The synonymy of *Haplochromis pharyngalis* and *Haplochromis petronius* (Cichlidae)

Nathan Vranken[1,2], Maarten Van Steenberge[2,3,4], Akonkwa Balagizi[5] & Jos Snoeks[1,2]

[1]Royal Museum for Central Africa, Biology department, Section Vertebrates, Leuvensesteenweg 13, 3080 Tervuren, Belgium
[2]KU Leuven, Laboratory of Biodiversity and Evolutionary Genomics, Department of Biology, Charles Deberiotstraat 32, 3000 Leuven, Belgium
[3]Royal Belgian Institute of Natural Sciences, Operational Directorate Taxonomy and Phylogeny, Vautierstraat 29, 1000 Brussels, Belgium
[4]Masaryk University, Department of Botany and Zoology, Kotlářská 2, 611 37 Brno, Czech Republic
[5]Université Officielle de Bukavu, Département de Biologie, Bukavu, Democratic Republic of the Congo

Correspondence

Nathan Vranken; email: nathan.vranken@africamuseum.be; tel.: +32 27695632

Funding

This research was conducted within the framework of the BELSPO (Belgian Science Policy) funded BRAIN project “HIPE”: Human impacts on ecosystem health and resources of Lake Edward. The fieldwork of MVS was supported by the FWO (Research Foundation – Flanders, V435116N) and the King Leopold III Fund for Nature Exploration and Conservation.

Abstract (max 90 words)

Haplochromis pharyngalis and *H. petronius*, two endemic cichlids from the Lake Edward system (Uganda, DR Congo), are very similar in general morphology, but have been reported to differ in pharyngeal jaw morphology and distribution. We analysed 51 morphometrics and various qualitative characteristics of 48 specimens from different localities. The morphological traits of both species strongly overlap and differences in the pharyngeal jaw morphology correspond to a geographic morphocline. We conclude that all specimens belong to one valid species, *H. pharyngalis*, and consider *H. petronius* to be a synonym.

Keywords

East African Great Lakes, geographical variation, haplochromines, polymorphism, taxonomy, *Thoracochromis*

The Lake Edward system, consisting of the basins of Lakes Edward and George, is inhabited by an estimated 60–100 endemic species of *Haplochromis* Hilgendorf, 1888 (Greenwood, 1973, Vranken *et al.*, 2019a). Two of these, *H. pharyngalis* Poll & Damas, 1939 and *H. petronius* Greenwood, 1973, have a unique phylogenetic position within the assemblage. They belong to one of the two ancestral lineages that, through introgressive hybridisation, may have been at the origin of the Lake Victoria region superflock (LVRS) (Seehausen *et al.*, 2003; Meier *et al.*, 2017). This lineage is the Nilotic lineage *sensu* Meier et al. (2017), the other has been referred to as the Congolese lineage and included *H. stappersii* Poll, 1943 from Lake Tanganyika. The LVRS is a monophyletic flock of ~700 species that evolved rapidly within the last 100–200 ka, hereby representing one of the most impressive adaptive radiations in vertebrates and a well-established model system in evolutionary biology (Verheyen *et al.*, 2003; Meier *et al.*, 2017; Salzburger, 2018). All species of *Haplochromis* from the Lake Edward system, except for *H. pharyngalis* and *H. petronius*, belong to the LVRS (Seehausen *et al.*, 2003) and display an impressive diversity in morphology, especially in trophic morphology (Greenwood, 1980). While *H. pharyngalis* and *H. petronius* have a trophic morphology similar to many species of the LVRS, they differ by their very small and embedded chest scales that merge abruptly into the large flank scales, i.e., a ‘*Thoracochromis’* Greenwood, 1979 squamation (sensu Greenwood, 1979). This scale pattern, however, is, within the Lake Edward system, not unique to these two species, as we observed a similar pattern in the algivorous *H. fuscus* Regan, 1925. This species remained unstudied in recent phylogenetic studies but ranged by Greenwood (1980) in his genus ‘*Neochromis*’ Regan, 1920, which differs from *‘Thoracochromis’* by a very strongly convex *v*. concave to convex head and a short and deep *v.* relatively long and more shallow lower jaw set with 3–8 *v*. 2–3 rows of inner teeth.

Greenwood (1973) reported that *H. pharyngalis* differed slightly from *H. petronius* by smaller chest scales, a scaleless *v.* scaled ventral margin of the cheek, fewer ceratobranchial gill rakers (6 *v.* 7–8), and a more strongly developed pharyngeal apparatus that was set with molariform *v.* stout teeth. These morphological differences were small and have been reported to vary highly in other haplochromine species (Snoeks, 1994; Smits *et al.*, 1996). Previously, these species were said to be restricted to Lake Edward for *H. pharyngalis* and Lake George for *H. petronius* (Greenwood, 1973), while later studies reported both species from the Kazinga Channel that connects these lakes (Seehausen *et al.*, 2003; Meier *et al.*, 2017). Hitherto, the taxonomic status, morphological variation, and distribution of *H. pharyngalis* and *H. petronius* remained ambiguous, especially given the recent desiccation (4–5 ka ago) of Lake George and the Kazinga Channel (Lærdal *et al.*, 2002). Therefore, we investigated 48 specimens with a '*Thoracochromis'* morphology from various locations within the Lake Edward system (Figure 1a). These were grouped a priori by catch localities, i.e., Lake Edward (LE), the mouth of the Kazinga Channel (MK), the Kazinga Channel (K), and Lake George (LG). To explore the morphological variation among specimens, 27 measurements and 24 counts were taken following Vranken *et al.* (2019a) (Table S1) and the following qualitative characteristics were observed and described following Barel *et al.* (1976, 1977):. lateral neurocranial outline, dorsal head profile, lateral snout outline, maxillary posterior extension, caudal fin outline, dentition of the oral and pharyngeal jaws, and colour pattern in vivo (from pictures) and in alcohol. In doing so, we combined the morphological species concept (morphometric traits) and the specific mate recognition concept (dominant male colour patterns), which proved to be a strong approach in *Haplochromis* taxonomy (Witte & Witte-Maas, 1987; Snoeks, 1994).

The morphological variation among specimens was investigated by principal component analyses (PCA) of the variation-covariation matrix of 25 log-transformed measurements, excluding pectoral and pelvic fin lengths (Table S2), and of the correlation matrix of 22 raw counts, excluding the invariable counts (anal fin spines and caudal peduncle scales) (Table S3). Principal component (PC) 1 (93.7% of variance) of the former analysis had positive values of a similar magnitude for all variables and, therefore, was interpreted as a proxy for size (Vranken *et al.*, 2019a,b,c; Zelditch *et al.*, 2004). The second PC

(2.0%) was mainly determined by the length of the dentigerous area of the lower pharyngeal jaw. In the analysis of the counts, PC 1 (14.0%) was determined by the numbers of pectoral-pelvic scales and infraorbital cheek scales (Figure 1b). These characters were mentioned by Greenwood (1973) to differentiate *H. pharyngalis* from *H. petronius*. We plotted PC 2 (measurements) against PC 1 (counts) (Figure 1b). On both axes, specimens from LE clustered mainly in the negative parts, while those from LG (and K) clustered mainly in the positive parts. Specimens from MK scored around zero on both axes and overlapped with all other groups. Hereby, the overall morphological variation corresponded to a continuous morphocline by catch locality. Axes of both PCAs were also plotted against SL to evaluate potential size inferences, but additional patterns were absent (not shown). To reveal possible diagnostic differences between the groups, all variables were compared by Mann-Whitney *U* (MW*U*) tests with sequential Bonferroni correction for each inter-group comparison (Table S4). All tests were performed on subsamples of specimens of similar-size classes (MW*U*(SL): $P > 0.5$). No significant differences ($P < 0.05$) were found, except for the shorter pelvic fins of specimens of both sexes from LE in comparison to those from LG [24.3–27.6 (26.1) *v.* 28.0–34.4 (30.8) % SL]. The colour of the pelvic fins of dominant males, black with a white-blue first ray, was more distinct in specimens from LG (and K) than in specimens from LE. Possibly, the pelvic fins play a role in social interaction and are more conspicuous in specimens from LG to compensate for the lower visibility in LG than in LE (Beadle, 1932).

Specimens from LE differed mostly from those from LG by a more strongly developed lower pharyngeal bone, set with sub-molariform to molariform *v.* stout to sub-molariform teeth (Figure 1c). In *Haplochromis*, a strongly developed pharyngeal bone is often linked to a molluscivorous diet (Witte & Van Oijen, 1990). Greenwood (1973) observed that specimens from LG were insectivorous, while the gut of a single specimen from LE was dissected and contained mostly snail and insect remains. Furthermore, on RX-images of all specimens, mollusc remains were observed in the guts of specimens from LE, but not in those from LG, K, and MK. The differences in trophic morphology were more pronounced in large specimens (> 80 mm SL) as the shape of the lower pharyngeal bone changed with size (SL) in specimens from LE. The dentigerous area increased in length [r=0.704 (p=0.011)] and decreased in width [r=-0.600 (p=0.039)] in comparison to the length and width of the bone, respectively. These patterns were absent in specimens from other localities. The differences in pharyngeal apparatus development in specimens from LE compared to those from LG could be explained by the higher abundance of molluscs and the larger size of some snail species in LE (Mandahl-Barth, 1954). The absence of oral mollusc-shelling species of *Haplochromis* in LG provides a further indication that the mollusc faunas of both lakes differ (Vranken *et al.*, 2019c).

Besides the differences in pelvic fin length and pharyngeal apparatus morphology, specimens from all localities were indistinguishable from each other in overall morphology, oral dentition, and dominant male colour pattern (Figure 1d). Some of the diagnostic differences on which Greenwood (1973) distinguished *H. pharyngalis* from *H. petronius* were observed to display weak geographical trends between LE (n=12) and LG (n=13), i.e., fewer ceratobranchial gill rakers (6–8 *v.* 7–9), more infraorbital cheek scales (4–5 *v.* 3–5), and more pectoral-pelvic scales (8–11 *v.* 7–9). Differences in the size of chest and nape scales and squamation pattern of the cheek were, however, absent. All morphological traits overlapped strongly to completely and had intermediate values in specimens from MK and K, hereby representing continuous morphoclines (Table S1). We conclude that all specimens belong to one biological species that includes all type specimens of *H. pharyngalis* and *H. petronius.* Given that the name *H. pharyngalis* has priority, *H. petronius* is placed into synonymy. Below, a redescription of *H. pharyngalis* is presented and a lectotype is designated.

Haplochromis pharyngalis **Poll & Damas, 1939**

(Figures 1, S1, S2; Tables 1, S1)

Haplochromis petronius Greenwood, 1973; *Thoracochromis pharyngalis* (Poll & Damas, 1939) and *Thoracochromis petronius* (Greenwood, 1973): Greenwood, 1979.

Lectotype: MRAC 65724; Lake Edward, Bugazia: 0°23'40.8"S 29°23'02.0"E; 16/05/1935 [80.7 mm SL].

Paralectotypes: MRAC 65725–65726 (n=2); same data as lectotype [76.5, 86.7 mm SL].

Other material examined:

BMNH 1972.6.2.1 (n=1, holotype of *H. petronius*) & 2–10 (n=3 of 9, paratypes of *H. petronius*); Lake George, Kashaka Bay: 0°04'58.0"S 30°10'33.6"E; 23/01/1968 [70.7–83.8 mm SL]. MRAC 2016.035.P.0184–185 (n=2); Mukutu Kihinga, rocky offshore of Mweya, Lake Edward: 0°11'31.2"S 29°52'26.4"E; 24/10/2016 [71.1, 93.2 mm SL]. MRAC 2016.035.P.0186 (n=1); Mouth of Kazinga Channel, Lake Edward 0°12'32.4"S 29°53'06.0"E Exp. HIPE1 Uganda 24/10/2016 [88.7 mm SL]. MRAC 2016.035.P.0187 (n=1) & 188–195 (n=7 of 8); Kazinga Channel, near Queen Elisabeth Bush Lodge: 0°08'09.6"S 30°02'27.6"E; 27/10/2016 [87.5–102.4 mm SL]. MRAC 2016.035.P.0196–197 (n=2); Kazinga Channel, near Queen Elisabeth Bush Lodge: 0°08'09.6"S 30°02'27.6"E; 4/11/2016 [68.6, 90.4 mm SL]. MRAC 2017.006.P.0245–253 (n=3 of 9) & 254–293 (n=4 of 40); Mouth of Kazinga Channel, hard substrate, Lake Edward: 0°12'14.4"S 29°52'37.2"E; 23/03/2017 [72.9–80.7 mm SL]. MRAC 2017.006.P.0313–321 (n=4 of 9); Rwenshama, rocky shore, Lake Edward: 0°24'05.7"S 29°46'35.1"E; 26/03/2017 [77.9–96.8 mm SL]. MRAC 2018.008.P.0319–320 (n=1 of 2); Kashaka bay, west rocky shore, Lake George: 0°05'02.0"S 30°07'38.4"E; 28/01/2018 [97.2 mm SL]. MRAC 2018.008.P.0324–327 (n=3 of 4); Kashaka bay, north of inlet, Lake George: 0°04'52.2"S 30°10'47.3"E; 2/02/2018 [74.9–78.5 mm SL]. RBINS 25610–25616 (n=4 of 7); Mouth of Kazinga Channel, Lake Edward: 0°12'32.4"S 29°53'06.0"E; 24/10/2016 [73.5–88.7 mm SL]. RBINS 25617–25646 (n=5 of 30); Kashaka bay, south of inlet, Lake George: 0°05'04.6"S 30°10'45.6"E; 2/02/2018 [60.5–66.9 mm SL]. RBINS 25647–25662 (n=1 of 16); Kayanja offshore, Lake Edward: 0°05'34.8"S 29°45'28.8"E; 31/03/2017 [85.1 mm SL].

Description: Body generalised sensu Barel *et al.* (1976), dorsal and anal fin bases long. Dorsal head profile weakly convex in small specimens (< 70 mm SL), anterior part concave and posterior part convex with skin somewhat thickened in large specimens (> 70 mm SL). Snout generalised in length, blunt, and with an inclination of 40–45°. Eyes small; interorbital region narrow; cheeks deep. Jaws isognathous and rounded; gape large and with a gentle inclination of 25–35°. Lower jaw short and upper jaw generalised. Maxilla reaches level between anteriormost points of orbit and pupil. Lips large sensu Vranken *et al.* (2019b). Neurocranium generalised with deep and wedge-shaped supraoccipital crest (Figure S1b). Chest scales very small, round, and embedded in skin; transition to flank scales abrupt between pectoral and pelvic fin bases. Scaleless anteroventral and ventral parts of cheek; scaleless area of 3–4 scale lengths just anterior of first dorsal fin spine.

Outer oral teeth stout and weakly embedded in oral mucosa. Necks straight and cylindrical; crowns recurved and weakly flattened laterally. Outer teeth of small specimens (<75 mm SL) bicuspid; major cusps bluntly pointed to rounded, equilateral, and with very small flanges (i.e., flattened protrusion laterally implanted on cusp); minor cusps large and straight up; cusp gaps broad. In large specimens (>

80 mm SL), a mixture of bi- and unicuspid outer teeth; major cusps very bluntly pointed, equilateral, and without flanges; minor cusps small and slightly horizontally inclined; cusp gaps narrow. In all specimens, dental arcades rounded and long. Outer teeth regularly and closely set with ½ tooth width between adjacent teeth. In both jaws, posterior outer teeth mostly unicuspid; in upper jaw, 2–3 posteriormost outer teeth enlarged; in lower jaw, anterior outer teeth implanted slightly procumbent at 20–30°. Tooth bands slender with 2–3 rows of inner teeth that are set on 1–2 outer tooth widths from outer row and that diminish laterad until only outer row remains posteriorly. In small specimens (< 75 mm SL), inner teeth stout, bluntly pointed, and strongly tricuspid; in large specimens (> 75 mm SL), inner teeth weakly tri- to unicuspid. Anterior inner and outer teeth often somewhat abraded.

Lower pharyngeal bone equally deep over entire length and highly variable in form: from greatly enlarged, deep, and set with molariform teeth in four median rows, to stout, relatively shallow, and set with stout teeth in two median rows (Figures 1c & S1c). Lateral teeth slender and bevelled with major cusps bluntly pointed, cusp gaps concave and wide, and minor cusps stout and small to reduced. Posteriormost teeth from molariform to stout with major cusps bluntly pointed, minor cusps reduced, and cusp gaps wide. Median row with 7–10 teeth; posterior transverse row with 20–28 teeth.

Ceratobranchial gill rakers of outer row of first gill arch, unifid, short, blunt, and with posteriormost rakers rarely anvil-shaped. Anteriormost part of ceratobranchial mostly covered by papillose tissue and papillae present on inner margins of anterior gill rakers. Epibranchial gill rakers slender.

Caudal fin rounded to weakly emarginate. Dorsal and anal fins reach to level between caudal fin base and ¼ caudal fin length in females, between caudal fin base and 1/2 caudal fin length in dominant males. Pectoral fins extend to level between two scale lengths anterior and one scale length posterior to anal opening; pelvic fins to level between anal opening and first anal fin spine in females, just before anal fin to first soft anal fin ray in dominant males; first ray of pelvic fin slightly produced in males.

Colouration in live: Dominant males: flanks green-yellow with blue sheen and 5–8 dark, slender, and faint vertical stripes; dorsal part of head and anterior part of dorsum crimson with rose-purple sheen, gently fading posteriad; belly, chest, branchiostegal rays black (Figures 1d & S2a). Operculum green-yellow; cheeks white-grey with blue sheen; snout, lacrimal, lips, and lower jaw turquoise to blue. Head with broad lacrimal stripes and faint nostril, interorbital, and supraorbital stripes. Pectoral fins hyaline;

pelvic fins black with blueish-white leading edge. Dorsal fin dusky with crimson sheen, yellow base, crimson lappets; anal fin dusky with dark spines, crimson distal part and 2–8 small egg spots (size equal to distance between rays); caudal fin hyaline to dusky and with yellow base and crimson distal part. Posterior part of dorsal fin and whole caudal fin strongly maculated. Sub-dominant males: similar to dominant males, except for white chest and belly, yellow flanks, and hyaline base of anal fin. Females and juveniles: Dorsum greyish; flank, cheek and operculum beige with yellow sheen, and belly and chest white (Figure S2a). Snout and lacrimal dusky with blueish sheen and faint lacrimal stripes. Pectoral and caudal fins hyaline, all other fins white. Dorsal and anal fins with black lappets, anal fin with 3–5 small spots resembling egg spots; posterior part of dorsal fin and caudal fin with faint maculations.

Colouration in preserved specimens: Body brown; flanks with 5–8 slender and faint vertical stirpes; chest and cheeks light brown; head with faint nostril and interorbital stripes and broad lachrymal stripes (Figure S1a). In dominant males, snout, and horizontal arm of preoperculum dark. In all specimens, pectoral fins hyaline and caudal fin hyaline to dusky and strongly maculated. In females, pelvic, dorsal, and anal fins dusky. In dominant males, pelvic fins black and with first ray blue, dorsal and anal fins dark and with hyaline posterodistal part and black lappets between spines, anal fin with 2–8 small egg spots with hyaline borders.

Distribution and ecology: Endemic to Lakes Edward and George; in Lake George, rare outside of Kashaka Bay. Occurs in littoral zones over hard substrates. Specimens from Lake George insectivorous (Greenwood, 1973), those from Lake Edward both insectivorous (Chironomidae and Ephemeroptera) and molluscivorous.

Differential diagnosis: *Haplochromis pharyngalis* differs from all species from the Lake Edward system, except *H. fuscus*, by a rounded caudal fin; very small, round, and deeply embedded chest scales (7–11 pectoral-pelvic scales); small nape scales, and dominant males with white-blue first ray of pelvic fins. Differs from *H. fuscus* (n=3) by an acute *v.* blunt snout with a more shallow inclination (40–45 *v.* 45–60°), rounded *v.* nearly squared dental arcades, and fewer rows of inner oral teeth [2–3 (rarely 4) *v.* 4–5]. Shares with *H. elegans* Trewavas, 1933 (n=25) and *H. aeneocolor* Greenwood, 1973 (n=9) a generalised *Haplochromis* morphology. Differs from both by 3–5 *v.* 2–3 infraorbital cheek scales, deeper cheeks [24.0–31.2 (28.2) *v.* 19.2–23.8 (21.4) and 20.1–24.4 (22.3) % HL], slightly smaller eyes [26.9–33.1 (29.7) *v.* 29.9–36.2 (34.4) and 29.7–35.0 (32.5) % HL], and dominant males with green-yellow *v.* blue and yellow flanks, respectively (Kayenbergh, unpublished results). Some specimens from Lake Edward share with *H. mylodon* Greenwood, 1973, *H. concilians* Vranken *et al.*, 2019c, *H. placodus* Poll & Damas, 1939, and *H. malacophagus* Poll & Damas, 1939 an enlarged pharyngeal apparatus set with molariform teeth. Differs from all by recurved *v.* straight outer oral teeth and from *H. mylodon* and *H. concilians* by the colour pattern of dominant males with green-yellow *v.* blue flanks and faint *v.* well-defined nostril and interorbital stripes; the latter is also diagnostic in preserved specimens.

Acknowledgements

We thank E. Decru (RMCA), M. Mulongaibalu (Université Officielle de Bukavu, DRC), and L. Wasswa (Ugandan Fisheries Department) for their help in collecting specimens. We are grateful to M. Parrent (RMCA) and O. Pauwels (RBINS) for curatorial services. Pictures of the lectotype and the lower pharyngeal bones were taken using the digitisation facility of the RMCA in the framework of the BELSPO-funded DIGIT04 project.

References

Barel, C. D. N., Witte, F. & Van Oijen, M. J. P. (1976) The shape of the skeletal elements in the head of a generalized *Haplochromis* species: *H. elegans* Trewavas 1933 (Pisces, Cichlidae). *Netherlands Journal of Zoology* **26**, 163–265.

Barel, C. D. N., Van Oijen, M. J. P., Witte, F. & Witte-Maas, E. L. M. (1977) An introduction to the taxonomy and morphology of the haplochromine cichlidae from Lake Victoria. *Netherlands Journal of Zoology* **27**, 333–380.

Beadle, L. C. (1932) Scientific results of the Cambridge expedition to the East African lakes, 1930-1. The waters of some East African lakes in relation to their fauna and flora. *Journal of the Linnean Society of London, Zoology* **38**, 157–211.

Greenwood, P. H. (1973) A revision of the *Haplochromis* and related species (Pisces: Cichlidae) from Lake George, Uganda. *Bulletin of the British Museum (Natural History) Zoology* **25**, 139–242.

Greenwood, P. H. (1979) Towards a phyletic classification of the ‘genus’ *Haplochromis* (Pisces, Cichlidae) and related taxa, part I. *Bulletin of the British Museum (Natural History) Zoology* **35**, 265–322.

Greenwood, P. H. (1980) Towards a phyletic classification of the ‘genus’ *Haplochromis* (Pisces, Cichlidae) and related taxa, part II. *Bulletin of the British Museum (Natural History) Zoology* **39**, 1–101.

Lærdal, T., Talbot, M. R. & Russell, J. M. (2002) Late Quaternary sedimentation and climate in the lakes Edward and George area, Uganda-Congo. *East African great lakes: lmnology, palaeolimnology and bodiversity* **12**, 429–470.

Mandahl-Barth, G. (1954) The freshwater mollusks of Uganda and adjacent territories. *Annalen Koninklijk Museum van Belgisch-Congo, Zoologische Wetenschappen - Annales du Musée Royal du Congo Belge, Sciences Zoologiques* **32**.

Meier, J. I., Marques, D. A., Mwaiko, S., Wagner, C. E., Excoffier, L. & Seehausen, O. (2017) Ancient hybridization fuels rapid cichlid fish adaptive radiations. *Nature Communications* **8**, 14363.

Poll, M. (1939) Poissons. In *Exploration du Parc National Albert Mission H. Damas (1935-1936)* p. 73 Bruxelles: Institut des Parcs Nationaux du Congo Belge.

Salzburger, W. (2018) Understanding explosive diversification through cichlid fish genomics. *Nature Reviews Genetics* **19**, 705–717.

Seehausen, O., Koetsier, E., Schneider, M. V., Chapman, L. J., Chapman, C. A., Knight, M. E., Turner, G. F., Alphen, J. J. M. v. & Bills, R. (2003) Nuclear markers reveal unexpected genetic variation and a Congolese-Nilotic origin of the Lake Victoria cichlid species flock. *Proceedings of the Royal Society B: Biological Sciences* **270**, 129–137.

Smits, J. D., Witte, F. & Van Veen, F. G. (1996) Functional changes in the anatomy of the pharyngeal jaw apparatus of *Astatoreochromis alluaudi* (Pisces, Cichlidae) and their effects on adjacent structures. Biological Journal of the Linnean Society **59**, 389–409.

Snoeks, J. (1994) *The haplochromine fishes (Teleostei, Cichlidae) of Lake Kivu, East Africa: a taxonomic revision with notes on their ecology*. Tervuren, Belgium: Royal Museum for Central Africa.

Verheyen, E., Salzburger, W., Snoeks, J. & Meyer, A. (2003) Origin of the superflock of cichlid fishes from Lake Victoria, East Africa. *Science* **300**, 325–329.

Vranken, N., Van Steenberge, M. & Snoeks, J. (2019a) Grasping ecological opportunities: not one but five paedophagous species of *Haplochromis* (Teleostei: Cichlidae) in the Lake Edward system. *Hydrobiologia* **832**, 105–134.

Vranken, N., Van Steenberge, M., Kayenbergh, A. & Snoeks, J. (2019b) The lobed-lipped species of *Haplochromis* (Teleostei, Cichlidae) from Lake Edward, two instead of one. *Journal of Great Lakes Research*.

Vranken, N., Van Steenberge, M. & Snoeks, J. (2019c) Similar ecology, different morphology: the oral mollusc shellers from Lake Edward. *Journal of Fish Biology*.

Witte, F. & Van Oijen, M. J. P. (1990) Taxonomy, ecology and fishery of Lake Victoria haplochromine trophic groups. *Zoologische Verhandelingen* **262**, 1–47.

Witte, F. & Witte-Maas, E. L. M. (1987) Implications for taxonomy and morphology of intra-specific variation in haplochromine cichlids of Lake Victoria. With descriptions of five zooplankivorous species. In Witte, F. (1987) *From Form to Fishery*. Leiden, Netherlands: University Leiden.

Zelditch, M. L., Swiderski, D. L., Sheets, H. D. & Fink, W. L. (2004) *Geometric morphometrics for biologists: a primer*. London: Elsevier Academic Press.