

Nothobranchius poppi, a new species of seasonal killifish (Cyprinodontiformes: Nothobranchiidae) from ephemeral wetlands of the lower Luapula River floodplain (upper Congo drainage: DR Congo)

Béla Nagy*, Auguste Chocha Manda**,***
and Emmanuel J. W. M. N. Vreven****,*****

Nothobranchius poppi, new species, is described from ephemeral wetlands in the upper Lubi River system, a left bank affluent of the lower Luapula River drainage (upper Congo River drainage) in the Democratic Republic of the Congo. It is identified as belonging to the *N. brieni* species group that is endemic to the upper Congo River and upper and middle Zambezi River drainages in south-central Africa. Members of this species group are characterised by a combination of colour pattern features in the male: light blue scales with broad brown-red borders creating a reticulated pattern on body; brown-red spots on proximal portion of median fins; and, caudal and anal fins with either a pattern of dark distal and light subdistal bands or, on the caudal fin an overlaying light blue iridescent distal band. *Nothobranchius poppi* is distinguished from all other members of this species group by: (i) a unique colour pattern in the male combining median fins with an irregular red-brown reticulated pattern and an overlaying light blue iridescent distal band; an anal fin lacking a subdistal band but having, rather, a narrow red-brown margin on fin-ray tips; (ii) significant differences in morphometric and meristic characters; (iii) molecular analysis of the mitochondrial COI barcoding gene, identifying a phylogenetically distinct lineage; and (iv) unique cytogenetic characteristics showing a multiple sex chromosome system with diploid number $2n = 49$ for males and $2n = 50$ for females. *Nothobranchius poppi*, like all congeners, completes its seasonal life cycle in ephemeral freshwater wetlands, making it highly vulnerable to habitat degradation. These wetlands are increasingly threatened by human activities such as agriculture, water abstraction, urban expansion, industrial pollution, and mining. Protecting the integrity of these habitats year-round is essential to preserve their unique seasonal biodiversity. The description of this new species from the lower Luapula River drainage aims to highlight the urgent need for stronger freshwater wetland conservation efforts by both national and international stakeholders.

* 15, voie de la Liberté, 77870 Vulaines sur Seine, France. E-mail: bela.nagy@neuf.fr

** Université de Lubumbashi, Unité de recherche en Biodiversité et Exploitation durable des Zones Humides, P.O. Box 1825, Lubumbashi, Democratic Republic of the Congo.

*** Royal Museum for Central Africa, Vertebrate Section, Ichthyology, Leuvensesteenweg 13, 3080 Tervuren, Belgium. E-mail: emmanuel.vreven@africamuseum.be

**** National Research Foundation - South African Institute for Aquatic Biodiversity (NRF-SAIAB), P.O. Box 94, Makhanda, South Africa

conservation/protection measures. Conservation measures should then focus on selecting and designating key sites for habitat protection, sustainable water management, pollution control, community engagement, and monitoring to ensure the long-term viability of the species and its seasonal wetland habitats.

Lack of conservation/protection of ephemeral wetlands is a general problem for species relying on seasonal conditions, such as the species of the genus *Nothobranchius*, in general. Therefore, awareness should be further raised to all humans that there is an increasing threat for these and other seasonal animals occupying these habitats. Therefore, ephemeral wetlands should be partially conserved and protected, ensuring that not all are converted to agricultural land or urbanized for anthropogenic purposes.

Comparative material. *Nothobranchius chochamandai*: RMCA 2013-022-P-0194, holotype, male, 29.7 mm SL; RMCA 2013-022-P-0195, paratype, male, 27.9 mm SL; RMCA 2014-008-P-0003-0006, paratypes, 4 males, 23.7–31.9 mm SL; and RMCA 2014-008-P-0001, paratype, male, 35.2 mm SL; DR Congo: middle Luapula drainage: Lufutishi system, Kasomeno Township.

N. cooperi: RMCA 2013-028-P-0035, holotype, male, 25.8 mm SL; and RMCA 2013-028-P-0028-0034, paratypes, 7 males, 20.9–24.6 mm SL; Zambia: middle Luapula drainage; upper Mansa River system, Mansa Township.

N. ditte: RMCA 2016-027-P-0001, holotype, male, 33.0 mm SL; and RMCA 2016-027-P-0002-0009, paratypes, 8 males, 31.1–38.9 mm SL; DR Congo: southwestern Lake Mweru basin: Katate system, Kilwa Township.

N. malaissei: RMCA 73-24-P-952, holotype, male, 36.4 mm SL; RMCA 73-24-P-914-919, paratypes, 4 males, 36.5–43.2 mm SL; and RMCA 73-24-P-947-951, paratypes, 2 males 37.0–38.7 mm SL, DR Congo: lower Luapula drainage, Luizi system: Kabiasha Village.

N. milvertzi: RMCA 2012-027-P-0001, holotype, male, 36.9 mm SL; and RMCA 2012-027-P-0002-0008, paratypes, 7 males, 30.5–36.0 mm SL; Zambia: north-eastern Lake Mweru basin, Lushiba Marsh: Chienga Village.

N. sainthousei: RMCA 2015-027-P-0001, holotype, male, 32.9 mm SL; and RMCA 2015-027-P-0002-0008, paratypes, 7 males, 24.1–40.8 mm SL; Zambia: middle Luapula drainage, Mweshi Village.

Acknowledgments

We thank Thomas Popp (DKG), Bauchet Katemo Manda (UNILU) and Emmanuel Abwe (UNILU) for sharing field data, Gábor Petneházy who joined the expedition in 2016, and Augustin Kalumba (UNILU) for assistance in the field in 2023, Zora Gabsi (MNHN) and Nalani Schnell (MNHN) for digital radiography, Thomas Litz (DKG) for providing literature and Miguël Parrent (RMCA) for managing the collected specimens deposited at the RMCA.

Literature cited

- Abell, R., M. L. Thieme, C. Revenga, M. Bryer, M. Kottelat, N. Bogutskaya, B. Coad, N. Mandrak, S. Contreras-Balderas, W. Bussing, M. L. J. Stiassny, P. Skelton, G. R. Allen, P. Unmack, A. Naseka, R. Ng, N. Sindorf, J. Robertson, E. Armijo, J. V. Higgins, T. J. Heibel, E. Wikramanayake, D. Olson, H. L. López, R. E. Reis, J. G. Lundberg, M. H. Sabaj Perez & P. Petry. 2008. Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience*, 58: 403–414.
- Ahl, E. 1926. Neue oder selten importierte Fische, III. *Blätter für Aquarien- und Terrarienkunde*, 37: 346–348.
- Baur, H. & C. Leuenberger. 2011. Analysis of ratios in multivariate morphometry. *Systematic Biology*, 60: 813–825.
- Broadley, D. G. & F. P. D. Cotterill. 2004. The reptiles of southeast Katanga, an overlooked 'hot spot'. *African Journal of Herpetology*, 53: 35–61.
- Cellerino, A., D. R. Valenzano & M. Reichard. 2016. From the bush to the bench: the annual *Nothobranchius* fishes as a new model system in biology. *Biological Reviews*, 91: 511–533.
- Cotterill, F. P. D., B. Nagy, B. R. Watters & D. U. Bellstedt. 2016. Tracking Quaternary and Neogene landscape evolution through the geocodynamics of fishes: unique proxy of tenures and mode of Africa's dambos and depocentres. *Quaternary International*, 404: 210.
- de Winter, J. C. F., D. Dodou & P. A. Wieringa. 2009. Exploratory factor analysis with small sample sizes. *Multivariate Behavioral Research*, 44: 147–181.
- Dorn, A., E. Ng'oma, K. Janko, K. Reichwald, M. Polačik, M. Platzer, A. Cellerino & M. Reichard. 2011. Phylogeny, genetic variability and colour polymorphism of an emerging animal model: the short-lived annual *Nothobranchius* fishes from southern Mozambique. *Molecular Phylogenetics and Evolution*, 61: 739–749.
- Dorn, A., A. Z. Musilova, M. Platzer, K. Reichwald & A. Cellerino. 2014. The strange case of East

- African annual fishes: aridification correlates with diversification for a savannah aquatic group? *BMC Evolutionary Biology*, 14: 210.
- Dytham, C. 2011. *Choosing and using statistics: a biologist's guide*. Third edition. Wiley-Blackwell, Chichester, 320 pp.
- Ewulonu, U. V., R. Haas & B. J. Turner. 1985. A multiple sex chromosome system in the annual killifish, *Nothobranchius guentheri*. *Copeia*, 2: 503–508.
- Flügel, T. J., F. D. Eckardt & F. P. D. Cotterill. 2015. The present day drainage patterns of the Congo river system and their Neogene evolution. Pp. 315–337 in: M. J. de Wit, F. Guillocheau & M. C. J. de Wit. (eds.), *Geology and resource potential of the Congo basin*. Springer, Berlin, 417 pp.
- Folmer, O., M. Black, W. Hoeh, R. Lutz & R. Vrijenhoek. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3: 294–299.
- Fricke, R., W. N. Eschmeyer & R. Van der Laan. 2024. Eschmeyer's catalog of fishes: genera, species, references. Available from <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>. Electronic version accessed 15 Jan 2025.
- Goudie, A. S. 2005. The drainage of Africa since the cretaceous. *Geomorphology*, 67: 437–456.
- Guillocheau, F., R. Chelalou, B. Linol, O. Dauteuil, C. Robin, F. Mvondo, Y. Callec & J.-P. Colin. 2015. Cenozoic landscape evolution in and around the Congo basin: constraints from sediments and planation surfaces. Pp. 271–313 in: M. J. de Wit, F. Guillocheau & M. C. J. de Wit. (eds.), *Geology and resource potential of the Congo basin*. Springer, Berlin, 417 pp.
- Hall, T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41: 95–98.
- Hilgendorf, F. M. 1891. Eine Aufzählung der von Emin Pascha und Dr. Stuhlmann gesammelten Fische und Krebse. *Sitzungs-Berichte der Gesellschaft Naturforschender Freunde zu Berlin*, 1: 18–20.
- Hoedeman, J. J. 1958. The frontal scalation pattern in some groups of tooth carps (Pisces, Cyprinodontiformes). *Bulletin of Aquatic Biology*, 1: 23–28.
- Hospodářská, M., P. Mora, A. C. Voleníková, A. Al-Rikabi, S. A. Simanovsky, T. Pavlica, M. Altmanová, K. Janečková, J. Štundlová, N. Tolar, M. Jankásek, M. Hříman, T. Liehr, M. Reichard, E. Y. Krysanov, P. Ráb, C. Englert, P. Nguyen, & A. Sember. 2024. Sex chromosome turnover in African annual killifishes of the genus *Nothobranchius*. *bioRxiv* (preprint)
- Hughes, R. H. & J. S. Hughes. 1992. *A directory of African wetlands*. IUCN, Gland and Cambridge & UNEP, Nairobi, 820 pp.
- IUCN. 2012. *IUCN Red List Categories and Criteria: Version 3.1. Second edition*. IUCN, Gland and Cambridge, 32 pp.
- James, F. C. & C. E. McCulloch. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? *Annual Review of Ecology and Systematics*, 21: 129–166.
- Jubb, R. A. 1971. A new *Nothobranchius* (Pisces, Cyprinodontidae) from southeastern Rhodesia. *Journal of the American Killifish Association*, 8: 12–19.
- Jubb, R. A. 1981. *Nothobranchius*. T. F. H., Neptune City, 61 pp.
- Kitano, J. & C. Peichel. 2012. Turnover of sex chromosomes and speciation in fishes. *Environmental Biology of Fishes*, 94: 549–558.
- Kitano, J., S. Ansai, Y. Takehana & Y. Yamamoto. 2024. Diversity and convergence of sex determination mechanisms in teleost fish. *Annual Review of Animal Biosciences*, 12: 233–259.
- Krysanov, E., T. Demidova & B. Nagy. 2016. Divergent karyotypes of the annual killifish genus *Nothobranchius* (Cyprinodontiformes; Nothobranchiidae). *Comparative Cytogenetics*, 10: 439–445.
- Krysanov, E. & T. Demidova. 2018. Extensive karyotype variability of African fish genus *Nothobranchius* (Cyprinodontiformes). *Comparative Cytogenetics*, 12: 387–402.
- Krysanov, E. Y., B. Nagy, B. R. Watters, A. Sember & S. A. Simanovsky. 2023. Karyotype differentiation in the *Nothobranchius ugandensis* species group (Teleostei, Cyprinodontiformes), seasonal fishes from the east African inland plateau, in the context of phylogeny and biogeography. *Comparative Cytogenetics*, 17: 13–29.
- Lavoué, S. 2012. *Petrocephalus* Marcusen 1854 (Osteoglossomorpha, Mormyridae) of the Bangweulu-Mweru ecoregion (Luapula River system, Congo basin), with the description of a new species. *Journal of Natural History*, 46: 2159–2178.
- Lévêque, C. 1997. Biodiversity dynamics and conservation, the freshwater fish of tropical Africa. University Press, Cambridge, xii + 438 pp.
- Lévêque, C., T. Oberdorff, D. Paugy, M. L. J. Stiassny & P. A. Tedesco. 2008. Global diversity of fish (Pisces) in freshwater. *Hydrobiologia*, 595: 545–567.
- Lindholm, A. & F. Breden. 2002. Sex chromosomes and sexual selection in poeciliid fishes. *The American Naturalist*, 160: 214–224.
- MacCallum, R. C., K. F. Widaman, S. Zhang & S. Hong. 1999. Sample size in factor analysis. *Psychological Methods*, 4: 84–99.
- Mayden, R. L. 1999. Consilience and a hierarchy of species concepts: advances toward closure on the species puzzle. *Journal of Nematology*, 31: 95–116.
- Mayden, R. L. 2002. On biological species, species concepts and individuation in the natural world. *Fish and Fisheries*, 3: 171–196.
- McDonald, J. H. 2008. *Handbook of biological statistics*. Sparky House, Baltimore, 287 pp.
- Minitab. 2010. [Statistical computer software]. Version 16.2.1. Minitab, Inc., State College.

- Moore, A. E. & P. A. Larkin. 2001. Drainage evolution in south-central Africa since the break-up of Gondwana. *South African Journal of Geology*, 104: 47–68.
- Moore, A. E., F. P. D. Cotterill, M. Main & H. Williams. 2007. The Zambezi River. Pp. 311–332 in: A. Gupta. (ed.), *Large rivers: geomorphology and management*. John Wiley, New York, 712 pp.
- Moore, A. E., F. P. D. Cotterill & F. D. Eckardt. 2012. The evolution and ages of Makgadikgadi palaeo-lakes: consistent evidence from Kalahari drainage evolution. *South African Journal of Geology*, 115: 385–413.
- Nagy, B. 2014a. *Nothobranchius milvertzi*, a new species of killifish from the Lushiba Marsh in the Lake Mweru drainage, Zambia (Teleostei: Cyprinodontiformes: Nothobranchiidae). *Ichthyological Exploration of Freshwaters*, 24: 347–360.
- Nagy, B. 2014b. *Nothobranchius chochamandai*, a new species of annual killifish from the Luapula drainage, Democratic Republic of Congo (Cyprinodontiformes: Nothobranchiidae). *Ichthyological Exploration of Freshwaters*, 25: 167–183.
- Nagy, B. 2014c. *Nothobranchius flagrans*, a new species of annual killifish from the Lufira drainage, Democratic Republic of Congo (Cyprinodontiformes: Nothobranchiidae). *Ichthyological Exploration of Freshwaters*, 25: 259–276.
- Nagy, B. 2015. Life history and reproduction of *Nothobranchius* fishes. *Journal of the American Killifish Association*, 47: 182–192.
- Nagy, B. 2018. *Nothobranchius ditte*, a new species of annual killifish from the Lake Mweru basin in Democratic Republic of Congo (Teleostei: Nothobranchiidae). *Ichthyological Exploration of Freshwaters*, 28: 115–134.
- Nagy, B. 2025. Review of cyprinodontiform fishes in the upper Congo drainage with descriptions of four new species of seasonal *Nothobranchius* (Nothobranchiidae) and a new species of ‘*Lacustricola*’ lampeye (Procatopodidae) in South-Eastern DR Congo. *Ecology and Diversity*, 2, 10006.
- Nagy, B., F. P. D. Cotterill & D. U. Bellstedt. 2016. *Nothobranchius sainthousei*, a new species of annual killifish from the Luapula River drainage in northern Zambia (Teleostei: Cyprinodontiformes). *Ichthyological Exploration of Freshwaters*, 27: 233–254.
- Nagy, B., B. R. Watters, P. D. W. van der Merwe, F. P. D. Cotterill & D. U. Bellstedt. 2017. *Nothobranchius cooperi* (Teleostei: Cyprinodontiformes) a new species of annual killifish from the Luapula River drainage, northern Zambia. *African Journal of Aquatic Science*, 42: 201–218.
- Nagy, B., B. R. Watters, P. D. W. van der Merwe, F. P. D. Cotterill & D. U. Bellstedt. 2020. Review of the *Nothobranchius ugandensis* species group from the inland plateau of eastern Africa with descriptions of six new species (Teleostei: Nothobranchiidae). *Ichthyological Exploration of Freshwaters*, 30: 21–73.
- Nagy, B. & B. R. Watters. 2021. A review of the conservation status of seasonal *Nothobranchius* fishes (Teleostei: Cyprinodontiformes), a genus with a high level of threat, inhabiting ephemeral wetland habitats in Africa. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 32: 199–216.
- Peters, N. 1963. Zur Embryonalentwicklung bodenleuchtender Zahnkarpfen. *Die Aquarien und Terrarien Zeitschrift*, 16: 201–204.
- Peters, W. C. H. 1868. Über eine neue Untergattung der Flederthiere so wie über neue Gattungen und Arten von Fischen. *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 1868: 145–148.
- Pinceel, T., B. Vanschoenwinkel, P. Deckers, A. Grégoir, T. Ver Eecke & L. Brendonck. 2015. Early and late developmental arrest as complementary embryonic bet-hedging strategies in African killifish. *Biological Journal of the Linnean Society*, 114: 941–948.
- Poll, M. 1938. Poissons du Katanga (bassin du Congo), récoltés par le professeur Paul Brien. *Revue de Zoologie et de Botanique Africaines*, 30: 389–423.
- Popp, T. 2015. Der Upemba Nationalpark. *Deutsche Killifisch Gemeinschaft Journal*, 47: 29–35.
- Quinn, G. P. & M. J. Keough. 2002. *Experimental design and data analysis for biologists*. University Press, Cambridge, 553 pp.
- Radda, A. C. 1969. *Fundulosoma thierryi* und ihre Verwandten (Cyprinodontiformes: Rivulinae). *Aquaria*, 16: 159–164.
- Rambaut, A. 2018. Figtree ver. 1.4.4. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh. <http://tree.bio.ed.ac.uk/software/figtree/>
- Reichard, M. 2015. The evolutionary ecology of African annual fishes. Pp. 133–158 in: N. Berois, G. García & R. O. de Sá (eds), *Annual fishes: life history strategy, diversity, and evolution*. CRC Press, Boca Raton, 327 pp.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, 43: 223–225.
- Ronquist, F. & J. P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19: 1572–1574.
- Seegers, L. 1997. Killifishes of the world: old world killifish II. *Aqualog, A.C.S., Mörfelden-Walldorf*, 112 pp.
- Shidlovskiy, K. M., B. R. Watters & R. H. Wildekamp. 2010. Notes on the annual killifish species *Nothobranchius rachovii* (Cyprinodontiformes; Nothobranchiidae) with the description of two new species. *Zootaxa*, 2724: 37–57.
- Sievers, F., A. Wilm, D. G. Dineen, T. J. Gibson, K. Karplus, W. Li, R. Lopez, H. McWilliam, M. Remmert, J. Söding, J. D. Thompson & D. G. Higgins. 2011. Fast, scalable generation of high-quality protein multiple sequence alignments using Clustal Omega. *Molecular Systems Biology*, 7: 579.
- Simanovsky, S. A., T. B. Demidova, V. E. Spangenberg, S. N. Matveevsky, K. G. Ordzhonikidze, O. L. Kolomiets & E. Y. Krysanov. 2019. Multiple sex chromosome system X1X2Y in African killifish genera *Nothobranchius* and *Fundulosoma* (Cyprinodont-

- tiformes). *Frontiers in Marine Science Conference, Abstract, XVI European Congress of Ichthyology*.
- Skelton, P. H. 1994. Diversity and distribution of freshwater fishes in east and southern Africa. *Annals of the Royal Central Africa Museum, Zoology*, 275: 95–131.
- Skelton, P. H. 2001. A complete guide to the freshwater fishes of Southern Africa. Struik Publishers, Cape Town, xiv + 395 pp.
- Snoeks, J., I. J. Harrison & M. L. J. Stiassny. 2011. The status and distribution of freshwater fishes. Pp. 43–91 in: W. R. T. Darwall, K. G. Smith, D. J. Allen, R. A. Holland, I. J. Harrison & E. G. E. Brooks. (eds.), *The diversity of life in African freshwaters: under water, under threat. An analysis of the status and distribution of freshwater species throughout mainland Africa*. IUCN, Cambridge and Gland, 347 pp.
- Sokal, R. R. & F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. Third edition. Freeman, New York, 880 pp.
- Sokal, R. R. & F. J. Rohlf. 2009. *Introduction to biostatistics*. Second edition. Dover Publications, Mineola, 382 pp.
- Stamatakis, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30: 1312–1313.
- Symoens, J. J. 1987. Region 7: Zaire basin. Pp. 401–456 in: M. J. Burgis, J. J. Symoens & P. Compère. (eds.), *African wetlands and shallow water bodies*. Office de la Recherche Scientifique et Technique Outre-Mer, Paris.
- Thieme, M. L., R. Abell, M. L. J. Stiassny, P. H. Skelton, B. Lehner, G. G. Teugels, E. Dinerstein, A. Kamdem-Toham, N. D. Burgess & D. Olson. 2005. *Freshwater ecoregions of Africa and Madagascar: a conservation assessment*. Island Press, Washington, Covelo & London, 483 pp.
- Valdesalici, S. 2010. *Nothobranchius boklundi* (Cyprinodontiformes: Nothobranchiidae): a new annual killifish with two male colour morphs from the Luangwa River basin, Zambia. *Aqua, International Journal of Ichthyology*, 16: 51–60.
- Valdesalici, S. & R. H. Wildekamp. 2004. A new species of the genus *Nothobranchius* Peters, 1868 from the Lufwa river basin, Katanga province, Democratic Republic of Congo (Pisces, Cyprinodontiformes, Aplocheilidae). *Annali del Museo Civico di Storia Naturale Giacomo Doria*, 96: 241–251.
- Valdesalici, S. & R. H. Wildekamp. 2005. A new species of the genus *Nothobranchius* (Cyprinodontiformes: Nothobranchiidae) from Luapula River basin, Zambia. *Aqua, International Journal of Ichthyology*, 9: 89–96.
- Valdesalici, S. & G. Amato. 2011. *Nothobranchius oestergaardi* (Cyprinodontiformes: Nothobranchiidae), a new annual killifish from Mweru Wantipa Lake drainage basin, northern Zambia. *Aqua, International Journal of Ichthyology*, 17: 111–119.
- Valdesalici, S., R. Bills, A. Dorn, K. Reichwald & A. Cellerino. 2012. *Nothobranchius niassa* (Cyprinodontiformes: Nothobranchiidae), a new species of annual killifish from northern Mozambique. *Ichthyological Exploration of Freshwaters*, 23: 19–28.
- van der Hoeven, J.C.M., I. M. Bruggeman, G. M. Alink & J. H. Koeman. 1982. The killifish *Nothobranchius rachowi*, a new animal in genetic toxicology. *Mutation Research/Environmental Mutagenesis and Related Subjects*, 97: 35–42.
- van der Merwe, P. D. W., F. P. D. Cotterill, M. Kandziora, B. R. Watters, B. Nagy, T. Genade, T. J. Flügel, D. S. Svendsen & D. U. Bellstedt. 2021. Genomic fingerprints of palaeogeographic history: the tempo and mode of rift tectonics across tropical Africa has shaped the diversification of the killifish genus *Nothobranchius* (Teleostei: Cyprinodontiformes). *Molecular Phylogenetics and Evolution*, 158: 106988.
- Van Steenberge, M., E. Vreven & J. Snoeks. 2014. The fishes of the Upper Luapula area (Congo basin): a fauna of mixed origin. *Ichthyological Exploration of Freshwaters*, 24: 329–345.
- Vanderplank, F. L. 1940. A study of *Nothobranchius taeniopygus* in its natural habitat. *The Aquarist*, 10: 247–249.
- Watters, B. R. 2009. The Ecology and Distribution of *Nothobranchius* Fishes. *Journal of the American Killifish Association*, 42: 37–76.
- Watters, B. R. 2015. A classification of *Nothobranchius* fish habitats. *Journal of the American Killifish Association*, 47: 152–180.
- Watters, B. R., R. H. Wildekamp & K. M. Shidlovskiy. 2015. Description and biogeography of *Nothobranchius capriiviensis*, a new species of annual killifish from the Zambezi Region of Namibia (Cyprinodontiformes: Nothobranchiidae). *Journal of the American Killifish Association*, 47: 97–133.
- Watters, B. R., B. Nagy, P. D. W. van der Merwe, F. P. D. Cotterill & D. U. Bellstedt. 2019. Review of the *Nothobranchius taeniopygus* species group from central and western Tanzania with descriptions of five new species and redescription of *Nothobranchius taeniopygus* (Teleostei: Nothobranchiidae). *Ichthyological Exploration of Freshwaters*, 29: 239–278.
- Wildekamp, R. H. 1978. Redescription of *Nothobranchius brieni* Poll, 1938 and the description of three new *Nothobranchius* species (Pisces, Cyprinodontidae) from the province of Shaba, Zaire. *Revue de Zoologie Africaine*, 92: 341–354.
- Wildekamp, R. H. 2004. A world of killies. Atlas of the oviparous cyprinodontiform fishes of the world. Volume 4. The American Killifish Association, Elyria: 398 pp.
- Wildekamp, R. H. & J. Rosenstock. 1989. Anmerkungen zu den *Nothobranchius*-Arten Sambias mit der Beschreibung von *Nothobranchius kafuensis* spec. nov. (Cyprinodontiformes; Nothobranchiinae). *Die Aquarien und Terrarien Zeitschrift*, 42: 413–419.

- Wildekamp, R. H., B. R. Watters & K. M. Shidlovskiy. 2014. Review of the *Nothobranchius neumanni* species group with descriptions of three new species from Tanzania (Cyprinodontiformes: Nothobranchiidae). *Journal of the American Killifish Association*, 47: 2-30.
- Wiley, E. O. 1978. The evolutionary species concept reconsidered. *Systematic Zoology*, 27: 17-26.
- Worthington, E. B. 1933. The fishes (other than Cichlidae) of Lake Bangweulu and adjoining regions, including descriptions of three new species. *Annals and Magazine of Natural History*, Ser. 10, 12: 34-52.
- Zar, J. H. 2010. *Biostatistical analysis*. Fifth edition. Pearson/Prentice-Hall, Upper Saddle River, xii + 944 pp.
- Zuur, A. F., E. N. Ieno & G. M. Smith. 2007. *Analysing ecological data (statistics for biology and health)*. Springer, New York, 672 pp.

Received 27 December 2024

Revised 31 March 2025

Accepted 16 January 2026

The whole contribution can be purchased as PDF file.

Availability

Generally all our publications are available as PDF files; full publications as a general rule after the printed version is out of print. If you have questions concerning particular contributions please contact us by e-mail:

pdf@pfeil-verlag.de.

The PDF files are protected by copyright.

The PDF file may be printed for personal use.

The reproduction and dissemination of the content or part of it is permitted.

It is not allowed to transfer the digital personal certificate or the password to other persons.

Prices

Books: Prices are to be found in the catalog.

Articles in journals and single contributions or chapters in books:

10 EURO basic price per order (including the first 10 pages),
and

0.50 EURO per page, beginning with the 11th page.

Page numbers are found in the contents of the publications.

Orders

Use our order form for PDF files or send your order informal per e-mail (pdf@pfeil-verlag.de). The only accepted payment is by credit card. While using the order form for PDF files, your data will be transmitted by secure link (ssl). You also may send the informations informally by e-mail, fax, phone or mail.

Handling

As soon as possible, depending on our business hours and your order, you will receive your PDF file together with the certificate and password by e-mail.

Larger PDF files can be downloaded from our webpage, if necessary.

Your invoice will be sent out by e-mail after we charged your credit card.

To open the encrypted PDF files you have to install your personal certificate after your first order. All PDF files with the same certificate can be opened from that time on.

Dieser Beitrag kann als PDF-Datei erworben werden.

Verfügbarkeit von PDF-Dateien

Prinzipiell sind von allen unseren Publikationen PDF-Dateien erhältlich. Komplette Publikationen in der Regel erst nachdem die gedruckte Version vergriffen ist. Anfragen bezüglich bestimmter Beiträge richten Sie bitte per E-Mail an pdf@pfeil-verlag.de.

Die PDF-Dateien sind urheberrechtlich geschützt.

Ein Ausdruck der PDF-Dateien ist nur für den persönlichen Gebrauch erlaubt.

Die Vervielfältigung von Ausdrucken, erneutes Digitalisieren sowie die Weitergabe von Texten und Abbildungen sind nicht gestattet.

Das persönliche Zertifikat und das Passwort dürfen nicht an Dritte weitergegeben werden.

Preise

Bücher: Die Preise sind dem Katalog zu entnehmen. Zeitschriftenbeiträge und einzelne Kapitel aus Sammelbänden bzw. Büchern:

10 EURO Grundbetrag pro Bestellung (einschließlich der ersten 10 Seiten),
und

0,50 EURO pro Seite ab der 11. Seite.

Den Umfang der Beiträge entnehmen Sie bitte den Inhaltsverzeichnissen.

Bestellungen

Bestellungen sind mit dem PDF-Bestellformular oder formlos per E-Mail (pdf@pfeil-verlag.de) an uns zu richten. Die Bezahlung ist ausschließlich per Kreditkarte möglich. Bei Verwendung unseres Bestellformulars werden die Kreditkartendaten über eine gesicherte Verbindung (ssl) übermittelt. Sie können die Daten aber auch formlos per E-Mail, Fax, Post oder telefonisch übermitteln.

Abwicklung

So bald wie möglich, aber abhängig von unseren Bürozeiten und der gewünschten Bestellung, schicken wir Ihnen die PDF-Datei(en) zusammen mit Ihrem persönlichen Zertifikat und dem zugehörigem Passwort per E-Mail. Größere Dateien bieten wir Ihnen gegebenenfalls zum Herunterladen an.

Der fällige Betrag wird von Ihrer Kreditkarte abgebucht und Sie erhalten die Rechnung ebenfalls per E-Mail.

Um die verschlüsselten PDF-Dateien öffnen zu können, muss bei der ersten Bestellung das passwortgeschützte persönliches Zertifikat installiert werden, welches anschließend auf dem Rechner verbleibt. Alle mit diesem Zertifikat verschlüsselten Dateien können anschließend auf diesem Rechner geöffnet werden.