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## Research article

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# *Protomelas krampus*, a new paedophagous cichlid from Lake Malawi (Teleostei, Cichlidae)

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**Abstract.** A new paedophagous species of *Protomelas*, *P. krampus* sp. nov., is described from Lake Malawi. It has been found in Lukoma Bay in Tanzania, near Mara Point in Mozambique, and at Otter Point, Chizumulu, the Likoma Islands and Mazinzi Reef in Malawi. This species is placed in the genus *Protomelas* based on its melanin pattern, which comprises a continuous midlateral stripe. A morphometric study was done to compare this species with its congeners and similar species of *Hemitaeniochromis* and *Caprichromis*. It differs from most congeners by having only one inner tooth row. Furthermore, *P. krampus* sp. nov. differs from *P. insignis*, *P. spilopterus*, *H. brachyrhynchus*, *H. urotaenia*, *Caprichromis liemi* and *C. orthognathus* by its shorter premaxillary pedicel, shorter prepectoral distances and dentition. It also differs largely in its melanin pattern from the paedophagous species *C. liemi*, *C. orthognathus*, *Diplotaxodon greenwoodi* and *Naevochromis chrysogaster*, as well as *H. brachyrhynchus* and *H. urotaenia*. *Protomelas krampus* sp. nov. has been observed to ram mouth-brooding cichlids from above to feed on their eggs or larvae.

**Keywords.** Cichliformes, East Africa, mouth-brooding cichlids, Mozambique, trophic ecology.

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## Introduction

Lake Malawi is home to about 800 to 1000 species of endemic cichlids (Snoeks 2000; Konings 2016). Because of their explosive speciation, species can be difficult to delineate and many species complexes and genera still need to be taxonomically resolved.

In Lake Malawi, haplochromines constitute the major part of the cichlids. The endemic genus *Protomelas* Eccles & Trewavas, 1989 currently encompasses 14 to 16 valid species (Konings 2016; Froese & Pauly

2019; Fricke *et al.* 2020). The genus is characterized by a typical melanin pattern with a well-developed continuous midlateral band from one eye length behind the opercle to the caudal fin and a dorsolateral band that may be spotted. Jaws are short and the length of the premaxillary pedicel is less than one third that of the head. Representatives of this genus have bicuspid anterior outer teeth that may be replaced by unicuspid teeth in adults; posterior outer teeth are simple (Eccles & Trewavas 1989). One species, *Haplochromis urotaenia* Regan, 1922, was placed in a newly described genus, *Hemitaeniochromis* Eccles & Trewavas, 1989, based on its melanin pattern having a typical discontinuous midlateral band (Eccles & Trewavas 1989). For a long time, it remained the sole species within this genus. Several undescribed species were attributed to the genus and later *Protomelas spilopterus* (Trewavas, 1935) was transferred by some authors to *Hemitaeniochromis* (see, e.g., Turner 1996; Snoeks & Hanssens 2004; Oliver 2012; Konings 2016). In addition, Oliver (2012) described a new species based on two specimens with a similar melanin pattern, *H. brachyrhynchus* Oliver, 2012. There is, however, major confusion on the precise delimitation of the genera *Protomelas* and *Hemitaeniochromis* (Snoeks & Hanssens 2004; Oliver 2012).

Already in 1983, McKaye & Kocher observed an undescribed paedophagous species near Otter Point, Lake Malawi. This species seemed to differ from *Caprichromis orthognathus* (Trewavas, 1935) by its melanin pattern and behaviour (McKaye & Kocher 1983). Eccles & Trewavas (1989) suggested that this undescribed cichlid might be *P. spilopterus*, which is a suspected paedophage based on the resemblance of the jaws and pharyngeal teeth with those of known paedophagous species in Lake Victoria. Based on its head shape and behaviour, as observed by Konings (1989, 2016), it seems, however, to be an undescribed species, which was referred to as *Protomelas* sp. ‘paedophage’ and later *Hemitaeniochromis* sp. ‘paedophage’ (see, e.g., Konings 1989, 2016). Snoeks & Hanssens (2004) also mentioned a possibly paedophagous species, *Protomelas* sp. ‘paedophage’, stating that this may be the same species as observed by Konings (1989). These authors placed the only two available specimens in the genus *Protomelas* because of its continuous midlateral stripe. McKaye & Kocher (1983) noted that paedophagous species, i.e., *Caprichromis liemi* (McKaye & Mackenzie, 1982) and *C. orthognathus*, may change colour depending on their prey species. Therefore, as Turner (1996) already noted, it is not possible to rule out that this undescribed species may be conspecific to either of the species in *Caprichromis* Eccles & Trewavas, 1989 or congeneric based solely on its melanin pattern. A morphological analysis was needed to compare this undescribed paedophagous species with similar taxa.

Three confirmed paedophagous species have currently been described from Lake Malawi. *Protomelas spilopterus* has short, oblique jaws with thick gums and one or two inner tooth rows. Both *Caprichromis liemi* and *C. orthognathus* have a melanin pattern with a diagonal stripe running from the nape to the base of the caudal fin. The teeth on the lower jaw are embedded in thick gums. Especially *C. orthognathus* has a steeply inclined mouth (Eccles & Trewavas 1989; Konings 2016). In addition to *P. spilopterus*, *C. liemi* and *C. orthognathus*, two more species are suspected of having a paedophagous diet (Stauffer & McKaye 1986; Eccles & Trewavas 1989). *Diplotaxodon greenwoodi* Stauffer & McKaye, 1986 is a widespread deep-water species. The genus *Diplotaxodon* Trewavas, 1935 is characterized by the lack of distinct markings such as bars or spots on the body. Its lower jaw protrudes and the teeth on the lower jaw are embedded in thick gums. *Diplotaxodon greenwoodi* has a steeply inclined mouth, large eyes and one to three inner tooth rows (Stauffer & McKaye 1986; Trewavas & Eccles 1989; Snoeks 2004). *Naevochromis chrysogaster* (Trewavas, 1935) has a suprapectoral spot, a midlateral spot covering the lateral line, a supranal spot positioned between the lateral lines and a precaudal spot. The chin is prominent and thick. It has a broad mouth and fleshy lips that embed the teeth. There is one inner row of teeth in the upper and two in the lower jaw (Eccles & Trewavas 1989; Konings 2016).

As is clear from various discussions (e.g., Eccles & Trewavas 1989; Snoeks 2004; Oliver 2012; Konings 2016) there is still some confusion regarding the classification of species within the genera *Protomelas*

and *Hemitaeniochromis*. In this study, we follow the classification provided by Eccles & Trewavas (1989), expanded by Oliver (2012). It is, however, clear that a taxonomical revision of the species in the genera *Protomelas* and *Hemitaeniochromis* is necessary. For now, we suggest including the newly described paedophagous species in the genus *Protomelas* based on its continuous midlateral band and short jaws, following Snoeks & Hanssens (2004). We await a further revision of the complex for a final generic allocation. Below, the species that is new to science is described as *Protomelas krampus* sp. nov.

## Material and methods

In total, 44 specimens of *Protomelas*, *Hemitaeniochromis* and *Caprichromis* in the collections at the Royal Museum of Central Africa, Tervuren, and the Natural History Museum, London, were examined: five specimens of *C. liemi*, five of *C. orthognathus*, one of *H. brachyrhynchus*, five of *H. urotaenia*, eleven of *H. sp. 'insignis like'* (*sensu* Snoeks & Hanssens 2004), four of *P. insignis*, two of *P. krampus* sp. nov. and eleven of *P. spilopterus*.

The measurements and counts performed here follow Snoeks (2004). Two additional measurements, as described by Oliver (2012), were taken: the snout width and belly length. Also, the gape inclination, the angle between the midlateral line and the anteriormost tip of the upper jaw, was measured. In total, 21 length measurements, 13 counts (including the number of vertebrae via X-rays), one angle (gape inclination) (see Tables 4 and 5) and some qualitative observations on the body and head shape, dentition, and the colour pattern in alcohol were made.

Principal component analysis (PCA) was performed in Past3 (Hammer *et al.* 2001) to explore the multivariate data set. Measurements were log-transformed and the covariance matrix was used. When using log-transformed measurements, the individual loadings of all variables on the first principal component (PC 1) are of the same magnitude and sign, and PC 1 can therefore be regarded as a proxy for multivariate size (Jolicoeur 1963; Snoeks 2004; Van Steenberge *et al.* 2015). The correlation matrix was used for the raw meristic data.

## Repositories

MRAC = Musée royal de l'Afrique centrale, Tervuren, Belgium (used traditionally for collections of the Royal Museum of Central Africa)

BMNH = British Museum of Natural History, London, UK (used traditionally for collections of the Natural History Museum)

## Abbreviations used in text

HL = head length

PC = principal component

PCA = principal component analysis

SL = standard length

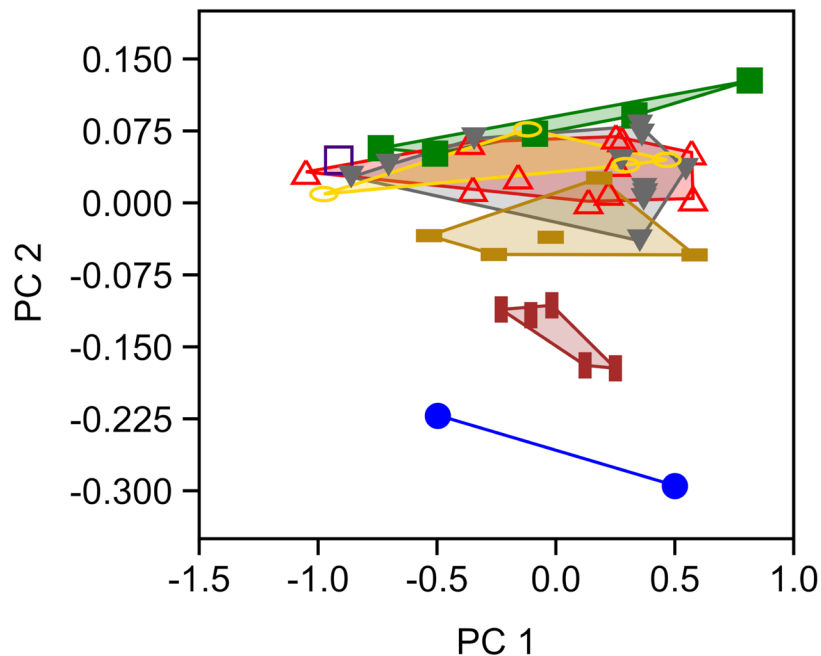
## Results

### *Comparative morphometrics*

A PCA on 21 log-transformed measurements including all specimens showed a clear separation of *Protomelas krampus* sp. nov. from all other species in the negative part of PC 2 on the second principal axis (Fig. 1). In general morphology, it seems to be most similar to *C. orthognathus*. The most important loadings on PC 2 are of the premaxillary pedicel length, cheek depth, belly length, caudal peduncle length, interorbital width and dorsal fin base (Table 1). In a comparison with both species of *Caprichromis*, *P. krampus* sp. nov. remains clearly separated on the third principal axis (Fig. 2). The most important

**Table 1.** Loadings of PC 1, PC 2 and PC 3 of the principal component analysis of 21 log-transformed measurements of all specimens in the analysis.

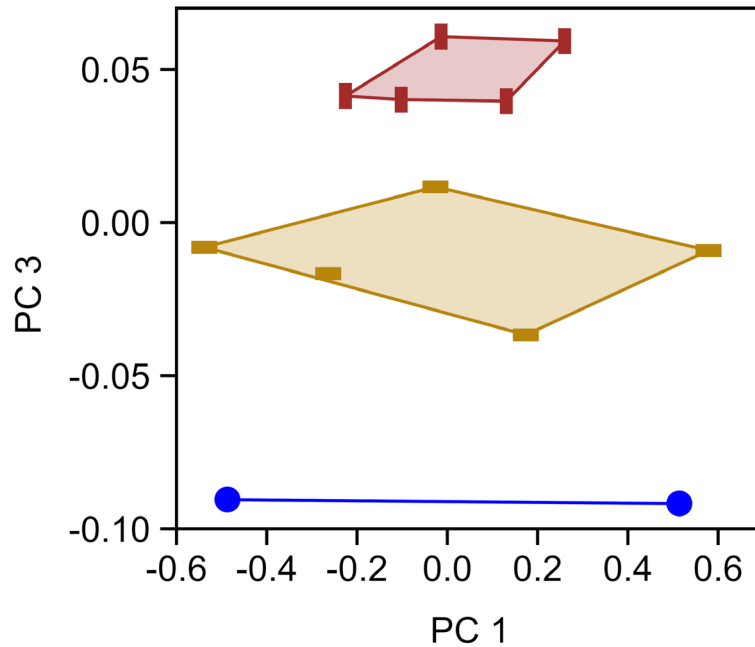
Measurement	PC1	PC 2	PC 3
Standard length	0.21	-0.16	0.03
Body depth	0.23	-0.05	0.18
Prepectoral distance	0.20	0.08	-0.05
Predorsal distance	0.21	0.16	0.01
Preventral distance	0.21	-0.05	0.05
Preanal distance	0.21	-0.11	-0.02
Dorsal fin base length	0.22	-0.22	0.07
Anal fin base length	0.20	-0.18	0.05
Caudal peduncle length	0.22	-0.25	0.12
Caudal peduncle depth	0.24	-0.17	0.11
Belly length	0.21	-0.27	-0.08
Head width	0.22	0.16	0.29
Head length	0.20	0.10	-0.10
Premaxillary pedicel length	0.18	0.61	-0.14
Snout length	0.24	0.19	-0.31
Lacrimal depth	0.26	0.14	-0.55
Cheek depth	0.26	-0.33	-0.19
Eye diameter	0.14	0.19	0.33
Inter orbital width	0.24	0.24	0.48
Snout width	0.24	0.13	0.07
Lower jaw length	0.22	-0.04	-0.17
% variance	90.77%	3.04%	2.13%



**Fig. 1.** Scatter plot of PC 1 against PC 2 for a principal component analysis of 21 log-transformed measurements of all specimens studied (n=44). *Protomelas krampus* sp. nov. = blue dot; *Hemitaeniochromis brachyrhynchus* Oliver, 2012 = purple square; *H. urotaenia* (Regan, 1922) = green square; *Hemitaeniochromis* sp. ‘*insignis* like’ = red triangle; *P. spilopterus* (Trewavas, 1935) = grey inverted triangle; *P. insignis* (Trewavas, 1935) = golden diamond; *Caprichromis liemi* (McKaye & Mackenzie, 1982) = light brown dash; *C. orthognathus* (Trewavas, 1935) = dark brown rectangle.

**Table 2.** Loadings of PC 1, PC 2 and PC 3 of the principal component analysis of 21 log-transformed measurements of both species of *Caprichromis* Eccles & Trewavas, 1989 and *P. krampus* sp. nov.

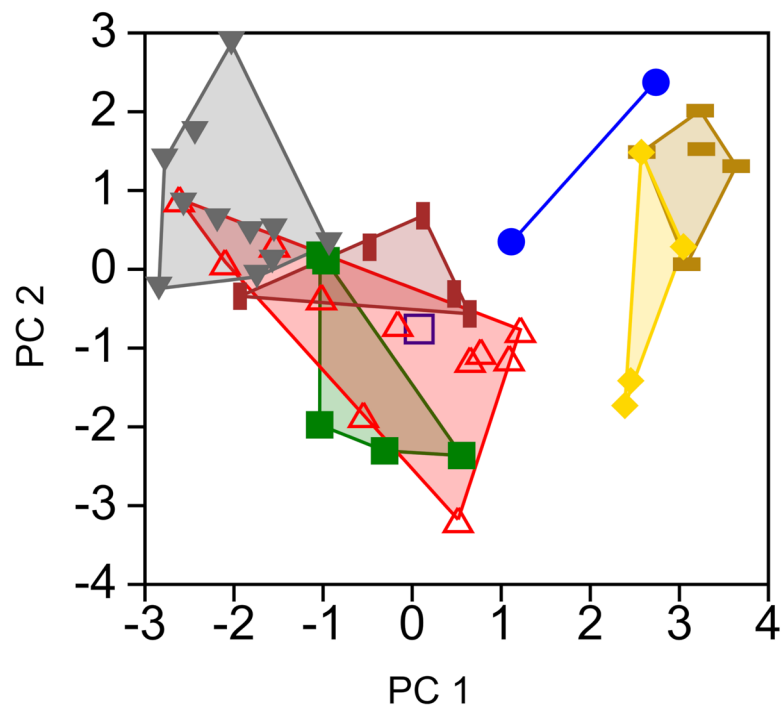
Measurement	PC1	PC 2	PC 3
Standard length	0.21	-0.10	-0.12
Body depth	0.20	0.08	-0.21
Prepectoral distance	0.20	0.17	-0.04
Predorsal distance	0.20	0.19	0.07
Preventral distance	0.22	0.04	-0.24
Preanal distance	0.23	0.01	-0.09
Dorsal fin base length	0.22	-0.06	-0.26
Anal fin base length	0.19	-0.08	-0.08
Caudal peduncle length	0.23	-0.32	0.21
Caudal peduncle depth	0.25	-0.15	0.02
Belly length	0.22	-0.20	0.10
Head width	0.22	-0.11	0.29
Head length	0.20	0.13	-0.09
Premaxillary pedicel length	0.15	0.61	0.52
Snout length	0.23	0.35	-0.34
Lacrimal depth	0.22	0.33	-0.16
Cheek depth	0.30	-0.29	-0.10
Eye diameter	0.15	-0.10	-0.04
Inter orbital width	0.25	-0.13	0.39
Snout width	0.23	-0.03	0.26
Lower jaw length	0.22	0.02	-0.00
% variance	86.45%	9.34%	1.90%



**Fig. 2.** Scatter plot of PC 1 against PC 3 for a principal component analysis of 21 log-transformed measurements of *Protomelas krampus* sp. nov., *Caprichromis liemi* (McKaye & Mackenzie, 1982) and *C. orthognathus* (Trewavas, 1935) (n=12). *P. krampus* sp. nov. = blue dot; *C. liemi* = light brown dash; *C. orthognathus* = dark brown rectangle.

**Table 3.** Loadings of PC 1 and PC 2 of the principal component analysis of 13 counts.

Counts	PC 1	PC 2
Longitudinal line	0.33	-0.37
Upper lateral line	0.26	-0.06
Lower lateral line	0.24	-0.37
Lower gill rakers	0.05	0.08
Upper gill rakers	0.08	0.09
Dorsal fin spines	0.31	-0.20
Dorsal fin rays	0.25	0.57
Anal fin rays	0.29	0.45
Pectoral fin rays	0.07	-0.26
Vertebrae	0.43	-0.05
Inner teeth rows	0.22	0.05
Upper teeth	0.40	-0.10
Lower teeth	0.34	0.22
% variance	29.05%	12.70%



**Fig. 3.** Scatter plot of PC 1 against PC 2 for a principal component analysis of 13 counts of all specimens studied (n=44). *Protomelas krampus* sp. nov. = blue dot; *Hemitaeniochromis brachyrhynchus* Oliver, 2012 = purple square; *H. urotaenia* (Regan, 1922) = green square; *Hemitaeniochromis* sp. ‘*insignis* like’ = red triangle; *P. spilopterus* (Trewavas, 1935) = grey inverted triangle; *P. insignis* (Trewavas, 1935) = golden diamond; *Caprichromis liemi* (McKaye & Mackenzie, 1982) = light brown dash; *C. orthognathus* (Trewavas, 1935) = dark brown rectangle.

loadings on PC 3 are for the premaxillary pedicel length, the interorbital width, the snout length, the head width, the dorsal fin base and the snout width (Table 2).

In a PCA on the raw meristics, the picture was less clear. Still, *P. krampus* sp. nov. was separated from all other species (Fig. 3), mostly on PC 1. The most important loadings on PC 1 are of the number of vertebrae, the number of both upper and lower jaw teeth, the number of longitudinal line scales, the

number of dorsal fin spines and the number of anal fin rays. On PC 2, the highest loadings are the number of dorsal fin rays, the number of anal fin rays, the number of scales on the lower lateral line, the number of longitudinal line scales, the number of pectoral fin rays and the number of outer lower jaw teeth (Table 3).

### **Taxonomy**

Phylum Chordata Haeckel, 1874  
 Class Actinopterygii Klein, 1885  
 Order Cichliformes Betancur *et al.*, 2013  
 Family Cichlidae Bonaparte, 1840  
 Subfamily Pseudocrenilabrinae Fowler, 1934  
 Tribe Haplochromini Poll, 1986

Genus *Protomelas* Eccles & Trewavas, 1989

*Protomelas* Eccles & Trewavas, 1989: 40 (type species: *Chromis kirkii* Günther, 1894, by original designation).

#### ***Protomelas krampus* sp. nov.**

[urn:lsid:zoobank.org:act:5C1913C2-E6C9-43CD-BB1C-5522DFC60B8C](https://doi.org/10.21203/rs.3.rs-1111111/v1)

Figs 4–5; Tables 4–5

### **Diagnosis**

*Protomelas krampus* sp. nov. differs from most species of *Protomelas*, i.e., *P. annectens* (Regan, 1922), *P. fenestratus* (Trewavas, 1935), *P. kirkii* (Günther, 1894), *P. labridens* (Trewavas, 1935), *P. macrodon* Eccles, 1989, *P. marginatus* (Trewavas, 1935), *P. pleurotaenia* (Boulenger, 1901), *P. similis* (Regan, 1922), *P. spilonotus* (Trewavas, 1935), *P. taeniolatus* (Trewavas, 1935), *P. triaenodon* (Trewavas, 1935) and *P. virgatus* (Trewavas, 1935), by having only one inner tooth row, whereas the other species have two rows.

It can be distinguished from *P. spilopterus* by a shorter premaxillary pedicel (17.0–19.2 vs 21.8–28.4% HL), a larger gape inclination (70–80 vs 40–60°), a shallower body (33.3–34.3 vs 36.0–42.8% SL), a smaller predorsal (27.4–29.1 vs 33.4–37.4% SL) and prepectoral distance (29.4–29.8 vs 31.8–40.0% SL), a shorter and more slender head (length 27.8–29.2 vs 30.4–34.6% SL and width 39.3–40.3 vs 41.4–50.7% HL, respectively), and a smaller interorbital width (22.9–23.4 vs 25.0–33.6% HL). In addition, *P. krampus* sp. nov. has more gill rakers on the outer epibranchial (further mentioned as upper gill rakers) than *P. spilopterus* (5 vs 3–4) and more vertebrae (31–32 vs 29). The inner teeth are tricuspid in *P. krampus* sp. nov. while mixed unicuspid/tricuspid or unicuspid in *P. spilopterus*. The outer teeth of the lower jaw of *P. krampus* sp. nov. are oriented straight up, whereas those of *P. spilopterus* are angled forward, except for in one specimen which has slightly inwards curved teeth.

*Protomelas krampus* sp. nov. differs from *P. insignis* by a shorter premaxillary pedicel (17.0–19.2 vs 27.9–30.0% HL), a deeper cheek (31.6–40.2 vs 23.2–28.5% HL), the larger gape inclination (70–80 vs 30°), a smaller predorsal (27.4–29.1 vs 34.2–35.9% SL) and prepectoral distance (29.4–29.8 vs 32.7–35.4% SL), a shorter and more slender head (length 27.8–29.2 vs 31.6–34.3% SL and width 39.3–40.3 vs 41.3–44.8% HL, respectively), a shallower lacrimal (19.6–20.4 vs 21.4–22.4% HL), a smaller interorbital width (22.9–23.4 vs 26.9–32.8% HL), and a longer lower jaw (37.7–38.8 vs 31.2–37.3% HL). The upper jaw has fewer outer teeth in *P. krampus* sp. nov. than in *P. insignis* (37–40 vs 43–50). Outer lower jaw teeth are straight in *P. krampus* sp. nov. but curved inwards in *P. insignis*.

*Protomelas krampus* sp. nov. differs from the undescribed species mentioned by Snoeks & Hanssens (2004) as *Hemitaeniochromis* sp. ‘*insignis* like’ by a shorter premaxillary pedicel (17.0–19.2 vs 24.7–30.7% HL), a deeper cheek depth (31.6–40.2 vs 22.5–28.8% HL), a larger gape inclination (70–80 vs 40–60°), a shorter predorsal (27.4–29.1 vs 33.5–38.3% SL) and prepectoral distance (29.4–29.8 vs 31.1–38.1% SL), a shorter and more slender head (length 27.8–29.2 vs 31.3–34.5% SL and width 39.3–40.3 vs 40.8–46.8% HL, respectively), and a longer lower jaw (37.7–38.8 vs 28.9–35.0% HL). *Protomelas krampus* sp. nov. has more gill rakers on the outer epibranchial than *H.* sp. ‘*insignis* like’ (5 vs 3–4). There are more dorsal fin rays in *P. krampus* sp. nov. than in *H.* sp. ‘*insignis* like’ (11–12 vs 9–10). The outer teeth of the lower jaw of *P. krampus* sp. nov. are oriented straight up, whereas those of *H.* sp. ‘*insignis* like’ are angled forward.

*Protomelas krampus* sp. nov. differs from both species of the genus *Hemitaeniochromis* by its continuous midlateral stripe, which places it in *Protomelas*, whereas *H. urotaenia* and *H. brachyrhynchus* have an anteriorly spotted stripe.

In addition, *P. krampus* sp. nov. differs from *H. urotaenia* by a shorter premaxillary pedicel (17.0–19.2 vs 27.5–28.9% HL), a deeper cheek (31.6–40.2 vs 27.3–30.6% HL), a larger gape inclination (70–80 vs 30–50°), a longer dorsal fin base (53.6–58.3 vs 49.3–50.5% SL), a shorter predorsal (27.4–29.1 vs 37.0–38.7% SL) and prepectoral distance (29.4–29.8 vs 35.2–36.7% SL), a shorter and more slender head (length 27.8–29.2 vs 34.9–37.3% SL and width 39.3–40.3 vs 40.5–42.5% HL respectively), and a shallower lacrimal (19.6–20.4 vs 22.7–23.3% HL). *Protomelas krampus* sp. nov. has more vertebrae (31–32 vs 30), more gill rakers on the outer epibranchial (5 vs 2–4) and more dorsal fin rays (11–12 vs 9–10) than *H. urotaenia*. *Protomelas krampus* sp. nov. has only one inner tooth row with tricuspid teeth, whereas *H. urotaenia* has two rows of mostly unicuspid teeth. The outer lower jaw teeth are straight in *P. krampus* sp. nov., whereas they are curved inwards in *H. urotaenia*.

*Protomelas krampus* sp. nov. differs from *H. brachyrhynchus* by a shorter premaxillary pedicel (17.0–19.2 vs 27.1% HL), a deeper cheek (31.6–40.2 vs 21.4% HL), a larger gape inclination (70–80 vs 45°), a shallower body (33.3–34.3 vs 37.7% SL), a shorter predorsal (27.4–29.1 vs 37.8% SL), preventral (39.0–44.4 vs 46.1% SL) and prepectoral distance (29.4–29.8 vs 37.0% SL), a shorter anal fin base length (18.3–18.8 vs 21.2% SL), a shorter and more slender head (27.8–29.2 vs 35.3% SL and 39.3–40.3 vs 43.8% HL, respectively), a longer snout (33.3–34.2 vs 30.1% HL), a deeper lacrimal (19.6–20.4 vs 17.2% HL), a smaller eye (22.5–27.0 vs 32.2% HL), and a longer lower jaw (37.7–38.8 vs 32.9% HL). *Protomelas krampus* sp. nov. has more vertebrae (31–32 vs 30), upper gill rakers (5 vs 4) and dorsal fin rays (11–12 vs 10) than *H. brachyrhynchus*. The outer teeth of the lower jaw of *P. krampus* sp. nov. are oriented straight up, whereas those of *H. brachyrhynchus* are angled forward and slightly outwards.

*Protomelas krampus* sp. nov. differs from the paedophagous species of the genus *Caprichromis* by its melanin pattern: it has a midlateral band from behind the opercle to the base of the caudal fin, whereas species of *Caprichromis* have a diagonal stripe from the nape to the base of the caudal fin.

*Protomelas krampus* sp. nov. further differs from *C. orthognathus* by a shorter premaxillary pedicel (17.0–19.2 vs 21.9–25.4% HL) and a shorter prepectoral distance (29.4–29.8 vs 30.2–33.4% SL). There are more soft dorsal fin rays in *P. krampus* sp. nov. than in *C. orthognathus* (11–12 vs 10) and more gill rakers on the outer epibranchial (5 vs 3–4). *Protomelas krampus* sp. nov. has fewer outer teeth in the lower jaw (31–36 vs 42–50).

*Protomelas krampus* sp. nov. differs from *C. liemi* by a shorter premaxillary pedicel (17.0–19.2 vs 24.7–28.0% HL), a deeper cheek (31.6–40.2 vs 25.5–29.5% HL), a larger gape inclination (70–80 vs



30–60°), a shallower body (33.3–34.3 vs 36.1–38.6% SL), shorter predorsal (27.4–29.1 vs 35.0–36.7% SL) and prepectoral distances (29.4–29.8 vs 34.2–36.5% SL), a shorter and wider head (length 27.8–29.2 vs 31.9–33.6% SL and width 39.3–40.3 vs 35.9–38.2% HL, respectively), and a shallower lacrimal (19.6–20.4 vs 20.8–23.9% HL). There are fewer scales along the upper lateral line in *P. krampus* sp. nov. than in *C. liemi* (20–23 vs 25–27). *Protomelas krampus* sp. nov. has fewer outer teeth in the upper jaw (37–40 vs 44–47) and lower jaw (31–36 vs 44–59) than *C. liemi*.

*Protomelas krampus* sp. nov. differs from *Diplotaxodon greenwoodi* by the lack of a melanin pattern in the latter species. It has isognathous jaws, whereas *D. greenwoodi* has a protruding lower jaw.

*Protomelas krampus* sp. nov. differs from *Naevochromis chrysogaster* by its melanin pattern, which consists of three large spots on the lateral sides in the latter instead of a continuous midlateral line. It has a more strongly inclined gape than *N. chrysogaster*. *Protomelas krampus* sp. nov. has only one inner tooth row on the lower jaw, whereas *N. chrysogaster* has two.

### Etymology

The specific name, ‘*krampus*’, is a noun in apposition and was chosen in reference to the European folklore character Krampus. This demon puts naughty children in a bag and takes them away, which is reminiscent of a paedophagous behaviour. The goat-like appearance of Krampus also implicitly refers to the head-butting behaviour of the species. The same implicit reference to this behaviour is also found in the genus name *Caprichromis* of other paedophagous species of Lake Malawi.

### Material examined

#### Holotype

TANZANIA • ♀; Lake Malawi, Lukoma Bay; 11°22.50' S, 34°52.00' E; 11 Jan. 1998; SADC/GEF Taxonomy team leg.; 116.1 mm SL; MRAC 99-041-P-4768.

#### Paratype

MOZAMBIQUE • 1 ♂; Lake Malawi, Mara Rocks; 12°11.34' S, 34°41.73' E; 22 May 1998; SADC/GEF Taxonomy team leg.; 181.1 mm SL; MRAC 99-041-P-4767.

#### Comparative material

*Hemitaeniochromis brachyrhynchus* (Oliver, 2012)

MALAWI • 1 paratype; Lake Malawi, Nkhata Bay, south bay; 11°36.22' S, 34°19.16' E; 27 Sep. 1997; SADC/GEF Taxonomy team leg.; 81.6 mm SL; MRAC 99-041-P-1746.

*Hemitaeniochromis urotaenia* (Regan, 1922)

MALAWI • 2 specs; Lake Malawi, Kande Bay, S of Bandawe; 11°56.47' S, 34°09.41' E; 3 Jun. 1997; SADC/GEF Taxonomy team leg.; 142.2–182.7 mm SL; MRAC 99-041-P-1738-1739 • 3 specs [of 5 in lot]; Lake Malawi, Nkhotakota; 12°52.95' S, 34°19.33' E; 22 Sep. 1997; SADC/GEF Taxonomy team leg.; 87.8–119.0 mm SL; MRAC 99-041-P-1741-1745.

*Hemitaeniochromis* sp. “*insignis* like”

MALAWI • 3 specs; Lake Malawi, Chipoka to Makanjila, SW arm and SE arm; 14°00.62' S, 34°37.29' E; 18 Nov. 1997; SADC/GEF Taxonomy team leg.; 122.0–148.5 mm SL; MRAC 99-041-P-1747-1749 • 1 spec.; Lake Malawi, Nkhotakota; 12°52.95' S, 34°19.34' E; 22 Sep. 1997; SADC/GEF Taxonomy team leg.; 76.9 mm SL; MRAC 99-041-P-1750 • 1 spec.; Lake Malawi, Senga Bay; 13°45.13' S, 34°29.22' E; 8 Jun. 1997; SADC/GEF Taxonomy team leg.; 145.2 mm SL; MRAC 99-041-P-1773 • 2 specs; Lake Malawi, Chipoka to Makanjila, SW arm and SE arm; 13°52.45' S, 34°54.74' E; 9 Oct. 1997; SADC/

GEF Taxonomy team leg.; 139.7–172.4 mm SL; MRAC 99-041-P-2625-2626 • 1 spec.; Lake Malawi, Chipoka to Makanjila, SW arm and SE arm; 13°57.77' S, 34°43.37' E; 10 Oct. 1997; SADC/GEF Taxonomy team leg.; 142.7 mm SL; MRAC 99-041-P-2627 • 1 spec.; Lake Malawi, SW arm; 14°07.00' S, 34°44.30' E; 18 Dec. 1996; SADC/GEF Taxonomy team leg.; 169.0 mm SL; MRAC 99-041-P-1755.

MOZAMBIQUE • 1 spec.; Lake Malawi, Chiwanga Bay; 12°39.03' S, 34°46.56' E; 11 Apr. 1998; SADC/GEF Taxonomy team leg.; 111.9 mm SL; MRAC 99-041-P-1753 • 1 spec.; Lake Malawi, Chiwanga Bay; 12°39.03' S, 34°46.56' E; 11 Apr. 1998; SADC/GEF Taxonomy team leg.; 117.8 mm SL; MRAC 99-041-P-1754.

*Protomelas spilopterus* (Trewavas, 1935)

MALAWI • lectotype, 3 paralectotypes; Lake Malawi, South End; 1925; 147.1–166.0 mm SL; BMNH 1935.6.14.644-647 • 2 paralectotypes [of 3 in lot]; Lake Malawi, Mwaya; 1925; 149.1–153.4 mm SL; BMNH 1935.6.14.649-651 (2 of 3) • 5 paralectotypes [of 6 in lot]; Lake Malawi, Monkey Bay; 1925; 85.5–160.4 mm SL; BMNH 1935.6.14.652-657.

*Protomelas insignis* (Trewavas, 1935)

MALAWI • lectotype, 3 paralectotypes; Lake Malawi, Monkey Bay; 1925; 81.7–161.0 mm SL; BMNH 1935.6.14.839-843.

*Caprichromis liemi* (McKaye & Mackenzie, 1982)

MALAWI • 1 spec.; Lake Malawi, Chipoka to Makanjila, SW arm and SE arm; 14°00.62' S, 34°37.29' E; 18 Nov. 1997; SADC/GEF Taxonomy team leg.; 129.2 mm SL; MRAC 99-041-P-2647.

MOZAMBIQUE • 1 spec.; Lake Malawi, Chilola Bay; 12°06.45' S, 34°46.79' E; 7 Apr. 1998; SADC/GEF Taxonomy team leg.; 117.9 mm SL; MRAC 99-041-P-2648 • 1 spec.; Lake Malawi, Tchulutcha Reef, Metangula; 12°42.19' S, 34°47.46' E; 25 May 1998; SADC/GEF Taxonomy team leg.; 173.2 mm SL; MRAC 99-041-P-2649 • 2 specs; Lake Malawi, Namisse, S of Cobue; 12°10.08' S, 34°42.97' E; 24 May 1998; SADC/GEF Taxonomy team leg.; 103.2–144.4 mm SL; MRAC 99-041-P-5018-5019.

*Caprichromis orthognathus* (Trewavas, 1935)

MALAWI • 1 spec.; Lake Malawi, Mazinzi Bay, SE arm; 4 Sep. 1980; D.S.C. Lewis leg.; 146.7 mm SL; MRAC 81-02-P-33 • 1 spec.; Lake Malawi; 25 Jun. 1962; 154.1 mm SL; MRAC 191849.

MOZAMBIQUE • 1 spec.; Lake Malawi, Chiwanga Bay; 12°38.52' S, 34°46.37' E; 10 Apr. 1998; SADC/GEF Taxonomy team leg.; 122.0 mm SL; MRAC 99-041-P-2644 • 2 specs; Lake Malawi, Chiwanga Bay; 12°38.81' S, 34°46.68' E; 10 Apr. 1998; SADC/GEF Taxonomy team leg.; 128.3–131.4 mm SL; MRAC 99-041-P-2645-2646.

*Diplotaxodon greenwoodi* (Stauffer & McKaye, 1986)

MALAWI • 1 spec.; Lake Malawi, Senga Bay; 13°45.25' S, 34°40'30" E; 8 Jun. 1997; SADC/GEF Taxonomy team leg.; MRAC 1999-041-P-10765 • 1 spec.; Lake Malawi, Chipoka to Makanjila, SW arm and SE arm; 13°57'46.19" S, 34°43'22.19" E; 10 Oct. 1997; SADC/GEF Taxonomy team leg.; MRAC 1999-041-P-10766.

MOZAMBIQUE • 1 spec.; Lake Malawi, Chilola Bay, 2<sup>nd</sup> bay of Cobue; 12°00'44.39" S, 34°47'16.80" E; 8 Apr. 1998; SADC/GEF Taxonomy team leg.; MRAC 1999-041-P-10768.

TANZANIA • 1 spec.; Lake Malawi, Weismann Bay; 9°30'46.80" S, 34°00'19.80" E; 14 Jan. 1998; SADC/GEF Taxonomy team leg.; MRAC 1999-041-P-10767.

*Naevochromis chrystogaster* (Trewavas, 1935)

MALAWI • 1 spec.; Lake Malawi, Mdoka; 10°19'00.01" S, 34°12'00" E; May 1989; A. Konings leg.; MRAC 1991-095-P-0037 • 1 spec.; Lake Malawi, Cape Ngombo near Makanjila Point; 13°44'07.19" S, 34°51'16.20" E; 13 Nov. 1997; SADC/GEF Taxonomy team leg.; MRAC 1999-041-P-8524.

TANZANIA • 1 spec.; Lake Malawi, Lutara, N of bay; 10°25'57.61" S, 34°33'33.59" E; 11 Nov. 1998; SADC/GEF Taxonomy team leg.; MRAC 1999-041-P-5205.

### Description

Based on holotype and one paratype (see Figs 4–5 and Tables 4–5). Qualitative observations are described in the context of Lake Malawi haplochromine cichlids as conducted by Snoeks (2004).

**BODY.** Moderately elongate.

**HEAD.** Profile somewhat steep, clearly concave at eye level. Snout above upper jaw convex. Mouth very steep, vertically orientated with a gape inclination of 70–80°. Premaxillary pedicel small. Jaws



**Fig. 4.** Photographs of preserved specimens of *Protomelas krampus* sp. nov. **A.** Holotype (RMCA 99-041-P-4768). **B.** Paratype (RMCA 99-041-P-4767). Melanin pattern strongly faded.

**Table 4.** Measurements for *Protomelas krampus* sp. nov. (holotype and paratype), compared with the ranges and means of the examined specimens of *P. insignis* (Trewavas, 1935), *Hemitaeniochromis* sp. ‘*insignis* like’, *P. spilopterus* (Trewavas, 1935), *Hemitaeniochromis brachyrrhynchus* Oliver, 2012, *H. urotaenia* (Regan, 1922), *Caprichromis liemi* (McKaye & Mackenzie, 1982) and *C. orthognathus* (Trewavas, 1935).

	<i>P. krampus</i> sp. nov.		<i>P. insignis</i>	<i>H. sp. ‘insignis</i> like’	<i>P. spilopterus</i>	<i>H. brachyrrhynchus</i>	<i>H. urotaenia</i>	<i>C. orthognathus</i>	<i>C. liemi</i>
	Holotype	Paratype							
Morphometrics			Range, mean (n=4)	Range, mean (n=11)	Range, mean (n=11)	(n=1)	Range, mean (n=5)	Range, mean (n=4)	Range, mean (n=5)
Standard length (SL) in mm	116.1	181.1	81.7–161.0 (128.9)	76.9–172.4 (135.8)	85.5–166.0 (137.8)	81.6	87.8–182.7 (125.6)	122.0–154.1 (136.5)	103.2–173.2 (133.6)
Gape inclination (in degrees)	70	80	30 (30)	35–60 (47.3)	40–60 (45.9)	45	30–50 (41)	70–90 (80.5)	30–60 (48)
<b>As %SL:</b>									
Body depth	33.3	34.3	33.8–37.0 (35.6)	34.2–40.3 (37.2)	36.0–42.8 (38.9)	37.7	31.5–35.5 (33.6)	32.5–34.8 (33.8)	36.1–38.6 (37.4)
Head length	27.8	29.2	31.6–34.3 (32.5)	31.3–34.6 (33.0)	30.4–34.6 (32.9)	35.3	34.9–37.3 (36.1)	29.3–31.1 (30.3)	31.9–33.6 (32.8)
Precoracal distance	29.4	29.8	32.7–35.4 (33.7)	31.1–38.1 (34.5)	31.8–40.0 (35.3)	37.0	35.2–36.7 (36.2)	30.2–33.4 (32.0)	34.2–36.5 (35.2)
Predorsal distance	29.0	27.4	34.2–35.9 (34.9)	33.5–38.3 (35.7)	33.4–37.4 (36.2)	37.8	37.0–38.7 (37.6)	31.3–33.4 (32.5)	35.0–36.7 (35.6)
Preventral distance	39.0	44.4	40.1–42.9 (41.7)	38.6–48.3 (43.6)	41.2–51.0 (46.0)	46.1	41.7–45.4 (43.4)	39.7–44.1 (42.2)	42.8–48.7 (44.5)
Preamal distance	62.3	69.8	67.5–70.1 (68.8)	63.7–72.7 (69.3)	64.7–72.1 (69.1)	70.0	66.0–69.9 (67.7)	67.2–70.3 (68.4)	68.5–72.6 (70.7)
Dorsal fin base	53.6	58.3	52.0–58.7 (56.3)	50.5–56.6 (53.3)	49.8–57.6 (54.1)	54.3	49.3–50.5 (50.1)	52.9–54.3 (53.7)	55.3–56.6 (55.7)
Anal fin base	18.2	18.8	17.9–19.3 (18.6)	16.6–20.1 (18.1)	17.8–20.7 (19.4)	21.2	17.4–20.2 (19.0)	18.4–19.3 (18.9)	18.3–19.9 (19.2)
Caudal peduncle length	17.2	19.6	17.5–17.8 (17.7)	15.9–19.5 (18.1)	17.5–19.3 (18.4)	15.7	17.0–19.4 (18.2)	18.5–20.9 (19.4)	15.4–18.1 (17.0)
Caudal peduncle depth	11.6	12.6	12.3–13.2 (12.7)	11.3–13.7 (12.5)	11.4–14.1 (12.6)	12.6	11.3–12.8 (11.9)	12.3–13.2 (12.6)	11.2–13.4 (12.2)
Belly length	27.8	29.5	28.3–29.8 (29.2)	27.3–32.3 (29.7)	23.4–29.0 (26.1)	28.5	26.6–28.7 (27.8)	29.2–32.6 (30.5)	24.5–31.4 (28.5)
<b>As %HL:</b>									
Head width	39.3	40.3	41.3–44.8 (43.4)	40.8–46.8 (43.2)	41.4–50.7 (46.6)	43.8	40.5–42.5 (41.9)	40.7–45.5 (43.3)	35.9–38.2 (37.0)
Premaxillary pedicel length	19.2	17.0	27.9–30.0 (29.3)	24.7–30.7 (29.0)	21.8–28.4 (26.3)	27.1	27.5–28.9 (28.0)	21.9–25.4 (23.7)	24.7–28.0 (27.0)
Snout length	34.2	33.3	32.7–39.3 (36.4)	30.6–36.4 (33.6)	30.8–37.8 (33.9)	30.1	34.1–37.5 (35.6)	31.4–33.7 (32.2)	34.8–39.6 (37.2)
Lachrymal depth	20.4	19.6	21.4–22.4 (21.9)	17.4–25.3 (20.6)	13.6–22.7 (19.0)	17.2	22.7–23.3 (23.0)	18.6–22.4 (20.3)	20.8–23.9 (22.3)
Cheek depth	31.6	40.2	23.2–28.5 (25.7)	22.5–28.8 (26.0)	22.6–31.9 (27.4)	21.4	27.3–30.6 (29.0)	29.2–37.0 (33.1)	25.5–29.5 (27.7)
Eye diameter	27.0	22.5	23.7–29.9 (25.6)	21.6–30.5 (25.8)	24.9–30.4 (27.2)	32.2	21.6–27.6 (24.4)	22.7–25.4 (23.9)	19.5–24.6 (21.8)
Snout width	30.8	32.2	27.7–34.5 (31.5)	27.9–34.8 (32.3)	30.2–40.8 (34.9)	29.2	31.8–37.2 (34.2)	32.9–36.0 (34.2)	28.4–31.8 (30.0)
Interorbital width	22.9	23.4	26.9–32.8 (29.3)	23.3–30.6 (25.8)	25.0–33.6 (29.8)	22.1	23.2–26.0 (24.9)	23.2–28.2 (25.8)	20.4–23.6 (21.6)
Lower jaw length	37.7	38.8	31.2–37.3 (34.4)	28.9–35.0 (32.7)	29.6–39.1 (36.1)	32.9	37.6–40.6 (39.0)	37.8–39.2 (38.4)	33.6–38.4 (36.2)

**Table 5.** Meristics for *Protomelas krampus* sp. nov. (holotype and paratype), compared with the ranges of the examined specimens of *P. insignis* (Trewavas, 1935), *Hemitaeniochromis* sp. ‘*insignis* like’, *P. spilopterus* (Trewavas, 1935), *Hemitaeniochromis brachyrhynchus* Oliver, 2012, *H. urotaenia* (Regan, 1922), *Caprichromis liemi* (McKaye & Mackenzie, 1982) and *C. orthognathus* (Trewavas, 1935).

Meristics	<i>P. krampus</i> sp. nov.		<i>P. insignis</i> (n=4)	<i>H. sp. ‘insignis like’</i> (n=11)	<i>P. spilopterus</i> (n=11)	<i>H. brachyrhynchus</i> (n=1)	<i>H. urotaenia</i> (n=5)	<i>C. orthognathus</i> (n=4)	<i>C. liemi</i> (n=5)
	Holotype	Paratype							
Longitudinal series	32	31	31–34	30–34	29–31	33	30–34	31–33	32–33
Upper lateral line	23	20	23–26	21–27	19–26	22	21–24	21–25	25–27
Lower lateral line	14	17	13–17	13–16	12–15	14	13–17	13–15	13–16
Upper gill rakers	5	5	4–5	3–4	3–4	4	2–4	3–4	3–5
Lower gill rakers	11	10	9–13	11–12	9–12	10	9–11	9–12	11–12
Dorsal fin spines	17	17	16–18	16–18	15–16	17	16–17	15–17	17
Dorsal fin rays	11	12	10–11	9–10	10–11	10	9–10	10	10–11
Anal fin rays	9	10	9–10	8–9	8–10	9	9	9	9–10
Pectoral fin rays	15	13	14–15	13–15	12–15	14	14–15	13–14	11–14
Upper oral jaw teeth	37	40	43–50	24–46	21–38	37	35–48	33–42	44–47
Lower oral jaw teeth	31	36	34–42	24–34	23–36	32	25–37	42–50	44–59
Inner teeth rows	1	1	2	1–2	1–2	1	1–2	1–3	1–2
Vertebrae	31	32	31	29–31	29	30	30	30–31	31



**Fig. 5.** Photograph of preserved paratype (RMCA 99-041-P-4767) of *Protomelas krampus* sp. nov., shortly after preservation.

isognathous. Lower jaw long. Posterior side of lower jaw protrudes anteriorly. Anterior side of lower jaw slightly wider than posterior side. Deep chin. Larger specimen with larger mouth inclination and deeper chin. Lip longer than half length of lower jaw. Lips normal. Lower lip with mucosa embedding teeth. Preopercle also inclined. Long and slender gill rakers.

**TEETH.** Outer row of teeth on upper and lower jaws mostly unequally bicuspid and some posterior teeth unicuspid in smaller specimen; anterior teeth exclusively unicuspid on both jaws of larger specimen. Teeth straight and not curved inwards. Anterior cusps of teeth on outer row in both jaws larger than posterior cusps in smaller specimen. Anterior teeth larger than posterior teeth in smaller specimen. One inner row of irregularly placed tricuspid teeth on both jaws in smaller specimen. Posterior and inner teeth in larger specimen not readily observable, being to a large extent or fully covered by fleshy gums. Teeth closely set (space between teeth about half to one tooth width).

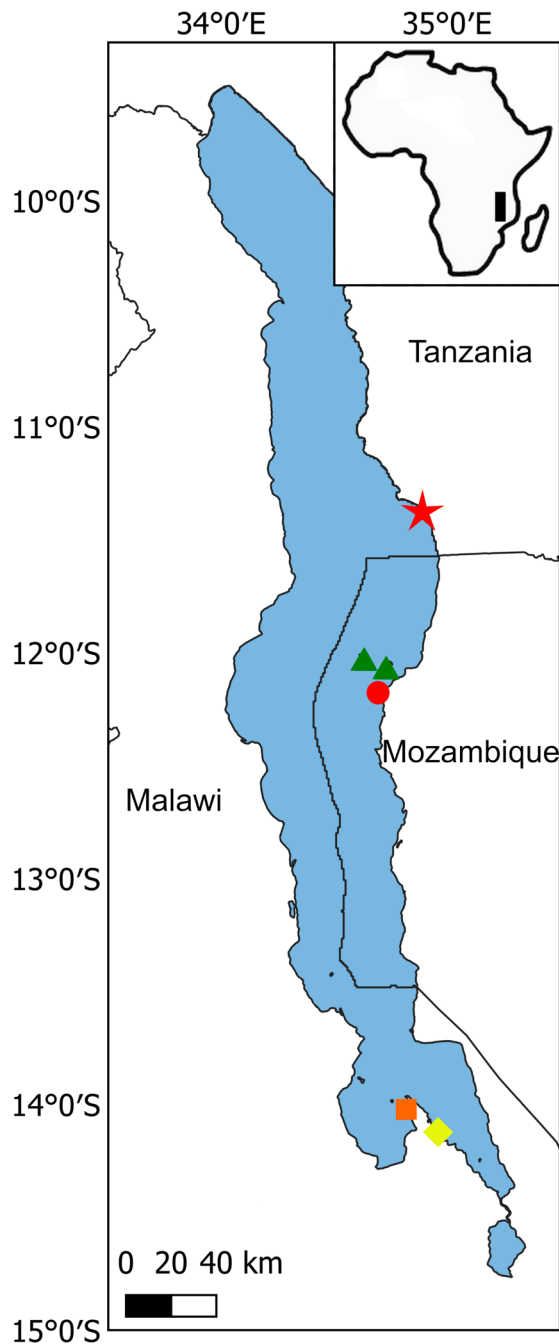
**FINS.** Pectoral fin origin behind level of dorsal fin origin in smaller specimen. Position of pectoral fin origin unknown in larger specimen because of damage. Pelvic fin origin positioned slightly more backwards than level of dorsal fin origin. Pectoral fin of holotype and pelvic fin in both types almost to level of anus. Anal fin anterior to level of first soft dorsal fin ray. Small scales on base of caudal fin rays.



**Fig. 6.** Photograph of live specimen of *Protomelas krampus* sp. nov. (specimen not preserved; length unknown) (copyright Ad Konings).

**Colour pattern in life**

Based on a photograph by Konings (2016) (Fig. 6). Body generally greyish. Head and pectoral fin base yellowish. Pelvic fin with white distal part of leading edge. Five orange-brownish eggspots on anal fin. Continuous dark midlateral band from about one eye length behind opercle to caudal fin. Supralateral row of dark spots. Dark spots also present just below dorsal fin. Some spots are arranged in an interrupted vertical bar pattern.



**Fig. 7.** Distribution map of *Protomelas krampus* sp. nov. Red star = holotype; red dot = paratype; green triangles = possible sightings by Konings (2016); orange square = possible sighting by McKaye & Kocher (1983); yellow diamond = possible sighting by Stauffer (pers. comm.). Inset: map of Africa with indication of area of Lake Malawi.

### Colour pattern in preserved specimens

Based on photographs by McKaye & Kocher (1983) and Snoeks (2004) (Fig. 5). Body generally brown or greyish. Dorsum somewhat darker than belly. Darker on dorsal parts of head and body contiguous with dorsal fin base. Clear dark maculae on spiny part of dorsal fin, possibly also on soft dorsal fin part and caudal fin. Continuous dark midlateral band from one eye length or about three scales behind opercle to caudal fin. One supralateral and one subdorsal row of dark spots. Some spots as subtle, incomplete vertical bars. Both types currently pale-coloured, probably due to light exposure (Fig. 4).

### Geographical distribution (Fig. 7)

The specimens of *P. krampus* sp. nov. were found in Lukoma Bay (11°22.50' S, 34°52.00' E), south of Mbamba Bay, Lake Malawi (Tanzania) and at rocks just south of Mara Point (12°11.34' S, 34°41.73' E), Aldeia Mala, Lake Malawi (Mozambique), at depths of 32.5–33.2 m. Three other specimens that also may belong to this species were caught near Otter Point (14°03' S, 34°49' E), Mangochi, Lake Malawi (Malawi), at a depth of 7–20 m (McKaye & Kocher 1983). It has also been observed near Chizumulu and Likoma Islands (Konings 2016) and Mazinzi Reef (Stauffer, pers. comm.). Hence the species has a confirmed distribution in the central-eastern part of the lake, but it may also occur in the southern part.

### Ecology

The behaviour and ecology of specimens most likely belonging to this species have been observed by McKaye & Kocher (1983) and Konings (1989, 2016). They observed this species feeding on eggs and fry while stealing them from mouth-brooding females of other cichlid species. The paedophage rams these females from above on the snout and the brooding females may release some eggs or larvae upon this impact. The brood can then be snatched by *P. krampus* sp. nov. The inclined position of the mouth enables the fish to immediately grab the brood since it is already in a good position relative to the prey after ramming from above (Konings 1989, 2016).

### Discussion

Based on its melanin pattern, the new species was assigned to the genus *Protomelas*. Eccles & Trewavas (1989) conducted an extensive review of the characteristics of all species of *Protomelas*. Based on these descriptions, only those species that are similar to the new paedophage species, *P. krampus* sp. nov., were included in the morphometric part of this study. Since *P. krampus* sp. nov. has only one inner tooth row, all twelve species with two or more inner rows (see diagnosis) were excluded from the detailed morphometric analyses. *Electochromis ornatus* (Regan, 1922), which according to Oliver (2012) and Konings (2016) belongs to *Protomelas*, was also excluded based on the number of inner tooth rows and melanin pattern as described by Eccles & Trewavas (1989). Only *P. spilopterus*, which was suggested by Eccles & Trewavas (1989) to be the undescribed paedophage species observed by McKaye & Kocher (1983), and *P. insignis* were retained for the morphometric comparison, as well as an undescribed species from this genus mentioned by Snoeks & Hanssens (2004) with some similar traits, *H. sp.* 'insignis like'. In the morphometric analyses it was found that *P. krampus* sp. nov. is distinguished from its congeners among others by its large gape inclination, very short premaxillary pedicel, deep cheek, long lower jaw, deep chin, short and slender head, small interorbital width, and shorter predorsal and prepectoral distance.

Both *C. orthognathus* and *P. krampus* sp. nov. have been observed showing a similar ramming behaviour (McKaye & Kocher 1983; Konings 2016), though the number of observations is limited; therefore, their strikingly similar morphology is probably linked to their food acquisition. The shorter head, the deep chin and short premaxillary pedicel of *P. krampus* sp. nov. enhance the aspect of an enlarged ventral part of the head. This may be an adaptation to the ramming behaviour typical of this species. *Caprichromis orthognathus* rams from beneath, whereas *P. krampus* sp. nov. rams from above with the ventral part



of the head. When the chin is enlarged, it is easier to use it as a ram from this orientation and possibly to have more impact on the snout of the prey. This may also explain the large gape inclination. The different angle of attack and slight differences in morphology may be explained by niche partitioning (McKaye & Kocher 1983). The precise phylogenetic relationships between the paedophagous species should, however, be further studied with genetic analyses and a thorough taxonomic revision.

During our analyses, it became clear that there may be an additional undescribed species within the genus *Protomelas*. The lectotype of *P. spilopterus* and one paralectotype (tag 2583 within BMNH 1935.6.14.652-657) differ from the other paralectotypes in several features. The head of these two specimens is steeper and the neurocranial crest appears to be more rounded. They show a clear chin, whereas the other paralectotypes lack a chin. The jaws of the lectotype and some paralectotypes are rounded, while the others have wide and anteriorly flattened jaws. The lacrimal appears to be somewhat larger and has a more rounded anterior side in the lectotype and paralectotype compared to the other paralectotypes. The caudal fin of the lectotype and paralectotype is emarginate, whereas the other paralectotypes of *P. spilopterus* have a truncate caudal fin with a longer dorsal lobe than ventral lobe. Furthermore, the lectotype has bicuspid teeth, the second cusp of which is very small, in the outer row on both jaws, and a mixture of uni- and tricuspid teeth on the two inner rows. Its teeth are curved inwards. The teeth of all paralectotypes are angled forwards and are uniquely unicuspid and conical, and there is only one inner tooth row on both jaws. The deepest point of the body occurs at the level of the pectoral fin origin in the lectotype and posterior to the pectoral fin origin in most paralectotypes. The eggspots on the anal fin of the lectotype are placed in three rows: the distal row with seven spots, the middle row with three spots and one spot in the proximal row. Only one other paralectotype has eggspots in two rows with five spots on the distal row and four or five spots on the proximal row. A more detailed study is necessary to assess whether or not the type series is polyspecific.

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