

Freshwater crabs (Brachyura: Potamoidea: Deckeniidae) from the Andrafiarana-Andavakoera protected area in northern Madagascar, including a new genus and species, *Dianathelphusa antsahabe* n. sp.

Neil Cumberlidge¹ & Savel R. Daniels²

¹ Department of Biology, Northern Michigan University, Marquette, Michigan 49855, USA

Email: ncumberl@nmu.edu

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

Email: srd@sun.ac.za

Abstract

A collection of freshwater crabs of the family Deckeniidae from the Andrafiarana-Andavakoera protected area in northern Madagascar made recently by S. M. Goodman and colleagues comprised three species in three genera. The collection included a new genus and species (*Dianathelphusa antsahabe* n. gen. et n. sp.), one species of the genus *Skelosophusa* Ng & Takeda, 1994 (*S. gollardi* (Bott, 1965)) and one species of *Hydrothelphusa* A. Milne-Edwards, 1872 (*H. madagascariensis* A. Milne-Edwards, 1872). This new genus is defined based on molecular evidence combined with morphological characters and is here compared with, and distinguished from, other closely related freshwater crabs occurring in Madagascar. This work increases the diversity of the Malagasy freshwater crab fauna by raising the number of genera to 15, and the number of species to 28. The molecular work also revealed three other novel genera that will be described elsewhere.

Keywords: DIANA Region, Anjakely, Antsahabe, Binara, PHP Andrafiarana-Andavakoera

Résumé détaillé

Une collection de crabes d'eau douce de la famille des Deckeniidae du Paysage Harmonieux Protégé (PHP) d'Andrafiarana-Andavakoera, dans le nord de Madagascar, réalisée récemment par S. M. Goodman et ses collègues de l'Association Vahatra comprenait trois espèces réparties en trois genres. Cette aire protégée se trouve dans une zone isolée et largement dépourvue de routes, dans la région DIANA et au sud-est de la Réserve Spéciale

d'Ankarana. L'investigation a pour but d'inventorier la biodiversité, tout en essayant de porter une attention particulière sur les taxa encore mal connus comme les crabes. Les crabes ont été collectés dans trois vestiges de forêts: Anjakely (360-750 m), Antsahabe (300-420 m) et Binara (200-600 m). La zone est depuis plusieurs années, exposée au problème de déforestation et diverses activités d'exploitation anthropique, expliquant ainsi l'état actuel du PHP, défini par ses quelques fragments et blocs isolés d'habitats naturels comme observés sur la chaîne Andavakoera, la chaîne Andrafiarana et le massif calcaire d'Antsahabe. La végétation naturelle résulte des influences simultanées des facteurs climatiques, topographiques et édaphiques, et constituée par deux principales classes, à savoir la forêt dense humide semi-décidue et la forêt dense sèche caducifoliée. Cette dernière est composée de deux variantes édaphiques, notamment celle qui est sur formation karstiques ou *tsingy* (Antsahabe) et celle qui se développe sur un sol faiblement ferrallitique et ferrisol.

Cette étude s'agit du premier signalement de la faune de crabe d'eau douce de cette zone. La collection comprenait un nouveau genre et une nouvelle espèce (*Dianathelphusa antsahabe* n. gen. et n. sp.), une espèce du genre *Skelosophusa* Ng & Takeda, 1994 (*S. gollardi* (Bott, 1965)) et une espèce d'*Hydrothelphusa* A. Milne-Edwards, 1872 (*H. madagascariensis* A. Milne-Edwards, 1872). Ce nouveau genre est défini sur la base de preuves moléculaires combinées à des caractères morphologiques et est ici comparé et distingué d'autres crabes d'eau douce étroitement apparentés et présents à Madagascar. Ces travaux augmentent la diversité de la faune du crabe d'eau douce malgache en portant le nombre de genres à 15 et le nombre d'espèces à 28. Les travaux moléculaires ont également révélé trois autres genres nouveaux qui seront décrits ailleurs.

Mots clés : Région de DIANA, Anjakely, Antsahabe, Binara, PHP d'Andrafiarana-Andavakoera

Introduction

The freshwater crabs reported on here were collected during a systematic survey of the fauna of the Andrafiarena-Andavakoera protected area (Paysage Harmonieux Protégé, Category V) of Andrafiarena-Andavakoera in the ex-Province of Antsiranana, DIANA Region, in the Districts of Antsiranana II and Ambilobe in northern Madagascar made by S. M. Goodman and colleagues. The survey aimed to document the local biodiversity and to identify species that may be new to science and/or threatened. The freshwater crab collections were made in three different forested parts of the Andrafiarena-Andavakoera protected area: Anjakely (at 360 m), Antsahabe (300–420 m), and the Binara (800 m). The Andrafiarena-Andavakoera protected area lies in a remote and largely road less area to the southeast of the Réserve Spéciale d'Ankarana. The native vegetation of the Andrafiarena range is dominated by tropical forest, but large areas of these forests have been cleared, and the Andrafiarena-Andavakoera protected area represents one of the few remaining zones of natural habitat in this portion of Madagascar. The natural vegetation of the Andrafiarena-Andavakoera complex consists of moist semi-deciduous forests on the mountain slopes of the Andrafiarena range and dry deciduous forests on the karst formations (*tsingy*) (Tahinarivony & Goodman, 2025, herein). This diversity of habitats supports a rich biodiversity, but this is the first report of the freshwater crab fauna of this immediate area.

The collection of freshwater crabs included species from three genera: a new genus and species (*Dianathelphusa antsahabe* n. sp.), one species of *Skelosophusa* Ng and Takeda, 1994 (*S. gollardi* (Bott, 1965), and one species of *Hydrothelphusa* A. Milne-Edwards, 1872 (*H. madagascariensis* A. Milne-Edwards, 1872). These genera and species belong to the exclusively Afrotropical freshwater crab family Deckeniidae Ortmann, 1897, subfamily Hydrothelphusinae Bott, 1955 (Cumberlidge & Daniels, 2022). The diagnostic characters of these species are summarized here, because the specimens belong to either a little-known species (*S. gollardi* Bott, 1965) (Cumberlidge & Sternberg, 2002), a new species (*Dianathelphusa antsahabe* n. sp.), or to a better-known species (*H. madagascariensis*) (Cumberlidge *et al.*, 2024). All 14 genera of Malagasy freshwater crabs currently recognized are endemic to Madagascar (*Agora* Cumberlidge, Soma, Leever & Daniels, 2020, *Boreathelphusa* Cumberlidge, 2010, *Crosnautes* Leever, Daniels, Soma &

Cumberlidge, 2022, *Foza* Reed & Cumberlidge, 2006, *Glabrithelphusa* Cumberlidge, Klaus, Meyer & Koppin, 2015, *Hydrothelphusa*, *Madagapotamon* Bott, 1965, *Malagasya* Cumberlidge & Sternberg, 2002, *Marojejy* Cumberlidge, Boyko & Harvey, 2002, *Nheena* Cumberlidge, Soma, Leever & Daniels, 2023a, *Skelosophusa* Ng & Takeda, 1994, *Toamasina* Leever, Daniels, Soma & Cumberlidge, 2022, *Vahatra* Leever, Daniels, Soma & Cumberlidge, 2022, and *Vichai* Cumberlidge, Daniels, Soma & Leever, 2023b) (Bott, 1965; Cumberlidge & Sternberg, 2002; Reed & Cumberlidge 2006; Cumberlidge *et al.*, 2007, 2015, 2020, 2021, 2023a, 2023b, 2024, 2025; Cumberlidge & Meyer, 2009; Cumberlidge, 2010; Meyer *et al.*, 2014; Leever *et al.*, 2022). The new genus is established here based on morphological and phylogenetic evidence and represents the 15th genus and 28th recognized species of freshwater crab from Madagascar. Diagnoses of the new genus and of each species, and illustrations of the characters of the carapace, chelipeds, thoracic sternum, and gonopods are provided.

Methods

All of the specimens collected by S. M. Goodman and colleagues are deposited in the Field Museum of Natural History (FMNH), Chicago, USA. Freshwater crabs from the Analakely Market in Antananarivo and from Lokobe on Nosy Be were collected by the last author and are included in Figure 1 of the present study. All specimens or tissue samples were preserved in either absolute (96%) or 70% ethanol.

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. The barcoding mitochondrial locus cytochrome oxidase subunit one (COI) was used to examine the taxonomic diversity among the Malagasy freshwater crabs because this locus has been employed successfully by a number of authors to reconstruct evolutionary relationships among African freshwater crabs (Daniels *et al.*, 2002, 2006, 2015, 2023; Klaus *et al.*, 2006; Phiri & Daniels, 2013, 2014, 2016; Gouws *et al.*, 2015; Daniels & Klaus, 2018). 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, 2023; Mengel & Daniels, 2024).

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. 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. Bayesian inferences (BI) 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. 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. The resultant tree topologies were used to evaluate taxonomically important characters of the Malagasy freshwater crabs.

Taxonomy

Taxonomically important characters such as the 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 calipers and are given in millimeters (mm). Measurements of the subterminal articles (SA) 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 TA/SA junction and ending at the TA tip. The length of the TA of G1 and G2 relative to the length of the SA 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 Davie *et al.* (2015) and the classification follows Cumberlidge and Daniels (2022). The following abbreviations are used: A1–6, pleomeres 1–6 respectively; ASL, altitude above sea level in meters; BI, Bayesian inferences; 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; FMNH = Field Museum of Natural History, Chicago, USA; FW, front width measured along anterior frontal margin between inner angles of orbits; G1, first gonopod; G2, second gonopod; ML, maximum likelihood; P2–5, pereopods 2–5 (ambulatory legs 1–4, respectively).

Results

Phylogenetics

Novel COI sequences were deposited in GenBank (Accession numbers PQ846668-PQ846674). Both the BI and ML trees recovered near identical topologies, hence only the ML tree topology is shown and discussed herein (Figure 1). The Malagasy freshwater crab fauna was retrieved as monophyletic, and *Vichai cyanalepou* Cumberlidge, Daniels, Soma & Leever, 2023 formed a divergent basal lineage on the tree. Two highly divergent clades (A & B) were present in the remainder of the tree topology. In Figure 1 clade A, *Marojejy longimerus* Cumberlidge, Boyko & Harvey, 2002 was basal to *Boreathelphusa ugwowi* (Cumberlidge & Sternberg, 2002) that was a sister group to *Skelosophusa*; that clade was sister to *Toamasina clarki* Leever, Daniels, Soma & Cumberlidge, 2022, that formed a sister group to *Vahatra ambohitra* (Reed & Cumberlidge, 2006). The latter clade was in turn sister to *Madagapotamon humberti* Bott, 1965, which was sister to

Dianathelphusa antsahabe n. sp. (FMNH 16195A and FMNH 16154). In addition, these latter two genera were sister to a new as-yet undescribed genus from Nosy Be off the northwestern coast of Madagascar. The phylogeny (Figure 1) placed FMNH 16154 and

FMNH 16195A in a lineage close to *Madagapotamon humberti*. The holotype of *D. antsahabe* n. sp. (FMNH 16153) and another specimen of this species (FMNH 16155), are both morphologically identical to the sequenced specimens (FMNH 16154, a subadult

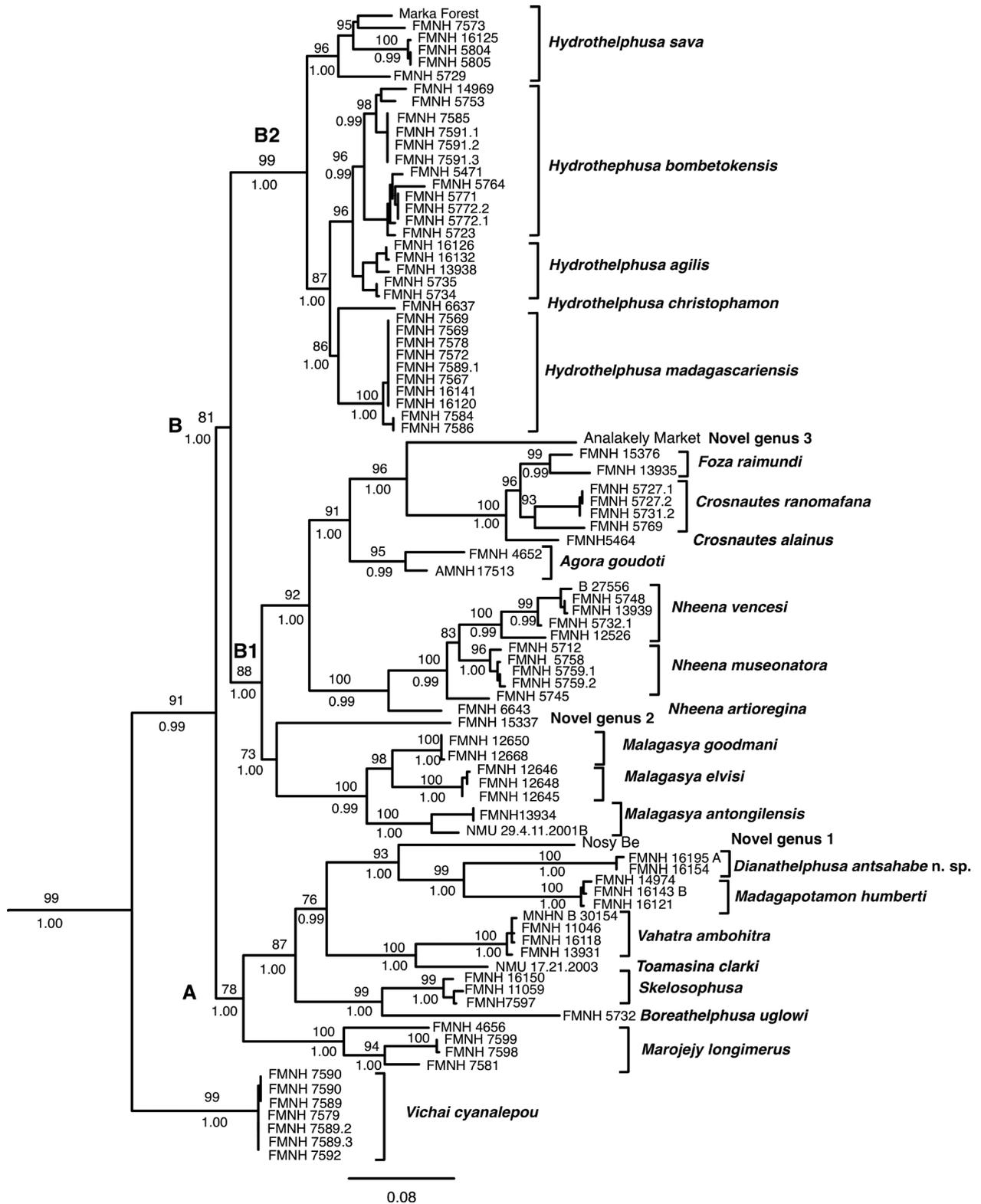


Figure 1. Maximum likelihood tree topology for the COI locus for the Malagasy freshwater crabs (outgroups removed). Values above nodes for bootstrapping (%) and below the nodes for posterior probability (pP). Only bootstrap values > 75% are shown, while only posterior probability values > 0.95 are shown on the tree topology.

female paratype, CW 22.9 mm and FMNH 16195A, a subadult female, CW 16.2 mm) and were collected from the same locality at the same time, so all four of these specimens are recognized here as *D. antsahabe* n. sp.

In Figure 1 clade B, two highly divergent clades were evident (B1 and B2). In clade B1, the monophyletic *Malagasya* (with *M. antongilensis* Rathbun, 1904 sister to *M. elvisi* Cumberlidge, Soma, Leever & Daniels, 2020, sister to *M. goodmani* Cumberlidge, Boyko & Harvey, 2002) was sister to a novel, as-yet undescribed genus (FMNH 15337) from Marojejy National Park in the SAVA Region of northern Madagascar. The latter two genera (*Malagasya* plus the new genus from Marojejy) were sister to a monophyletic *Nheena* comprising three species (*N. artioregina* Cumberlidge, Soma, Leever & Daniels, 2023, sister to *N. museonatarata* Cumberlidge, Soma, Leever & Daniels, 2023, sister to *N. vencesi* Cumberlidge, Marijnissen & Thompson, 2007), with *Nheena* being sister to a clade for *Agora goudoti* (Milne Edwards, 1853), *Crosnautes*, *Foza raimundi* Reed & Cumberlidge, 2006, and the specimen from the Analakely Market in Antananarivo (representing an additional novel genus). Clade B2 was exclusively comprised of *Hydrothelphusa* species, with *H. madagascariensis* sister to *H. christophamon* Cumberlidge, Soma, Leever & Daniels, 2024 with the latter clades being sister to *H. agilis* A. Milne-Edwards, 1872 sister to *H. bombetokensis* Rathbun, 1904, and these four species were sister to *H. sava* Cumberlidge, Robinson & Daniels, 2024.

Systematics

Infraorder Brachyura Linnaeus, 1758

Superfamily Potamoidea Ortmann, 1896

Family Deckeniidae Ortmann, 1897

Subfamily Hydrothelphusinae Bott, 1955

Genus *Dianathelphusa* n. gen.

(Figures 2-4)

LSIDurn:lsid:zoobank.org:pub:292F0819-FB8F-4A2A-8CF9-13980AAAEC36

Type species

Dianathelphusa antsahabe n. sp. by present designation and by monotypy.

Type material

Holotype: FMNH 16153 (SMG-22247), adult male (CW 28.7 mm), Madagascar, ex-Antsiranana Province, DIANA Region, Antsiranana II District,

Andrafiarena-Andavakoera protected area, Antsahabe Forest, 2.8 km NW Anjakely (village) (12.894°S, 49.294°E, 360 m), coll. S. M. Goodman, 29 November 2023, in pitfall trap 5, in disturbed dry deciduous forest on limestone plateau (*tsingy*).

Paratypes: FMNH 16154 (SMG-22248), subadult female (CW 22.9 mm), claw cracked before preservation, Madagascar, ex-Antsiranana Province, DIANA Region, Antsiranana II District, Andrafiarena-Andavakoera protected area, Antsahabe Forest, 2.8 km NW Anjakely (village) (12.894°S, 49.294°E, 360 m), coll. S. M. Goodman and V. Soarimalala, 29 November 2023, by hand, in dry deciduous forest on limestone plateau (*tsingy*). FMNH 16155 (SMG-22285) subadult female (CW 22.9 mm), claw cracked before preservation, Madagascar, ex-Antsiranana Province, DIANA Region, Antsiranana II District, Andrafiarena-Andavakoera protected area, Antsahabe Forest, 2.8 km NW Anjakely (village) (12.894°S, 49.294°E, 360 m), coll. S. M. Goodman and V. Soarimalala, 29 November 2023, by hand, dry deciduous forest on limestone plateau (*tsingy*). FMNH 16195 (SMG-22200), subadult female (CW 16.2 mm), Madagascar, ex-Antsiranana Province,

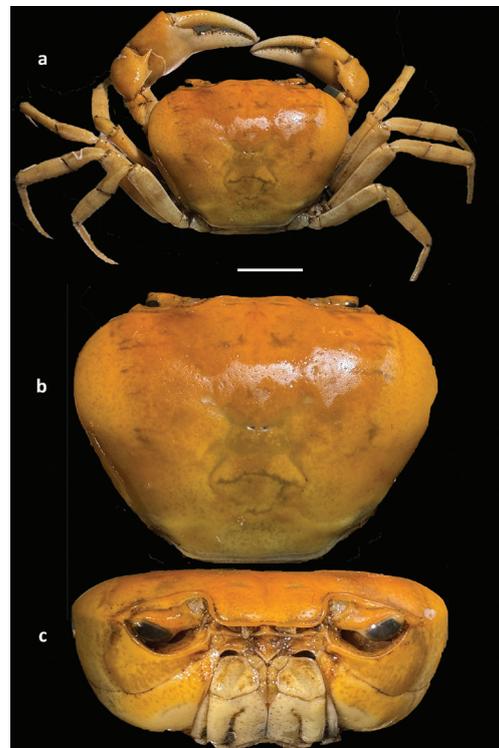


Figure 2. *Dianathelphusa antsahabe* n. sp. adult male holotype, CW 28.7 mm, from Andrafiarena-Andavakoera protected area, Antsahabe Forest, Madagascar (FMNH 16153): **a**) whole animal, dorsal view; **b**) carapace, dorsal view; **c**) carapace, frontal view. Scale bar: a = 9.7 mm; b = 5.5 mm; c = 5.3 mm.

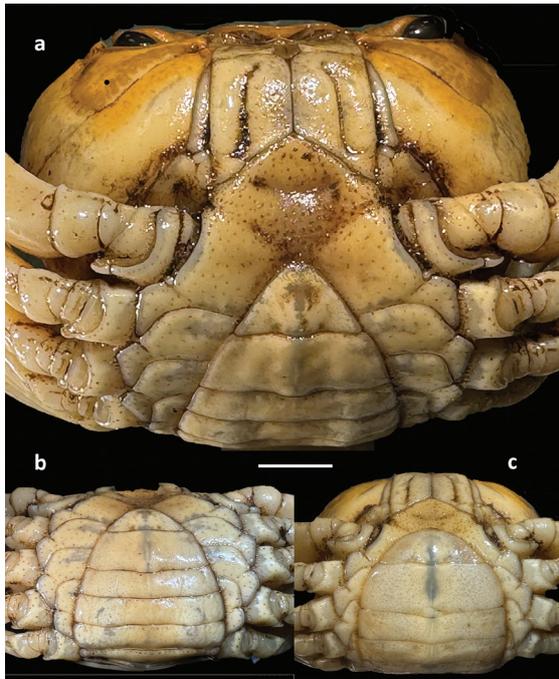


Figure 3. *Dianathelphusa antsahabe* n. sp. adult male holotype, CW 28.7 mm, from Andrafiarana-Andavakoera protected area, Antsahabe Forest, Madagascar (FMNH 16153): **a**) anterior thoracic adult male sternum showing partial pleon with telson; **b**) posterior thoracic adult female sternum showing complete pleon with telson; **c**) anterior thoracic adult female sternum showing pleon with telson. Scale bar: a = 6.8 mm; b = 10.6 mm; c = 10.6 mm.

DIANA Region, Antsiranana II District, Andrafiarana-Andavakoera protected area, Antsahabe Forest, 2.8 km NW Anjakely (village) (12.894°S, 49.294°E, 360 m), coll. S. M. Goodman, 28 November 2023, in pitfall trap 5, dry deciduous forest on limestone plateau (*tsingy*).

Diagnosis

Entire carapace surface smooth; epibranchial tooth small, acute, close to exorbital tooth, positioned in line with postorbital margin (Figure 2a & b); shallow notch between exorbital, epibranchial teeth; carapace lateral margin smooth; suborbital, subhepatic, pterygostomial regions of branchiostegite smooth; epistomial tooth triangular, deflexed, edges granular (Figure 2c), mandibular palp with medium-sized anterior lobe on terminal article; third maxilliped ischium with deep vertical sulcus, distal end curving medially, ending before meeting medial margin, third maxilliped exopod with shortened flagellum ($\sim 0.5 \times$ merus length) (Figure 4a). Sternal suture S2/3 not completely traversing sternum, sides not meeting sternal margins; S3/4 broad, V-shaped, deepest at

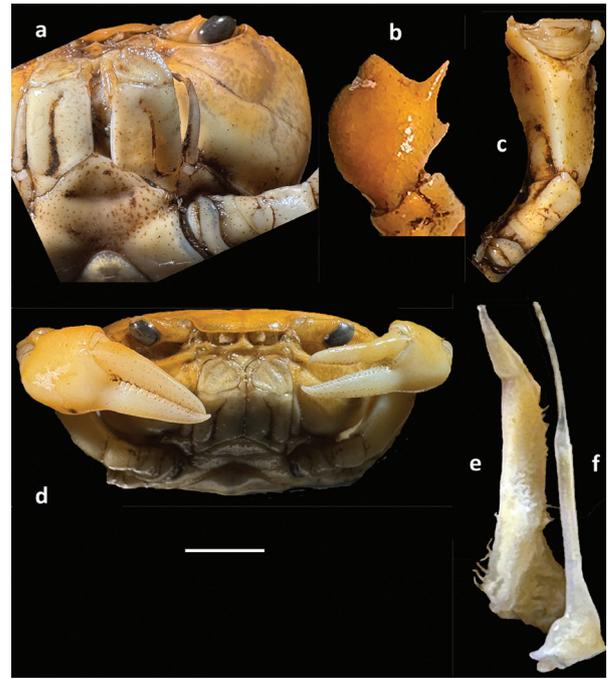


Figure 4. *Dianathelphusa antsahabe* n. sp. adult male holotype, CW 28.7 mm, from Andrafiarana-Andavakoera protected area, Antsahabe Forest, Madagascar (FMNH 16153): **a**) specimen tilted upwards to show details of the characters of the branchiostegite; **b**) right cheliped carpus; **c**) right cheliped merus and ischium, underside; **d**) frontal view of subadult female showing right and left chelae; **e**) right G1 ventral view; **f**) right G2 ventral view. Scale bar: a = 8.7 mm; b = 5.8 mm; c = 5.7 mm; d = 10.0 mm; e, f = 0.3 mm.

edges, meeting anterior margin of sternopleonal cavity; S4/5 meeting pleon short distance from telson/PL6 suture; S6/7 meeting midpoint of lateral margin of PL5; episternal sulci S4/E4, S5/E5, S6/E6, S7/E7 all distinct, short, not complete, not meeting sternal segment (Figure 3a & b); posterior inferior margin of cheliped merus lined with small faint granules, anterior inferior margin of cheliped merus smooth, distal tooth obscure (Figure 4c); cheliped ischium margin smooth, rounded (Figure 4c); telson lateral margins straight, apex rounded (Figure 3a-c); ambulatory legs (P2–5) stout, not elongated (Figure 2a); G1TA dorsal side broadest proximally, distal half curving slightly upward, tip broad (Figure 4e); G2TA long (G2TA/G2SA = 0.7), flagellum-like, straight (Figure 4f). Small-sized species, largest known specimen CW 28.7 mm, pubertal molt between CWs 24 and 28 mm.

Description

Based on holotype, adult male. Carapace outline transversely oval, extremely high (CH/CW 0.44);

front narrow (FW/CW = 0.3), deflexed; entire carapace surface smooth. Epibranchial tooth small, acute, close to exorbital tooth, positioned in line with postorbital margin; carapace lateral margin curved evenly outward, smooth, continuous with posterolateral margin; postfrontal crest faint, incomplete, not traversing entire carapace, epigastric crests faint, in line with postorbital margin, postorbital crests faint, ending before meeting epibranchial tooth; cardiac, urogastric sulci faint, semicircular sulcus deep, cervical sulcus broad, faint, long, not meeting postorbital crest (Figure 2a & b). Suborbital, subhepatic, pterygostomial regions of branchiostegite smooth; vertical sulcus on branchiostegite curved, granular, running downward from base of epibranchial tooth to epimeral sulcus (Figure 2c). Epistomial tooth triangular, deflexed, edges granular (Figure 2c). Mandibular palp terminal article bilobed, anterior lobe on terminal article conspicuous, medium-sized. Exopod of third maxilliped reaching to lower half of merus, exopod with shortened flagellum (less than half merus length), ischium with deep vertical sulcus, distal end curving medially, ending before meeting medial margin (Figures 3a & 4a). Sternal suture S1/2 short, faint; S2/3 not completely traversing sternum, sides not meeting sternal margins; S3/4 broad, V-shaped, deepest at edges, meeting anterior margin of sternopleonal cavity; S4/5 meeting pleon short distance from telson/PL6 suture; S6/7 meeting midpoint of lateral margin of PL5; episternal sulci S4/E4, S5/E5, S6/E6, S7/E7 all distinct, short, not complete, not meeting sternal segment (Figure 3a-c). Left chela largest, proximal half of cutting edge of fixed finger (pollex of propodus) with four small molars, small teeth distally; cutting edge of movable finger (dactylus) with small teeth proximally, one larger tooth midway (Figure 2a); right chela smaller than left chela, dentition same as right chela (Figure 2a); lower margin of propodus of both chelae slightly indented medially (Figure 2a). Female chelae left larger than right, both not greatly enlarged compared to male (Figure 3d). Distal tooth on inner margin of cheliped carpus large, pointed; proximal tooth significantly smaller, acute, rest of margin smooth (Figure 4b). Posterior inferior margin of cheliped merus lined with small faint granules, anterior inferior margin of cheliped merus smooth, distal tooth obscure; superior side of cheliped merus roughened by granules; cheliped ischium margins smooth, rounded (Figure 4c). Ambulatory legs P2–5 stout (Figure 2a). Male pleon plus telson triangular, tapered distally, widest at PL3, narrowest at telson; PL6

relatively broad, with convex lateral margins; telson outline with straight lateral margins, apex rounded (Figure 3a & b); subadult female pleon widened, but not yet meeting coxae of P2–5; subadult female pleon wider than adult male pleon (Figure 3b–c). Sulcus between G1TA-G1SA faint on ventral side, distinct on dorsal side; G1TA medium length (G1TA/G1SA = 0.3), dorsal side slim, broadest proximally, distal half curving slightly upward, tip broad; G1SA with distinct raised rounded shoulder on external margin near G1TA-G1SA junction (Figure 4e). Broad, trapezoid dorsal membrane on dorsal side of G1TA-G1SA junction; superior margin of G1 dorsal membrane diagonal, inferior margin J-shaped, lateral margin broad, mesial margin narrow (Figure 4e). G2TA long (G2TA/G2SA = 0.7), flagellum-like, straight (Figure 4f). Small-sized species, largest known specimen CW 28.7 mm, pubertal molt between CWs 24 and 28 mm

Color

In life, this species is pale brown dorsally and pale cream ventrally and at the tips of the chelae. This is superficially similar to *Madagapotamon humberti*, which also has a pale-colored carapace but its elongated walking legs are usually much darker. Preserved specimens are uniformly pale brown dorsally and cream colored ventrally, with pale ambulatory legs that are an even lighter than the carapace (Figure 2a).

Distribution

Dianathelphusa antsahabe n. gen & n. sp. is only known from the locality at Andrafiarana-Andavakoera in the DIANA Region of northern Madagascar and appears to be an endemic species with a narrow range.

Type locality

Madagascar, ex-Antsiranana Province, DIANA Region, Antsiranana II District, Andrafiarana-Andavakoera protected area, Antsahabe Forest, 2.8 km NW Anjakely (village) (12.894°S, 49.294°E, 360 m).

Etymology

The genus name, *Dianathelphusa*, refers to DIANA (an acronym for **D**iego I & II - **A**mbilobe - **N**osy Be - **A**mbanja), the administrative region in northern Madagascar where the holotype was collected. The

name is used as a Latin noun in nominative singular and is feminine. *Thelphusa* from the Greek, used to define freshwater crabs.

Species included

Dianathelphusa antsahabe n. sp.

Habitat

All of the specimens of *Dianathelphusa antsahabe* n. sp. were taken in the Antsahabe Forest with dry deciduous forest (*tsingy*) located a few kilometers from the village of Anjakely. This locality is in the Andrafiarana-Andavakoera protected area where this species lives in crevices on the karst limestone plateau in areas without any permanent water sources, at least on the surface. Interestingly, crabs were observed to become more active after rains. *Dianathelphusa antsahabe* n. sp. was caught either at night in a pitfall trap, or during the day by hand, and clearly this species spends a lot of its time on land (and, therefore, breathing air). In terms of its specialized habitat and terrestrial habits, *D. antsahabe* n. sp. is similar to the better-known long-legged karst specialist species *Madagapotamon humberti*, which is found in the nearby Réserve Spéciale d'Ankarana and in several other localities in northern Madagascar (Cumberlidge *et al.*, 2015).

Comparisons

Dianathelphusa n. gen. shares clade A (Figure 1) with six other genera: *Madagapotamon*, *Vahatra*, *Toamasina*, *Skelosophusa*, *Boreathelphusa*, and *Marojejy*. The characters that separate *Dianathelphusa* n. gen. from these other genera are as follows. *Dianathelphusa* n. gen. can be distinguished from *Madagapotamon* by the length of the flagellum of the exopod of the third maxilliped, which is well developed in *Dianathelphusa* n. gen. (Figure 4a), but almost absent, and reduced to a short stub in *Madagapotamon* (Cumberlidge & Sternberg, 2002: Figure 5h).

Dianathelphusa n. gen. can be distinguished from *Vahatra* as follows. The epistomial tooth edges are granular in *Dianathelphusa* n. gen. (Figure 2c) (vs smooth epistomial tooth edges in *Vahatra* (Leever *et al.*, 2022: Figure 1c)); sternal suture S2/3 does not completely traverse the sternum and its sides do not meet the sternal margins, and S3/4 is broad, U-shaped, and is deepest in the middle with its central part meeting the anterior margin of the sternopleonal cavity in *Dianathelphusa* n. gen. (Figure 3a) (vs a S2/3

that completely traverses the sternum, and the S3/4 is broad, U-shaped, deepest at the sides and it does not meet the anterior margin of the sternopleonal cavity in *Dianathelphusa* n. gen. (Leever *et al.*, 2022: Figure 1e)); S4/5 meets the pleon a short distance from the telson/PL6 suture, and S6/7 meets PL5 at the midpoint of its lateral margin in *Dianathelphusa* n. gen. (Figure 3a) (vs S4/5 meets the pleon at the telson/PL6 suture, and S6/7 meets PL6 at the midpoint of its lateral margin in *Vahatra* (Leever *et al.*, 2022: Figure 1e)); the episternal sulci S4/E4, S5/E5, S6/E6, S7/E7 that are all distinct, short, not complete, and do not meet the adjacent sternal segment in *Dianathelphusa* n. gen. (Figure 3a & b) (vs episternal sulci S4/E4, S5/E5, S6/E6, S7/E7 are all obscure in *Vahatra* (Leever *et al.*, 2022: Figure 1e)); the posterior inferior margin of the cheliped merus is lined with small faint granules, while the anterior inferior margin of the cheliped merus is smooth and the distal tooth is obscure in *Dianathelphusa* n. gen. (Figure 3c) (vs both of the inferior margins of the cheliped merus are lined with small, rounded teeth and the distal tooth is large in *Vahatra* (Leever *et al.*, 2022: Figure 4e)); and *Dianathelphusa* n. gen. is a small-sized species (largest known specimen has a CW 28.7 mm, with a pubertal molt between CWs 24 and 28 mm) (vs *Vahatra* which is a medium-sized species, where the largest known specimen has a CW 50 mm, with a pubertal molt between CWs 37 and 43 mm (Leever *et al.*, 2022)).

Dianathelphusa n. gen. can be distinguished from *Toamasina* as follows. The margin of the cheliped ischium of *Dianathelphusa* n. gen. is smooth and rounded (Figure 4c) (vs a cheliped ischium margin lined with small teeth in *Toamasina* (Leever *et al.*, 2022: Figure 4g & h)); the S4/5 thoracic sternal sulcus of *Dianathelphusa* n. gen. meets the pleon on the margin of the telson (Figure 3a) (vs an S4/5 sulcus that meets the pleon at the PL6/telson suture in *Toamasina* (Leever *et al.*, 2022: Figure 1f)); the exopod of the third maxilliped has a medium-length flagellum (less than the merus length) in *Dianathelphusa* n. gen. (Figure 4a) (vs a third maxilliped exopod with a long flagellum (equal to the merus length) in *Toamasina* (Leever *et al.*, 2022: Figure 2f)); the ambulatory legs (P2–5) are short ($\Sigma P2-5/CW = 5.7$) in *Dianathelphusa* n. gen. (Figure 2a) (vs ambulatory legs (P2–5) that are of medium length ($\Sigma P2-5/CW = 6.4$) in *Toamasina* n. gen. (Leever *et al.*, 2022: Table 3); the G1TA is broadest proximally with a distal half that curves upward and ends in a broad tip in *Dianathelphusa* n. gen. (Figure

4e) (vs a G1TA that is widest at the midpoint, with a distal half that is straight and ends in a pointed tip (Leever *et al.*, 2022: Figure 5d & e)).

Dianathelphusa n. gen. is distinguished from *Boreathelphusa* and *Skelosophusa* by the size of the flap on the mandibular palp, that of *Dianathelphusa* n. gen. is medium sized ($0.3 \times$ TS length), whereas that of *Boreathelphusa* and *Skelosophusa* is noticeably small, reduced to a small ledge ($0.1 \times$ TS length) (Cumberlidge & Sternberg, 2002: Figure 4h-k). Finally, the new genus can be distinguished from *Marojejy* by the small notch-like space between the exorbital and epibranchial teeth in *Dianathelphusa* n. gen. (Figures 2a & 3a) (vs a wide space between these teeth in *Marojejy* (Cumberlidge & Sternberg, 2002: Figures 1a-c & 2f)). The stout ambulatory legs (P2–5) (not elongated or slim) and eyestalks and corneas of normal length and size of *Dianathelphusa* n. gen. (Figure 2a) 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: Figures 2f & 8f).

***Dianathelphusa antsahabe* n. sp.**

(Figures 2-4)

LSIDurn:lsid:zoobank.org:pub:292F0819-FB8F-4A2A-8CF9-13980AAEC36

Type species

Dianathelphusa antsahabe n. sp. by present designation and by monotypy.

Material examined

Same as for the genus.

Type material

Same as for the genus.

Type locality

Same as for the genus.

Diagnosis

Same as for the genus.

Description

Same as for the genus.

Habitat

Same as for the genus.

Etymology

The species is named for the Antsahabe Forest, in the Andrafiarena-Andavakoera protected area, which lies in the DIANA Region, Antsiranana II District, 2.8 km NW of the village of Anjakely in northern Madagascar. The specific epithet is used as a Latin noun in genitive singular and treated as masculine.

Comparisons and Remarks

Same as for genus

***Skelosophusa gollardi* Bott, 1965**

(Figure 5)

Material

FMNH 16150A (SMG-22113B), subadult F (CW 27.1 mm, CL 19.6 mm, CH 10.6 mm, FW 7.9 mm) claw cracked before preservation, Madagascar, ex-Antsiranana Province, DIANA Region, Ambilobe District, Andrafiarena-Andavakoera protected area,

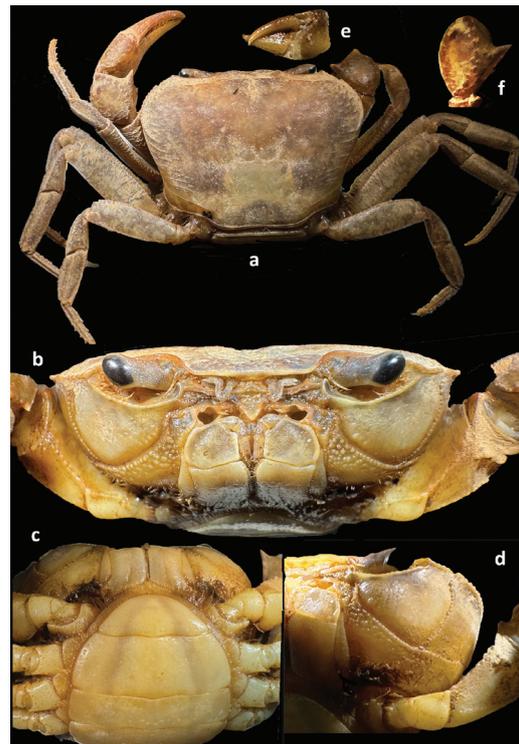


Figure 5. *Skelosophusa gollardi* Ng & Takeda, 1994, subadult female, CW 27.1 mm, from Andrafiarena-Andavakoera protected area, Binara-Andavakoera Forest, Madagascar (FMNH 16150A): **a**) whole animal, dorsal view; **b**) carapace, frontal view; **c**) anterior thoracic adult female sternum showing pleon with telson; **d**) specimen tilted upwards to show details of the characters of the branchiostegite. Scale bar: a = 12.3 mm; b = 7.3 mm; c = 12.3 mm; d = 7.3 mm.

Binara-Andavakoera Forest, 5.4 km E of Ankatsaka, next to the Ambaratra River (13.101°S, 49.240°E, 300 m ASL), coll. S. M. Goodman, 19 November 2023, caught by hand during the day, in disturbed moist semi-deciduous forest in shallow pools in river with flowing water in a gallery habitat. This river is a tributary of the Loky River.

Diagnosis

Carapace outline transversely oval (wider than long, CW/FW = 3.4, CL/FW = 2.5), moderately arched (CH/FW = 1.3); exorbital, epibranchial teeth both low, blunt, continuous with lateral margin; anterior carapace surface smooth, with granules and carinae in anterolateral, posterolateral regions; epigastric and postorbital crests both faint but detectable (Figure 5a); frontal margin straight, front deflexed (Figure 5b); cervical groove very short, shallow; pterygostomial region mostly smooth, inferior part with field of sparse short setae and a few small granules near third maxilliped (Figure 5b-d); mandibular palp two-segmented, terminal article with flat basal thickening at junction between segments; ischium of third maxilliped ischium with faint vertical sulcus (Figure 5b); anterior, posterior inferior margins of ischium of chela smooth (Figure 5b); distal tooth of cheliped carpus large, wide, with pointed tip; proximal carpal tooth small, rest of margin smooth (Figure 5b & d). Posterior inferior margin of cheliped merus lined with small faint granules, anterior inferior margin of cheliped merus smooth, distal meral tooth small; superior side of cheliped merus roughened by granules; cheliped ischium margins smooth, rounded (Figure 5b); walking legs (P2–5) normal length, neither elongated nor shortened (Figure 5a), ratio length merus P5 to CW = 0.5; anterior, posterior margin of P5 propodus granular (Figure 5a); branchiostegite suborbital, subhepatic regions mostly smooth with few faint granules (Figure 5b-d); small sized species, adult size range beginning at CW 28 mm.

Comparisons

The following morphological characters justify including this specimen in *Skelosophusa gollardi* Bott, 1965 (Bott, 1965; Cumberlidge & Sternberg, 2002). The anterior carapace surface and the carapace lateral margin are both smooth with granules and carinae in the anterolateral and posterolateral regions; the epibranchial tooth is distinct, rounded, and low; the posterior end of the carapace lateral

margin curves inward and is not continuous with the posterolateral margin; the exorbital tooth is small and broad; the epibranchial tooth is small, acute, close to the exorbital tooth and continuous with the lateral margin which is granular (Figure 5a); he epigastric and postorbital crests are smooth and do not touch; the carapace cervical groove is very short and shallow; the suborbital and subhepatic regions of the branchiostegite are smooth (Figure 5a), as is the upper part of the pterygostomial region but the lower part of the pterygostomial region has a field of dense field of setae; the mandibular palp has a small hard ledge-like process at the junction of the terminal article-subterminal segment; and the cheliped ischium margins are smooth and rounded (Figure 5b-d). *Skelosophusa gollardi* is a small sized species (adult at CWs between 24 and 28 mm).

Skelosophusa gollardi can be distinguished from *S. eumeces* Ng & Takeda, 1994 by the epigastric and postorbital crests that are faint and not joined together in *S. gollardi* (Figure 4a) (vs epigastric and postorbital crests that are distinct, rugose, and joined together in *S. eumeces*), the carapace cervical groove is short and faint in *S. gollardi* (Figure 5a) (vs a carapace cervical groove that is broad and distinct in *S. eumeces*) and the lower part of pterygostomial region of the branchiostegite has a dense field of setae in *S. gollardi* (Figure 5b) (vs a smooth lower part of the pterygostomial region of the branchiostegite that lacks a dense field of setae in *S. eumeces*). *Skelosophusa gollardi* can be distinguished from *S. prolixa* Ng & Takeda, 1994 by the carapace cervical groove, which is short and faint in *S. gollardi* (Figure 5a) (vs a carapace cervical groove which is long and deep in *S. prolixa*). One difference between the subadult female from Andrafiarena-Andavakoera (FMNH 16150A) and the adult male holotype of *S. gollardi* from the Ankarana Special Reserve is the length of the walking legs (P2–5) that are stout and not elongated in the specimens from Andrafiarena-Andavakoera, but elongated, and slender in the holotype of *S. gollardi* (Bott, 1965: Plate V, Figures 19–21)).

Skelosophusa is distinguished from its closest relative, *Boreathelphusa uglowi*, as follows. The ischium of the third maxilliped of *Skelosophusa* has a distinct vertical sulcus, whereas in *B. uglowi* the third maxilliped ischium is smooth.

Remarks

Skelosophusa gollardi was previously known only from a single specimen (CW 23 mm, MNHN-B 5165)

held in the Muséum national d'histoire naturelle, Paris, collected by R. Decary in 1939 from the 'Grotte de l'Ankara' (= a cave in the Réserve Spéciale d'Ankarana), in the DIANA Region of northern Madagascar. The Réserve Spéciale d'Ankarana is known for its *tsingy* rock formations with canyons and underground cave networks, and for its seasonal dry forests. The specimen from Ankarana was first described 26 years later as *Madagapotamon gollardi* Bott, 1965 (Bott, 1965). Since then no other specimens of this species have been collected. This species was transferred into *Skelosophusa* by Ng and Takeda, 1994, and redescribed by Cumberlidge and Sternberg, 2002. The locality of the specimen reported on here from the Andrafiarena-Andavakoera protected area (a subadult female, CW 28.7 mm, FMNH 16150A) lies about 20 km southeast of the Réserve Spéciale d'Ankarana. Because this specimen is a subadult female, the characters of the gonopods and male sternum are unavailable, but the majority of its other characters conform to the diagnosis of the species. This record represents a range extension for this little-known species.

Conservation

Skelosophusa gollardi was most recently assessed for The IUCN Red List of Threatened Species in 2016, and was listed as Data Deficient (DD) because it is too poorly known to carry out an extinction risk assessment (Cumberlidge, 2016a). The new record for this species leaves *S. gollardi* in the same category (DD) because two localities are still not enough to make a conservation assessment using the IUCN Red List protocols.

Genus *Hydrothelphusa* A. Milne-Edwards, 1872

Hydrothelphusa madagascariensis A. Milne-Edwards, 1872

(Figures 6-8)

Material

FMNH 16149 (SMG-22112), adult male (CW 56.5 mm) claw cracked before preservation, Madagascar, ex-Antsiranana Province, DIANA Region, Ambilobe District, Andrafiarena-Andavakoera protected area, Binara-Andavakoera Forest, 5.4 km E Ankatsaka, next to Ambaratra River (13.101°S, 49.240°E, 300 m ASL), coll. S. M. Goodman, 19 November 2023, by hand, in disturbed moist semi-deciduous humid forest; found during the day in shallow pools in a river with flowing water in



Figure 6. *Hydrothelphusa madagascariensis* A. Milne-Edwards, 1872, subadult female, CW 56.4 mm, from Andrafiarena-Andavakoera protected area, Binara-Andavakoera Forest, Madagascar (FMNH 16149): **a**) whole animal, dorsal view; **b**) carapace, dorsal view. Scale bar: a = 28.9 mm; b = 12.2 mm.

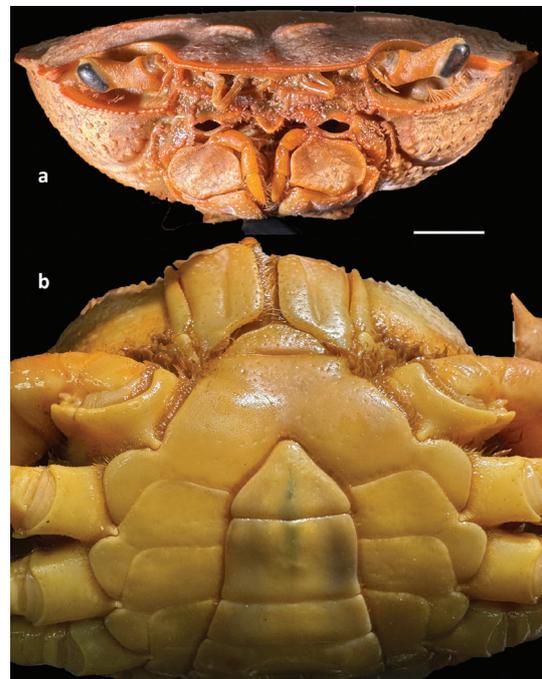


Figure 7. *Hydrothelphusa madagascariensis* A. Milne-Edwards, 1872, subadult female, CW 56.4 mm, from Andrafiarena-Andavakoera protected area, Binara-Andavakoera Forest, Madagascar (FMNH 16149): **a**) carapace, frontal view; **b**) anterior thoracic adult male sternum showing partial pleon with telson. Scale bar: a = 12.2 mm; b = 14.3 mm.

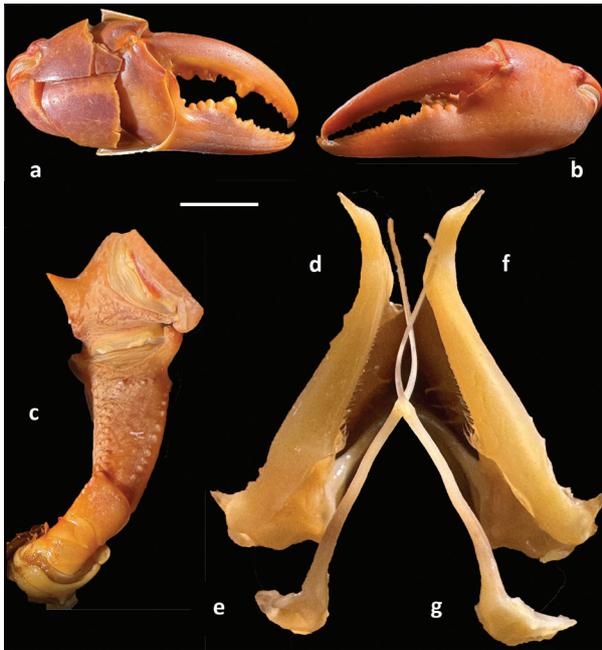


Figure 8. *Hydrothelphusa madagascariensis* A. Milne-Edwards, 1872, subadult female, CW 56.4 mm, from Andrafiarana-Andavakoera protected area, Binara-Andavakoera Forest, Madagascar (FMNH 16149): **a**) frontal view of right chela (damaged); **b**) frontal view of left chela; **c**) right cheliped merus and ischium, underside; **d**) right G1 ventral view; **e**) right G2 ventral view; **f**) left G1 ventral view; **g**) left G2 ventral view. Scale bar: a = 8.9 mm; b = 7.0 mm; c = 7.6 mm; d–g = 0.3 mm.

a gallery habitat. This river is a tributary of the Loky River. FMNH 16150 (SMG-22113A), subadult male (CW 35.4 mm) claw cracked before preservation. Same collection details as FMNH 16149. FMNH 16151 (SMG-22114), subadult male (CW 21.1 mm). Same collection details as FMNH 16149. FMNH 16152 (SMG-22115), subadult male (CW 20.9 mm) claw cracked before preservation. Same collection details as FMNH 16149. FMNH 16156 (SMG-22350), adult male (CW 47.8 mm) claw cracked before preservation, Madagascar, ex-Antsiranana Province, DIANA Region, Ambilobe District, Andrafiarana-Andavakoera protected area, Anjakely Forest, 1.3 km SE Anjakely (village) (12.913°S, 49.328°E, 420 m ASL), coll. V. Soarimalala and S. M. Goodman, 4 December 2023, by hand, in slightly disturbed moist semi-deciduous forest, in a river about 40 m above the Piscine Naturelle. FMNH 16157 (SMG-22351), adult male (CW 59.5 mm), claw cracked before preservation, Madagascar, ex-Antsiranana Province, DIANA Region, Ambilobe District, Andrafiarana-Andavakoera protected area, Anjakely Forest, 1.3 km SE Anjakely (village) (12.913°S, 49.328°E, 420 m ASL), coll. V. Soarimalala and S. M. Goodman 4,

December 2023, by hand, from slightly disturbed moist semi-deciduous forest, in a river about 300 m above the Piscine Naturelle. FMNH 16158 (SMG-22369), juvenile male (CW 18.6 mm), Madagascar, ex-Antsiranana Province, DIANA Region, Ambilobe District, Andrafiarana-Andavakoera protected area, at the edge of the Anjakely Forest, along the Teganjahahely River (12.914°S, 49.317°E, 300 m ASL), coll. A. P. Raselimanana, 2 December 2023, by hand at night, in permanent running water passing through rafia swamp.

Diagnosis

Inferior margins of cheliped merus lined by either large teeth or large granules; anterior carapace texture roughened, not smooth; anterolateral regions of carapace distinctly granular with short distinct carinae; inferior lateral margin of cheliped merus with single row of granules leading to distal meral tooth; frontal margin slightly indented, margin granular; front moderately deflexed; suborbital margin lined with granules; lower margins of cheliped merus, ischium lined by granules, not teeth.

Comparisons

This species was recently illustrated in a revision of the genus *Hydrothelphusa* and identification keys to the species of this genus were provided (Cumberlidge *et al.*, 2024: Figures 1b, 2b, 3b, 4b, 5c & d, 6b, g, h, 7c–e, 8b, f, & j). The following morphological characters justify including the specimens from the Andrafiarana-Andavakoera protected area in *Hydrothelphusa* (Cumberlidge *et al.*, 2024). The carapace outline is transversely oval with wide frontal and posterior margins (each approximately one-third × carapace width) (Figure 6a & b); the mandibular palp consists of two articles and its terminal article is bilobed, with a medium-sized anterior lobe (MPAL/MPTA 0.5) at the junction between the two articles; the third maxilliped ischium has a deep vertical sulcus, and the exopod has a long flagellum (Figure 7a & b); sternal sulcus S2/3 is deep and horizontal, and S3/4 is shallow and either U- or Y- shaped; episternal sulci S4/E4, S5/E5, S6/E6, S7/E7 are all obscure (Figure 7a); the ambulatory legs (P2–5) are either stout or medium length ($\Sigma P2-5/CW$ 5.4–6.7) (Figure 6a), but not exceptionally elongated (i.e., with a $\Sigma P2-5/CW > 7.0$); the male pleon is long, slim, and triangular, with a bell-shaped telson whose sides are indented (Figure 7b); the G1TA is medium length (G1TA/G1SA = 0.3) and is widened in the midpoint by

a rounded lobe; the G1SA has a distinct disto-lateral triangular shoulder-like projection at the junction of the segments (Figure 8d & f); and the G2TA is long ($G2TA/G2SA = 0.7$), flagellum-like and straight (Figure 8e & g).

Hydrothelphusa madagascariensis most closely resembles *H. sava* Cumberlandidge, Robinson & Daniels, 2025, and the distribution of both species overlaps in northern Madagascar. For example, *H. sava* is known from the Marojejy National Park, the Montagne des Français protected area (both in the SAVA Region), and the Montagne d'Ambre National Park (in the DIANA Region). These two species share the following characters. In both species, the anterior carapace surface has fields of granules and carinae, the exorbital tooth is large, the lateral margin behind the epibranchial tooth is raised and granulated (Figure 5a; Cumberlandidge *et al.*, 2025: Figures 1a & 2b), the suborbital margins (Figure 6a; Cumberlandidge *et al.*, 2025: Figure 2a), the cheliped ischium margins, and cheliped merus inferior margins are all granulated (Figure 7c; Cumberlandidge *et al.*, 2025: Figure 3d & e), and the distal tooth on the cheliped carpus inner margin is a long, slender spine (Figure 7c; Cumberlandidge *et al.*, 2025: Figure 3e).

Hydrothelphusa madagascariensis can be distinguished from *H. sava* as follows. The inner margin of the cheliped carpus has a single small tooth behind the proximal tooth in *H. madagascariensis* (Figure 8c) (vs a cheliped carpus with large granules behind the proximal tooth in *H. sava* (Cumberlandidge *et al.*, 2025: Figure 3e)). The adult size is in the large body size range (adult at CW 70 mm) in *H. madagascariensis* (Figure 5a) (vs a medium body size range (adult at CW 50 mm) in *H. sava*) (Cumberlandidge *et al.*, 2025: Figure 1a). The carapace frontal margin projects straight out in *H. madagascariensis* (Figure 6a) (vs a carapace frontal margin that is slightly deflexed in *H. sava*) (Cumberlandidge *et al.*, 2025: Figure 2a). The distal tooth on the inner margin of the cheliped carpus is large with a wide base and tapers distally to form a broad triangle in *H. madagascariensis* (Figure 7c) (vs a distal tooth on the inner margin of the cheliped carpus that is a large, slim, and narrow, and tapers to form a triangular spine in *H. sava* (Cumberlandidge *et al.*, 2025: Figure 3e)). The medial, lateral inferior margins of cheliped merus are lined by small pointed teeth in *H. madagascariensis* (Figure 8c) (vs medial, lateral inferior margins of the cheliped merus that are lined by small granules in *H. sava*) (Cumberlandidge *et al.*, 2025: Figure 3d & e). The lateral inferior margin of the

cheliped merus is lined by small granules but lacks a second row of granules in *H. madagascariensis*) (Figure 8c) (vs a lateral inferior margin of cheliped merus that has a second row of small granules in *H. sava* (Cumberlandidge *et al.*, 2025: Figure 3d)

Conservation

Hydrothelphusa madagascariensis was most recently assessed for The IUCN Red List of Threatened Species in 2016, and is listed as Least Concern (Cumberlandidge, 2016b). The new records for this species presented here still leaves *H. madagascariensis* in the same category (LC) (Cumberlandidge *et al.*, 2017).

Discussion

Our phylogenetic results (Figure 1) revealed the presence of four new Malagasy freshwater crab genera, of which *Dianathelphusa antsahabe* n. sp. from Andrafiarana-Andavakoera is described herein. These results point to the exceptional diversity of the Malagasy freshwater crab fauna and clearly suggest that additional sampling is likely to unmask further novel diversity. The remaining three new genera identified during the present study will be described elsewhere and when more material becomes available. We note that *Crosnautes* is not monophyletic suggesting that further taxonomic refinement is required. The Malagasy Hydrothelphusinae now comprises 15 genera that are all endemic to Madagascar (*Agora*, *Boreathelphusa*, *Crosnautes*, *Dianathelphusa*, *Foza*, *Glabrithelphusa*, *Hydrothelphusa*, *Madagapotamon*, *Malagasya*, *Marojejy*, *Nheena*, *Skelosophusa*, *Toamasina*, *Vahatra*, and *Vichai*, plus three as yet undescribed genera) (Bott, 1965; Cumberlandidge & Sternberg, 2002; Reed & Cumberlandidge, 2006; Cumberlandidge & Meyer, 2009; Cumberlandidge, 2010; Meyer *et al.*, 2014; Cumberlandidge *et al.*, 2007, 2015, 2020, 2021, 2023a, 2023b, 2024, 2025; Leever *et al.*, 2022).

Madagascar's freshwater decapod fauna is undoubtedly rich in comparison with other similar-sized and better-studied areas of Africa. For example, both South Africa (1,222,000 km², 36 species, two genera, Cumberlandidge & Daniels, 2022; Daniels *et al.*, 2023, Peer *et al.*, 2023; Mengel & Daniels, 2024) and Angola (1,248,000 km², nine species, one genus, Cumberlandidge & Tavares, 2006; Cumberlandidge *et al.*, 2021) have a territorial area of about twice that of Madagascar (587,040 km²), but both have substantially fewer genera (all potamonautids) when

compared to Madagascar (28 species, 15 genera, all dekeniids). The high degree of endemism shown by Madagascar's freshwater crabs is similar to the pattern shown by several other invertebrate and vertebrate groups, and reflects the long absence of biotic exchange between the island and the mainland that has resulted in genetic isolation and remarkable radiations within Madagascar's fauna and flora (Antonelli *et al.*, 2022). Interestingly, the majority of Madagascar's freshwater crab species are restricted to the island's northern regions of DIANA and SAVA that represents less than 10% of the island's area. This species richness in the north of the island may be due to northern Madagascar's wealth of habitats including moist semi-deciduous and dry deciduous forests, and karst landscapes in areas showing considerable topographic variation.

Acknowledgements

This work was made possible by the material collected from Madagascar over a number of years by S. M. Goodman of the Field Museum of Natural History (FMNH), Chicago, USA and Association Vahatra, Antananarivo, Madagascar; as well as numerous colleagues associated with Association Vahatra. Marty Prydzia and Sean Keogh of the FMNH are also thanked for kindly loaning specimens used in this study and for hosting a visit by the first author. We thank Steve Goodman for comments on an earlier version of this article.

References

- Antonelli, A., Smith, R. J., Perrigo, A. L., Crottini, A., Hackel, J., Testo, W., Farooq, H., Torres Jiménez, M. F., Andela, N., Andermann, T., Andriamanohera, A. M., Andriambololonera, S., Bachman, S. P., Bacon, C. D., Baker, W. J., Belluardo, F., Birkinshaw, C., Borrell, J. S., Cable, S., Canales, N. A., Carrillo, J. D., Clegg, R., Clubbe, C., Cooke, R. S. C., Damasco, G., Dhanda, S., Edler, D., Faurby, S., de Lima Ferreira, P., Fisher, B. L., Forest, F., Gardiner, L. M., Goodman, S. M., Grace, O. M., Guedes, T. B., Henniges, M. C., Hill, R., Lehmann, C. E. R., Lowry, P. P., Marline, L., Matos-Maraví, P., Moat, J., Neves, B., Nogueira, M. G. C., Onstein, R. E., Papadopoulos, A. S. T., Perez-Escobar, O. A., Phelps, L. N., Phillipson, P. B., Pironon, S., Przelomska, N. A. S., Rabarimanarivo, M., Rabehevitra, D., Raharimampionona, J., Rajaonah, MT, Rajaonary, F, Rajaovelona, LR, Rakotoarinivo, M, Rakotoarisoa, AA, Rakotoarisoa, S. E., Rakotomalala, H. N., Rakotonasolo, F., Ralaiveloarisoa, B. A., Ramirez-Herranz, M., Randriamamonjy, J. E. N., Randriamboavonjy, T., Randrianasolo, V., Rasolohery, A., Ratsifandrihamanana, A. N., Ravololomanana, N., Razafiniary, V., Razanajatovo, H., Razanatsoa, E., Rivers, M., Sayol, F., Silvestro, D., Vorontsova, M. S., Walker, K., Walker, B. E., Wilkin, P., Williams, J., Ziegler, T., Zizka, A. & Ralimanana, H. 2022. Madagascar's extraordinary biodiversity: Evolution, distribution, and use. *Science*, 378 (6623).
- Bott, R. 1955. Die Süßwasserkrabben von Afrika (Crust. Decap.) und Ihre Stammesgeschichte. *Annales du Musée du Congo Belge, Tervuren, (Belgique)*, C Zoologie, (3, 3), 3 (1): 209-352.
- Bott, R. 1965. Die Süßwasserkrabben von Madagaskar. *Bulletin du Muséum national d'Histoire naturelle*, 37 (2): 335-350.
- Cumberlidge, N. 1999. *The freshwater crabs of West Africa. Family Potamonautidae. Faune et Flore Tropicales*. Vol. 35. Institut de Recherche pour le Développement, Paris.
- Cumberlidge, N. 2010. *Boreathelphusa*, a replacement name for *Boreas* Cumberlidge and Sternberg, 2002 (Crustacea: Brachyura: Potamonautidae), preoccupied by *Boreas* Morris, 19870 (Bryozoa: Hippothoidae). *Zootaxa*, 2450: 68.
- Cumberlidge, N. 2016a. *Skelosophusa gollardi*. *The IUCN Red List of Threatened Species* 2016: e.T134762A87566628 <https://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T134762A87566628.en>. Accessed on 15 December 2024.
- Cumberlidge, N. 2016b. *Hydrothelphusa madagascariensis*. *The IUCN Red List of Threatened Species* 2016: e.T134480A87565253. <https://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T134480A87565253.en>. Accessed on 10 December 2024.
- Cumberlidge, N. & Daniels S. R. 2022. A new multilocus phylogeny reveals overlooked diversity in African freshwater crabs (Potamonautidae Bott, 1970): A major revision with new higher taxa and genera. *Zoological Journal of the Linnean Society*, 194: 1268-1311.
- Cumberlidge, N. & Meyer, K. S. 2009. A new species of *Foza* Reed & Cumberlidge, 2006, from northern Madagascar (Decapoda, Brachyura, Potamoidea, Potamonautidae), with a redescription of *F. goudoti* (H. Milne Edwards, 1853) comb. n., and comments on *Skelosophusa prolixa* Ng & Takeda, 1994. *ZooKeys*, 18: 77-89.
- Cumberlidge, N. & Sternberg, R. V. 2002. The freshwater crabs of Madagascar (Decapoda: Potamoidea: Potamonautidae). *Zoosystema*, 24 (1): 41-79.
- Cumberlidge, N. & Tavares, M. 2006. Remarks on the freshwater crabs of Angola, southwestern Africa, with the description of *Potamonautes kensleyi*, new species (Brachyura: Potamoidea: Potamonautidae). *Journal of Crustacean Biology*, 26 (2): 248-257.
- Cumberlidge, N., Marijnissen, S. A. E. & Thompson, J. 2007. *Hydrothelphusa vencesi*, a new species of freshwater crab (Brachyura: Potamoidea: Potamonautidae) from southeastern Madagascar. *Zootaxa*, 1524: 61-68.

- 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, Potamonautidae). *European Journal of Taxonomy*, 109: 1-15.
- Cumberlidge, N., Rasamy Razanabolana, J., Ranaivoson, C. H., Randrianasolo, H. H., Sayer, C., Máiz-Tomé, L., Van Damme, D. & Darwall, W. R. T. 2017.** Updated extinction risk assessments of Madagascar's freshwater decapod crustaceans reveal fewer threatened species but more Data Deficient species. *Malagasy Nature*, 12: 32-41.
- Cumberlidge, N., Soma, J. B., Leever, E. M. & Daniels, S. R. 2020.** Molecular and morphological analyses identify new lineages within the Madagascan freshwater crab fauna: *Agora* n. gen. for *Thelphusa goudoti* H. Milne Edwards, 1853, and a phytotelmic new species of *Malagasya* Cumberlidge and Sternberg, 2002 (Brachyura, Potamonautidae, Deckeniinae). *Journal of Crustacean Biology*, 1-16.
- Cumberlidge, N., Soma, J. B., Leever, E. M., Clark, P. F. & Daniels, S. R. 2021.** Description of a new genus and two new species of freshwater crabs (Decapoda: Brachyura: Potamonautidae) from southeastern Madagascar. *Journal of Crustacean Biology*, 43, 1-13.
- Cumberlidge, N., Soma, J. B., Leever, E. M. & Daniels, S. R. 2023a.** *Nheena* n. gen., a new Madagascan freshwater crab genus for *Hydrothelphusa vencesi* Cumberlidge, Marijnissen & Thompson, 2007, with two new species of this genus (Brachyura: Potamoidea: Deckeniidae). *Journal of Crustacean Biology*, 43: 1-13.
- Cumberlidge, N., Daniels, S. R., Soma, J. B. & Leever, E. M. 2023b.** *Vichai cyanapelou* n. gen. et sp. nov. (Deckeniidae: Hydrothelphusinae), a new genus and new species of freshwater crab from Madagascar. *Journal of Natural History*, 57: 463-474.
- Cumberlidge, N., Soma, J. B., Leever, E. M. & Daniels, S. R. 2024.** A revision of the Madagascan freshwater crab genus *Hydrothelphusa* A. Milne Edwards, 1872 (Brachyura, Deckeniidae, Hydrothelphusinae), with a new species of this genus from northern Madagascar. *Crustaceana*, *Christoph D. Schubart Memorial Issue*, 97 (5-9): 687-707.
- Cumberlidge, N., Robinson, G. E. & Daniels, S. R. 2025.** A new collection of freshwater crabs from northern Madagascar with the description of a new species of *Hydrothelphusa* A. Milne-Edwards, 1872 (Brachyura: Deckeniidae: Hydrothelphusinae). *Zootaxa*, 5601 (3): 533-544.
- Daniels, S. R. & Klaus, S. 2018.** Divergent evolutionary origins and biogeographic histories of two freshwater crabs (Brachyura: *Potamonautes*) on the West African conveyor belt islands of São Tomé and Príncipe. *Molecular Phylogenetics and Evolution*, 127: 119-128.
- 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.
- 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.** Multi-locus phylogeny of the Afrotropical freshwater crab fauna reveals historical drainage connectivity and transoceanic dispersal since the Eocene. *Systematic Biology*, 64 (4): 549-567.
- Daniels, S. R., Busschau, T., Gullacksen, G., Marais, H., Gouws, G. & Barnes, A. 2023.** Cryptic and widespread: A recipe for taxonomic misidentification in a freshwater crab species (Decapoda: Potamonautidae: *Potamonautes sidneyi*) as evident from species delimitation methods. *Zoological Journal of the Linnean Society*, 197: 1005-1033.
- Davie, P. J. F., Guinot, D. & Ng, P. K. L. 2015.** Anatomy and functional morphology of Brachyura. In *Treatise on zoology – anatomy, taxonomy, biology*, eds. P. Castro, P. J. F. Davie, D. Guinot, F. Schram & C. von Vaupel Klein, pp. 11-63. The Crustacea 9 Part C. Brill, Leiden.
- Gouws, G., Peer, N. & Perissinotto, R. 2015.** MtDNA lineage diversity of a potamonautid freshwater crab in KwaZulu-Natal, South Africa. *Koedoe*, 57: 1-12.
- 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.
- Leever, E. M. & Daniels, S. R., Soma, J. B. & Cumberlidge, N. 2022.** Two new genera and a new species of freshwater crabs from northern Madagascar (Brachyura: Potamoidea: Deckeniidae). *Journal of Natural History*, 56: 241-263.
- Linnaeus, C. 1758.** *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Vol. 1, Edn. 10. *Impensis Direct. Laurentii Salvii, Holmiae* [= Stockholm].
- Mengel, K. & Daniels, S. R. 2024.** Hiding in the hills: Evidence for two novel mountain-dwelling freshwater crabs of *Potamonautes* (Decapoda: Brachyura: Potamonautidae) from South Africa. *Journal of Crustacean Biology*, 44 (2): ruae026, <https://doi.org/10.1093/jcabi/ruae026>
- Meyer, S. K., Cumberlidge, N. & Koppin, K. C. 2014.** A new genus and species of freshwater crab from Madagascar (Decapoda, Brachyura, Potamoidea, Potamonautidae). *Zootaxa*, 3884 (1): 65-72.
- Milne-Edwards, A. 1872.** Note sur les Crabes d'eau douce de Madagascar. *Bibliothèque de l'Ecole pratique des Hautes Etudes, Section Sciences Naturelles*, 5 (8): 1-3.
- Milne-Edwards, H. 1853.** Observations sur les affinités zoologiques et la classification naturelle des Crustacés. *Annales des Sciences Naturelles, Zoologie, Série 3*, 20: 163-228.

- Ortmann, A. E. 1896.** Das System der Decapoden-Krebse. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie de Thiere*, 9: 409-453.
- Ortmann, A. E. 1897.** Carcinologische Studien. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie de Thiere*, 10: 256-372.
- Peer, N., Gouws, G., Maliwa, L., Barker, N., Juby, P. & Perissinotto, R. 2023.** Description of a new montane freshwater crab (Arthropoda, Malacostraca, Decapoda, Potamonautidae) from the Eastern Cape, South Africa. *ZooKeys*, 1160: 89-108.
- Posada, D. 2008.** jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution*, 25: 1253-1256.
- Rathbun, M. 1904.** Les crabes d'eau douce (Potamonidae). *Nouvelles Archives du Muséum d'Histoire naturelle* 6 (4): 255-312.
- Reed, S. K. & Cumberlidge, N. 2006.** *Foza raimundi*, a new genus and species of potamonautid freshwater crab (Crustacea: Decapoda: Potamoidea) from northern Madagascar. *Proceedings of the Biological Society of Washington*, 119 (1): 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.
- Stamatakis, A., Hoover, P. & Rougemont, J. 2008.** A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology*, 57: 758-771.
- Tahinarivony, J. & Goodman, S. M. 2025.** Description of the Paysage Harmonieux Protégé d'Andrafiarena-Andavakoera, Madagascar, and the 2023 biological inventory of the protected area. In A floral and faunal inventory of the Andrafiarena-Andavakoera protected area of northern Madagascar, eds. S. M. Goodman & J. A. Tahinarivony. *Malagasy Nature*, 19: 1-31.