

Interochromis, a new genus of the Tanganyikan cichlid fish

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A new genus, *Interochromis*, is erected on the basis of morphological and ecological reviews on a cichlid species, *Limnotilapia loocki*, endemic to Lake Tanganyika. This species is an epilithic algal grazer, not browser, feeding mainly on unicellular algae, as in *Petrochromis*, and also a maternal mouthbrooder incubating larger eggs as in *Petrochromis*. Its intestinal coiling pattern is of the *Petrochromis* type and more complicated than that of the browsers. Osteologically, the shapes of the neurocranium, maxilla and suspensorial complex are similar to those of *Petrochromis*. Its jaw dentition is intermediate between that of grazers and browsers. The outer jaw teeth, except lateral ones, have the bicuspid crown bent linguad well with the slender stalk and are clearly larger than inner teeth, which have the tricuspid crown. *L. loocki* differs from a congener, *L. dardennii*. It resembles the grazers, *Petrochromis* spp., rather than the browsers, *Simochromis* spp., *Pseudosimochromis curvifrons* and *Tropheus moorii*. Though it has been proposed to synonymise the genus *Limnotilapia* with the genus *Simochromis*, it seems reasonable that *L. loocki* should be placed in a distinct new genus.

There has been much argument about the taxonomic status of the genus *Limnotilapia*.¹⁻⁴ On the basis of their shared osteological features, Greenwood¹ proposed to synonymise the genus *Limnotilapia* with the genus *Simochromis*. Poll² considered that morphological features in *Limnotilapia* are distinct from those in *Simochromis*, giving his opinion that the two genera be retained separately. However, he treated *L. loocki* as a member of the genus *Simochromis* (*S. loocki*). Yamaoka^{3,4} showed that the jaws, including jaw teeth and suspensorial complex of *L. loocki*, are not similar to those in *Simochromis*. In recent years the jaw and tooth morphology of *Limnotilapia loocki* Poll was found to be intermediate between those of the genus *Petrochromis* (a grazer) and *Simochromis*, *Tropheus*, *Pseudosimochromis* and *Limnotilapia dardennii* (all browsers),³ all of which are members of the same lineage inferred both from intestinal ontogeny⁵ and allozyme data.⁶ In this study, we describe the morphology of the intestinal coiling and syncranium bones, the feeding behaviour, food and breeding habits of *L. loocki*, an algal feeder endemic to Lake Tanganyika, occurring in the shallow rocky area of the shore.⁷ We, then, compare them with those of *Simochromis* spp. and review the taxonomic status of *L. loocki* from both morphological and ecological points of view.

Materials and methods

All materials but type specimens examined in the present study were deposited in the Department of Biology, Faculty of Science, Kochi University, Kochi, Japan (BSKU). Collection localities of *L. loocki* and other species were Kigoma in Tanzania and near Luhanga in Congo, respectively. For *L. loocki*, samplings were made in November and December 1983 by M.H. and T.K., and for other species, from November 1979 to November 1981 by K.Y.

For morphological study of the intestine, 10 specimens of *L. loocki* (BSKU 82704-82713, 37.6-121.4 mm in SL; standard length, 3 males, 3 females, 4 unknown) were used. The IP value refers to the number of intersecting points between coiling loops and a line set vertical to the body axis at the middle part of the intestinal mass.⁵ The IR value refers to the ratio of intestine length to standard length.

Specimens used for comparative osteological study are listed below. The specimens comprise *L. loocki* ($n = 4$, BSKU 82704-82707, 37.6-121.4 mm SL), *Limnotilapia dardennii* ($n = 5$, BSKU 82714-82718, 25.2-142.3), *Petrochromis polyodon* ($n = 4$, BSKU 82719-82722, 10.6-165.3), *P. fasciolatus* ($n = 4$, BSKU 82723-82726, 12.3-114.4), *P. orthognathus* ($n = 4$, BSKU 82727-82730, 16.7-114.3), *Pseudosimochromis curvifrons* ($n = 3$, BSKU 82731-82733, 14.3-89.4), *Simochromis diagramma* ($n = 5$, BSKU 82734-82738, 14.3-132.5), *S. babaulti* ($n = 3$, BSKU 82739-82741, 24.6-64.8), *S. marginatus* ($n = 3$, BSKU 82742-82744, 20.1-74.8), *Tropheus moorii* ($n = 4$, BSKU 82745-82748, 14.3-98.7). Skeletons were stained with alizarin red S. Glycerol was used as a clearing agent. The osteological nomenclature follows mainly Barel *et al.*⁸

We examined the holotype (RG106261, 73.4 mm SL, Kigoma, Tanzania, 24 Jan., 1947) and two paratypes (RG 106262, 57.9 mm SL, Kigoma, Tanzania, 9 Jan., 1947 and RG106265, 57.0 mm SL, Albertville, Congo, 10 Feb., 1947) deposited in the Royal Museum of Central Africa at Tervuren, Belgium. The holotype had been dissected at the parts of the pharyngeal bone and the gill arch. One paratype (RG106262) also had been dissected.

Information on the body coloration in life could be given from 8-mm movie film taken underwater at Kigoma where the holotype was collected. Concerning the coloration of fixed specimens, we used five examples (63.4-109.0 mm SL) collected at Kasenga.

Field observations were conducted in the coastal waters at Kigoma, Tanzania, and Kasenga Point, about 7 km north-east of Mpulungu, Zambia. *L. loocki* were found both in a shallow habitat (*c.* 1 m deep), composed of stones, rubble and reeds along the shore, and in a deeper habitat (*c.* 10 m deep), composed mainly of rocks and rocks on a sandy or muddy bottom. Especially at Kasenga Point, this species is dominant along the rocky shore.

Observations on general feeding behaviour were carried out by snorkeling in November and December, 1983 and January, 1984 at Kigoma by M.H. and T.K. The first author conducted underwater observations using SCUBA in October, 1996 along the shore at Kasenga Point. Feeding behaviour of adults was recorded by 8-mm movie camera or digital video camera (Sharp Digital Viewcam VL-DC1). To analyse the feeding behaviour, two parameters were measured; grazing speed (GS) and bites per bout (frequency of mouth-opening and mouth-closing per each pressing of the mouth against the rock surface).^{9,10} The number of adult individuals observed for the feeding behaviour was 9.

For stomach content analyses, nine large, mature specimens were caught on 11 and 13 December and 16 small, immature

ones on 22 November, 1983. Formalin solution (c. 10%) was injected into the body cavity to fix the digestive tract just after sampling in the field. The stomach contents were analysed by the points method¹¹ and the occurrence method.

Results and discussion

Intestine

The intestine occupied most of the ventral cavity as a voluminous mass and only the right gonad was developed in both males and females. The intestinal coiling pattern of *L. loocki* is certainly of the *Petrochromis* type, and probably of the *Petrochromis* subtype.⁵ The minimum IP value observed was 19 (found in the 42.3-mm SL specimen). The smallest specimen available, 37.6 mm SL, showed 21 IP and its IR was 4.29. The haplochromine loop extended well rostrad in the specimen. Maximum values of IP and IR were 35 and 6.88, respectively. Both IP and IR values increased with growth and thus there was no distinct species-specific IP value (Fig. 1).

IP values of *L. loocki* throughout growth (Fig. 1) are larger than those of *Simochromis* spp., *T. moorii*, *Ps. curvifrons* and *L. dardennii* (cf. Yamaoka⁵). The contrast in IP values between *L. loocki* and *L. dardennii* is especially conspicuous. The latter species reaches the maximum value (19) at about 70 mm SL and has the simplest coiling pattern within 10 species with a *Petrochromis* subtype of intestinal morphology. Larger specimens of *L. dardennii* show even smaller values (13, 15 or 17).⁵ The intestinal morphology of *L. loocki* is similar to that of *Petrochromis* rather than of browsers.

Neurocranium

The neurocranium of the algal feeding cichlids from Lake Tanganyika varies considerably not only in shape but in stoutness. Especially conspicuous interspecific differences in its morphology are exhibited in the ethmovomerine bloc (Yamaoka, unpub.). Reinthal¹² stated that for rock-dwelling cichlids from Lake Malawi the primary area of specific neurocranial shape variation within the group was the vomer region.

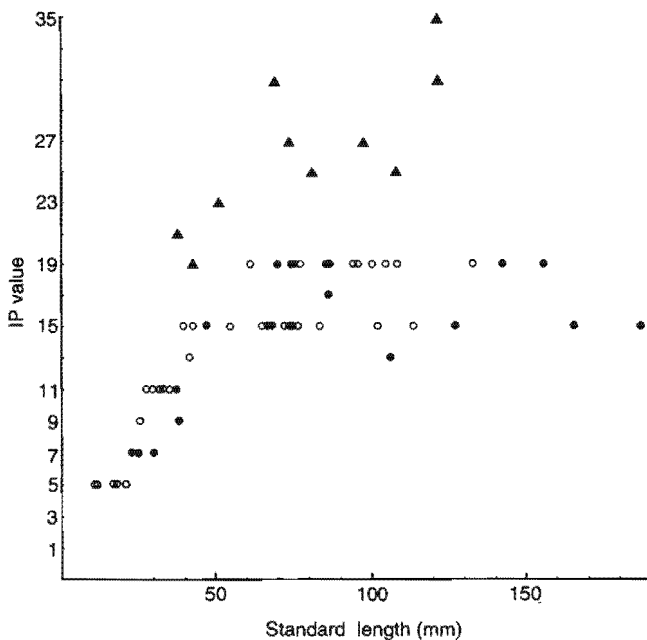


Fig. 1. Relation between standard length and IP value. Triangles, *Limnotilapia loocki*; filled circles, *L. dardennii*; open circles, *Simochromis diagramma*. Data on *L. dardennii* and *S. diagramma* modified from Yamaoka.⁵

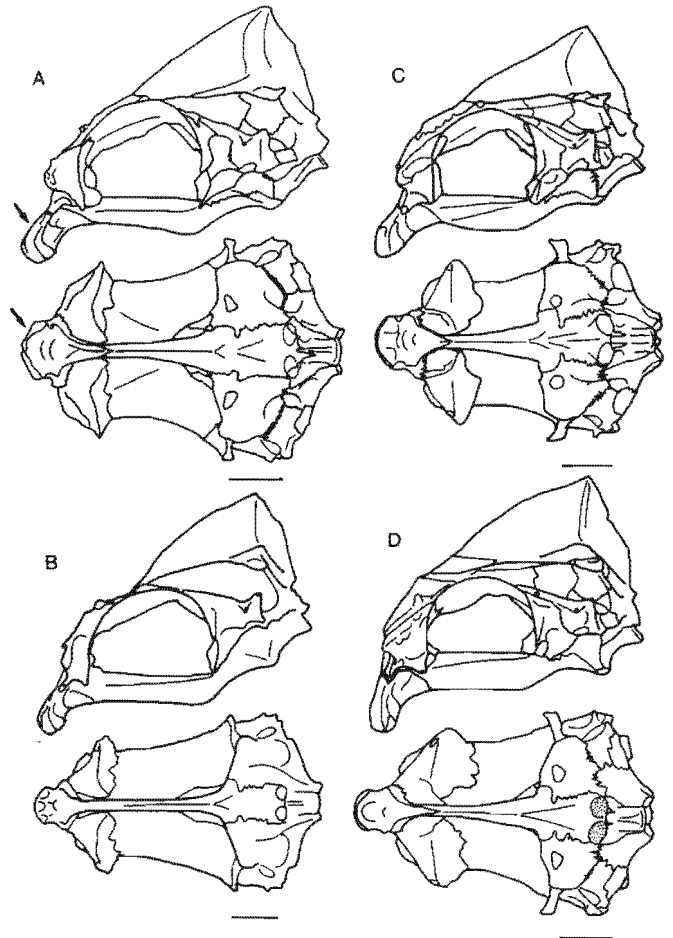


Fig. 2. Lateral (top) and ventral (bottom) views of the neurocranium. A, *Limnotilapia loocki* (BSKU 82704, 121.4 mm SL); B, *L. dardennii* (BSKU 82715, 142.2 mm SL); C, *Petrochromis orthognathus* (BSKU 82730, 114.3 mm SL); D, *Simochromis diagramma* (BSKU 82736, 132.5 mm SL). Arrow shows the ethmovomerine block. Scale = 5 mm.

The vomer is a main component of the ethmovomerine bloc. It is a median bone, forming the rostromost cap of the neurocranium and consists of two portions, a rostral head and a caudal stalk. The dorsal face of the rostral head functions as a basis on which the ascending arms of the premaxilla slide with an intervention of the rostral cartilage on mouth opening and closing. The neurocraniad condyle of the maxilla also slides on the latero-ventro-rostral face through the submaxillary meniscus. It is, therefore, clear that the ethmovomerine bloc plays an important role in feeding.

The ethmovomerine bloc of *L. loocki* has the following two features. First, the rostral head of the bloc projects rostroventrad and is large or moderate in width in ventral view. Second, the rostradorsal wall of the bloc is not steep in lateral view (Fig. 2). The two features are shared by *Petrochromis* spp. By contrast, *Simochromis* spp., *Pseudosimochromis curvifrons* and *Tropheus moorii* are distinctly different in terms of these two features. The rostral head of the bloc projects rather ventrad, and is relatively suppressed and small in width. Its rostradorsal wall is much or considerably decurved and steep in lateral view (Fig. 2). *L. dardennii* shows an intermediate, mosaic character state between that of *L. loocki* and of *Simochromis* spp., *Pseudosimochromis curvifrons* and *Tropheus moorii*. Its rostral head projects rostroventrad but is small in width, and the rostradorsal wall is not steep in lateral view.

The shape of the neurocranium of *L. loocki* is similar to that of grazers not only from Lake Tanganyika but also from Lake

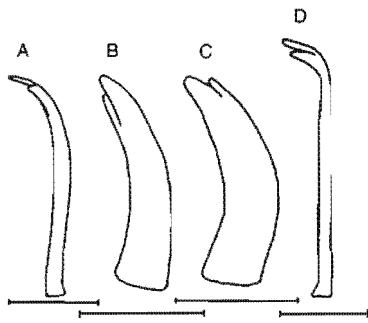


Fig. 3. Lateral view of outer tooth on lower jaw. A, *Limnotilapia loocki* (BSKU 82704, 121.4 mm); B, *L. dardennii* (BSKU 82714, 142.3 mm); C, *Simochromis diagramma* (BSKU 82736, 132.5 mm); D, *Petrochromis fasciolatus* (BSKU 82725, 114.4 mm). Scale = 1 mm.

Malawi. Reinthal¹² showed lateral views of the neurocranium of three Malawian epilithic algal feeding cichlids, *Pseudotropheus zebra*, *P. tropheops* and *Labeotropheus fuelleborni*. *L. loocki* is similar in neurocranial shape to *P. zebra*, which brushes loose aufwuchs from the rock surface,¹³⁻¹⁵ i.e. it is a grazer.

Jaw dentition

The morphology of the jaw teeth in *L. loocki* is unique among algal-feeding cichlids from Lake Tanganyika.³ It has the following distinctive features: 1) The teeth are arranged seemingly haphazardly, but they can be assigned to several tooth rows, and form a considerably wide tooth band similar to that of *P. fasciolatus*; 2) though the crown of outer jaw teeth is bicuspid as in browsers (*L. dardennii*, *Simochromis* spp., *Pseudosimochromis curvifrons*, *Tropheus moorii*), the long and flexible stalk of each outer jaw tooth and its backward curving crown are similar to those found in *Petrochromis* spp. (Fig. 3); and 3) the outer bicuspid teeth are movable, not attached firmly to the jaw bone as found in *Tilapia melanopleura* (now *Tilapia rendallii*) and *Tilapia nilotica* (now *Oreochromis niloticus*), which show the similar jaw tooth crown to that of *L. loocki* among Tanganyikan cichlids.⁷ Though the type specimens examined in the present study are small (holotype; 92 mm TL), their jaw dentition generally agreed with the above descriptions.

According to Poll,^{2,7} Yamaoka^{3,9} and Brichard,¹⁶ all jaw teeth are tricuspid in members of the genus *Petrochromis* and many of them have relatively long stalks with backward curving crowns. The bicuspid crown of the outer jaw teeth in *L. loocki* is, therefore, clearly different from the tricuspid jaw teeth in *Petrochromis* spp. However, other morphological aspects of the jaw dentition are similar to those of *Petrochromis* spp. We suggest that the morphology of the jaw dentition in *L. loocki* is intermediate between that of grazers and browsers.

In the above browsers, the outer jaw teeth are firmly fixed to the alveolar surface of the jaw and each tooth is not strongly curved backward at the crown.^{3,10} This dentition surely enables them to cut filamentous algae off a substrate. By contrast, on a functional-morphological basis, it seems almost impossible to cut off filamentous algae with such 'soft' dentition in *L. loocki*. In the original description of this species, Poll¹⁷ stated that the basal part of the jaw teeth is not fixed firmly.

Maxilla

The dorsal end of the neurocraniad condyle of the maxilla in *L. loocki* makes a triangular or circular facet in

dorsal view. This feature is shared with *Petrochromis* spp. By contrast, that in *Simochromis* spp., *Pseudosimochromis curvifrons*, *Tropheus moorii* and *L. dardennii* makes an elongate, oval-shaped facet (Fig. 4).

Generally, the neurocraniad condyle of the maxilla plays an important role in mouth opening in acanthopterygians and articulates with the vomer through the submaxillary meniscus.¹⁸ That is, the condyle functions as a mediator between the premaxilla with jaw dentitions and the base of jaw actions, the neurocranium. A form of the facet therefore seems to be correlated with the quality of the jaw action on feeding. The triangular or circular facet found in *L. loocki* and *Petrochromis* spp., grazers, may adjust itself easily to the diverse force applied from different directions. In contrast, the elongate, oval facet in *Simochromis* spp., *Pseudosimochromis curvifrons*, *Tropheus moorii* and *L. dardennii*, all browsers, may not be well adapted to diverse forces from several directions but be restricted to coping with a powerful force from a limited direction.

This speculation is consistent with the difference in foraging methods in natural habitats between grazers and browsers.^{9,10} According to Yamaoka,^{9,10} members of the genus *Petrochromis* open their mobile mouth and press the wide tooth band against every rock surface and edge that the mouth can reach. That is, they can adjust their jaw dentition to even minute topographic features of the substrate. *L. loocki*'s feeding behaviour is very similar to that of *Petrochromis* spp. Furthermore, there is no firm connection between the symphyseal articulation facet of the jaw and its counterpart, which controls the jaw action, in *L. loocki* and *Petrochromis* spp.³ This allows the two sides of the jaw to be less restricted by each other. Electromyographic study shows that *Petrotilapia tridentiger*, an epilithic algal scraper from Lake Malawi, which is morphologically and ecologically equivalent to *Petrochromis* spp.,^{15,19} adjusts the action of its bands of teeth against an irregular substrate, by modulating bilaterally asymmetrical muscle activity.²⁰ It is, therefore, probable that *Petrochromis* spp. have the same asymmetrical muscle firing system as found in *Petrotilapia tridentiger*. This modulating system might place the burden of diverse forces from various directions on the neurocraniad condyle of the maxilla.

In sharp contrast to the looseness of the symphyseal articulation in grazers, in the browsers *Simochromis* spp., *Pseudosimochromis curvifrons*, *Tropheus moorii* and *L. dardennii* it is tight.³ The tight symphyseal articulation will restrict bilaterally asymmetrical jaw action, but enable fish to perform precise and hard biting as a result of using right and left jaws as one unit. Small browsing marks²¹ and raps heard in the water whenever *T. moorii*

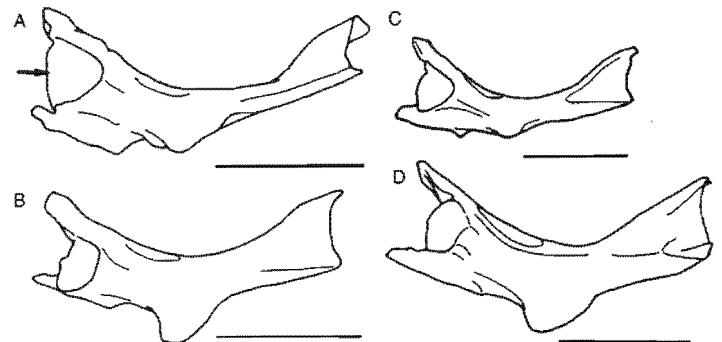


Fig. 4. Dorsal view of the maxilla. A, *Limnotilapia loocki* (BSKU 82704, 121.4 mm); B, *L. dardennii* (BSKU 82714, 142.3 mm); C, *Petrochromis orthognathus* (BSKU 82730, 114.3 mm); D, *Simochromis diagramma* (BSKU 82736, 132.5). Arrow shows articular facet of the neurocraniad condyle. Scale = 5 mm.

bites against a rock surface¹⁰ support this conclusion. The elongate, oval-shaped facet of the neurocranium condyle may be correlated with the force applied from particular directions when browsers bite.

Suspensorial complex

According to Yamaoka,⁴ the suspensorial complex in *L. loocki* shares mainly the following features with *Petrochromis* spp. and *L. dardennii*: 1) the ventrorostral margin of the complex at the ectopterygoid and quadrate runs almost vertically parallel to the caudal margin of the vertical limb of the preoperculum; and 2) the mesethmoidad process and lateroethmoidad articulation facet of the palatine are situated well dorsad. Some complementary descriptions are needed concerning the second feature. Thus, the dorsal level of the mesethmoidad process and lateroethmoidad articulation facet is almost the same and a notch develops between them (Fig. 5).

Simochromis spp., *Pseudosimochromis curvifrons* and *Tropheus moorii* have the characteristic feature that the whole rostral part of the complex protrudes rostrad, and as a result its ventrorostral margin (mainly at the ectopterygoid) has a weak rostral inclination and is not parallel to the caudal margin of the preoperculum.⁴ In addition to this, the lateroethmoidad articulation facet of the palatine tends to project more dorsad than the mesethmoidad process. This trend is conspicuous in *Ps. curvifrons* and *T. moorii* (Fig. 5). The notch observed between mesethmoidad process and lateroethmoidad articulation facet, developed in members of the genera *Limnotilapia* and *Petrochromis* in this study, is not obvious.

Yamaoka⁴ placed *L. dardennii* as a member of the same group as *L. loocki* and *Petrochromis* spp. However, we think it better to place the species between grazers (*L. loocki* and *Petrochromis* spp.) and browsers (*Simochromis* spp., *Pseudosimochromis curvifrons* and *Tropheus moorii*), because the positional relation between ventrorostral margin of the complex and caudal margin of the vertical limb of the preoperculum seems to be intermediate between the two groups.

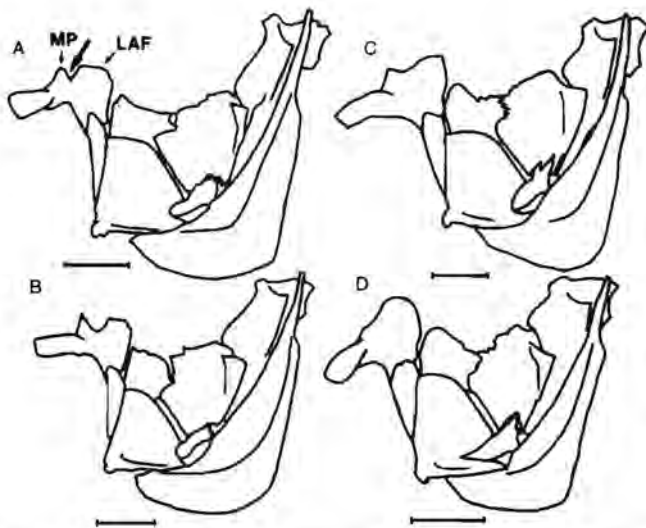


Fig. 5. Lateral view of the suspensorial complex. A, *Limnotilapia loocki* (BSKU 82704, 121.4 mm); B, *Petrochromis orthognathus* (BSKU 82730, 114.3 mm); C, *Simochromis diagramma* (BSKU 82736, 132.5 mm); D, *Pseudosimochromis curvifrons* (BSKU 82733, 89.4 mm). MP and LAF show the mesethmoidad process and lateroethmoidad articulation facet, respectively. Large arrow shows a notch between MP and LAF. Scale = 5 mm.

Table 1. Behavioural characters of adult individuals of *Limnotilapia loocki*.

No. of fish observed	9
Range of TL (cm)	c. 11–13
No. of bites per bout: mean \pm s.d. (no. of bouts observed)	2.67 \pm 1.11 (180)
GS: mean \pm s.d. (observation times)	3.53 \pm 0.55 (90)

Feeding behaviour

Adults were common in the deeper habitat. They foraged singly and pressed the mouth against the rock surface, scraping usually with a few bites per bout (Table 1). This feeding behaviour seems to be basically the same as that found in *Petrochromis* spp. and has been suggested to be adapted for scraping unicellular algae off rocks.⁹ A series of short repeated bites which are common to browsers, such as *Simochromis* spp., *T. moorii*, *Ps. curvifrons* and *L. dardennii*¹⁰ were not observed. However, occasionally a single bite with a lateral swing of the head was performed as is usual in browsers. Adults did not feed on the sandy or muddy bottom at Kigoma and Kasenga Point, but Y. Yanagisawa (pers. comm.) observed feeding action on the muddy bottom, at a depth of about 30 m, along the northwestern shore of the lake in Congo; many minute crateriform feeding marks were also found there.

Young were common in the shallow habitat, and usually scraped the surface of stones, but sometimes they pecked at the root mat of reeds near the shore. The number of bites per bout among the young (50–80 mm TL) was higher than for adults. The mean value of this character in the adult was not large (2.67), which was very similar to that (2.74) of a grazing species, *Petrochromis orthognathus*.⁹ The number of bites per bout decreased from young to adult. This trend is also found in *P. orthognathus*.¹⁰

The GS of *L. loocki* did not show a clear change with growth. The mean value of GS in the adult stage (3.53) was rather large compared with *Petrochromis* spp.⁹ The value for the adult stage was intermediate between *P. orthognathus* and *P. fasciatus*, which show the second fastest and fastest GS, respectively. Faster feeding speed has been suggested to be the most generalised feature for feeding behaviours.^{9,22}

Yamaoka¹⁰ has demonstrated on the basis of field observations that there are two major feeding methods in epilithic algal-feeding cichlids from Lake Tanganyika; grazing and browsing. The feeding behaviour of adult *L. loocki* is similar to that of the grazer, *P. orthognathus* or *P. fasciatus* and clearly different from that observed in the browsers, *Simochromis* spp., *T. moorii*, *Ps. curvifrons* and its congener, *L. dardennii*.¹⁰ Thus, *L. loocki* can be categorised as a grazer in terms of feeding behaviour.

Food

Stomach content analysis (Table 2) showed that *L. loocki* took mainly epilithic algae. They ingested mainly unicellular algae (diatoms), not filamentous algae, both at the young and adult stages. Adults did not feed on any animal material, but, in contrast, about half the specimens of young fish fed on a small amount of benthic animals. All specimens observed ingested sand.

According to Takamura,²³ *Petrochromis* spp. feed on unicellular algae whereas *Simochromis* spp., *T. moorii* and *Ps. curvifrons* feed on filamentous algae. *Limnotilapia dardennii*, a congener of *L. loocki*, has a tendency towards omnivory.²⁴ As for the food, *L.*

Table 2. Dietary composition of young and adult specimens of *Limnotilapia loocki*.

No. of specimens	Young (16)		Adult (9)	
	Points (%)	Frequency (%)	Points (%)	Frequency (%)
Range of SL (mm)	37.2–62.4		101.4–122.4	
Food items	Points (%)	Frequency (%)	Points (%)	Frequency (%)
Microfilamentous algae	5.8	88	1.1	11
Filamentous algae	9.6	94	6.5	44
Unicellular algae	56.9	100	64.5	100
Plant tissue	4.2	38	2.2	22
Shales	0.4	6	-	-
Ostracods	0.4	6	-	-
Shrimps	6.2	12	-	-
Ephemeroptera	0.8	12	-	-
Diptera	2.7	31	-	-
Hemiptera	0.4	6	-	-
Sand	12.7	100	25.8	100

loocki is similar to *Petrochromis* spp. in taking unicellular algae. This is also supported by Poll,⁷ who records the intestine in specimens of this species as being full of bottom mud and diatoms.

Breeding habits

One mouthbrooding specimen (110.6 mm SL) was collected in the offshore boulder area at a depth of 4 m. It was a female which incubated 22 eggs; the egg size was 6.64 ± 0.17 mm along the major axis and 4.97 ± 0.19 mm in diameter (mean \pm s.d., $n = 10$). The egg size belongs to the largest class among the Tanganyikan cichlids and is similar to that of *Petrochromis* spp. (6.0–7.1 mm along major axis) rather than that of *Simochromis* spp. (4.5–5.2 mm).²⁵ Only the right gonad is present.

Although the spawning act was not observed, courtship display by large (c. 15 cm TL) males towards visiting females was often seen: the male quivered his tail in a head-up position by the side of a rock. No special 'nest' was made by the male, and the courtship site was not restricted to a single rock. These characteristics of courtship site resemble those of *Petrochromis* rather than those of *Simochromis*.²⁵

These morphological and ecological data show that *L. loocki* is more closely related to members of the genus *Petrochromis*, which are grazers, than those of the browsers *Simochromis*, *Pseudosimochromis*, *Tropheus* and *L. dardennii*¹⁰, though, on the evidence of each morphological character, for example, the jaw teeth of both grazers and browsers manifest a mosaic of character states.

According to Greenwood,¹ the morphological gap found in the premaxilla and dentary between the type species of the genera *S. diagramma* and *L. dardennii* is bridged when one examines *L. loocki*, the morphology of whose bones is intermediate between the two species. However, the differences in the outline of these bones, viewed from below, between *S. diagramma* and *L. dardennii* may be related to the differences in their feeding behaviour. *S. diagramma* takes mainly filamentous algae,²³ for which a straight and wide anterior jaw margin is more fitted than a curved one because the former can press a wider jaw margin to the rock surface than the latter on a flat rock surface on each bite. *L. dardennii* has a tendency towards omnivory,²⁴ that is, it must take diverse foods for which a non-specialised, gently curved jaw seems to be suitable. The differences in the outline of the

premaxilla and dentary are suggested to be more closely related with feeding behaviours than phylogenetic relationships.

Limnotilapia loocki, *L. dardennii* and *Simochromis* spp. have been pointed out to share slender-shafted, recurved, outer jaw teeth, suggesting that there would be no grounds for treating *Limnotilapia* and *Simochromis* as distinct genera.¹ The main reason for this supposition seems to be the tooth figures shown in the original paper¹⁷ and a familiar book.¹⁹ Despite its original description that each jaw tooth of *L. loocki* has the slender shaft,¹⁷ since the distal part of the outer jaw tooth was figured and its slender shaft, which is hidden in the labial papillae, was not shown, only the distal tooth part was probably misunderstood as the short and stout outer jaw tooth. As shown in Fig. 4, an outer jaw tooth in both *L. dardennii* and *S. diagramma* is very similar, not slender but rather stout, but that of *L. loocki* is clearly different from that in the two other species.

Recently, the shape of the oral jaw teeth has been suggested to be highly variable and thus is not a reliable character for taxonomic purposes.²⁶ We intend to make a comparative morphological and ecological study of certain species inhabiting both the northern and southern parts of Lake Tanganyika to elucidate the degree of variation within each species.

Based on the above facts, we propose to place *L. loocki* in a new genus, *Interochromis*. The third species of the genus *Limnotilapia*, *L. trematocephala*, is not treated here, because it probably belongs to a different lineage and should not be included in the genus.¹

Interochromis gen. nov.

Type species: *Limnotilapia loocki* Poll, 1949.

Diagnosis

The genus is distinguishable from other genera in the family Cichlidae by the following combination of characters. Outer jaw teeth generally bicuspid and inner ones all tricuspid. Bicuspid teeth clearly larger than tricuspid ones. Outer jaw teeth, except lateral ones on the dentigerous lateral arms, movable (not firmly attached to jaw bone) and brown bicuspid crown bent linguad well with slender, long stalk. Gill-rakers on lower limb of first left arch 10–15. Only right gonad present.

Descriptions

This genus is endemic to Lake Tanganyika with only one species: *L. loocki* (Poll, 1949). Body rather deep. Upper jaw meets the lower almost evenly in front (isognathous). Outer jaw teeth are generally movable and have the brown bicuspid crown bent linguad well with the slender, long stalk. Outer teeth clearly larger than inner teeth generally having the tricuspid crowns. Jaw teeth arranged seemingly haphazardly, but counted into several rows (maximum 8), form tooth band in adults. The intestinal coiling pattern is surely of the *Petrochromis* type and there is no species-specific IP value. Only right gonad present.

Body depth 2.48–2.68 times standard length (holotype, 2.48; paratypes, 2.57 and 2.55). D. XVIII–XX, 8–9 (holotype, XVIII, 8; paratypes, XVIII, 8 and XVIII, 9) A. III, 6–7 (holotype, III, 6; paratypes, III, 6 and III, 7). Numbers of lateral-line scales 32–33 (holotype, 33; paratypes, 31 and 33). Gill-rakers on lower limb of first left arch 10–15. Vertebrae 31–32 [15–16 (abdominal) + 15–16 (caudal)]. Maximum size c. 150 mm TL.

Colour in life: Dorsum brown. Ventral part of body whitish. Nine brown vertical stripes on flank. Head with yellowish patches and especially at roof region of orbit conspicuous. Ventral fin whitish. Spine part of anal fin orange. Several yellow egg

dummies on anal fin. Caudal fin with dark parts at dorsal and ventral region.

Colour in formalin: Dorsum dark brown and head brown. Ventral part of body whitish brown. Especially in smaller specimens, 9 dark brown stripes conspicuous on flank. Caudal striped with many brown circular maculations.

Conclusions

A morphological and ecological study showed that *Limnotilapia loocki* Poll, 1949 (Cichlidae, from Lake Tanganyika) differs in certain respects from *L. dardennii*, and that it resembles the grazer *Petrochromis* rather than the browsers *Simochromis* spp., *Ps. curvifrons* and *T. moorii*. Though it has been proposed to synonymise genus *Limnotilapia* with genus *Simochromis*, we think it reasonable to place *L. loocki* in a distinct genus. A new genus *Interochromis* is proposed.

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- Greenwood P.H. (1979). Towards a phyletic classification of the genus *Haplochromis* (Pisces, Cichlidae) and related taxa. Part 1. *Bull. Br. Mus. nat. Hist. (Zool.)* **35**, 265–322.
- Poll M. (1986). Classification des Cichlidae du lac Tanganika: Tribus, genres et espèces. *Acad. r. Belg. Mem. classe sci.* **45**, 1–163.
- Yamaoka K. (1987). Comparative osteology of the jaw of algal-feeding cichlids (Pisces, Teleostei) from Lake Tanganyika. *Rep. Usa Mar. Biol. Inst. Kochi Univ.* **9**, 87–137.
- Yamaoka K. (1988). Comparative osteology of the suspensorial complex of algal-feeding cichlids (Pisces, Teleostei) from Lake Tanganyika. *Afr. Stud. Monogr.* **9**, 65–84.
- Yamaoka K. (1985). Intestinal coiling pattern in the epilithic algal-feeding cichlids (Pisces, Teleostei) of Lake Tanganyika, and its phylogenetic significance. *Zool. J. Linn. Soc.* **84**, 235–261.
- Nishida M. (1991). Lake Tanganyika as an evolutionary reservoir of old lineages of East African cichlid fishes: Inferences from allozyme data. *Experientia* **47**, 974–979.
- Poll M. (1956). Poissons Cichlidae. Resultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. r. sci. nat. Belg.* **3(5B)**, 1–619.
- Barel C.D.N., Witte F. and van Oijen M.J.P. (1976). The shape of the skeletal elements in the head of the generalized *Haplochromis* species: *H. elegans* Trewavas 1933 (Pisces, Cichlidae). *Neth. J. Zool.* **26**, 163–265.
- Yamaoka K. (1982). Morphology and feeding behaviour of five species of genus *Petrochromis* (Teleostei, Cichlidae). *Physiol. Ecol. Japan* **19**, 57–75.
- Yamaoka K. (1983). Feeding behaviour and dental morphology of algae scraping cichlids (Pisces: Teleostei) in Lake Tanganyika. *Afr. Stud. Monogr.* **4**, 77–89.
- Hynes H.B.N. (1950). The food of freshwater sticklebacks, with a review of method used in studies of the food of fishes. *J. Anim. Ecol.* **19**, 36–58.
- Reinthal P.N. (1990). Morphological analyses of the neurocranium of a group of rock-dwelling cichlid fishes (Cichlidae: Perciformes) from Lake Malawi, Africa. *Zool. J. Linn. Soc.* **98**, 123–139.

- Fryer G. (1959). The trophic interrelationships and ecology of some littoral communities in Lake Nyasa with special reference to the fishes, and a discussion of the evolution of a group of rock-frequenting Cichlidae. *Proc. zool. Soc. Lond.* **132**, 153–281.
- Holzberg S. (1978). A field and laboratory study of the behaviour and ecology of *Pseudotropheus zebra* (Boulenger), an endemic cichlid of Lake Malawi (Pisces: Cichlidae). *Z. zool. Syst. Evol.-forsch.* **16**, 171–187.
- Ribbink A.J., Marsh B.A., Marsh A.C., Ribbink A.C. and Sharp B.J. (1983). A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi. *S. Afr. J. Zool.* **18**, 149–310.
- Brichard P. (1989). *Cichlids and All the Other Fishes of Lake Tanganyika*. T.F.H. Publications, New Jersey.
- Poll M. (1949). Deuxième série de Cichlidae nouveaux recueillis par la Mission hydrobiologique belge au lac Tanganika (1946–1947). *Bull. Inst. r. sci. nat. Belg.* **25**, 1–55.
- Alexander R.McN. (1967). The functions and mechanisms of the protrusible upper jaws of some acanthopterygian fish. *J. Zool. (Lond.)* **151**, 43–64.
- Fryer G. and Iles T.D. (1972). *The Cichlid Fishes of the Great Lakes of Africa; Their Biology and Evolution*. Oliver & Boyd, Edinburgh.
- Liem K.F. (1980). Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Amer. Zool.* **20**, 295–314.
- Takamura K. (1983). Interspecific relationship between two Aufwuchs eaters *Petrochromis polyodon* and *Tropheus moorei* (Cichlidae) of Lake Tanganyika. *Physiol. Ecol. Japan* **20**, 59–69.
- Yamaoka K. (1991). In *Cichlid Fishes: Behaviour, Ecology and Evolution*, ed. M.H.A. Keenleyside, chap. 7, pp. 151–172. Chapman & Hall, London.
- Takamura K. (1984). Interspecific relationships of aufwuchs-eating fishes in Lake Tanganyika. *Environ. Biol. Fish.* **10**, 225–241.
- Hori M., Yamaoka K. and Takamura K. (1983). Abundance and micro-distribution of cichlid fishes on a rocky shore of Lake Tanganyika. *Afr. Stud. Monogr.* **3**, 25–38.
- Kuwamura T. (1986). Parental care and mating systems of cichlid fishes in Lake Tanganyika: a preliminary field survey. *J. Ethol.* **4**, 129–146.
- Verheyen E., Ruber L., Snoeks J. and Meyer A. (1996). Mitochondrial phylogeography of rock-dwelling cichlid fishes reveals evolutionary influence of historical lake level fluctuations of Lake Tanganyika, Africa. *Phil. Trans. r. Soc. Lond. B*, **351**, 797–805.

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