atsinanana Region ($-17.286667S, 49.408333E$), 10 m ASL, in pitfall traps, coll. S.M. Goodman, April 1997 (AMNH 17531). FMNH 4652 was divided into two lots, to make a gift to AMNH, so FMNH 4652 and AMNH 17531 both have the same collection data.

Diagnosis: As for genus.

Redescription (based on NMU NC1987): Carapace ovoid, noticeably wide (CW/FW 4.2), highly arched (CH/FW 1.9), dorsal surface smooth, urogastric groove deep, distinct; cervical groove distinct, long, ending just before meeting postfrontal crest; semi-circular groove, both cervical grooves deep, long, curving distinctly outward; postfrontal crest distinct, prominent, completely crossing carapace, meeting anterolateral margins of carapace at epibranchial teeth (Figs. 2A, 3A); exorbital tooth faint, low; epibranchial tooth small but distinct, low (Figs. 2A, 3A); carapace anterolateral surface smooth, posterolateral surface with striae; carapace branchiostegal sidewall with vertical, longitudinal sutures dividing it into 3 regions (suborbital, subhepatic, pterygostomial) (Fig. 4A); longitudinal suture beginning at respiratory opening, curving backward across sidewall dividing suborbital, subhepatic regions from pterygostomial region (Fig. 4A); vertical sulcus on carapace branchiostegal wall curving to meet anterolateral margin at epibranchial tooth (Fig. 4A), dividing suborbital from subhepatic regions (Fig. 4A). Subhepatic region of branchiostegal wall smooth, suborbital region smooth except for rows of large granules along longitudinal groove, inferior part of pterygostomial region smooth (lacking granules or setae), superior part with rows of large granules along longitudinal suture.

Mandibular palp 2-segmented; terminal segment (TS) bilobed, with small distinct anterior lobe ($0.44 \times$ TS length; Fig. 5F, G). Third maxilliped exopod with long flagellum; ischium with distinct vertical groove (Fig. 3B). Sternal sulcus S2/3 prominent, horizontal, completely crossing sternum; S3/4 V-shaped, distinct, completely crossing sternum, midpoint ending just before meeting anterior margin of subpleonal cavity (Fig. 3B). Episternal sulci S4/E4, S5/E5, S6/E6, S7/E7 faint or missing (Fig. 3B).

Male chelipeds subequal; fingers slim, elongated. Right (major) cheliped dactylus relatively stout, straight, with 2 medium teeth proximally, one medium tooth medially; fixed finger (pollex) with 3 large teeth proximally (Fig. 4B); dactylus, propodus of left cheliped straight, propodus large teeth proximally (Fig. 4C); distal tooth on cheliped carpus inner margin large with pointed tip, proximal tooth conspicuously small (Fig. 4D); medial inferior margin of cheliped merus with small distinct distal tooth followed by row of granules (Fig. 4D, E).

Male pleon triangular, sides slightly indented; telson rounded at distal margin (Fig. 3B). G1 TA short (TA/SS 0.26), directed outwards at 35° angle to longitudinal axis of G1 SS. G1 SS tube-like, tapering slightly from broad basal margin to distal margin ($0.3 \times$ SS basal margin); ventral face of SS with raised triangular flap extending halfway across segment forming roof of chamber for G2, flap tapering diagonally from broad base to narrow point at SS/TA junction (Fig. 5D); dorsal surface of SS entirely smooth, distal part with broad dorsal membrane (maximum length $0.13 \times$ SS length) at TA/SS junction (Fig. 5A–D). G2 TA long (TA/SS 0.65), almost as long as G2 SS (Fig. 5E),

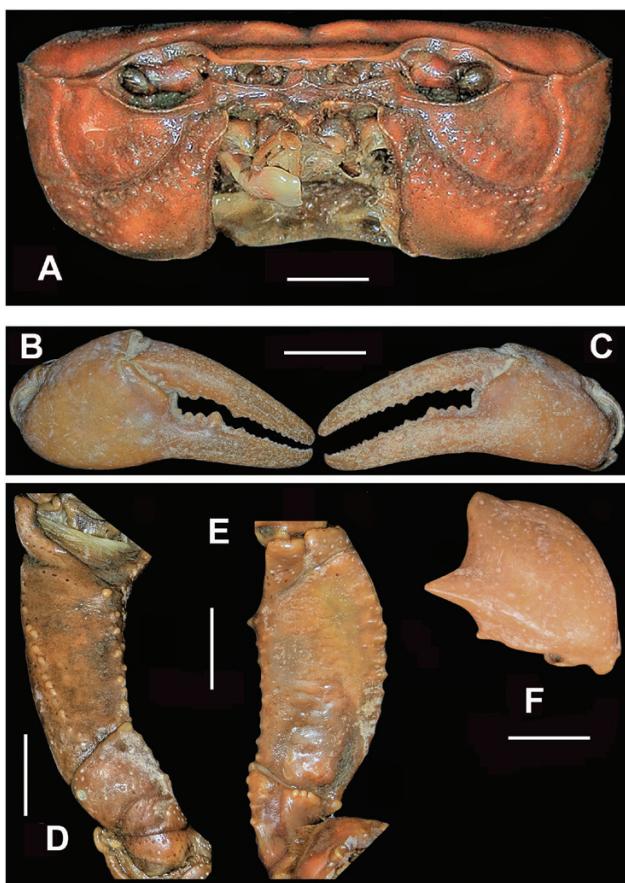


Figure 4. *Agora goudotii* (H. Milne Edwards, 1853, n. comb.), voucher specimen, male CW 45.3 mm, from Analakely Market in Antananarivo, Madagascar (NMU NC1987). Carapace frontal view (A), frontal view right (B) and left (C) chelipeds, right cheliped merus underside (D), right cheliped merus dorsal view (E), right cheliped carpus dorsal view (F). Scale bars: A = 5 mm; B, C = 10 mm; D–F = 6.7 mm. This figure is available in colour at *Journal of Crustacean Biology* online.

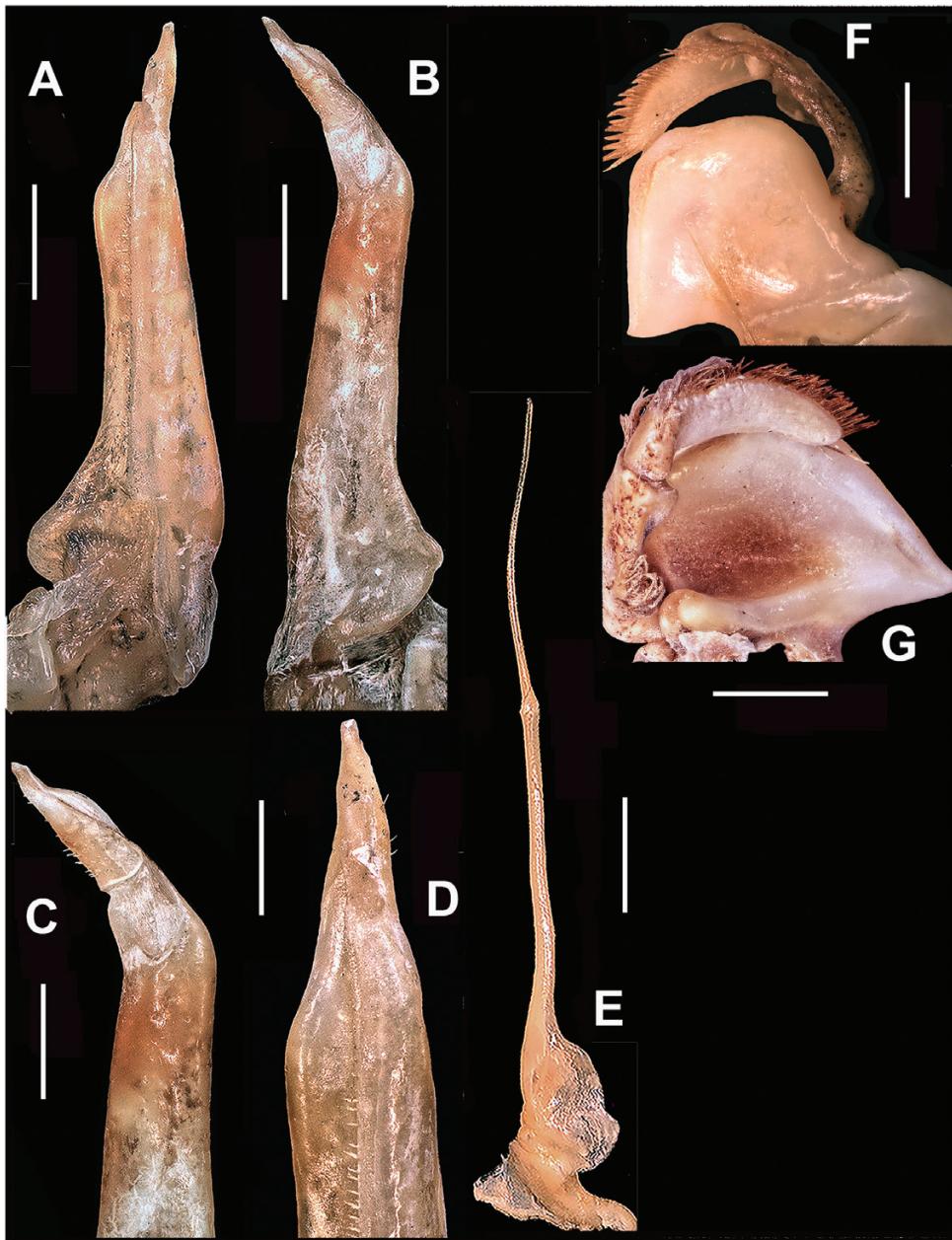


Figure 5. *Agora goudoti* (H. Milne Edwards, 1853, **n. comb.**), voucher specimen, male CW 45.3 mm, from Analakely Market in Antananarivo, Madagascar (NMU NC1987). Right G1 ventral view (**A**), right G1 dorsal view (**B**), right G1 dorsal view detail of TA and of SS junction (**C**); right G1 superior view (**D**), right G2 ventral view (**E**), mandible frontal view (**F**), mandible posterior view (**G**). Scale bars: A = 2.2 mm; B = 2.1; C = 1.7 mm; D = 1.3 mm; E = 2.9 mm; F = 2.5 mm; G = 2.9 mm.

flagellum-like, tip straight, in line with longitudinal axis of G2 TA. Adult at CW 45.3 mm.

Colour in life: Carapace dark brown, maroon, underside pale yellow to brown.

Molecular analysis: The three specimens (FMNH 4652, AMNH 17513, NMU NC1987) sequenced have morphological characters of the carapace shared with those of the type specimen of *T. goudoti* (Fig. 2). All three specimens form a well-supported clade that is recognized here as *Agora n. gen.*, which is phylogenetically distinct from all of the other specimens of Malagasy freshwater crabs included herein (Fig. 1).

The phylogenetic studies of Daniels *et al.* (2006, 2015) included FMNH 4652, but each one assigned this specimen to a

different genus. For example, Daniels *et al.* (2006: table 1, fig. 1) treated FMNH 4652 as *Hydrothelphusa goudoti* because it was part of a lineage (although positioned basally) that included *H. agilis* and *H. madagascariensis*, and that was also separate from *F. raimundi* (the type species of *Foza*). Daniels *et al.* (2015: table 2, fig. 1) subsequently followed Cumberlidge & Meyer (2009) and treated FMNH 4652 as *Foza goudoti*. We nevertheless found FMNH 4652 to occupy a completely different lineage from either *Hydrothelphusa* or *Foza*, and so we have established *Agora n. gen.* to accommodate this specimen (NMU NC1987) and its close relatives (AMNH 17513).

Remarks: *Thelphusa goudoti* H. Milne Edwards, 1853 was the first freshwater crab to be described from Madagascar, and has long been recognised as a distinct species. The generic assignment of this species,

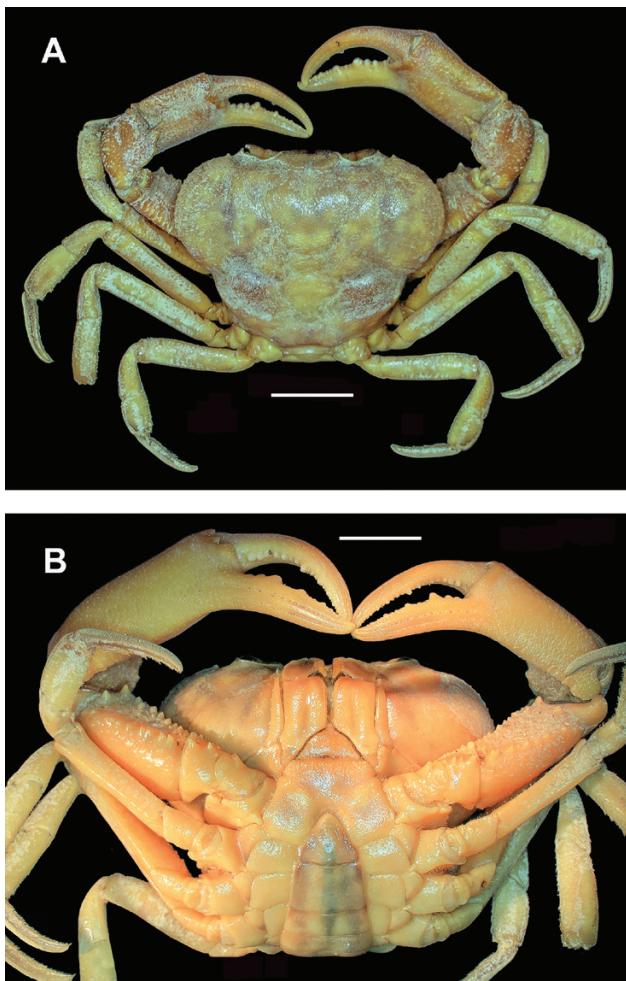


Figure 6. *Malagasya elvisi* n. sp. holotype, male CW 39 mm, from Bobankorana forest, Sava region, Madagascar (FMNH 12646). Whole animal, dorsal view (A), whole animal, ventral view (B). Scale bars: A, B = 6.7 mm. This figure is available in colour at *Journal of Crustacean Biology* online.

however, has been less stable and has been revised several times (De Man, 1892, 1898; Rathbun, 1904; Pretzmann, 1961; Bott, 1965; Sternberg & Cumberlidge, 2002; Cumberlidge & Meyer, 2009). It is herein revised once again. The present reassignment of *A. goudoti* n. comb. to *Agora* n. gen. is made on the basis of similarities of characters of the carapace, thoracic sternum, third maxilliped, and cheliped of the voucher specimen of *A. goudoti* n. comb., which unite the present specimens with the type specimen of *T. goudoti*. *Agora goudoti* n. comb. is distinguished from other species of Malagasy freshwater crabs by a unique suite of characters of the mandible, carapace, and gonopods (see remarks section for genus). *Agora goudoti* n. comb. is characterized by its unusual carapace proportions: it has the widest, longest and most highly arched carapace of any species in this genus, its carapace has a distinctive groove pattern with long, outward curved cervical grooves resembling cow horns, and the P5 merus is remarkably short.

We have examined the holotype of *Potamon* (*Potamon*) *methueni* Calman, 1913 and agree with Cumberlidge & Sternberg (2002) and Cumberlidge & Meyer (2009) that *P. (P.) methueni* Calman, 1913, is a junior synonym of *T. goudoti*. The holotype of *P. (P.) methueni* is similar to *A. goudoti* n. comb. in a number of characters. Both specimens have a wide and highly arched carapace with a smooth dorsal surface, smooth carapace sidewall regions, a postfrontal crest that completely crosses the carapace meeting the anterolateral margins, a small but distinct epibranchial tooth, a third maxilliped whose exopod has a long flagellum, and whose ischium has a distinct vertical groove, and a 2-segmented mandibular palp with

a bilobed terminal segment with a small distinct anterior lobe. We note, however, that the thoracic sternal sulcus S3/4 of *P. (P.) methueni* differs from that of *A. goudoti* n. comb., which is faint and reduced to two short side notches and does not completely cross the sternum in the former, and deep and completely crosses the sternum in the latter. We do not accept Bott's (1965) opinion that *P. (P.) methueni* is a junior synonym of *Madagapotamon ankarahare* (Nobili, 1906).

Habitat: The collectors of the original specimens of *A. goudoti* provided few habitat notes, but the distributional range maps indicate that this genus occurs in the Madagascar Eastern Highlands freshwater ecoregion (581) (Abell et al., 2008). The ecoregion includes a narrow band of mountains extending north-south along the eastern length of the island. This eco-region experiences high rainfall (2,500–3,000 mm annually), its rivers flow over rocks year-round, and there are numerous rapids and waterfalls. The vegetation at lower elevations of the Eastern Highlands consists of dense evergreen forest, but there are thickets and shrublands at higher elevations (above 1,800 m).

Conservation status: An IUCN conservation assessment of *A. goudoti* n. comb. has not yet been carried out, but this species (as *Foza goudoti*) was assessed in the Least Concern category by Cumberlidge et al. (2018) in a recent review of the extinction risk status of the freshwater decapods of Madagascar. We have herein restricted the range of *A. goudoti* n. comb., which now has a smaller extent of occurrence. This may affect its conservation status, which now needs to be reassessed.

Family Potamonautesidae Bott, 1970

Subfamily Deckeniinae Ortmann, 1897

Tribe Hydrothelphusini Colosi, 1920

Malagasya Cumberlidge & Sternberg, 2002

Type species: *Potamon* (*Parathelphusa*) *antongilensis* Rathbun, 1905 by original designation, gender feminine.

Malagasya elvisi n. sp.

(Figs. 6–9, 10E, F, 11C, F, I, L, Supplementary material Table S1)

Type material: (FMNH 12646), adult male, holotype (designated herein) (CW 39, CL 29.2, CH 12.5, FW 7.8 mm), Sub-prefect of Vohemar, Bobankora forest, western slope, at Antsahalalina, 9.9 km southeast of Daraina, Sava region (−13.2258, 49.7511), from transitional lowland forest, 145 m ASL, in a tuft of *Pandanus* sp. leaves 4 m off the ground, coll. M. Raheriarisena, 2003. Paratypes (same details as holotype). (FMNH 12648), adult female (CW 37.2, CL 28.2, CH 12.5, FW 8.3 mm); (FMNH 12645) subadult female (CW 23.3, CL 17.6, CH 6.8, FW 5.9 mm); (FMNH 12647). FMNH 12645, FMNH 12646, and FMNH 12648 sequenced in present study (Supplementary material Table S1).

Comparative material: *Malagasya antongilensis* (FMNH 13934), adult male (CW 21.1 mm) coll. V. Soarimalala (DNA sequenced herein), Moramanga District, d'Ambohimanaivo Village, Alaotra-Mangoro region (−18.7933, 48.3344); (FMNH 14994) adult male (CW 30.9, CL 22.7, CH 11.5, FW 8.3 mm), coll. D.L. Ramanjisoa and S.M. Goodman, 21 November 2015, along the main road, Atsinanana region, near Reserve Naturelle Integrale [de Betampona], Analanjirofo region (−17.9103S, 49.1969E), low altitude, 321 m ASL.

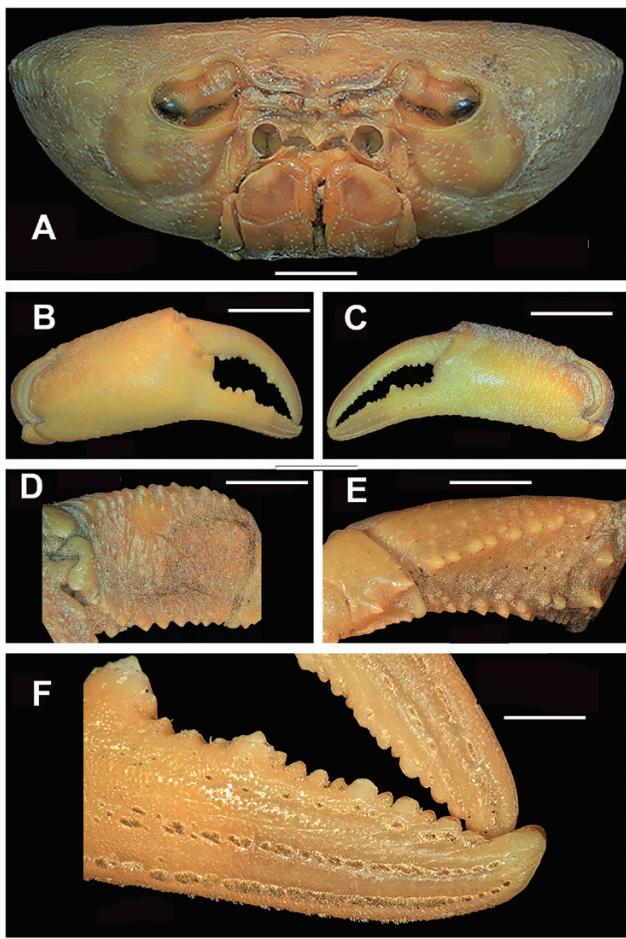


Figure 7. *Malagasya elvisi* n. sp. holotype, male CW 23 mm, from Bobankorana forest, Sava region, Madagascar (FMNH 12646). Carapace frontal view (A), chelipeds frontal view right (B), left (C), right cheliped merus underside (D), right cheliped merus superior view (E), detail of pollex of right cheliped propodus (F). Scale bars: A, D, E = 5 mm; B, C = 10 mm; F = 1.8 mm.

Malagasya goodmani (FMNH 12668), adult male (CW 25.5, CL 18.9, CH 8.6, FW 6.1 mm) (DNA sequenced herein), coll. E. Ihtceue and J. Rozalimanahaka, 20 April 2004, caught in pitfall trap, 10 m ASL, Station Forestière de Tampolo, 10 km NW Fenentre-Est, Atsinanana region (-17.2833S, 49.4167E); *M. goodmani* holotype (FMNH 4651) (DNA sequenced by Daniels et al., 2015), adult male (CW 23.0, CL 17.6, CH 6.8, FW 4.7 mm), Station forestière de Tampolo, Atsinanana region (-17.283889, 49.401389). *M. goodmani* paratypes: (FMNH 4651) adult female (CW 23.5, CL 18.4, CH 8.0, CH 5.4 mm), juvenile male (CW 12.6, CL 10.6, CH 4.2, FW 3.1 mm); (AMNH 17530) male sub-adult (CW 16.5 mm); (AMNH 17530a) adult female, ovigerous (CL 18.1 mm), coll. S.M. Goodman, in leaf axils of *Pandanus* sp., 4 April 1997, Station Forestière de Tampolo, Atsinanana region (-17.03333S, 49.40833E) 152 m ASL; ovigerous female (CL 20.3 mm) (AMNH 17830), coll. S.M. Goodman. 15–22 October 1996, in leaf axils of *Pandanus* sp., near tributary of Manantenina River, 100 km northwest of Manantenina, Reserve Naturelle Integrale de Marojejy, Sava region (-14.43333S, 49.761667E) 674 m ASL.

Diagnosis: Anterolateral margin of carapace with row of small granules; cheliped carpus proximal tooth reduced to small granule, followed by second small granule; major cheliped with

highly arched dactylus forming long oval gape with 5 large teeth on fixed finger (pollex) of propodus; tips of fingers touching but not overlapping.

Description: Based on holotype male from Forêt de Bomankora, Sava region, CW 39 mm (FMNH 12646). Carapace outline heart-shaped, elongated (CL/FW 3.7), high (CH/FW 1.6), widened anteriorly (CW/FW 5.0), tapering sharply posteriorly. Exorbital tooth missing, continuous with supraorbital, suborbital margins; epibranchial tooth small pointed. Front granular, frontal margin noticeably narrow (one-fifth CW), midpoint interrupted by distinct notch. Lateral, medial flagellae of antennules extremely reduced, lateral larger than medial. Anterolateral carapace surface regions granular; branchial, semi-circular, urogastric, cardiac, grooves deep; cervical grooves deep, long, ending before meeting postorbital crests. Postfrontal crest incomplete, epigastric crests positioned posteriorly to epibranchial teeth, epigastric crests clearly separated from postorbital crests; postorbital crests faint, marked by widely-spaced granules, not meeting anterolateral margin. Carapace branchiostegal sidewall clearly divided into 3 parts by horizontal epimeral sulcus running across sidewall, curved vertical sulcus running from base of epibranchial tooth to epimeral sulcus, separating suborbital region from hepatic region. Suborbital, pteryostomial regions smooth except for row of granules along epimeral sulcus, subhepatic region with fields of distinct carinae.

Mandibular palp 2-segmented, terminal segment bilobed, with medium-sized anterior process (about $0.5 \times$ terminal segment) at junction between segments. Third maxilliped exopod reaching lower lateral corner of merus; exopod flagellum medium length, ischium with deep vertical groove. Sternal sulcus S1/2 barely visible; S2/3 broad, shallow, horizontal completely crossing sternum; S3/4 broad, shallow, completely crossing sternum, angling inward, not meeting anterior margin of sterno-pleonal cavity on S4; S4/5 meeting telson about one-third along its length; S5/6 meeting A6 about one-third along length of segment; S6/7 meeting A5 about one-third along length of A5. Episternal sulci S4/E4, S5/E5, S6/E6, S7/E7 smooth, all lacking visible groove.

Dactylus of right (major) cheliped slender (one-quarter height of palm), highly arched, with 2 large teeth, one proximal, one distal, lower margin of cheliped propodus lightly indented, pollex of propodus with 5 large teeth interspersed by series of smaller teeth, tips of closed fingers touching but not overlapping, enclosing long oval interspace; pollex of cheliped propodus with 2 horizontal lines of long setae grouped, evenly spaced (Fig. 7F). Anterior, posterior inferior margins of cheliped ischium with large teeth. Inferior margins of cheliped merus each lined by row of small rounded teeth; single large meral tooth on distal inner margin; superior surface of merus rough, finely granular. Inner margin of cheliped carpus with large, pointed distal tooth, proximal carpal tooth noticeably small, followed by second small tooth of equal size. Ambulatory legs (P2–5) long, slender: ratio of total length of P2/CW to P5/CW 1.22, 1.57, 1.92, 1.20 respectively; inner margins of propodi of P2–5 lined by small evenly spaced teeth; merus, carpus of P2–5 elongated, propodus P2–5 not elongated; outer margin of dactylus of P2–5 with thick covering of velvet-like setae, outer margin of propodus of P2–5 proximally lacking setae, distally with thick setae continuing along junction between propodus, dactylus (Fig. 8D).

Pleon slim, last 4 pleomeres (A3–A6) plus telson tapering inward forming long triangle, A3 widest, telson narrowest; telson with straight sides, triangular, not bell-shaped; A6 long, slightly longer than width of distal margin of A6. G1 TA short, less than one-half SS length (TA/SS 0.4); slim, cone-shaped, almost straight (angled about 4° inwards from longitudinal axis of G1 SS), tapering to slightly up-curved tip with clear apical opening; longitudinal groove on G1 TA wide near junction, narrowing sharply distally, clearly visible on ventral, superior sides, not visible

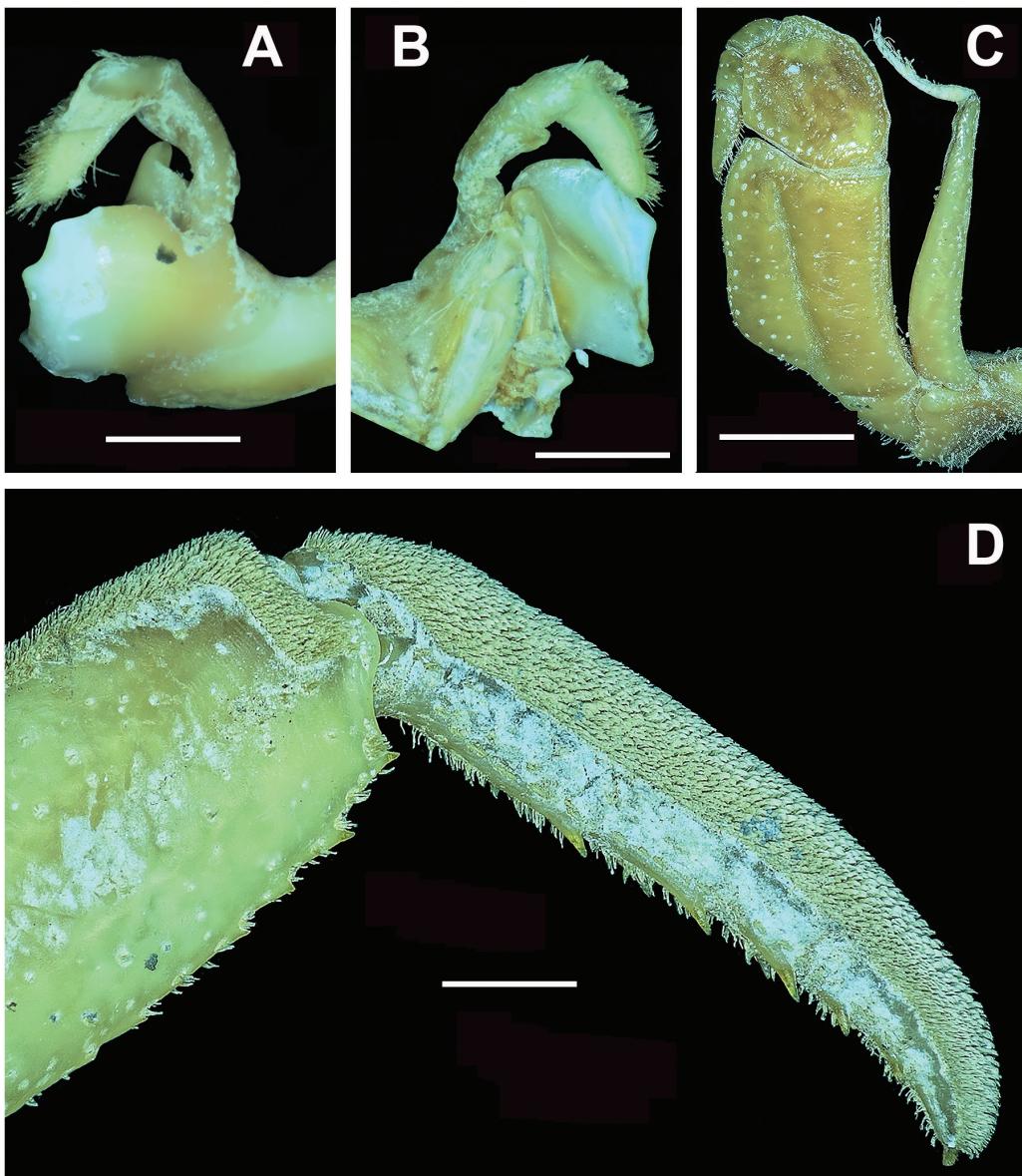


Figure 8. *Malagasya elvysi* n. sp. holotype, male CW 23 mm, from Bobankorana forest, Sava region, Madagascar (FMNH 12646). Mandible frontal view (A), mandible ventral view (B), detail of dactylus of right ambulatory leg 5 (C), left third maxilliped, frontal view, adult female paratype (FMNH 12648) same details as holotype (D). Scale bars: A = 1.0 mm; B, D = 1.4 mm; C = 2.9 mm.

on dorsal side; lateral, medial folds on ventral TA equal in height, width; G1 SS with distinct triangular shoulder on external margin near junction with TA; G1 TA/SS suture distinct on dorsal side but barely visible on ventral side; wide membrane on dorsal side of G1 TA/SS junction. G2 longer than G1; G2 TA flagellum-like, slightly shorter than SS (TA/SS 0.8), basal two-thirds straight, distal one-third inwardly curved.

Size: Largest adult male CW 39 mm.

Colour: Colour in life unknown. The preserved specimen is uniformly pale brown.

Habitat: *Malagasya elvysi* n. sp. is found in the high rainfall Madagascar Eastern Highlands freshwater ecoregion (581) in transitional evergreen lowland forest in association with screwpine leaves (*Pandanus* sp.). It was collected from a rainwater pool formed in the leaf axils of *Pandanus* sp. some 4 m above the ground. Phytotelm habitats

like this one are used by all three species of *Malagasya* (as well as several species of reptiles and amphibians) (Cumberlidge et al., 2005).

Distribution: Madagascar. *Malagasya elvysi* n. sp. is so far known only from the western part of the Forêt de Bobankora at Antsahalalina, 9.9 km southeast of Daraina (−13.2258S, 49.7511E) 157 m ASL, in the sous-prefect of Vohemar in Sava Region (Fig. 10C).

Type locality: The western part of the Forêt de Bobankora at Antsahalalina, 9.9 km southeast of Daraina (−13.2258, 49.7511) 157 m ASL, in the sous-prefect of Vohemar, in Sava Region, north eastern Madagascar.

Etymology: The new species is named for the unusual fields of dense short setae lining the margins of the dactyli and part of the propodi of P2–5, which gives the crab the appearance of wearing suede shoes on its feet (albeit a brown colour in the type specimen). The species epithet “elvysi” is a noun in apposition inspired by the



Figure 9. *Malagasya elvisi n. sp.* holotype, male CW 23 mm, from Bobankorana forest, Sava region, Madagascar (FMNH 12646), right G1 ventral view (A), right G1 dorsal view (B), right G1 dorsal view, detail of TA and of SS junction (C), right G1 superior view (D), right G2 ventral view (E), right G1 and G2 in situ (F). Scale bars: A, B = 1.67 mm; C = 2.2 mm; D, E = 1.4 mm; F = 2.9 mm.

song *Blue Suede Shoes* written by Carl Perkins and made famous by Elvis Presley.

Comparisons: All three species of *Malagasya* are found in the Madagascar Eastern Highlands freshwater ecoregion (581), with *M. antongilensis* being the most widespread species, being found from Diana region in the extreme north of the island, south along the forested highlands of the Eastern Highland freshwater ecoregion (in Sofia, Alaotra-Mangoro, Atsinanana, Analanjirofo, and Vatovavy-Fitovinany regions), and as far south as Anosy region, whereas *M. goodmani* is found in Atsinanana and Sava regions, and *M. elvisi n. sp.* only in Sava region (Fig. 12A–C). The three species of *Malagasya* form a clade that is genetically separate from the other Malagasy genera with *M. antongilensis* positioned basally to the other two taxa. *Malagasya antongilensis* is genetically separate from *M. goodmani* (with an uncorrected p-distance based on COI sequence data of 9.02%), whereas *M. elvisi n. sp.* and *M. goodmani* are sister species with an uncorrected p-distance of 8.97%.

Malagasya elvisi n. sp. is included in *Malagasya* on the basis of a number of morphological characters it shares with *M. antongilensis* and *M. goodmani*, such as a heart-shaped carapace, a markedly narrow carapace front, a mandibular palp with a bilobed terminal segment, propodi of P2–5 each with a distinctly toothed inner margin, and markedly elongated walking legs.

Malagasya elvisi n. sp. and *M. goodmani* can be distinguished from *M. antongilensis* as follows. The frontal margin of *M. antongilensis* is complete (interrupted in the middle by a deep notch in *M. elvisi n. sp.* and *M. goodmani*); the epigastric crests of *M. antongilensis* are in an advanced position on the carapace in line with the supraorbital margins (set further back in *M. elvisi n. sp.* and *M. goodmani*); the cheliped carpus of *M. antongilensis* has three small well-spaced teeth on the anterior margin following the distal spine (a smooth anterior margin in *M. elvisi n. sp.* and *M. goodmani*); the cheliped dactylus of *M. antongilensis* is not arched, encloses only a long narrow interspace when the cheliped fingers are touching, lacks large teeth, and the tips of the fingers are touching (arched with a wide oval interspace and large teeth and the tips of the fingers overlap in *M. elvisi n. sp.* and *M. goodmani*); the propodus of P5 of *M. antongilensis* is elongated (either normal or a little shorter than in *M. elvisi n. sp.* and *M. goodmani*); and the outer margins of the dactylus and propodus of P2–5 of *M. antongilensis* lack the thick covering of suede-like short setae (smooth outer margins in *M. elvisi n. sp.* and *M. goodmani*). The dorsal surfaces of the carapace and legs of *M. antongilensis* are uniformly dark purple/black, whereas the ventral side of the carapace and distal segments of the legs are cream (a multi coloured dorsal carapace (chocolate brown, dark red purple, lilac and gray) and deep red-brown legs dorsally, and pale orange ventrally in *M. goodmani*). We have no record of the colour of *M. elvisi n. sp.* when alive (it is a uniformly pale brown after over 12 months in ethanol).

Malagasya elvisi n. sp. is morphologically and phylogenetically closest to *M. goodmani* but the two species can be distinguished as follows. The anterolateral margin of *M. elvisi n. sp.* is lined by small granules (lined by small teeth in *M. goodmani*), the carapace FW of *M. elvisi n. sp.* is conspicuously narrow, one fifth as wide as the CW (CW/FW 5) (FW narrow, about one quarter as wide as CW (CW/FW 3.7) in *M. goodmani*); the carapace of *M. elvisi n. sp.* is very long, almost four times as long as the FW (CL/FW 5) (not elongated (CL/FW 2.7) in *M. goodmani*); the carapace of *M. elvisi n. sp.* is extremely arched, much higher than the front width (CH/FW 1.6) (not arched (CH/FW 1.2) in *M. goodmani*); the proximal tooth on the cheliped carpus of *M. elvisi n. sp.* is very small (large and pointed in *M. goodmani*). The new species is clearly geographically separate from *M. goodmani*, with the type locality of *M. elvisi n. sp.* being 130 km north of the most northerly locality for *M. goodmani*. The new locality for *M. goodmani* reported herein from Sava region extends the range of this species by some 400 km north of the type locality in Atsinanana region.

Conservation status: An IUCN conservation assessment of *M. elvisi n. sp.* has not yet been carried out, but given the fact that this species is known from only a few specimens that are all from a single locality (Bobankora forest, Madagascar), and that no immediate threats are known, it would probably be regarded as Data Deficient.

Nomenclatural statement: A life science identifier (LSID) number was obtained for the new species: urn:lsid:zoobank.org:pub: 97D882FC-2789-45A4-9070-3ED88C46023A.

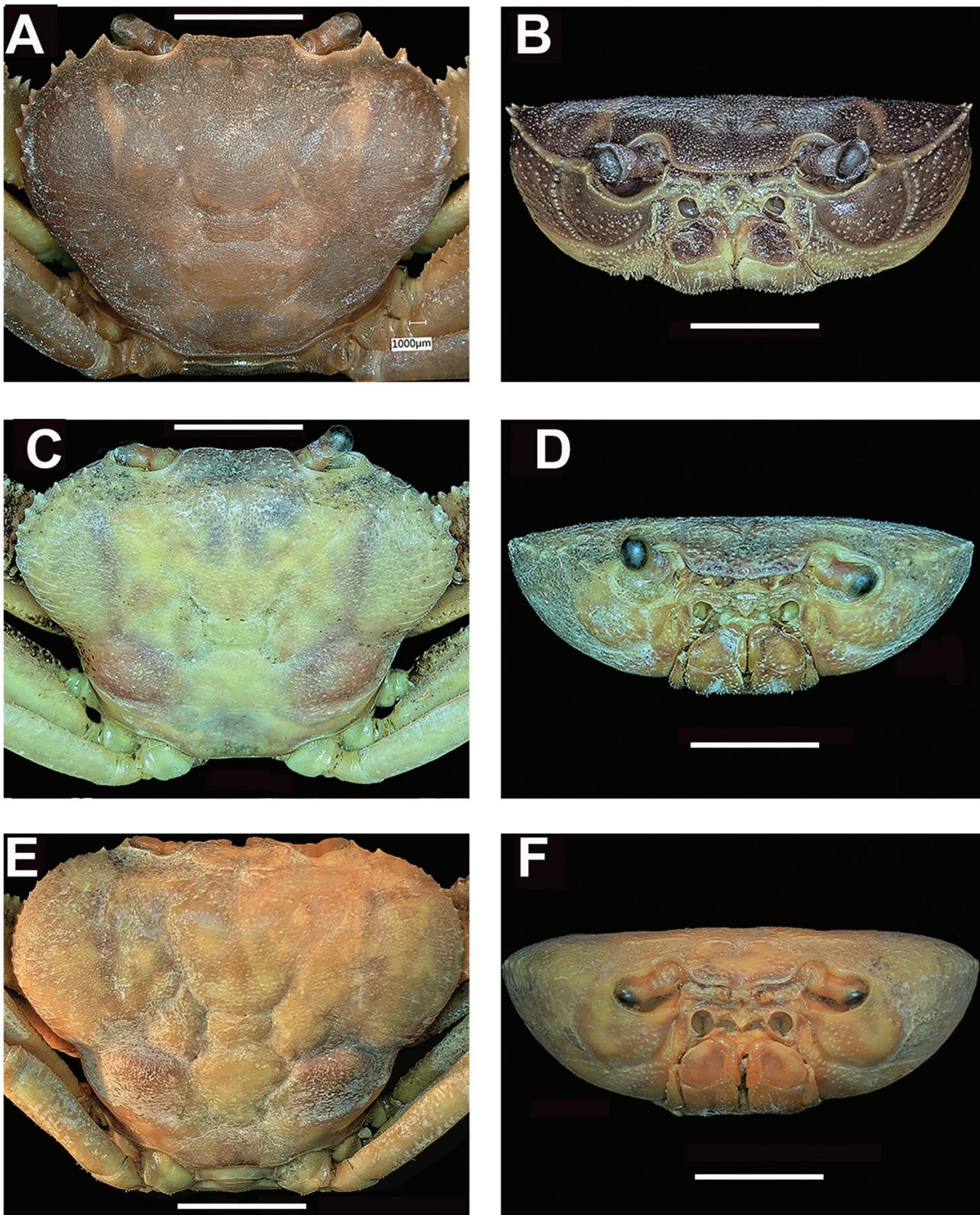


Figure 10. Comparisons of taxonomic characters of males of three species of *Malagasya*, *M. antongilensis* (FMNH 13934) (CW 21.1 mm) from Alaotra-Mangoro region, Madagascar (**A, B**), *M. goodmani* (FMNH 12668) (CW 25.5 mm) from Atsinanana Region, Madagascar (**C, D**), *M. elvisi n. sp.* (FMNH 12646) adult male CW 39 mm, from Sava Region, Madagascar (**E, F**). Dorsal view of carapace (**A, C, E**), frontal view of carapace (**B, D, F**). Scale bars: A–D = 6.7 mm; E, F = 10 mm. This figure is available in colour at *Journal of Crustacean Biology* online.

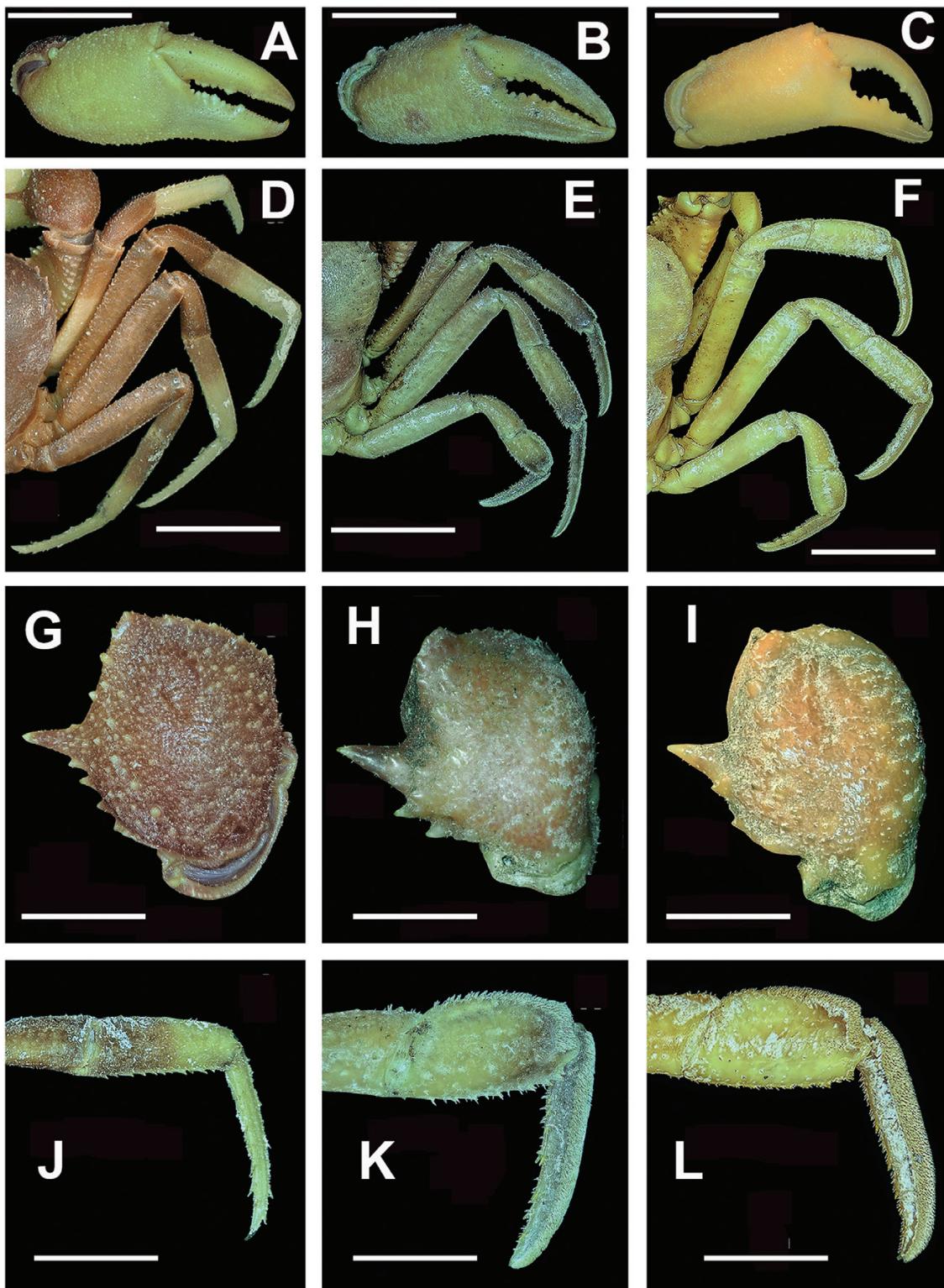


Figure 11. Comparisons of taxonomic characters of males of three species of *Malagasya*, *M. antongilensis* (FMNH 13934) (CW 21.1 mm) from Alaotra-Mangoro region, Madagascar (**A, D, G, J**), *M. goodmani* (FMNH 12668) (CW 25.5 mm) from Atsinanana Region, Madagascar (**B, E, H, K**), *M. elvisi* n. sp. (FMNH 12646) adult male CW 39 mm, from Bobankorana forest, Sava Region, Madagascar (**C, F, I, L**). Frontal view of right (major) cheliped (**A–C**), P3, P4, P5 right side (**D–F**), right cheliped carpus (**G–I**), P5 propodus and dactylus (**J–H**), P2 propodus and dactylus (**I**). Scale bars: A, B = 10.0 mm; C = 15.7 mm; D–F 10 mm; G, H = 3.3 mm; I = 5.7 mm; J, K = 2.9 mm; L = 5 mm. This figure is available in colour at *Journal of Crustacean Biology* online.

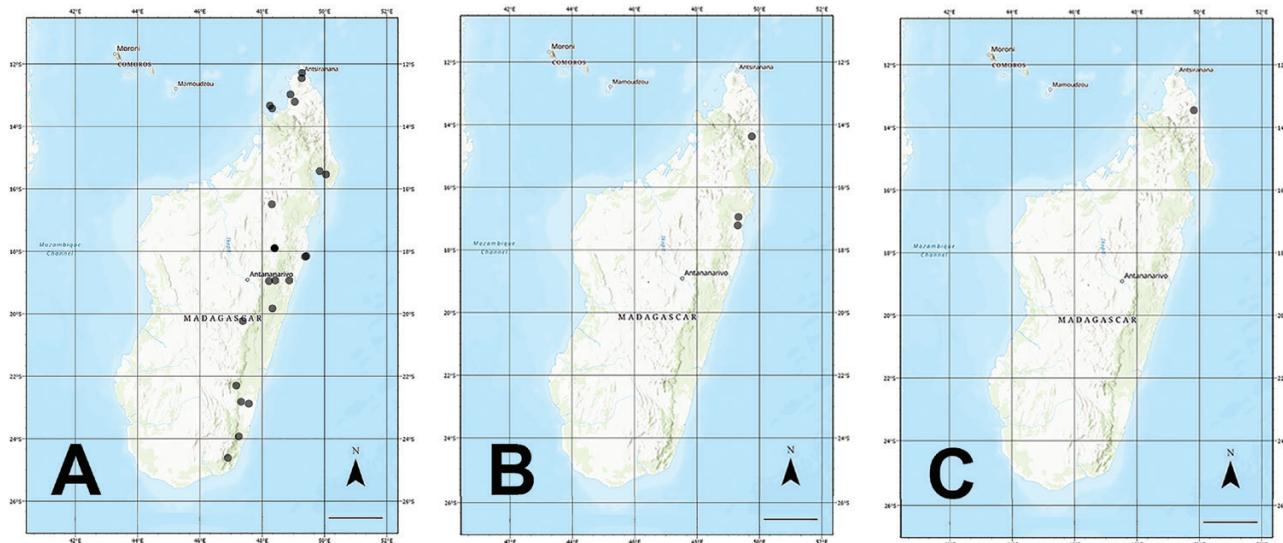


Figure 12. Distribution maps for three species of *Malagasy*, *M. antongilensis* (A), *M. goodmani* (B), and *M. elvysi* n. sp. (C). Scale bars: A–C = 190 mm.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

S1 Table. Museum accession numbers and their GenBank accession numbers.

ACKNOWLEDGEMENTS

The broad taxon sampling used in the present study was made possible by compiling specimens from Madagascar held in major museums in Europe, Asia, and the USA. A vast majority of specimens came from the collection of FMNH and were collected recently in Madagascar by Dr. Steven M. Goodman (FMNH). We are also grateful to Mr. Marty Prydzia, Dr. Joachim Gerber, and Dr. Janet Voight (FMNH) for kindly loaning specimens used in this study and for hosting visits by the first author. Drs. Peter K. L. Ng and Darren C. J. Yeo of the National University of Singapore are thanked for loaning specimens of *A. goudoti* n. comb. (ZRC 2000.2303). We also thank Dr. Paul F. Clark and Ms. Miranda Lowe (NHMW), who hosted visits by the first author. We are grateful to the anonymous reviewers and the Associate Editor for their helpful contributions that improved the manuscript.

REFERENCES

- Abell, R., Thieme, M.L., Revenga, C., Bryer, M., Kottelat, M., Bogutskaya, N., Coad, B., Mandrak, N., Balderas, S.C., Bussing, W., Stiassny, M.L.J., Skelton, P., Allen, G.R., Unmack, P., Naseka, A., Ng, R., Sindorf, N., Robertson, J., Armijo, E., Higgins, J.V., Heibel, T.J., Wikramanayake, E., Olson, D., López, H.L., Reis, R.E., Lundberg, J.G., Sabaj Pérez, M.H., & Petryet, P. 2008. Freshwater eco-regions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience*, **58**: 403–414.
- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In: *Breakthroughs in Statistics*, Vol. I (B.N. Petrov & F. Csáki, eds.), pp. 267–281. 2nd International Symposium on Information Theory, Tsahkadsor, Armenia, USSR, September 2–8, 1971, Akadémiai Kiadó, Budapest [republished in 1992 (S. Kotz & N. L. Johnson, eds), pp. 610–624, Springer-Verlag, New York].
- Balss, H. 1929. Crustacea V. Potamonautesidae. In: Contribution à l'étude de la faune du Cameroun. *Faune des Colonies Françaises*, III: 115–129, 1 pl.
- Beolens, B., Watkins, M. & Grayson, M. 2013. *The eponym dictionary of amphibians*. Pelagic Publishing, Exeter, UK.
- Bott, R. 1955. Die Süßwasserkrabben von Afrika (Crust., Decap.) und ihre Stammesgeschichte. *Annalen van het Koninklijk Museum van Belgisch Congo. C. Dierkunde. Reeks III*, **1**(3): 209–352.
- Bott, R. 1960. Crustacea (Decapoda): Potamonidae. In: *South African animal life. Results of the Lund University Expedition in 1950–1952* (B. Hanström, P. Brinck, & G. Rudebeck, eds.), **7**: 13–18.
- Bott, R. 1965. Die Süßwasserkrabben von Madagaskar. *Bulletin du Muséum National d'Histoire naturelle*, **37**: 335–350.
- Bott, R. 1969. Die Flusskrabben aus Asien und ihre Klassificaten (Crustacea, Decapoda). *Senckenbergiana biologica*, **50**: 359–366.
- Bott, R. 1970. Betrachtungen über die Entwicklungsgeschichte der Süßwasserkrabben nach der Sammlung des Naturhistorischen Museums in Genf/Schweiz. *Revue suisse de Zoologie*, **77**: 327–344.
- Calman, W.T. 1913. On freshwater decapod Crustacea (Families Potamonautesidae and Palaemonidae) collected in Madagascar by the Hon. Paul A. Methuen. *Proceedings of the Zoological Society of London*, **4**: 914–932.
- Cumberlidge, N. 1999. *The freshwater crabs of West Africa, Family Potamonautesidae*. *Faune et Flore Tropicales*, **Vol. 35**, IRD, Paris.
- Cumberlidge, N. 2010. *Boreathelphusa*, a replacement name for *Boreas* Cumberlidge and Sternberg, 2002 (Crustacea: Brachyura: Potamonautesidae), preoccupied by *Boreas* Morris, 19870 (Bryozoa: Hippothoidae). *Zootaxa*, **2450**: 68.
- Cumberlidge, N. 2014. An overview of the Afrotropical freshwater crab fauna: Diversity, biogeography, and conservation (Brachyura, Potamoidea, Potamonautesidae and Potamidae). In: *Advances in freshwater decapod systematics and biology* (D. Yeo, N. Cumberlidge & S. Klaus, eds.), *Crustaceana Monographs*, **19**: 71–99.
- Cumberlidge, N. & Clark, P.F. 1992. A new genus and species of freshwater crab from Cameroon, West Africa (Crustacea, Brachyura, Potamoidea, Potamonautesidae). *Bulletin of the British Museum of Natural History (Zoology)*, **58**: 149–156.
- Cumberlidge, N. & Meyer, K.S. 2009. A new species of *Foza* Reed & Cumberlidge, 2006, from northern Madagascar (Decapoda, Brachyura, Potamoidea, Potamonautesidae), with a redescription of *H. goudoti* (H. Milne Edwards, 1853) comb. n., and comments on *Skelosophusa prolixus* Ng & Takeda, 1994. *ZooKeys*, **18**: 77–89.
- Cumberlidge, N. & Sachs, R. 1989. Three new subspecies of the West African fresh-water crab *Liberonautes latidactylus* (DeMan, 1903) from Liberia, with notes on their ecology. *Zeitschrift für Angewandte Zoologie*, **76**: 425–439.
- Cumberlidge, N. & Sternberg, R. 2002. The freshwater crabs of Madagascar (Crustacea, Decapoda, Potamoidea). *Zoosystema*, **24**: 41–79.
- Cumberlidge, N., Boyko, C.B. & Harvey, A.W. 2002a. A new genus and species of freshwater crab (Decapoda, Crustacea, Potamoidea) from northern Madagascar, and a second new species associated with Pandanus leaf axils. *Journal of Natural History*, **36**: 65–77.
- Cumberlidge, N., Clark, P.F. & Baillie, J. 2002b. A new species of freshwater crab (Brachyura: Potamoidea: Potamonautesidae) from Príncipe,

- Gulf of Guinea, Central Africa. *Bulletin of the British Museum of Natural History (Zoology)*, **68**: 13–18.
- Cumberlidge, N., Fenolio, D.B., Walvoord, M.E. & Stout, J. 2005. Tree-climbing crabs (Potamonautilidae and Sesarmidae) from phytotelmic microhabitats in rainforest canopy in Madagascar. *Journal of Crustacean Biology*, **25**: 302–308.
- Cumberlidge, N., Klaus, S., Meyer, K.S. & Koppin, J.C. 2015. New collections of freshwater crabs from northern Madagascar, with the description of a new species of *Foza* Reed & Cumberlidge, 2006 (Brachyura, Potamonautilidae). *European Journal of Taxonomy*, **109**: 1–15.
- Cumberlidge, N., Marijnissen, S.A.E. & Thompson, J. 2007. *Hydrothelphusa vencesi*, a new species of freshwater crab (Brachyura: Potamoidea: Potamonautilidae) from southeastern Madagascar. *Zootaxa*, **1524**: 61–68.
- Cumberlidge, N., Reed, S.K. & Boyko, C.B. 2004. Distribution patterns of the Malagasy freshwater crabs (Crustacea: Decapoda: Brachyura). *Journal of Natural History*, **38**: 1133–1157.
- Cumberlidge, N., Sternberg, R. von. & Daniels, S.R. 2008. A revision of the higher taxonomy of the Afrotropical freshwater crabs (Decapoda: Brachyura) with a discussion of their biogeography. *Biological Journal of the Linnean Society*, **93**: 399–413.
- Cumberlidge, N., Rasamy Razanabolana, J., Ranaivoson, C.H., Darwall, W.R.T. & Máiz-Tomé, L. 2018. The status and distribution of freshwater decapod crustaceans. In: *The status and distribution of freshwater biodiversity in Madagascar and the Indian Ocean islands hotspot* (L. Máiz-Tomé, C.A. Sayer, & W.R.T. Darwall, eds.), Chapter 5, pp. 42–58. IUCN, Gland, Switzerland.
- Daniels, S.R. & Klaus, S. 2018. Divergent evolutionary origins and biogeographic histories of two freshwater crabs (Brachyura: Potamonautes) on the West African conveyer belt islands of São Tomé and Príncipe. *Molecular Phylogenetics and Evolution*, **127**: 119–128.
- Daniels, S.R., Cumberlidge, N., Pérez-Losada, M., Marijnissen, S.A.E., Crandall, K.A. 2006. Evolution of Afrotropical freshwater crab lineages obscured by morphological convergence. *Molecular Phylogenetics and Evolution*, **40**: 225–235.
- Daniels, S.R., Phiri, E.E., Klaus, S., Albrecht, C. & Cumberlidge, N. 2015. Multilocus phylogeny of the Afrotropical freshwater crab fauna reveals historical drainage connectivity and transoceanic dispersal since the Eocene. *Systematic Biology*, **64**: 549–567.
- Daniels, S.R., Stewart, B.A., Gouws, G., Cunningham, M. & Matthee, C.A. 2002. Phylogenetic relationships of the southern African freshwater crab fauna derived from multiple data sets reveal biogeographic patterning. *Molecular Phylogenetics and Evolution*, **25**: 511–523.
- Goodman, S.M. & Benstead, J.P. 2005. Updated estimates of biotic diversity and endemism for Madagascar. *Oryx*, **39**: 73–77.
- Gouws, G., Peer, N. & Perissinotto, R. 2015. MtDNA lineage diversity of a potamonautilid freshwater crab in KwaZulu-Natal, South Africa. *Koedoe*, **57**: 1–12.
- Hilgendorf, F. 1869. Ueber eine neue Gattung der kurzschwänzigen Krebse aus den Sammlungen des Baron von der Decken, *Deckenia imitatrix*. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*, **1**: 2.
- Klaus, S., Schubart, C.D. & Brandis, D. 2006. Phylogeny, biogeography and a new taxonomy for the Gecarcinucoidea Rathbun, 1904 (Decapoda: Brachyura). *Organism Diversity and Evolution*, **6**: 199–217.
- Latrelle, P.A. 1819. Salicoques, Carides, Latr. In: *Nouveau Dictionnaire d'Histoire naturelle ... Vol. 30*, pp. 68–73.
- Man, J.G. de. 1892. Decapoden des Indischen Archipels. In: Weber, M. (ed.): *Zoologische Ergebnisse Einer Reise nach Niederland Ost-Indien*, **2**: 265–527.
- Man, J.G. de. 1898. Note sur quelques espèces des genres *Paratelphusa* H.M.E. et *Potamon* Sav., Par. M. Leonard Fea pendant son voyage in Birmanie. *Annali del Museo Civico di Storia Naturale di Genova*, **19**: 384–440.
- Meyer, K.S., Cumberlidge, N. & Koppin, J.C. 2014. A new genus and species of freshwater crab from Madagascar (Decapoda, Brachyura, Potamoidea, Potamonautilidae). *Zootaxa*, **3884**: 65–72.
- Milne-Edwards, A. 1868. Description de quelques Crustacés nouveaux provenant des voyages de M. Alfred Grandidier à Zanzibar et à Madagascar. *Nouvelles Archives du Muséum d'Histoire naturelle*, **4**: 69–92.
- Milne-Edwards, A. 1869. Révision du genre *Thelphuse* et description de quelques espèces nouvelles faisant partie de la collection du Muséum. *Nouvelles Annales du Muséum d'Histoire naturelle*, **5**: 1–3.
- Milne-Edwards, A. 1872. Note sur les crabes d'eau douce de Madagascar. *Bibliothèque de l'École des hautes Études, Section Sciences naturelles*, **5**: 1–3.
- Milne-Edwards, A. 1887. Observations sur les affinités zoologiques et la Classification naturelle des Crustacés. *Annales des Sciences Naturelles*, Série 6, **4**: 121–149.
- Milne Edwards, H. 1837. *Histoires naturelles des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux*, Vol. 2. Librairie encyclopédique de Roret, Paris.
- Milne Edwards, H. 1853. Observations sur les affinités zoologiques et la classification naturelle des Crustacea. *Annales des Sciences naturelles, Zoologie*, **3**: 163–228.
- Ng, P.K.L. & Takeda, M. 1994. *Skelosophusa* (Crustacea, Decapoda, Brachyura), a new genus of potamonautilid freshwater crab from Madagascar, with descriptions of two new species. *Bulletin of the National Science Museum, Series A (Zoology)*, **20**: 161–172.
- Ng, P.K.L., Števčić, Z. & Pretzmann, G. 1995. A revision of the family Deckeniidae Ortmann, 1897 (Crustacea: Decapoda: Brachyura: Potamoidea), with description of a new genus (Gecarcinucidae: Gecarcinucoidea) from the (Gecarcinucidae: Gecarcinucoidea) from the Seychelles, Indian Ocean. *Journal of Natural History*, **29**: 581–600.
- Ng, P.K.L., Guinot, D. & Davie, P.J.F. 2008. Systema Brachyurorum: Part 1. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology*, **17**: 1–286.
- Nobili, G. 1906. Spedizione al Ruwenzori di S.A.R. Luigi Amedeo di Savoia Duca degli Abruzzi. 9. Crostacei. *Bollettino dei Musei di Zoologia e l'Anatomia Comparata, Torino*, **544**: 1–2.
- Nylander, J.A.A., Ronquist, F., Huelsenbeck, J.P. & Nieves-Aldrey, J.L. 2004. Bayesian phylogenetic analysis of combined data. *Systematic Biology*, **53**: 47–67.
- Phiri, E.E. & Daniels, S.R. 2013. Hidden in the highlands: the description and phylogenetic positioning of a novel endemic freshwater crab species (Potamonautilidae: *Potamonautes*) from Zimbabwe. *Invertebrate Systematics*, **27**: 530–539.
- Phiri, E.E. & Daniels, S.R. 2014. Disentangling the divergence and cladogenesis in the freshwater crab species (Potamonautilidae: *Potamonautes perlatus* sensu lato) in the Cape Fold Mountains, South Africa, with the description of two novel cryptic lineages. *Zoological Journal of the Linnean Society*, **170**: 310–332.
- Phiri, E.E. & Daniels, S.R. 2016. Multilocus coalescent species delimitation reveals widespread cryptic differentiation among Drakensberg mountain-living freshwater crabs (Decapoda: *Potamonautes*). *Invertebrate Systematics*, **30**: 60–74.
- Posada, D. 2008. jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution*, **25**: 1253–1256.
- Posada, D. & Buckley, T.R. 2004. Model Selection and Model Averaging in Phylogenetics: Advantages of Akaike Information Criterion and Bayesian Approaches Over Likelihood Ratio Tests. *Systematic Biology*, **53**: 793–808.
- Pretzmann, G. 1961. Die Reptantia der österreichischen Madagaskar-Expedition, 1958. *Mémoires de l'Institut Scientifique de Madagascar*, **4**: 161–165.
- Rambaut, A., Suchard, M. & Drummond, A. 2013. Tracer v1.6. A program for analyzing results from Bayesian MCMC programs such as BEAST & MrBayes [<http://tree.bio.ed.ac.uk/software/tracer>].
- Rathbun, M.J. 1904. Les crabes d'eau douce (Potamoniidae). *Nouvelles Archives du Muséum d'Histoire naturelle*, **6**: 255–312.
- Rathbun, M.J. 1905. Les crabes d'eau douce (Potamoniidae). *Nouvelles Archives du Muséum d'Histoire naturelle*, **7**: 159–322.
- Reed, S.K. & Cumberlidge, N. 2006. *Foza raimundi*, a new genus and species of potamonautilid freshwater crab (Crustacea: Decapoda: Potamoidea) from northern Madagascar. *Proceedings of the Biological Society of Washington*, **119**: 58–66.
- Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. 2012. MRBAYES 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, **61**: 539–542.
- Savigny, J.C. 1816. *Mémoires sur les animaux sans vertèbres*. Vol. 1. G. Dufour, Paris.
- Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood based phylogenetic analysis with thousands of taxa and mixed models. *Bioinformatics*, **22**: 2688–2690.
- Swofford, D.L. 2001. PAUP* Version 4.10. Phylogenetic Analysis Using Parsimony (and other methods), Illinois Natural History Survey, Champaign, IL, USA.
- Vences, M., Wollenberg, K.C., Vieites, D.R. & Lees, D.C. 2009. Madagascar as a model region of species diversification. *Trends in Ecology and Evolution*, **24**: 456–465.