Foza raimundi, a new genus and species of potamonautid freshwater crab (Crustacea: Decapoda: Potamoidea) from northern Madagascar

Sadie K. Reed and Neil Cumberlidge*

(SKR) Department of Biology, Program in Evolution, Ecology, and Organismal Biology, ASEC 185, University of Akron, Akron, Ohio 44325-3908, U.S.A., e-mail: skreed@kent.edu;
(NC) Department of Biology, Northern Michigan University, Marquette, Michigan 49855-5301, U.S.A., e-mail: ncumberl@nmu.edu

Abstract.—Foza raimundi, a new genus and species of freshwater crab from Antsiranana Province, northern Madagascar, is described from a high-altitude locality in the isolated Marojejy mountain range. The unusual combination of characters of the new species warrants the establishment of a new genus to accommodate this taxon. The new taxon is compared to the other species of freshwater crabs occurring in Madagascar. The Malagasy freshwater crabs belong to the Potamonautidae, a family found exclusively in the Afrotropical zoogeographic region. The new taxon is endemic to Madagascar, as are the other six genera and 12 species of freshwater crabs found there.

The most recent revision of the freshwater crabs of Madagascar (Cumberlidge & Sternberg 2002) recognized 12 species in six genera. The distribution of these endemic crustaceans was described in detail by Cumberlidge & Sternberg (2002) and by Cumberlidge et al. (2004); the latter authors also assessed the conservation status of each taxon. Of concern is the fact that ten Malagasy species were judged to be either threatened or extremely rare/endangered, and only two taxa (Hydrothelphusa agilis A. Milne-Edwards, 1872 and H. madagasacariensis (A. Milne-Edwards, 1872)) were considered to be secure (Cumberlidge et al. 2004). The high degree of endemism shown by the Malagasy freshwater crabs is a characteristic that they share with other terrestrial and freshwater organisms from this tropical island. These crabs are found in the lakes, streams, rivers, and adjacent terrestrial habitats throughout the island (Bott 1960, 1965: Ng & Takeda 1994; Cumberlidge 1999; Cumberlidge &

We report here on the discovery of a new genus and species of freshwater crab from a high altitude locality in an isolated mountain range in northern Madagascar. The specimens described here are distinctly different from all known taxa in a number of important morphological taxonomic characters including those of the mandible, gonopods, carapace, sternum, epistome, chelipeds, walking legs, and third maxilliped. This unusual combination of characters is sufficient to warrant the recognition of a new monotypic genus to accommodate this species. Foza raimundi, new genus, new species, is compared to the other genera and species of freshwater crabs from Madagascar. The new taxon is assigned to the Potamonautidae sensu Cumberlidge (1999) and Cumberlidge & Sternberg (2002).

Abbreviations.--Terminology is adapted from Cumberlidge (1999), and the

Sternberg 2002, 2003; Cumberlidge et al. 2004); there are also a number of reports of their presence in phytotelmic habitats in rainforest ecosystems (Cumberlidge et al. 2002, Cumberlidge et al. 2005).

^{*} Corresponding author.

classification used here follows that of Martin & Davis (2001). Abbreviations: cw, distance across the carapace at the widest point; cl, carapace length measured along the median line, from the frontal margin to the posterior margin; ch, carapace height, the maximum height of the cephalothorax); fw, front width measured along the frontal margin; s, thoracic sternite; s4/s5, s5/s6, s6/s7, s7/s8, sternal sulci between adjacent thoracic sternites; e, thoracic episternite; s4/e4, s5/e5, s6/e6, s7/e7, episternal sulci between adjacent thoracic sternites and episternites; a, abdominal segment; a6/a5, a7/a6, sutures between abdominal segments; p1-p5, pereopods 1-5; asl, above sea level. All measurements are given in mm. FMNH = Field Museum of Natural History, Chicago, Illinois, U.S.A.

Systematics

Subphylum Crustacea Brünnich, 1772 Order Decapoda Latreille, 1802 Infraorder Brachyura Latreille, 1802 Superfamily Potamoidea Ortmann, 1896 Family Potamonautidae Bott, 1970

Foza, n. gen.

Type species.—Foza raimundi, n. sp.

Diagnosis.-Frontal margin of carapace relatively narrow (fw/cw 0.25), sharply deflexed. Pterygostomial region of carapace sidewall with broad area of dense setae. Terminal article of gonopod 1 short, wide-tipped, broadly conical. Terminal article of gonopod 2 extremely long, flagellum-like, reaching anterior margin of sterno-abdominal cavity; flagellum of gonopod 2 curving inward distally, tip sharply curved inward, overall outline of flagellum forming "question mark" shape; distal parts of flagellae of both second gonopods overlapping one another, sometimes protruding from under closed abdominal telson.

Etymology.—Foza is derived from the Malagasy name "fosa" meaning freshwa-

ter crab. *Foza* is treated as a feminine noun. The spelling of the word "fosa" has been modified because of the potential for confusion that may arise from the similarity of the spelling and pronunciation of "fosa" to the generic name and common name of two common Malagasy carnivores. For example, the scientific name of the Malagasy civet or striped civet is *Fossa fossana* (Viverridae), while "fossa", also spelled "fosa", is the common name for the well-known Malagasy carnivore *Cryptoprocta ferox* (Cryptoproctidae) (Dollar 2000a, 2000b).

Remarks .- Foza, like all Malagasy freshwater crab taxa, is assigned to the Potamonautidae Bott, 1970, because of the common possession of a number of characters, including a two-segmented mandibular palp, a triangular abdomen, and a first gonopod with either a short or medium length terminal article (Cumberlidge 1999). Foza can be distinguished from the other Malagasy freshwater crab genera (Hydrothelphusa A. Milne-Edwards, 1872, Madagapotamon Bott, 1965, Skelosophusa Ng & Takeda, 1994, Marojejy Cumberlidge, Boyko, & Harvey, 2002, Malagasya Cumberlidge & Sternberg, 2002, and Boreas Cumberlidge & Sternberg, 2002) as follows: the first gonopod of Foza has a wide-tipped, broadly conical terminal article; the second gonopod has an extremely elongated and inwardly curved flagellum-like terminal article; the pterygostomial region has a dense field of setae, and the postfrontal crest is faint and incomplete with the weak epigastric crests positioned so far forward on the front that they almost touch the frontal margin. Interestingly, this discovery means that the Marojejy mountains are home to four species of freshwater crabs belonging to four genera, the other three taxa being Marojejy longimerus Cumberlidge, Boyko & Harvey, 2002, Skelosophusa eumeces Ng & Takeda, 1994. Hydrothelphsua and madagascariensis.

Foza is morphologically close to Malagasya because both taxa share a bilobed mandibular palp, elongated walking legs, a narrow deflexed front, and two pointed carpal teeth on the carpus of the cheliped. However, Foza can be distinguished from Malagasya by the anterolateral margin of the carapace, which is granular in Foza, but conspicuously toothed in Malagasya. Foza can be distinguished from Hydrothelphusa and Marojejy, the other Malagasy genera with a bilobed mandibular palp, as follows: the space between the exorbital and epibranchial teeth in Foza is very narrow as the result of the advanced position of the epibranchial tooth (which is so far forward that it almost touches the exorbital tooth), whereas in both Hydrothelphusa and Marojejy there is a wide space between these teeth. The long slender walking legs of Foza further distinguish this genus from Hydrothelphusa whose walking legs are shorter, and not unusually elongated. The eyestalks and corneas of Foza are of normal length and size, which distinguishes this genus from Marojejy whose eyestalks taper distally and whose corneas are very reduced.

Foza is distinguished from Skelosophusa and Boreas by the form of the terminal segment of the mandibular palp (which has an enlarged anterior process about 0.5 times as large as the posterior lobe in Foza, but only a small ledge-like anterior process in Skelosophusa and Boreas). The long slender walking legs of Foza distinguish this genus externally from Boreas whose walking legs are shorter, and not unusually elongated. Foza is distinguished from Madagapotamon by the terminal segment of the mandibular palp (which has a distinct lobe-shaped anterior process in Foza, but which is simple and lacking all evidence of an anterior process in Madagapotamon) and by the length of the flagellum of the exopod of the third maxilliped (which is a shortened flagellum in Foza, but a dramatically reduced short stub in *Madaga-potamon*).

Foza raimundi, new species Figs. 1 and 2

Holotype.—FMNH 7435: adult male (cw 22.9, cl 17, ch 10.9, fw 5.7 mm), Madagasacar, Antsiranana Province, Parc National de Marojejy (= Marojezy), 13 km SE Doany, on ridge between the Andranomazava and Antsahaberaoka Rivers (14°26.2'S, 49°37.2'E), caught by hand in undisturbed montane forest on slope with slightly wet ground, collected by Achille Ruselimanana, 29 Oct 2001.

Paratypes.-FMNH 7436: adult ovigerous female (cw 25.2, cl 18.6, ch 12.4, fw 6.1 mm), Antsiranana Province, Parc National de Marojejy (= Marojezy), 13 km SE Doany, on ridge between the Andranomazava and Antsahaberaoka Rivers (14°26.2'S, 49°37.2'E), 1070 m asl, found 20 cm below surface of soil, collected by S. M. Goodman, 29 Oct 2001; FMNH 7437: adult female ovigerous (cw 22.2, cl 17.4, ch 11.5, fw 5.7 mm), Antsiranana Province, Parc National de Marojejy (= Marojezy) $(14^{\circ}26.2'S)$, 49°37.2'E), 875 m asl, pitfall trap, collected by Voahangy & Bomoina, 11 Feb 2002; FMNH 7438: adult ovigerous female (cw 22.8, cl 15.7, ch 10.2, fw 6.6 mm), Antsiranana Province, Parc National de Marojejy (= Marojezy) (14° 26.2'S, 49°37.2'E), 850 m asl, pitfall trap, collected by M. Raheriasena & S. M. Goodman, 6 Feb 2002; FMNH 7439: juvenile (cw 10.9, cl 8.9, ch 5.6, fw 2.6 mm), Antsiranana Province, Parc National de Marojejy (= Marojezy), NW (14°26.2'S, 49°37.2'E), 810 m asl, pitfall trap, collected by V. Soarimalala & D. Raheriasena, 10 Feb 2002; FMNH 7440: juvenile (cw 11.3, cl 9.3, ch 5.8, fw 2.9 mm), Antsiranana Province, Parc National de Marojejy (= Marojezy) NW (14°26.2'S, 49°37.2'E), 810 m asl, pitfall trap, collected by V. Soarimalala & D.



Fig. 1. *Foza raimundi*, from Madagascar. Male holotype (FMNH 7435), cw 22.9 mm. A, cephalothorax, frontal aspect; B, cephalothorax, dorsal aspect; C, carpus and merus of right cheliped, inferior view; D, carpus and merus of right cheliped, superior view; E, right cheliped, frontal aspect; F, left cheliped, frontal aspect; G, right pereopod 4; H, right pereopod 5; I, sternum. Scale bar = 8 mm.



Fig. 2. *Foza raimundi*, from Madagascar. Male holotype (FMNH 7435), cw 22.9 mm. A, left third maxilliped; B, right gonopod 1, dorsal aspect; C, right gonopod 1, medial aspect, turned to show longitudinal groove; D, right gonopod 1, ventral aspect; E, right gonopod 2, ventral aspect. Female adult, paratype (FMNH 7437), cw 22.2 mm. F, sternum. Scale bar = 4 mm (B–E), 8 mm (A, F).

Rahotomalala, 11 Feb 2002; FMNH 7441: juvenile (cw 13.8, cl 10.5, ch 6.6, fw 3.6 mm) Antsiranana Province, Parc National de Marojejy (= Marojezy), NW (14°26.2'S, 49°37.2'E), 810 m asl, pitfall trap, collected by V. Soarimalala & D. Rahotomalala, 11 Feb 2002.

Diagnosis.—As for the genus.

Description.—Based on holotype, an adult male. Carapace outline transversely

oval, very high (ch/fw 2.0); front narrow (fw/cw 0.25), deflexed; epibranchial tooth small, pointed, extremely advanced in position, almost touching exorbital tooth; anterolateral margin evenly curved outward, lined by small granules, continuous with posterolateral margin, latter margin crossed by carinae; postfrontal crest faint to absent, postorbital crests lacking, epigastric crests faint, positioned forward on front almost touching frontal margin; deep mid-groove between epigastric crests forked posteriorly; cardiac, urogastric grooves deep, cervical grooves deep, short. Suborbital region of carapace sidewall smooth, subhepatic region smooth except for few carinae near posterolateral margin, pterygostomial region with broad area of dense setae, vertical sulcus on carapace sidewall curved, granular, running from base of epibranchial tooth to epimeral sulcus.

Epistomial tooth triangular, deflexed, edges smooth. Exopod of third maxilliped reaching to lower half of merus, flagellum of exopod with short flagellum, ischium with faint vertical groove, curving distally toward medial margin. Sternal sulcus s1/ s2 short, very faint; sternal sulcus s2/s3 completely crossing sternum; sternal sulcus s3/s4 a v-shaped groove, deep at edges, faint in middle; anterior sterno-abdominal cavity lined with short setae. Episternal sulci s4/e4, s5/e5, s6/e6, s7/e7 absent, smooth. Male abdomen slim, triangular, tapered, widest at a3 narrowest at a7 (telson); telson outline forming straightsided triangle with broad base, rounded apex. Sternal groove s4/s5 meeting abdomen at abdominal groove between a7/a6; sternal groove s6/s7 meeting a6 one quarter of segment length from a6/a5.

Terminal article of gonopod 1 very short (ratio of length of terminal article to subterminal segment 0.2), cone-shaped, directed slightly outward, straight, bristled, apical opening wide; lateral, medial folds on ventral terminal article of gonopod 1 equal in height, width, folds basally separated forming wide space, folds meeting midway along ventral face of article to form longitudinal groove that continues to tip of article; groove not visible on dorsal face; subterminal segment of gonopod 1 with distinct raised rounded shoulder on external margin near junction with terminal article. Junction between terminal article and subterminal segment of gonopod 1 not clear on ventral side. Terminal article, subterminal segment separated on dorsal side by broad, subtriangular dorsal membrane; superior margin of dorsal membrane formed by diagonal basal margin of terminal article, inferior margin of membrane formed by diagonal slightly sshaped distal edge of subterminal segment; lateral margin of dorsal membrane broad, medial margin of membrane narrow, forming medial junction between subterminal segment and terminal article.

Subterminal segments of gonopods 1 & 2 of equal length, but terminal article of gonopod 2 much longer than terminal article of gonopod 1. Terminal article of gonopod 2 flagellum-like, same length as subterminal segment of gonopod 2, reaching anterior margin of sterno-abdominal cavity; flagellum curving inward distally, tip sharply curved inward, overall outline of flagellum forming "question mark" shape; distal parts of flagellae of both second gonopods overlapping, sometimes protruding from under closed abdominal telson.

Dactylus of both chelipeds relatively slender, approximately one-third height of palm, cutting edge lined by small even teeth; upper margin of dactylus smooth; lower margin of propodus slightly indented. Fixed finger of propodus of major (right) cheliped slender with large fused molar in proximal region followed by series of small pointed teeth. First carpal tooth on inner margin of carpus of cheliped large, pointed; second carpal tooth smaller, pointed, followed by series of very small teeth. Medial, lateral margins of inferior face of merus of cheliped distinctly toothed, inferior face with pointed, granulated distal meral tooth; superior margin and superior face of merus of cheliped roughened by granules and short carinae; granules on medial margin of merus continuous with granules on medial margin of ischium of cheliped, inferior margin of ischium rounded, smooth. Walking legs (p2–p5) elongated (ratio of merus length of p5 to cw 0.4), slender, inner margins of propodi of p2 to p5 smooth.

Variation.—Anterior sternum of female with heavy field of setae, sterno-abdominal cavity broad, shallow. Adult female abdomen broad, shield-shaped, lateral margins covering coxa of walking legs, telson (a7) outline broad-based triangle with rounded apex. Chelipeds subequal, lacking enlargement of propodus palm, lacking large molar teeth on edges of fingers seen in adult male.

Size.—The largest known specimen is the male holotype, cw 22.9 mm. Adults as judged by size at pubertal molt beginning around cw 22 mm.

Live coloration.—Carapace uniformly deep purple, chelipeds and walking legs light brown, sternum and undersides of pereopods p1–p5 pale purple-yellow.

Distribution.—Foza raimundi is known only from a single locality in the Parc National de Marojejy (formerly the Réserve Naturelle Intégrale de Marojejy), in Antsiranana Province in northern Madagascar.

Remarks.—This species is distinguished from other Malagasy species by a unique combination of gonopod and carapace features (see Remarks under genus above). The discovery that the Marojejy mountain range supports three monotypic genera of freshwater crabs (*Foza, Marojejy*, and *Skelosophusa*) plus the widespread species *H. madagascariensis* (Cumberlidge et al. 2004) makes this isolated mountain range an area of great interest in terms of its biodiversity. The

Marojejy massif is a forested mountain range with a series of peaks some of which are more than 2000 m asl, situated between the Tsaratanana mountains to the northwest and the Masoala peninsula to the southeast. The climate of Marojejy is sub-humid and warm and receives heavy rain from mid-October to April (25°C average) and lighter rain from May to October (19°C average). The river Manantenina drains the Lokoho valley from west to east and empties into the Indian Ocean, whereas the river Andranomadiobe flows south from these mountains and the river Antongodriha flows north.

Ecology.—Crabs were caught in pitfall traps set in a partially disturbed mixed dry deciduous and humid forest at altitudes between 810 and 1070 m asl. Interestingly, in one case a crab was found burrowed 20 cm below the surface of the soil. These observations imply that this species spends at least some of its time on land, and indicates a degree of independence from permanent water sources. Furthermore, the branchial chambers of F. raimundi each house two different respiratory organs (both a dorsal pseudolung and ventral gills) that is noteworthy because pseudolungs are not widespread in potamonautids (Sternberg & Cumberlidge 2001). Foza shares this adaptation of its respiratory system with a select number of terrestrial Afrotropical freshwater land crabs such as *Globonautes* macropus Rathbun, 1898 from West Africa (Cumberlidge 1991, 1999); Deckenia imitatrix Hilgendorf, 1868 from East Africa; Madagapotamon humberti Bott, 1965 from Madagascar; and Seychellum alluaudi (A. Milne-Edwards & Bouvier, 1893) from the Seychelles (Sternberg & Cumberlidge 2001). Pseudolungs are widespread in neotropical pseudothelphusids (Rodriguez 1986), and were described in detail for several semi-terrestrial species by Diaz & Rodriguez (1977). Foza shares a superficially similar morphology with

other highly terrestrial true freshwater crabs (Potamidae, Potamiscinae) from Southeast Asia such as *Thaipotamon* Ng & Naiyanetr, 1993, *Pudaengon* Ng & Naiyanetr, 1995, and *Terrapotamon* Ng & Naiyanetr, 1998, no doubt through convergence (Ng & Naiyanetr 1993, 1995, 1998). Clearly, *F. raimundi*, as an airbreathing highly terrestrial species, is worthy of comparison with land crabs (including members of the predominantly marine families Ocypodidae and Grapsidae) that are highly adapted to life out of water.

Etymology.—The new species is named for the first author's father, Raymond Paul Reed II, nicknamed "Raimundo," to thank him for his extensive love and support throughout her graduate career during which time this species was discovered.

Acknowledgments

We thank Steven M. Goodman (Department of Zoology, FMNH) for his unparalleled field collecting skills and for making the specimens available to the authors, and we thank Janet Voight and Martin Pryzdia of the FMNH for hosting visits to the museum by both authors. The National Science Foundation (Grant no. 0075614) is thanked for its support.

Literature Cited

- Bott, R. 1960. Crustacea (Decapoda): Potamonidae. Pp. 13–18 *in* B. Hansström and others, eds., South African animal life. Results of the Lund University Expedition in 1950–1952.
 - —. 1965. Die Süßwasserkrabben von Madagaskar.—Bulletin du Muséum national d'Histoire naturelle Paris 37(2):335–350.
 - —. 1970. Die Süßwasserkrabben von Europa, Asien, Australien und ihre Stammesgeschichte.—Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft Deutsch 526:1–338.
- Brünnich, M. Th. 1772. Zoologiae fundamenta praelectionibus academicis accomodata. Grunde I Dyrelaeren. Hafniae et Lipsiae

[=Copenhagen and Leipzig]: Apud Frider. Christ. Pelt., 254 pp. [not seen; as cited in Holthuis, 1991].

- Dollar, L. 2000a. *Cryptoprocta ferox. In* IUCN 2004. 2004 IUCN Red List of Threatened Species. <www.redlist.org>.
- Dollar, L. 2000b. *Fossa fossana. In* IUCN 2004. 2004 IUCN Red List of Threatened Species. <www.redlist.org>.
- Cumberlidge, N. 1991. The respiratory system of *Globonautes macropus* (Rathbun 1898), a terrestrial fresh-water crab from Liberia (Parathelphusoidea, Gecarcinucidae).—Crustaceana 61(1):69–80.
- ——. 1999. The freshwater crabs of West Africa, family Potamonautidae.—Faune et Flore Tropicales, No. 35, IRD, Paris, 382 pp.
- —, & R. v. Sternberg. 2002. A taxonomic revision of the freshwater crabs of Madagascar (Decapoda: Potamoidea: Potamonautidae).—Zoosystema 24(1):41–79.
- —, & —, 2003. The freshwater crabs of Madagascar. Pp. 612–617 in S. Goodman and J. Benstead, eds., Madagascan Natural History. University of Chicago Press.
- —, C. B. Boyko, & A. W. Harvey. 2002. 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.
- —, S. K. Reed, & C. B. Boyko. 2004. Distribution patterns of the Malagasy freshwater crabs (Crustacea: Decapoda: Brachyura).—Journal of Natural History 38: 1133–1157.
- —, D. B. Fenolio, M. E. Walvoord, & J. Stout. 2005. Tree-climbing crabs (Potamonautidae and Sesarmidae) from phytotelmic microhabitats in rainforest canopy in Madagascar.— Journal of Crustacean Biology 25(2):302–308.
- Diaz, H., & G. Rodriguez. 1977. The branchial chamber of some terrestrial and semiterrestrial crabs.—Biological Bulletin 153:485– 504.
- Hilgendorf, F. 1868. Ueber eine neue Gattung der kurzschwanzigen Krebse aus den Sammlungen des Baron von der Decken, *Deckenia imitatrix.*—Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin 1869:2.
- Holthuis, L. B. 1991. Marine lobsters of the world. An annotated and illustrated catalogue of species of interest to fisheries known to date.—FAO species catalogue, vol. 13, and FAO Fisheries Synopsis no. 125. Rome: FAO i–vii, Pp 292.
- Latreille, P. A. 1802. Histoire Naturelle générale et particulière, des Crustacés et des Insectes, III:1–467.

- Martin, J. W., & G. E. Davis. 2001. An updated classification of the recent Crustacea.—Natural History Museum of Los Angeles County Contributions in Science 39:1–124.
- Milne-Edwards, A. 1872. Note sur les crabes d'eau douce de Madagascar.—Bibliographie école Hautes études (Séction Sciences naturelles) Paris 5(8):1–3.
- , & E. Bouvier. 1893. Sur une espèce nouvelle du genre *Deckenia* (Hilgendorf) recueilli par M. Alluaud aux Seychelles, Indian Ocean.— Annales des Sciences Naturelles (Zoologie), Paris 15:325–336.
- Ng, P. K. L., & P. Naiyanetr. 1993. New and recently described freshwater crabs (Crustacea: Decapoda: Brachyura: Potamidae, Gecarcinucidae and Parathelphusidae) from Thailand.—Zoologische Verhandeingen 284: 1–117, figs. 1–68.
 - , & ——. 1995. *Pudaengon*, a new genus of terrestrial crabs (Crustacea: Decapoda: Brachyura: Potamidae) from Thailand and Laos, with descriptions of seven new species.—
 Raffles Bulletin of Zoology, Singapore 43(2):355–376.
 - —, & ——. 1997. A revision of the genus Siamthelphusa Bott, 1968 (Crustacea: Decapoda: Brachyura: Parathelphusidae), with descriptions of five new species from Thailand.—Journal of Natural History 31(12): 1751–1784.

- —, & ——. 1998. Terrapotamon palian sp. nov., a second member of the terrestrial crab genus Terrapotamon (Decapoda, Brachyura, Potamidae) from southern Thailand.—Crustaceana 71(5):487–492.
- —, & M. Takeda. 1994. Skelosophusa (Crustacea, Decapoda, Brachyura), a new genus of potamonautid freshwater crab from Madagascar, with descriptions of two new species.—Bulletin of the National Science Museum, Tokyo, series A (Zoology) 20(4):161–172.
- Ortmann, A. 1896. Das system der Decapoden-Krebse.—Zoologische Jahrbuchner (Systematics) 9:409–453.
- Rathbun, M. J. 1898. Descriptions of three new species of fresh-water crabs of the genus *Potamon.*—Proceedings of the Biological Society of Washington 12:27–30.
- Rodriguez, G. 1986. Centers of Distribution of Neotropical Freshwater Crabs. Pp. 51–67 *in*R. H. Gore, & K. L. Heck, eds., Biogeography of the Crustacea.—Crustacean Issues 3, figs. 1–13.
- Sternberg, R. v., & N. Cumberlidge. 2001. Notes on the position of the true freshwater crabs within the brachyrhynchan Eubrachyura (Crustacea: Decapoda: Brachyura).—Hydrobiologia 449(1/3):21–39.

Associate Editor: Christopher B. Boyko