Zootaxa 3780 (3): 455–480
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3780.3.2
http://zoobank.org/urn:lsid:zoobank.org:pub:AFB77705-1519-413D-96CD-25EDE68A6C73

Descriptions of three new species of *Marcusenius* Gill, 1862 (Teleostei: Mormyridae) from South Africa and Mozambique

PHOLOSHI A. MAAKE[1, 2,3], OFER GON[1]& ERNST R. SWARTZ[1]

[1]*South African Institute for Aquatic Biodiversity (SAIAB), Private Bag 1015, Grahamstown 6140, South Africa.*
[2]*Department of Ichthyology and Fisheries Science, Rhodes University, P.O. Box 94,Grahamstown 6140, South Africa*
[3]*Corresponding author. E-mail: p.maake@gmail.com*

Abstract

Morphological and genetic studies of mormyrid fishes belonging to the genus *Marcusenius* from South Africa and Mozambique revealed four species of which three are described as new. *Marcusenius pongolensis* is widespread throughout the Incomati, Pongola and Kosi river systems, and sparsely represented in the Limpopo River system in South Africa. *Marcusenius krameri* **sp. nov.** is endemic to the Limpopo River system, and is the sister taxon of *M. caudisquamatus* **sp. nov.** from the Nseleni and Mhlatuze river systems in the KwaZulu-Natal Province of South Africa. The Ruvuma specimens were well differentiated from all southern and eastern African species of *Marcusenius*, and are therefore recognised as *M. lucombesi* **sp. nov.** Phylogenetic analysis of the mitochondrial cytochrome *b* gene showed that the three new species and *M. altisambesi* form a monophyletic lineage that is sister to a group containing *M. pongolensis* and *M. macrolepidotus*. *Marcusenius krameri* and *M. lucombesi* seems to prefer slow flowing reaches of rivers, whereas *M. pongolensis* and *M. caudisquamatus* seems to mainly inhabit rapid flowing sections of rivers with a rocky substrate. A key to the southern African species of *Marcusenius* is provided.

Key words: DNA barcoding, cytochrome *b,* genetics, genetypes, identification key, *Marcusenius*, morphology, Mozambique, South Africa, species descriptions

Introduction

Mormyrids have been of widespread research interest ever since Lissmann (1951) discovered that they produce and receive weak electric signals for the purposes of mating, communication and object-location (e.g. Lissmann & Machin 1958; Bennett 1971; Kirschbaum 1975; Szabo & Fessard 1974; Hopkins 1981, 1986, 2009; Kramer & Westby 1985; Bastian 1986; Hanika & Kramer 2000; Werneyer & Kramer 2005; Carlson *et al.* 2011). The electric organs of these fishes, located in the caudal peduncle, generate an electric signal, referred to as the electric organ discharge (EOD) that is often species-specific and has been used as a taxonomic character in systematic studies of this group (Alves-Gomes & Hopkins 1997; Boden *et al.* 1997; Moritz *et al.* 2009, Kramer *et al.* 2012; Kramer 2013a; Kramer *et al.* in press).

The genus *Marcusenius* is the largest genus of the Mormyridae, currently with 37 valid species, widely distributed from the Nilo-Sudan (Boden *et al.* 1997) to South Africa (Kramer *et al.* 2007). Since the systematic revision by Taverne (1971; 1972), many new species have been described (e.g. Bigorne & Paugy 1990; Boden *et al.* 1997; Kramer *et al.* 2007). Kramer (2013b) added a new species from West Africa, while Kramer and Wink (2013) described another from the Cunene River on the border between Angola and Namibia. Kramer *et al.* (2007) discovered that there are at least five species in southern Africa rather than a single widespread species. These are *M. macrolepidotus* (Peters, 1852) from the Lower Zambezi River; *M. angolensis* (Boulenger, 1905) from Cuanza River in Angola and *M. pongolensis* (Fowler, 1934) from the Incomati, Pongola, Kosi and Mhlatuze rivers in South Africa; they also described *M. devosi* from Kenya's Tana River and *M. altisambesi* from the Upper-Zambezi and Okavango river systems.

Accepted by W. Holleman: 5 Feb. 2014; published: 24 Mar. 2014

yielded congruent results with EODs, confirming its usefulness as a systematic character (Kramer *et al.* 2007; 2012; Kramer & Swartz 2010; Kramer & Van der Bank 2011).

Sequence analysis of the mitochondrial cyt *b* gene confirmed that specimens of *M. krameri*, *M. caudisquamatus* and *M. lucombesi* were distinct from each other (0.9–3.5% divergence, see Table 2) and all three species are distinct from *M. pongolensis* and *M. macrolepidotus* (2.0–5.8% divergence) (Figure 4). The level of cyt *b* genetic divergence between all the analysed species (0.9–6.8%) are comparable with species-level differences in other mormyrids, such as *Marcusenius* species assessed by Kramer *et al*. (2007) (1.5–8.5%), *Petrocephalus* species assessed by Lavoué *et al.* (2008) (1.5–14.5%) and by Kramer *et al.* (2012) (0.8–4.2%). Based on a molecular clock by Burridge *et al.* (2008) used in other mormyrid taxa such as *Pollimyrus* Taverne, 1971 (Kramer *et al.* in press), the divergences of the new species from their most recent ancestor (*M. altisambesi* of the Upper Zambezi) possibly occurred between 3.4 to 6.0 million years ago. The basal position of *M. altisambesi* within this group is consistent with the hypothesis that the Upper Zambezi discharged to the Indian Ocean through the Limpopo valley until about 2 million years ago (Moore & Larkin 2001; Skelton 2001).The geological reviews in Moore and Larkin (2001) and Stankiewicz and de Wit (2006) show that the headwaters of the lower Zambezi captured the middle Zambezi via the Kariba Gorge, where the middle Zambezi captured the Upper Zambezi via the Batoka Gorge, creating the present course of the main Zambezi River. This could explain the isolation of the three species in South Africa, but further research is required to understand relationships among all the *Marcusenius* species.

Acknowledgements

The research was funded by the National Research Foundation of South Africa (NRF, grant no. FA200705100020). We are grateful to the Ezemvelo KZN Wildlife and Mpumalanga Tourism and Parks Agency and their staff for their assistance and logistical support. We particularly thank Andre Hoffman, Francois Roux and the late Johan Engelbrecht for discussions and assistance in the field. Richard Simelane, Geelbooi Mashilo and Mpho Ramoejane also assisted in the field. We also thank landowners in the KZN, Mpumalanga and Limpopo provinces for access to their properties. We are also grateful for the assistance and advice given by Roger Bills, Albert Chakona and Taryn Bodill from SAIAB. Bernd Kramer (Zoological Institute, University of Regensburg, Germany) assisted in the field and helped to initiate this project. Gavin Gouws assisted with analysis and reviewed the manuscript. The authors acknowledge that opinions, findings and conclusions or recommendations expressed in this publication generated by the NRF supported research are that of the authors and that the NRF accepts no liability whatsoever in this regard.

References

Abuzinadah, O.A. (1995) Gill raker morphology in some Red Sea fishes of different feeding preferences. *JKAU: Marine Science,* 6, 93–122.
http://dx.doi.org/10.4197/mar.6-1.8

Alves-Gomes, J. & Hopkins, C.D. (1997) Molecular insights into the phylogeny of mormyriform fishes and the evolution of their electric organs. *Brain, Behaviour and Evolution,* 49, 324–351.
http://dx.doi.org/10.1159/000113001

Bastian, J. (1986) Electrolocation: behavior, anatomy and physiology. *In:* Bullock, T.H. & Heiligenberg, W. (Eds.), *Electroreception.* John Wiley & Sons, New York, pp. 577–612.

Bennett, M.V.L. (1971) Electroreception. *In:* Hoar, W.S. & Randall, D.J. (Eds.), *Fish Physiology.* Academic Press, London New York, pp. 493–574.

Bigorne, R. & Paugy, D. (1990) Description de *Marcusenius meronai*, espèce nouvelle de Mormyridae (Teleostei) de Sierra Leone. *Ichthyological Exploration of Freshwaters,* 1, 33–38.

Boden, G., Teugels, G.G. & Hopkins, C.D. (1997) A systematic revision of the large-scaled *Marcusenius* with description of a new species from Cameroon (Teleostei; Osteoglossomorpha; Mormyridae). *Journal of Natural History,* 31, 1645–1682.
http://dx.doi.org/10.1080/00222939700770881

Booth, A.J. & Khumalo, N. (2010) Age, growth and reproduction of *Marcusenius pongolensis*, *Oreochromis mossambicus* and *Schilbe intermedius* in an oligotrophic impoundment in Swaziland. *African Journal of Ecology,* 48, 481–489.
http://dx.doi.org/10.1111/j.1365-2028.2009.01136.x

Boulenger, G.A. (1898) Matériaux pour la faune du Congo. Poissons nouveaux du Congo. Première Partie. Mormyres. *Annales du Musée du Congo, Zoologie, Série I,* 1, 1–20.

Boulenger, G.A. (1899) A revision of the genera and species of the fishes of the family Mormyridae. *Proceedings of the Zoological Society of London*, 1898, 775–821.
Boulenger, G.A. (1905) Descriptions of four new freshwater fishes discovered by Dr. W. J. Ansorge in Angola. *Annals and Magazine of Natural History, Ser. 7*, 15 (89), 457–459.
Burridge, C.P., Craw, D., Fletcher, D. & Waters, J.M. (2008) Geological dates and molecular rates: Fish DNA sheds light on time dependency. *Molecular Biology and Evolution*, 25, 624–633.
http://dx.doi.org/10.1093/molbev/msm271
Carlson, B.A., Hasan, S.M., Hollmann, M., Miller, D.B., Harmon, L.J. & Arnegard, M.E. (2011) Brain evolution triggers increased diversification of electric fishes. *Science,* 332, 583–583.
http://dx.doi.org/10.1126/science.1201524
Chakrabarty, P. (2010) Genetypes: a concept to help intergrate molecular phylogenetics and taxonomy. *Zootaxa,* 2632, 67–68.
Crass, R.S. (1960) Notes on the freshwater fishes of Natal with descriptions of four new species. *Annals of the Natal Museum,* 14, 405–458.
Felsenstein, J. (1981) Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution,* 17, 368–376.
http://dx.doi.org/10.1007/bf01734359
Feulner, P.G.D., Kirschbaum, F., Mamonekene, V., Ketmaier, V. & Tiedemann, R. (2006) Adaptive radiation in African weakly electric fish (Teleostei: Mormyridae: *Campylomormyrus*): a combined molecular and morphological approach. *Journal of Evolutionary Biology,* 20, 403–414.
http://dx.doi.org/10.1111/j.1420-9101.2006.01181.x
Fowler, H.W. (1934) Fishes obtained by Mr. H.W. Bell-Marley chiefly in Natal and Zululand in 1929 to 1932. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 86, 405–514.
Gilchrist, J.D.F. & Thompson, W.W. (1913) The freshwater fishes of South Africa. *Annals of the South African Museum,* XI, 321–463.
Gill, T.N. (1862). On the West African genus *Hemichromis* and descriptions of new species in the Museums of the Academy and Smithsonian Institution. *Proceedings of the Academy of Natural Sciences of Philadelphia* 14, 134–139.
Günther, A.C.L.G. (1866) *Catalogue of the fishes in the British Museum. Catalogue of the Physostomi, containing the families Salmonidae, Percopsidae, Galaxidae, Mormyridae, Gymnarchidae, Esocidae, Umbridae, Scombresocidae, Cyprinodontidae, in the collection of the British Museum,* volume 6. London, pp. 1–368.
Hammer, Ø., Harper, D. & Ryan, P.D. (2001) PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica,* 4, 9.
Hanika, S. & Kramer, B. (2000) Intra-male variability of its communication signal in the weakly electric fish, *Marcusenius macrolepidotus* (South African form), and possible functions. *Behaviour*, 142, 145–166.
http://dx.doi.org/10.1163/1568539053627677
Hebert, P.D.N., Cywinska, A., Ball, S.L. & De Waard, J.R. (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society London B,* 270, 313–321.
Hopkins, C.D. (1981) On the diversity of electric signals in a community of mormyrid electricfish in West Africa. *American Zoologist,* 21, 211–222.
Hopkins, C.D. (1986) Behaviour of Mormyridae. *In:* Bullock T.H. & Heiligenberg, W. (Eds.), *Electroreception.* John Wiley & Sons, New York. pp. 527–576.
Hopkins, C.D. (2009) Electrical perception and communication. *In*: Squire L.R. (Ed.), *Encyclopedia of Neuroscience*, volume 3. Academic Press, Oxford, pp. 813–831.
Ivanova, N.V., Zemlak, T.S., Hanner, R.H. & Hebert, P.D.N. (2007) Universal primer cocktails for fish DNA barcoding. *Molecular Ecology Notes,* 7, 544–548.
http://dx.doi.org/10.1111/j.1471-8286.2007.01748.x
Kirschbaum, F. (1975) Development of the electric organ discharge in mormyrid and gymnotid fish (*Marcusenius* sp.and *Eigenmannia virescens*). *Experientia,* 1, 1290–1292.
http://dx.doi.org/10.1007/bf01945786
Kramer, C.Y. (1956) Extension of multiple range tests to group means with unequal number of replications. *Biometrics,* 12, 307–310.
http://dx.doi.org/10.2307/3001469
Kramer, B. (2013a) A morphological study on species of African *Mormyrus* (Teleostei: Mormyridae) and their electric organ discharges. *African Journal of Aquatic Science,* 38, 1–19.
http://dx.doi.org/10.1080/10236244.2013.796161
Kramer, B. (2013b) Differentiation in morphology and electrical signalling in four species of para- and sympatric *Marcusenius* (Teleostei: Mormyridae) from Côte d'Ivoire, West Africa. *Marine and Freshwater Behaviour and Physiology,* 46, 105–133.
http://dx.doi.org/10.2989/16085914.2012.745806
Kramer, B. & Swartz, E.R. (2010) A new species of slender Stonebasher within the *Hippopotamyrus ansorgii* complex from the Cunene River in southern Africa (Teleostei: Mormyridae). *Journal of Natural History,* 44, 2213–2242.
http://dx.doi.org/10.1080/00222931003764089

Kramer, B. & Van der Bank, F.H. (2000) The southern churchill, *Petrocephalus wesselsi*, a new species of mormyrid from South Africa defined by electric organ discharges, genetics, and morphology. *Environmental Biology of Fishes,* 59, 393–413.

Kramer, B. & Van der Bank, F.H. (2011) The Victoria Falls, a species boundary for the Zambezi Parrotfish, *Cyphomyrus discorhynchus* (Peters, 1852), and the resurrection of *Cyphomyrus cubangoensis* (Pellegrin, 1936) (Mormyridae: Teleostei). *Journal of Natural History,* 45, 2669–2699.
http://dx.doi.org/10.1080/00222933.2011.597945

Kramer, B. & Westby, G.W.M. (1985) No sex difference in the wave form of the pulse type electric fish, *Gnathnemus petersii* (Mormyridae). *Experientia,* 41, 1530–1531.
http://dx.doi.org/10.1007/bf01964790

Kramer, B. & Wink, M. (2013) East-west differentiation in the *Marcusenius macrolepidotus* species complex in southern Africa: the description of a new species for the lower Cunene River, Namibia (Mormyridae, Teleostei). *Journal of Natural History,* 47, 2327–2362.
http://dx.doi.org/10.1080/00222933.2013.798699

Kramer, B., Bills, R., Skelton, P. & Wink, M. (2012) A critical revision of the Churchill snoutfish, genus *Petrocephalus*, from southern and eastern Africa, with the recognition of *P. tanensis*, and the description of five new species (Teleostei, Mormyridae). *Journal of Natural History,* 46, 2179–2258.
http://dx.doi.org/10.1080/00222933.2012.708452

Kramer, B., Skelton, P.H., Van der Bank, F.H. & Wink, M. (2007) Allopatric differentiation in the *Marcusenius macrolepidotus* species complex in southern and eastern Africa: the resurrection of *M. pongolensis* and *M. angolensis*, and the description of two new species (Mormyridae, Teleostei). *Journal of Natural History,* 41, 647–708.
http://dx.doi.org/10.1080/00222930701250987

Kramer, B., Van der Bank, H., Flint, N., Sauer-Gürth H. & Wink M. (2003) Evidence for parapatric speciation in the mormyrid fish, *Pollimyrus castelnaui* (Boulenger, 1911), from the Okavango – Upper Zambezi river systems: *P. marianne* sp. nov., defined by electricorgan discharges, morphology and genetics. *Environmental Biology of Fishes*, 77, 47–70.

Kramer, B., Van der Bank, H. & Wink, M. (2013) Marked differentiation in a new species of dwarf stonebasher, *Pollimyrus cuandoensis sp. nov. (Mormyridae: Teleostei), from a contact zone with two sibling species of the Okavango and Zambezi rivers. Journal of Natural History,* 48 (7–8), 429–463.
http://dx.doi.org/10.1080/00222933.2013.807950

Larkin, M.A., Blackshields, G., Brown, N.P., Chenna, R., McGettigan, P.A., McWilliam, H., Valentin, F., Wallace, I.M, Wilm, A., Lopez, R., Thompson, J.D., Gibson, T.J & Higgins, D.G. (2007) Clustal W and Clustal X version 2.0. *Bioinformatics,* 23, 2947–2948.
http://dx.doi.org/10.1093/bioinformatics/btm404

Lavoué, S., Arnegard, M.E., Sullivan, J.P. & Hopkins, S.D. (2008) *Petrocephalus* of Odzala offer insights into evolutionary patterns of signal diversification in the Mormyridae, a family of weakly electrogenic fishes from Africa. *Journal of Physiology-Paris,* 102, 322–339.
http://dx.doi.org/10.1016/j.jphysparis.2008.10.003

Lissmann, H.W. (1951) Continuous electric signals from the tail of a fish *Gymnarchus niloticus* Curvier. *Nature London,* 167, 201–202.
http://dx.doi.org/10.1038/167201a0

Lissmann, H.W. & Machin, K.E. (1958) The mechanism of object location in *Gymnarchus niloticus* and similar fish. *Journal of Experimental Biology,* 35, 451–486.

Machordom, A. & Doadrio, I. (2001) Evidence of a Cenozoic Betic-Kabilian connection based on freshwater fish phylogeography (*Luciobarbus*, Cyprinidae). *Molecular Phylogenetics and Evolution*, 18, 252–263.
http://dx.doi.org/10.1006/mpev.2000.0876

McGarigal, K., Cushman, S. & Stafford, S. (2000) *Multivariate statistics for wildlife and ecology research*. Springer Verlag, New York, 283 pp.

Moore, A.E. & Larkin, P.A. (2001) Drainage evolution in south-central Africa since the breakup of Gondwana. *South African Journal of Geology,* 104, 47–68.
http://dx.doi.org/10.2113/104.1.47

Moritz, T., Engelmann, J., Linsenmair, K.E., & Von der Emde, G. (2009) The electric organ discharges of the *Petrocephalus* species (Teleostei: Mormyridae) of the Upper Volta system. *Journal of Fish Biology,* 74, 54–76.
http://dx.doi.org/10.1111/j.1095-8649.2008.02111.x

Peters, W.C.H. (1852) Einige neue Säugethiere und Flussfische aus Mossambique. *Monatsberichte der Königlich-Preussischen Akademie der Wissenschaften Berlin*, 1852, 273–276.

Pezzanite, B. & Moller, P. (1998) A sexually dimorphic basal anal-fin ray expansion in the weakly discharging electric fish *Gnathonemus petersii*. *Journal of Fish Biology,* 53, 638–644.
http://dx.doi.org/10.1111/j.1095-8649.1998.tb01007.x

Posada, D. & Crandall, K.A. (1998) MODELTEST: testing the model of DNA substitution. *Bioinformatics,* 14, 817–818.
http://dx.doi.org/10.1093/bioinformatics/14.9.817

SAS Institute Inc. (2007) *JMP Statistics and Graphic Guide.* Cary, NC, USA, 1076 pp.

Sabaj Pérez, M.H. (Ed) (2013) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Version 4.0 (28 June 2013) American Society of Ichthyologists and Herpetologists, Washington, DC. Available from: http://www.asih.org/node/204 (accessed 16 September 2013)

Skelton, P.H. (2001) *A complete guide to the freshwater fishes of southern Africa*. 2nd ed. Struik Publishers, Cape Town, South Africa, pp. 92–101.

Stankiewicz, J. & de Wit, M.J. (2006) A proposed drainage evolution model for Central Africa – Did the Congo flow east? *Journal of African Earth Science*, 44 (1), 75–84.

Sullivan, J.P. & Hopkins, C.D. (2005) A new *Stomatorhinus* (Osteoglossomorpha: Mormyridae) from the Ivindo River, Gabon, West Central Africa. *Zootaxa,* 847, 1–23.

Swofford, D.L. (2002) PAUP*. *Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4*. Sinaeur Assoc Inc., Sunderland, Massachusetts.

Szabo,T. & Fessard,A. (1974) Physiology of electroreceptors. *In:* Fessard, A. (Ed.), *Handbook of Sensory Physiology*. Springer-Verlag, Berlin Heidelberg New York, pp. 59–124.

Taverne, L. (1971) Ostéologie des genres *Marcusenius* Gill, *Hippopotamyrus* Pappenheim, *Cyphomyrus* Myers, *Pollimyrus* Taverne et *Brienomyrus* Taverne (Pisces Mormyriformes). *Annales Musée Royal de l'Afrique Centrale, Sciences Zoologiques,* 188, 144.

Taverne, L. (1972) Ostéologie des genres Mormyrus Linné, *Mormyrops* Müller, *Hyperopisus* Gill, *Isichthys* Gill, *Myomyrus* Boulenger, *Stomatorhinus* Boulenger et *Gymnarchus* Cuvier. Considérations générales sur la systématique des poissons de l'ordre des Mormyriformes. *Annales Musée Royal de l'Afrique Centrale, Sciences Zoologiques,* 200, 1–194.

Tukey, J.W. (1953) *The problem of multiple comparisons*. Princeton University, N.J., 396 pp. [unpublished manuscript]

Werneyer, M. & Kramer, B. (2005) Electric signalling and reproductive behaviour in a mormyrid fish, the bulldog *Marcusenius macrolepidotus* (South African form). *Japan Ethology,* 23, 113–125. http://dx.doi.org/10.1007/s10164-004-0136-0

APPENDIX 1. Additional material of the genus *Marcusenius* occurring in eastern and southern African river systems observed for vertebral and gill raker counts.

M. angolensis (Boulenger, 1905): SAIAB 84751, 11: 83–143 mm SL, Cuanza River, above confluence with Kawa River. SAIAB 84768: 105 mm SL, same collection data as previous lot. SAIAB 84707, 3: 107–124 mm SL, Lucala River. SAIAB 84735: 120 mm SL, Kawa River.

M. altisambesi Kramer, Skelton, Van der Bank & Wink, 2007: SAIAB 79136, 7: 129.3–180.0 mm SL, Lisiliki River, Upper Zambezi system. SAIAB 98584, 21, Kalimbeza channel backwater, Upper Zambezi System.

M. devosi Kramer, Skelton, Van der Bank & Wink, 2007: SAIAB 79138 (holotype), 102.5 mm SL, Tana River. SAIAB 79139 (Paratypes), 9: 96.6–116.7 mm SL, Tana River.

M. livingstonii (Boulenger, 1899): SAIAB 35825, 6. Lifune River, Lake Chiuta System. SAIAB 50153, 7: 49.1–60.8 mm SL, Pool in stream bed above Lake Chikukutu. SAIAB 73882, 116.6mm SL, Rovuma River. SAIAB 73883, 3: 82.4–105.7 mm SL, Rovuma River. SAIAB 35797, 4, Njerwa Beach, Lake Chiuta System. SAIAB 73853, 3: 44.1–64.6 mm SL, Nandanda River, Lugenda System.

M. macrolepidotus (Peters, 1852): SAIAB 61603, 4, Lagoon behind sugar fields, Lower Zambezi system. SAIAB 67369, 25: 69.4–148.1 mm SL, Lucite River, Lower Zambezi System. SAIAB 64835, 2: 135–140 mm SL, Maputo River, Maputo System.

M. multisquamatus Kramer, 2013: SAIAB 59455, 5: 123.6–156.4 mm SL, Ruacana River, Cunene system. SAIAB 186772, 7: 80.0–124.0 mm SL, Cunene system. SAIAB 59458, 2: 113.9–137.9 mm SL, Ruacana Gorge, Cunene system. SAIAB 28065, 3, Canal at Mahanene, Cunene System. SAIAB 87287, 180 mm SL, Cunene Lagoon, Cunene System.