

## Review of the *Nothobranchius ugandensis* species group from the inland plateau of eastern Africa with descriptions of six new species (Teleostei: Nothobranchiidae)

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The *Nothobranchius ugandensis* species group from the inland plateau of Kenya, Tanzania and Uganda is reviewed. Members of this group are characterized in males by the combination of characters of a light blue body coloration with red to red-brown scale margins; a frontal part of head red-brown; throat light blue or red; a uniform red or yellow caudal fin; and a light blue or yellow anal fin with red-brown spotted pattern. Six new species are identified, to raise total species richness to eleven. *Nothobranchius albertinensis*, Nagy, Watters & Bellstedt, new species, from the Albert Nile drainage in western and north-western Uganda, is characterized by a yellow dorsal fin with stripes in medial part parallel to fin rays; yellow anal fin without markings; and anal fin positioned anterior to dorsal fin. *Nothobranchius attenboroughi* Nagy, Watters & Bellstedt, new species, from the Grumeti and other lesser systems east of Lake Victoria in northern Tanzania, is characterized by a light blue anal fin with red-brown dots proximally and medially, and becoming yellow distally with narrow red-brown stripes parallel to fin rays. *Nothobranchius hoermanni* Nagy, Watters & Bellstedt, new species, from the upper Wembere drainage in central Tanzania, is characterized by a red throat; light blue anal fin with red-brown spots and stripes proximally and medially, and with a broad light blue distal zone without markings; pectoral fin hyaline with red-brown stripes parallel to fin rays; and exposed branchiostegal membrane red-brown, with cream distal margin. *Nothobranchius itigiensis* Nagy, Watters & Bellstedt, new species, from the uppermost Ruaha drainage and the Bahi Swamp area in central Tanzania, is characterized by a yellow anal fin with red-brown spots proximally, that merge medially to a pattern parallel to fin rays and are fused distally to form a marginal band. *Nothobranchius moameensis* Nagy, Watters & Bellstedt, new species, from the Moame system south of Lake Victoria in northern Tanzania, is characterized by a light blue anal fin with red-brown dots proximally and medially, and with light blue or yellow distal zone without markings. *Nothobranchius venustus* Nagy, Watters & Bellstedt, new species, from lesser systems in south-western Lake Victoria basin in north-western Tanzania, is characterized by a dorsal fin with a narrow light blue subdistal band and a narrow red-brown to black distal band; a light blue anal fin with irregular red-brown stripes perpendicular to fin rays proximally and medially, and orange with red-brown stripes parallel to fin rays in distal zone. The species group on the inland plateau in eastern Africa also includes *N. derhami*, *N. kardashevi*, *N. streltsovi*, *N. torgashevi* and *N. ugandensis*; furthermore *N. nubaensis* from southern Sudan and western Ethiopia is also included. Phylogenetic analysis of the sequences of their mitochondrial ND2 and COI, and nuclear Glyt, MyH6 and SNX33 gene sequences supports the genetic distinction of the six new species and confirms their position, together with all known members in the *N. ugandensis* species group.

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## Literature cited

- Ahl, E. 1935. Über neue oder seltene afrikanische Zahnkarpfen der Gattungen *Aphyosemion* und *Nothobranchius*. *Zoologischer Anzeiger*, 112: 123–129.
- Axelrod, H. R., W. E. Burgess, N. Pronek & J. G. Walls. 1993. Dr. Axelrod's atlas of freshwater aquarium fishes. Seventh edition. T. F. H., Neptune City, 1151 pp.
- Baker, R. J. & R. D. Bradley. 2006. Speciation in mammals and the genetic species concept. *Journal of Mammalogy*, 87: 643–662.
- Bartáková, V., M. Reichard, R. Blažek, M. Polačik & J. Bryja. 2015. Terrestrial fishes: rivers are barriers to gene flow in annual fishes from the African savanna. *Journal of Biogeography*, 42: 1832–1844.
- Beuning, K. R. M., K. Kelts, J. Russell & B. B. Wolfe. 2002. Reassessment of Lake Victoria–Upper Nile River paleohydrology from oxygen isotope records of lake sediment-cellulose. *Geology*, 30: 559–562.
- Boulenger, G. A. 1902. List of the cold-blooded vertebrates, hitherto recorded from the Uganda protectorate. Pp. 445–449, in H. Johnston (ed.), *The Uganda protectorate: an attempt to give some description of the physical geography, botany, zoology, anthropology, languages and history of the territories under British protection in East Central Africa, between the Congo Free State and the Rift Valley and between the first degree of South Latitude and the fifth degree of North Latitude*. Volume 1. Hutchinson, London.
- Bowden, E. 1995. *Nothobranchius* update 2. Killi-News, the *Journal of the British Killifish Association*, 357: 80–86.
- Castelló, J. R. 2016. *Bovids of the world: antelopes, gazelles, cattle, goats, sheep, and relatives*. Princeton Field Guides, Princeton University Press, Princeton and Oxford, 664 pp.
- Costa, W. J. E. M. 2018. Comparative morphology, phylogeny and classification of African seasonal killifishes of the tribe *Nothobranchiini* (Cyprinodontiformes: Aplocheilidae). *Zoological Journal of the Linnean Society*, 184: 115–135.
- Cotterill, F. P. D., P. J. Taylor, S. Gippoliti, J. M. Bishop & C. P. Groves. 2014. Why one century of phenetics is enough: response to 'are there really twice as many bovid species as we thought?' *Systematic Biology*, 63: 819–832.
- Darriba, D., G. L. Taboada, R. Doallo & D. Posada. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*, 9: 772.
- de Queiroz, K. 2007. Species concepts and species delimitation. *Systematic Biology*, 56: 879–886.
- de Rham, P. 1991. *Safaris poissons au Kenya*. Deuxième partie. *Aquarama*, 121: 21–30.
- Dorn A., Z. Musilová, 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, 1–13.
- Dytham C. 2011. *Choosing and using statistics: a biologist's guide*. Third edition. Wiley-Blackwell, Oxford, Chichester & Hoboken, 320 pp.
- Furness A. I., D. N. Reznick, M. S. Springer & R. W. Meredith. 2015. Convergent evolution of alternative developmental trajectories associated with diapause in African and South American killifish. *Proceedings of the Royal Society of London, Series B*, 282: 20142189.
- Greenwood, P. H. 1958. *The fishes of Uganda*. The Uganda Society, Kampala, 224 pp.
- Greenwood, P. H. 1966. *The fishes of Uganda*. Second edition. The Uganda Society, Kampala, 131 pp.
- Goudie, A. S. 2005. The drainage of Africa since the Cretaceous. *Geomorphology*, 67: 437–456.
- Groves, C. P. & P. Grubb. 2011. *Ungulate taxonomy*. John Hopkins University Press, Baltimore, 317 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.
- Hanssens, M. 2004. *Nothobranchius* sp. nov. 'Lake Victoria'. The IUCN red list of threatened species: e.T61274A12456568. IUCN, Gland, Switzerland & Cambridge, UK.
- Harrison, T. & M. L. Mbago. 1997. Introduction: paleontological and geological research in the Manonga Valley, Tanzania. Pp. 1–32 in: T. Harrison (ed.), *Neogene Paleontology of the Manonga Valley, Tanzania: a window into the evolutionary history of East Africa*. Springer, Boston.
- Hilgendorf, F. 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.
- Hilgendorf, F. 1905. *Fische von Deutsch und Englisch Ost-Afrika, gesammelt von Oscar Neumann, 1893–1895*. *Zoologische Jahrbücher Abteilung für Systematik, Geographie und Biologie der Tiere*, 22: 405–420.
- Hoedeman, J. J. 1958. The frontal scalation pattern in some groups of toothcarps (Pisces – Cyprinodontiformes). *Bulletin of Aquatic Biology*, 1: 23–28.
- Hughes, R. H. & J. S. Hughes. 1992. *A directory of African wetlands*. IUCN, Gland and Cambridge & UNEP, Nairobi, 820 pp.
- Jackson, I. J. 1971. Rainfall. Pp. 36–39 in: L. Berry (ed.), *Tanzania in maps: graphic perspectives of a developing country*. Africana Publishing Corporation, New York.
- 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.
- Johnson, T. C., C. A. Scholz, M. R. Talbot, K. Kelts, R. D. Ricketts, G. Ngobi, K. Beuning, I. Ssemmanda & J. W. McGill. 1996. Late Pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. *Science*, 273: 1091–1093.

- Jubb, R. A. 1981. *Nothobranchius*. T. F. H., Neptune City, 61 pp.
- Lambert J. W., M. Reichard & D. Pincheira-Donoso. 2019. Life fast, and diversify non-adaptively: evolutionary diversification of exceptionally short-lived annual killifishes. *BMC Evolutionary Biology*, 19: 10, 1–13.
- Langton, R. W. 1996. Wild collections of killifish, 1950–1995. Second edition. The American Killifish Association, Mishawaka, 70 pp.
- Langton, R. W. 2004. Wild collections of killifish, 1950–2003. The American Killifish Association, Mishawaka, 137 pp.
- Lévêque, C. 1997. Biodiversity dynamics and conservation: the freshwater fish of tropical Africa. University Press, Cambridge, xiii + 438 pp.
- Markofsky, J. & J. R. Matias. 1977. The effects of temperature and season collection on the onset and duration of diapause in embryos of the annual fish *Nothobranchius guentheri*. *The Journal of Experimental Zoology*, 202: 49–56.
- 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.
- Miller, M. A., W. Pfeiffer & T. Schwartz. 2010. Creating the CIPRES science gateway for inference of large phylogenetic trees. Pp. 1–8 in: Institute for Electrical and Electronics Engineers (ed.), Proceedings of the Gateway Computing Environments Workshop (GCE), 14 November 2010, New Orleans.
- Minitab. 2010. [Statistical computer software]. Version 16.2.1. Minitab, Inc., State College.
- Nagy, B. 2010. Collecting *Nothobranchius* in ‘The pearl of Africa’. *Nothobranchius Archives*, 1: 14–30.
- Nagy, B. 2014. *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. 2015. Life history and reproduction of *Nothobranchius* fishes. *Journal of the American Killifish Association*, 47: 182–192.
- Nagy, B. 2017a. Searching for a mystery *Nothobranchius* in Uganda. *Journal of the American Killifish Association*, 50: 162–174.
- Nagy, B. 2017b. Nous cherchions un mystérieux killifish en Ouganda. *L’Aquarium à la maison*, 125: 46–50.
- 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. & B. R. Watters. 2018a. Distribution and habitat conditions of *Nothobranchius* fishes in Uganda. *Journal of the American Killifish Association*, 51: 176–192.
- Nagy, B. & B. R. Watters. 2018b. Fishes that ‘fall from the sky with rain’. Pp. 59–60 in: C. A. Sayer, L. Máiz-Tomé & W. R. T. Darwall (eds.), Freshwater biodiversity in the Lake Victoria basin: guidance for species conservation, site protection, climate resilience and sustainable livelihoods. Cambridge, UK and Gland, Switzerland, IUCN, xiv+226 pp.
- 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.
- Neumann, W. 2004. Die Annuellen – eine Literaturstudie. *Deutsche Killifisch Gemeinschaft Journal*, 36: 67–79.
- Neumann, W. 2008. Prachtgrundkärpflinge – eierlegende Zahnkarpfen. *Deutsche Killifisch Gemeinschaft Journal*, Supplementheft, 9: 1–128.
- Nkwabi, A. K., J. Bukombe, H. Maliti, S. Liseki, N. Lesio & H. Kija. 2018. An overview of biodiversity in Tanzania and conservation efforts. Pp. 295–340 in: T. Pullaiah (ed.), *Global Biodiversity, Volume 3: selected countries in Africa*. CRC Press, Oakville.
- Nsubuga, F. W. N., O. J. Botai, J. M. Olwoch, C. J. deW Rautenbach, Y. Bevis & A. O. Adetunji. 2014. The nature of rainfall in the main drainage sub-basins of Uganda. *Hydrological Sciences Journal*, 59: 278–299.
- Okeyo, D. O. & W. O. Ojwang (eds.). 2015. A photographic guide to freshwater fishes of Kenya including riverine and lacustrine haplochromines. *Seriously Fish*, 354 pp. Available from [www.seriouslyfish.com/publications](http://www.seriouslyfish.com/publications). Accessed on 8 May 2019.
- Ollier, C. & C. Pain. 2000. *The origin of mountains*. Routledge, London, xxi + 378 pp.
- Østergaard, K. 1991. *Nothobranchius* in Sukumaland. *Journal of the American Killifish Association*, 24: 202–212.
- Paepke, H.-J. & L. Seegers. 1986. *Kritischer Katalog der Typen und Typoide der Fischesammlung des Zoologischen Museums Berlin. Teil 1. Atheriniformes. Mitteilungen aus dem Zoologischen Museum in Berlin*, 62: 135–186.
- Pellegrin, J. 1909. *Mission scientifique de Ch. Alluand en Afrique orientale (1908–1909). Poissons. Mémoires de la Société zoologique de France*, 22: 281–298.
- Peters, C. R., R. J. Blumenschine, R. L. Hay, D. A. Livingstone, C. W. Marean, T. Harrison, M. Armour-Chelu, P. Andrews, R. L. Bernor, R. Bonnefille & L. Werdelin. 2008. Paleoeology of the Serengeti-Mara Ecosystem. Pp. 47–94 in: A. R. E. Sinclair, C. Packer, S. A. R. Mduma & J. M. Fryxell (eds.), *Serengeti III: human impacts on ecosystem dynamics*, University of Chicago Press, Chicago and London.

- Peters, N. 1963. Zur Embryonalentwicklung bodenleicher Zahnkarpfen. Die Aquarien und Terrarien Zeitschrift, 16: 201–204.
- 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.
- 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.
- Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution, 43: 223–225.
- Roberts, T. R. 1975. Geographical distribution of African freshwater fishes. Zoological Journal of the Linnean Society, 57: 249–319.
- Rosenstock, J. 1989. Nothos I have known. Journal of the American Killifish Association, 22: 85–92.
- Rosenstock, J. 1991. A postscript to 'Nothobranchius of Sukumaland'. Journal of the American Killifish Association, 24: 209–212.
- Rosenstock, J. 1995. *Nothobranchius* from north to south. Killi-News, the Journal of the British Killifish Association, 36(2): 155–166.
- Rosenstock, J. 2011. 30 years of collecting *Nothobranchius*. *Nothobranchius* Archives, 2: 3–24.
- Roth, O. 2003. Warum *Nothobranchius*? Deutsche Killifisch Gemeinschaft Journal, 35: 58–62.
- Sainthouse, I. 1989. Some notes on the type locality of *N. robustus* and also the activities of Dr. F. L. Vanderplank in the nearby Shinyanga District circa 1940. Kill-News, the Journal of the British Killifish Association, 28(2): 7–12.
- Sainthouse, I. F. N. 1988. Interesting new *Nothobranchius*. Killi-News, the Journal of the British Killifish Association, 27(4): 11–13.
- Sayer, C. A., L. Máiz-Tomé & W. R. T. Darwall. 2018. Freshwater biodiversity in the Lake Victoria basin: guidance for species conservation, site protection, climate resilience and sustainable livelihoods. Cambridge, UK and Gland, Switzerland, IUCN, xiv + 226 pp.
- Scoon, R. N. 2018. Geology of national parks of central/southern Kenya and northern Tanzania: geotourism of the Gregory Rift Valley, active volcanism and regional plateaus. Springer, Berlin, i–xxxv + 221 pp.
- Scheel, J. J. 1990. Atlas of killifishes of the Old World. T. F. H., Neptune City, 448 pp.
- Seegers, L. 1987. From Kenya – two new killies. Today's Aquarium, 3: 7–8.
- Seegers, L. 1997. Aqualog: killifishes of the world: old world killis II. A. C. S., Mörfelden-Walldorf, 112 pp.
- Seegers L., L. De Vos & D. O. Okeyo. 2003. Annotated checklist of the freshwater fishes of Kenya (excluding the lacustrine haplochromines from Lake Victoria). Journal of East African Natural History, 92: 11–47.
- Shidlovsky, K. 2010. Collecting *Nothobranchius* in southwestern Tanzania. *Nothobranchius* Archives, 1: 18–27.
- 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.
- Stewart, K. M. 2001. The freshwater fish of Neogene Africa (Miocene-Pleistocene): systematics and biogeography. Fish and Fisheries, 2: 177–230.
- Stuhlmann, F. 1894. Mit Emin Pascha ins Herz von Afrika: ein Reisebericht mit Beiträgen von Dr. Emin Pascha, in seinem Auftrage geschildert von Franz Stuhlmann. Im amtlichen Auftrage der Kolonial-Abtheilung des Auswärtigen Amtes herausgegeben. Reimer, Berlin, 901 pp.
- Turner, A. & M. Antón. 2004. Evolving Eden: an illustrated guide to the evolution of the African large-mammal fauna. Columbia University Press, New York, 269 pp.
- Turner, B. J. 2009. The anthropologist's annuals: a personal memoir of Dr. Louis Leakey and *Nothobranchius*. Journal of the American Killifish Association, 42: 77–93.
- Valdesalici, S. 2012. *Nothobranchius kardashevi* and *Nothobranchius ivanovae* (Cyprinodontiformes: Nothobranchiidae): two new annual killifishes from the Katuma River drainage, western Tanzania. Aqua, International Journal of Ichthyology, 18: 191–198.
- Valdesalici, S. 2013. Travel to Kenya 2012. Journal of the American Killifish Association, 46: 19–32.
- Valdesalici, S. 2015. *Nothobranchius torgashevi* (Cyprinodontiformes: Nothobranchiidae), a new species of annual killifish with two male colour morphs from the Lake Eyasi basin, central Tanzania. Killi-Data Series, 2015: 17–30.
- 2016. *Nothobranchius streltsovi*, a new species of annual killifish with two male colour morphs from the Malagarasi drainage, central Tanzania (Teleostei: Cyprinodontiformes: Nothobranchiidae). Ichthyological Exploration of Freshwaters, 27: 153–161.
- Valdesalici, S. & G. Amato. 2019. *Nothobranchius derhami* (Cyprinodontiformes: Nothobranchiidae), a new species of seasonal killifish from western Kenya. Aqua, International Journal of Ichthyology, 25: 111–124.
- Valdesalici, S. & K. Kardashev. 2011. *Nothobranchius seegersi* (Cyprinodontiformes: Nothobranchiidae), a new annual killifish from the Malagarasi River drainage, Tanzania. Bonn Zoological Bulletin, 60: 89–93.
- Valdesalici, S., M. Bellemans, K. Kardashev & A. Golubtsov. 2009. *Nothobranchius nubaensis* (Cyprinodontiformes: Nothobranchiidae) a new annual killifish from Sudan and Ethiopia. Aqua, International Journal of Ichthyology, 15: 143–152.

- Van Damme, D. & M. Pickford. 2003. The late Cenozoic Thiaridae (Mollusca, Gastropoda, Cerithioidea) of the Albertine Rift valley (Uganda-Congo) and their bearing on the origin and evolution of the Tanganyikan thalassoid malacofauna. *Hydrobiologia*, 498: 1–83.
- Walch, R. 1995. Ein Juwel unter den *Nothobranchius*: *Nothobranchius* spec. 'Odinya K 86/9'. Deutsche Killifisch Gemeinschaft Journal, 27: 93–95.
- Watters, B. R. 1991. *Nothobranchius* species/populations in the hobby – past and present. *Journal of the American Killifish Association*, 24: 245–248.
- Watters, B. R. 2009. The ecology and distribution of *Nothobranchius* fishes. *Journal of the American Killifish Association*, 42: 37–76.
- Watters, B. R. 2014. 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 capriviensis*, a new species of annual killifish from the Zambezi Region of Namibia (Cyprinodontiformes: Nothobranchiidae). *Journal of the American Killifish Association*, 47 (2014 [2015]): 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*, IEF-1110: 1–41.
- Wildekamp, R. H. 1978. Redescription of *Nothobranchius brieri* 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. 1980. Investigations into the identity of *Nothobranchius taeniopygus* Hilgendorf, 1891, with reclassification of the subgenus *Zononothobranchius* Radda, 1969. *Journal of the American Killifish Association*, 13: 32–36.
- Wildekamp, R. H. 1989. Fisch-Safari in Uganda. *Die Aquarien und Terrarien Zeitschrift*, 42: 358–362.
- Wildekamp, R. H. 1990. Redescription of two lesser known *Nothobranchius* from central Tanzania, *N. taeniopygus* and *N. neumanni* (Cyprinodontiformes: Aplocheilidae). *Ichthyological Explorations of Freshwaters*, 1: 193–206.
- Wildekamp, R. H. 1994. The *Nothobranchius* species from Uganda, with description of a new polymorphic species (Cyprinodontiformes: Aplocheilidae). *Ichthyological Explorations of Freshwaters*, 5: 193–206.
- Wildekamp, R. H. 2004. A world of killies: atlas of the oviparous cyprinodontiform fishes of the world. Volume IV: the genera *Garmanella*, *Gnatholebias*, *Hubbsichthys*, *Hylopanchax*, *Hypospanchax*, *Jordanella*, *Laciris*, *Lamprichthys*, *Leptolebias*, *Leptolucania*, *Lucania*, *Maratecoara*, *Megalebias*, *Megupsilon*, *Micromoema*, *Millerichthys*, *Moema*, *Neofundulus*, *Nothobranchius*, *Orestias*, *Oxyzygonectes*, *Pachypanchax*, *Pantanodon*, *Papiliolebias*, *Pituna*, *Plataplochilus*, *Platypanchax*, and *Plesiolebias*. The American Killifish Association, Elyria, 398 pp.
- 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.
- Williams, M. A. & M. R. Talbot. 2009. Late Quaternary environments in the Nile basin. Pp. 61–72 in: H. J. Dumont (ed.), *The Nile: origin, environments, limnology, and human use*. Monographiae Biologicae, Volume 89. Springer, Dordrecht.
- Wilson, E. O. 1984. *Biophilia: the human bond with other species*. Harvard University Press, Cambridge, 160 pp.
- Wourms, J. B. 1965. Comparative observations on the early embryology of *Nothobranchius taeniopygus* (Hilgendorf) and *Aplocheilichthys pumilus* (Boulenger), with special reference on the problem of naturally occurring embryonic diapauses in Teleost fishes. *East African Freshwater Fisheries Research Organisation, Annual Report*, 1964: 68–73.
- 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, xxvi + 672 pp.

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