Taxonomy of Small-sized Cichlid Fishes in the Shell-bed Area of Lake Tanganyika

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Abstract Several species of small-sized cichlid fishes inhabit the shell-bed area at Rumonge, Burundi, in the northeastern part of Lake Tanganyika. Some of them are very similar in morphology to the known species occurring in rocky and sandy habitats, but their bodies are unusually small. Investigations of three such small-sized cichlids were made from taxonomic point of view, and it was concluded that they represent small morphs of *Altolamprologus compressiceps*, *Lamprologus callipterus* and *Neolamprologus mondabu*. Their small bodies and some minor morphological differences were interpreted as adaptations to the utilization of empty shells as brooding sites and shelters in the shell-bed environment.

Lake Tanganyika is the oldest of the Great Rift Valley lakes, and its shores consist of various types of habitats for cichlids and other freshwater fishes. A major fraction of the cichlid fishes inhabiting the lake live along the shoreline, mainly in rocky and sandy habitats, and the morphologically and behaviorally diverse species are included (Brichard, 1989; Konings and Dieckhoff, 1992; Nishida, 1991).

During expedition to Lake Tanganyika in 1992 and 1993, we collected specimens of several species of small-sized cichlids, which take care of eggs or young inside the shells of the gastropod, *Neothauma tanganicense*, from shell-bed area off the sandy coast of Rumonge, Burundi. The bottom of the shell-bed area is almost completely covered with empty shells of *N. tanganicense*, representing one of the most characteristic habitats of aquatic organisms in the lake (Sato and Gashagaza, in press). These small cichlid fishes from the shell-bed are morphologically similar to the species occurring in rocky and sandy habitats, but they become mature at very small sizes and do not grow large. For example, females of a species similar to *Altolamprologus compressiceps* are already mature at lengths less than 40 mm SL, and the largest specimen collected there was a mature male of 57.0 mm SL. Female *A. compressiceps* in rocky habitats usually attains maturity at sizes around 60 mm SL, with the largest male recorded being 120 mm SL (Gashagaza, 1991). Similar phenomena were also observed in the fishes resembling *Neolamprologus mondabu*, *Lamprologus callipterus* and some others. However, to date these fishes have not been studied taxonomically, and whether or not they represent small morphs of known species living in other habitats, or different undescribed species, is unclear. The identity of these small fishes is of great importance to the studies of geographical variation and morphological plasticity among Lake Tanganyikan cichlids, as well as to the ecological studies of the unique shell-bed environment.

The purpose of present study is to establish the identity of three small-sized cichlid fishes of the Rumonge shell-bed. In addition, the adaptive significance of small-sized body and other morphological modifications in this unique shell-bed environment are briefly discussed.

Materials and Methods

Study materials were collected on a shell-bed off the vast and flat sandy coast of Rumonge, about 75 km south of Bujumbura, Burundi (Fig. 1). The Rumonge shell-bed is a monotonous stretch of empty

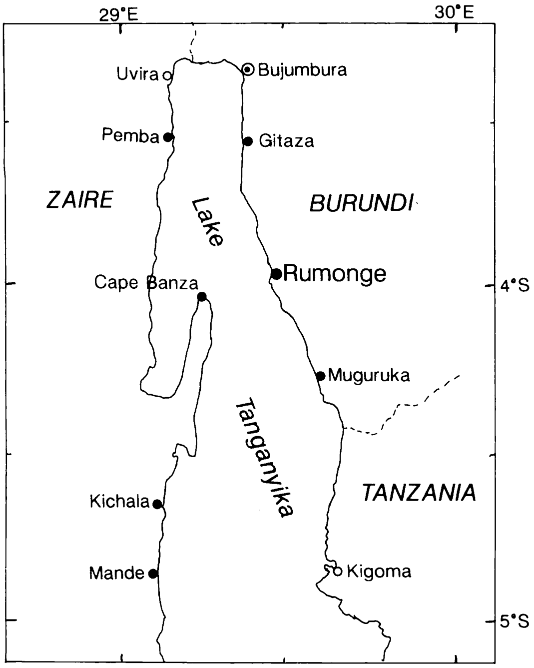

Fig. 1. Schematic map of northern part of Lake Tanganyika, showing collection sites (●).

gastropod shells of *Neothauma tanganicense* on the flat sandy bottom, extending for some kilometers from about 9 to at least 13 m in depth. Most exposed shells of *N. tanganicense* are heavily calcified. Some dead bivalve shells (*Iridina spekei*) and sponges are patchily distributed, but there is no aquatic vegetation.

Fish specimens were collected at different depths, using SCUBA, in November 1992, and January and September 1993. Shells accommodating fishes were sampled intensively by hand, and schooling and solitary fishes were caught using gill-nets. Fishes were transported alive to the laboratory for photography and then preserved in 10% formalin.

The Rumonge shell-bed specimens were compared with specimens of *Altolamprologus compressiceps*, *Lamprologus callipterus* and *Neolamprologus mondabu* collected from various localities in the lake (Fig. 1). Counts and measurements followed Hubbs and Lagler (1958), except for those of unpaired fins, the last ray being counted as two independent elements following Trewavas (1983). Materials from Rumonge and comparative materials (Table 1) are deposited in the fish collection of Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University (HUMZ). Some specimens from Fisheries Research Laboratory, Mie University (FRLM) were used for photography.

Results

Altolamprologus specimens from Rumonge (RA specimens)

The genus *Altolamprologus* Poll, 1986 is endemic to Lake Tanganyika and consists of two species: *A. compressiceps* (Boulenger, 1898) and *A. calvus* (Poll, 1978). Specimens from Rumonge (RA specimens) are characterized by the presence of scales on the nape and 9–10 anal spines, thereby differing from *A. calvus*, which lacks scales on nape and has 11–13 anal spines (Poll, 1978).

Mature male and female RA specimens (Fig. 2, top and second) are outstandingly smaller than mature specimens of conventional *A. compressiceps* (Fig. 2, third and bottom). Maximum sizes of males and females were 57.0 mm SL and 41.2 mm SL for RA specimens, and 114.8 mm SL and 66.9 mm SL for *Altolamprologus compressiceps*, respectively. Gashagaza (1991) reported the sizes of mature *A. compressiceps* as ranging from 80 to 120 mm SL (males), and from 55 to 80 mm SL (females).

Comparison of counts and measurements of RA specimens with those of *A. compressiceps* (Table 2) shows strong coincidence, except for scales on the lower lateral line. The lower lateral line scales were 3–9 in RA specimens, but the type specimens of *A. compressiceps* have 9–10 scales (Boulenger, 1898).

Morphologically, there are little differences between RA specimens and *Altolamprologus compressiceps*, including the distribution of scales on the occiput. Differences found are as follows: dorsal profile of head nearly straight, or only slightly concave in RA specimens, but concave in *A. compressiceps*; upper jaw reaching anterior margin of eye in RA specimens, but not reaching in *A. compressiceps*; dorsal fin base tending to be shorter in RA specimens (Fig. 3); clear vertical bands on body in RA specimens (Fig. 2), but vertical bands present only in young stages in *A. compressiceps* (Poll, 1956); light brown ground body color in all RA specimens, but very dark in large *A. compressiceps.*

RA females spawn inside empty shells, which are utilized as brooding sites for wrigglers. The females often stay at the entrance of the shell during the brooding period, and sometimes enter, possibly to

Table 1. List of study materials

No.	SL (mm)	Locality*	No.	SL (mm)	Locality*
Altolamprologus specimens from Rumonge (RA specimens):					
HUMZ 127264	52.1	RUM	HUMZ 133192	46.1	RUM
HUMZ 133193	48.1	RUM	HUMZ 133194	39.4	RUM
HUMZ 133195	46.0	RUM	HUMZ 133196	36.9	RUM
HUMZ 133197	48.5	RUM	HUMZ 133198	41.2	RUM
HUMZ 133199	40.9	RUM	HUMZ 133200	46.1	RUM
HUMZ 133201	57.0	RUM			
Altolamprologus compressiceps:					
HUMZ 127227	108.2	GIT	HUMZ 127251	62.9	GIT
HUMZ 127288	52.2	GIT	HUMZ 127298	58.1	GIT
HUMZ 127299	89.7	GIT	HUMZ 127377	55.9	GIT
HUMZ 127376	51.1	GIT	HUMZ 127378	64.0	GIT
HUMZ 127409	63.3	GIT	HUMZ 127410	66.9	GIT
HUMZ 127411	110.8	GIT	HUMZ 127678	50.8	CBA
HUMZ 127892	71.2	CBA	HUMZ 128137	62.9	CBA
HUMZ 128569	54.0	GIT	HUMZ 128570	64.9	GIT
HUMZ 132926	109.1	MAN	HUMZ 132927	114.8	MAN
HUMZ 132928	102.9	MAN	HUMZ 132929	88.9	MAN
HUMZ 132930	89.1	MAN	HUMZ 132931	86.0	MAN
HUMZ 132932	89.9	MAN	HUMZ 132933	60.3	MAN
Lamprologus specimens from Rumonge (RB specimens):					
HUMZ 133202	51.1	RUM	HUMZ 133203	45.1	RUM
HUMZ 133204	47.2	RUM	HUMZ 133205	47.0	RUM
HUMZ 133206	51.0	RUM	HUMZ 133207	49.3	RUM
HUMZ 133208	47.8	RUM	HUMZ 133209	43.0	RUM
HUMZ 133210	49.1	RUM	HUMZ 133211	45.4	RUM
HUMZ 133226	46.7	RUM	HUMZ 133227	35.8	RUM
HUMZ 133228	34.0	RUM			
Lamprologus callipterus:					
HUMZ 116469	68.9	PEM	HUMZ 116610	79.9	PEM
HUMZ 116771	74.8	PEM	HUMZ 116772	86.8	PEM
HUMZ 116807	53.5	PEM	HUMZ 117990	46.5	PEM
HUMZ 118108	50.0	PEM	HUMZ 118265	51.3	PEM
HUMZ 118269	58.7	PEM	HUMZ 127188	46.3	GIT
HUMZ 127148	58.7	GIT	HUMZ 127152	89.8	GIT
HUMZ 127313	53.0	GIT	HUMZ 127314	55.0	GIT
HUMZ 127317	86.9	GIT	HUMZ 127592	68.0	GIT
HUMZ 127652	46.0	GIT	HUMZ 128422	71.8	MUG
HUMZ 128423	60.8	MUG	HUMZ 128485	78.8	GIT
HUMZ 128690	68.1	GIT	HUMZ 132934	114.2	KIC
HUMZ 132935	100.0	KIC	HUMZ 132937	97.0	KIC
HUMZ 132938	107.8	KIC	HUMZ 132940	111.4	KIC
HUMZ 132941	115.9	KIC	FRLM 12734	42.0	ZAM
Neolamprologus specimens from Rumonge (RC specimens):					
HUMZ 127101	41.2	RUM	HUMZ 127111	37.9	RUM
HUMZ 127112	32.8	RUM	HUMZ 127268	32.8	RUM
HUMZ 127269	48.2	RUM	HUMZ 133212	44.1	RUM
HUMZ 133213	43.9	RUM	HUMZ 133217	43.8	RUM

Table 1. (continued)

No.	SL (mm)	Locality*	No.	SL (mm)	Locality*
Neolamprologus mondabu:					
HUMZ 116422	70.7	PEM	HUMZ 116425	51.9	PEM
HUMZ 116453	66.9	PEM	HUMZ 116571	64.9	PEM
HUMZ 116584	50.1	PEM	HUMZ 118090	82.3	PEM
HUMZ 118092	77.1	PEM	HUMZ 118094	71.0	PEM
HUMZ 118096	84.1	PEM	HUMZ 118112	43.8	PEM
HUMZ 118114	46.5	PEM	HUMZ 118116	51.5	PEM
HUMZ 118121	47.4	PEM	HUMZ 118122	44.8	PEM
HUMZ 118124	44.9	PEM	HUMZ 118279	62.0	PEM
HUMZ 127135	70.1	GIT	HUMZ 127137	41.2	GIT
HUMZ 127172	44.4	GIT	HUMZ 127174	41.9	GIT
HUMZ 127175	42.9	GIT	HUMZ 127176	42.9	GIT
HUMZ 127177	41.1	GIT	HUMZ 127217	76.3	GIT
HUMZ 127516	82.5	MUG	HUMZ 127542	40.9	GIT
HUMZ 127628	55.0	MUG	HUMZ 127630	47.1	MUG
HUMZ 127632	55.9	MUG	HUMZ 127633	65.4	MUG
HUMZ 127657	46.0	GIT	HUMZ 127658	43.7	GIT
HUMZ 127663	63.9	GIT			

* CBA, Cape Banza; GIT, Gitaza; KIC, Kichala; MAN, Mande; MUG, Muguruka; PEM, Pemba; RUM, Rumonge; ZAM, Wonzyie, Zambia.

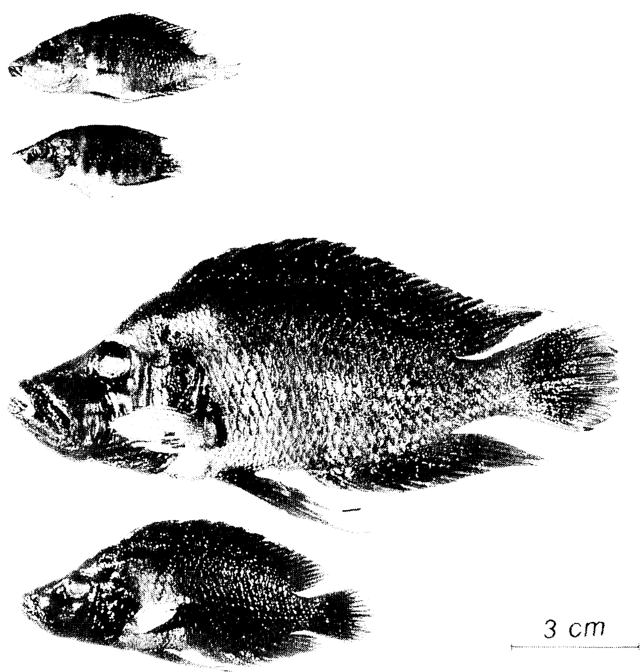

Fig. 2. RA specimens from Rumonge (*top two*) and *Altolamprologus compressiceps* from Gitaza (*bottom two*). From top to bottom: HUMZ 133200 (male, 46.1 mm SL), HUMZ 133196 (female, 36.9 mm SL), HUMZ 127411 (male, 110.8 mm SL), HUMZ 127410 (female, 66.9 mm SL).

ventilate the young. They rush into the shell when disturbed. RA males use other large empty shells as shelters when they were chased. In rocky areas, female *A. compressiceps* use small holes just sufficiently wide and deep to accommodate them (Gashagaza, 1991). Males control a large breeding territory, and use the rock undersurfaces or crevices as shelters.

Lamprologus specimens from Rumonge (RB specimens)

The genus *Lamprologus* Schilthuis, 1891 includes about ten species from Lake Tanganyika and the Zaire river basin. Specimens from Rumonge (RB specimens) are characterized by having 18–19 dorsal spines, 7–8 anal spines, and a rounded caudal fin. These characters suggest its closest affinity with *Lamprologus callipterus* (Boulenger, 1906), which is endemic to the lake.

Mature male RB specimens (Fig. 4, top) are extremely smaller than those of *L. callipterus* (Fig. 4, third). Maximum sizes of males were 51.1 mm SL for RB specimens, but 115.9 mm SL for *L. callipterus.* Sato (1994) also reported that sizes of mature

Table 2. Counts and measurements of RA specimens from Rumonge and *Altolamprologus compressiceps*

Characters	RA specimens	*A. compressiceps*	
	$n=11$	$n=25$	$(n=1)$*
Total length (mm)	—	—	(83.0)
Standard length (SL, mm)	36.9–57.0	50.8–114.8	—
Counts			
Dorsal spines	19–20	19–20	(20–21)
Dorsal softrays	5–6	5–6	(6)
Anal spines	9–10	9–10	(10)
Anal softrays	4–5	4–6	(5)
Pectoral fin rays	13	12–13	—
Pelvic fin rays	I, 5	I, 5	—
Caudal fin rays	14	12–14	—
Longitudinal scales	30–33	31–34	(32–33)
Upper lateral line scales	20–25	23–29	(22–23)
Lower lateral line scales	3– 9	6–11	(9–10)
Scales below lateral line	12–14	12–14	(12)
Gill rakers	13–16	13–16	(15)
Canine teeth (upper jaw)	5–6	5–6	(a few)
Canine teeth (lower jaw)	4	4	(a few)
Vertebrae	29–30	29–31	
Measurements (% SL)			
Body depth	35.1–38.9	34.5–42.5	
Head length	37.2–40.4	36.0–40.3	
Snout length	12.7–16.1	13.6–17.2	
Interorbital width	6.4–7.9	5.9–7.6	
Eye diameter	10.3–12.5	7.5–10.7	
Suborbital width	6.6–7.6	7.2–10.3	
Upper jaw length	15.3–17.5	13.1–18.0	
Longest dorsal spine	14.2–16.9	15.0–17.7	
Longest dorsal softray	13.8–23.9	16.9–32.3	
Longest anal spine	14.6–19.7	15.2–19.1	
Longest anal softray	16.5–23.5	17.7–29.1	
Longest pectoral ray	20.1–22.7	19.7–24.7	
Longest pelvic ray	25.4–38.8	28.2–47.7	
Dorsal fin base length	54.3–56.9	55.4–65.0	
Anal fin base length	27.2–30.7	28.0–33.5	
Caudal peduncle length	13.2–15.4	12.6–15.3	
Caudal peduncle depth	12.1–13.6	10.9–13.2	

* Numbers in parentheses are type data from Boulenger (1898).

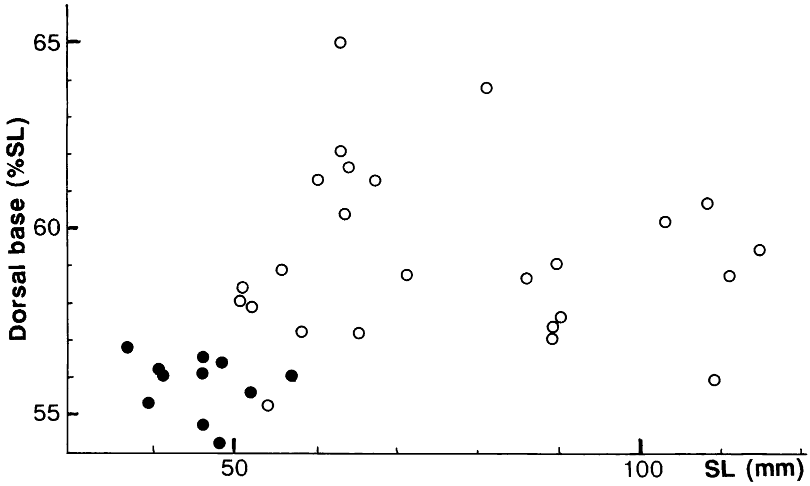

Fig. 3. Dorsal fin base length against SL in *Altolamprologus*. RA specimens (●), *A. compressiceps* from other localities (○).

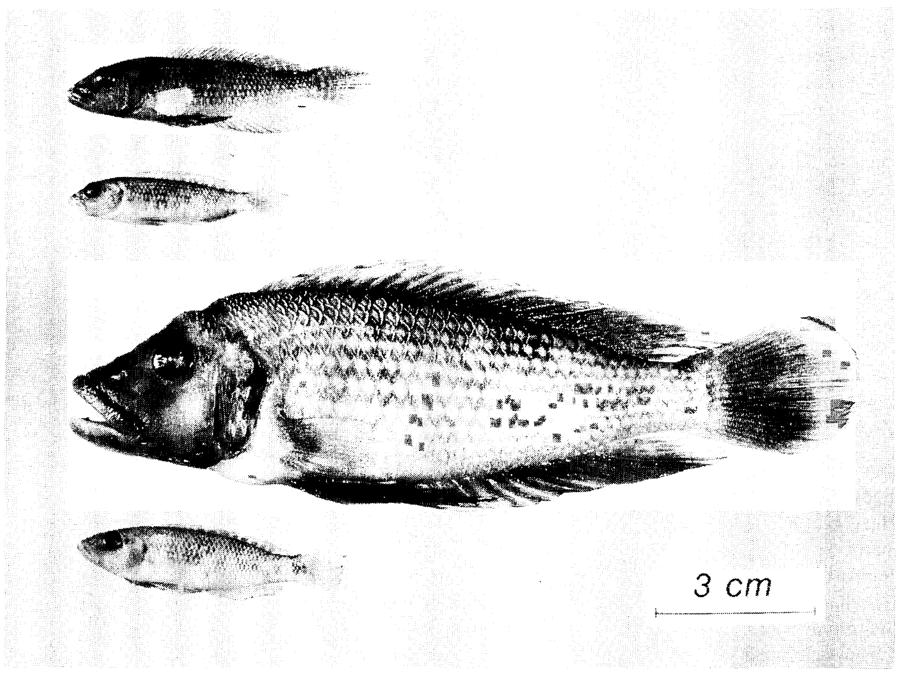

Fig. 4. RB specimens from Rumonge (*top two*) and *Lamprologus callipterus* from other localities (*bottom two*). From top to bottom: HUMZ 133226 (male, 46.7 mm SL), HUMZ 133227 (female, 35.8 mm SL), HUMZ 132941 (male, 115.9 mm SL) from Kichala, FRLM 12734 (female, 42.0 mm SL) from Wonzyie, Zambia.

territorial males in *L. callipterus* ranged from 83 to 111 mm SL, although there were some smaller mature males that performed alternative reproductive behavior. Female *L. callipterus* at other localities in the lake use shells as breeding sites, in the same way as RB females, and the size of locally-available shells is the major limiting factor of female size (Sato, 1994). Accordingly, the sizes of RB females and female *L. callipterus* did not differ greatly, and only differences between mature males from Rumonge and other localities are described herein.

Meristic counts and measurements of RB males coincide well with those of *L. callipterus* (Table 3), except for longitudinal scale counts. Longitudinal scales are 38–40 in the type specimens of *L. callipterus* (Boulenger, 1906), while RB and *L. callipterus* specimens examined in this study have 36–37 and 35–37 scales, respectively.

There are few differences in morphological features between RB and *L. callipterus* specimens. The dorsal fin base tends to be shorter in RB specimens. Other differences between similar-sized RB and *L. callipterus* males are the lengths of soft rays in dorsal and anal fins. RB specimens have longer and more pointed soft dorsal and anal fins (Fig. 5) than the same-sized *L. callipterus*. However, larger males of *L. callipterus* have longer and more pointed soft dorsal and anal fins than their smaller males.

Mature territorial males of *L. callipterus* at other sites carry and accumulate empty shells along rocky outcrops on the sandy bottom to make breeding nests (Sato, 1994), although they take refuge in crevices or under nearby rocks when disturbed. RB males, being small in size, lack the ability to transport shells, and they shelter inside shells when disturbed.

Table 3. Counts and measurements of RB specimens from Rumonge and *Lamprologus callipterus*

Characters	RB specimens	*L. callipterus*	
	n=10	*n*=27	(*n*=3)*
Total length (mm)	——	——	(90.0–125.0)
Standard length (SL, mm)	43.0–51.1	46.0–115.9	——
Counts			
Dorsal spines	18–19	18–20	(18–19)
Dorsal softrays	8–10	9–10	(9)
Anal spines	7–8	7–9	(8)
Anal softrays	7–9	7–9	(7–8)
Pectoral fin rays	13–14	14–15	——
Pelvic fin rays	I, 5	I, 5	——
Caudal fin rays	14–16	14	——
Longitudinal scales	36–37	35–37	(38–40)
Upper lateral line scales	21–26	21–28	(24–25)
Lower lateral line scales	9–15	9–17	(10–13)
Scales below lateral line	12–13	12–14	(10–11)
Gill rakers	12–13	11–13	(10–12)
Canine teeth (upper jaw)	8–10	6–10	(6–8)
Canine teeth (lower jaw)	6–9	4–10	(6–8)
Vertebrae	33–34	34–35	
Measurements (% SL)			
Body depth	23.9–27.7	23.0–32.8	
Head length	30.3–33.9	28.8–32.8	
Snout length	10.0–11.9	9.8–13.1	
Interorbital width	6.6–8.2	6.6–10.0	
Eye diameter	8.0–10.0	6.9–9.7	
Suborbital width	4.6–6.1	4.9–8.1	
Upper jaw length	11.5–14.5	9.9–14.3	
Longest dorsal spine	12.4–17.0	13.6–17.2	
Longest dorsal softray	19.5–24.4	13.0–23.3	
Longest anal spine	12.7–15.7	13.8–16.0	
Longest anal softray	18.4–21.4	13.3–21.9	
Longest pectoral ray	19.6–22.6	19.2–22.9	
Longest pelvic ray	23.5–30.3	20.5–31.7	
Dorsal fin base length	51.5–57.0	54.0–61.4	
Anal fin base length	25.3–28.9	26.1–31.9	
Caudal peduncle length	15.5–18.3	15.1–19.9	
Caudal peduncle depth	10.5–11.6	10.2–12.7	

* Numbers in parentheses are type data from Boulenger (1906).

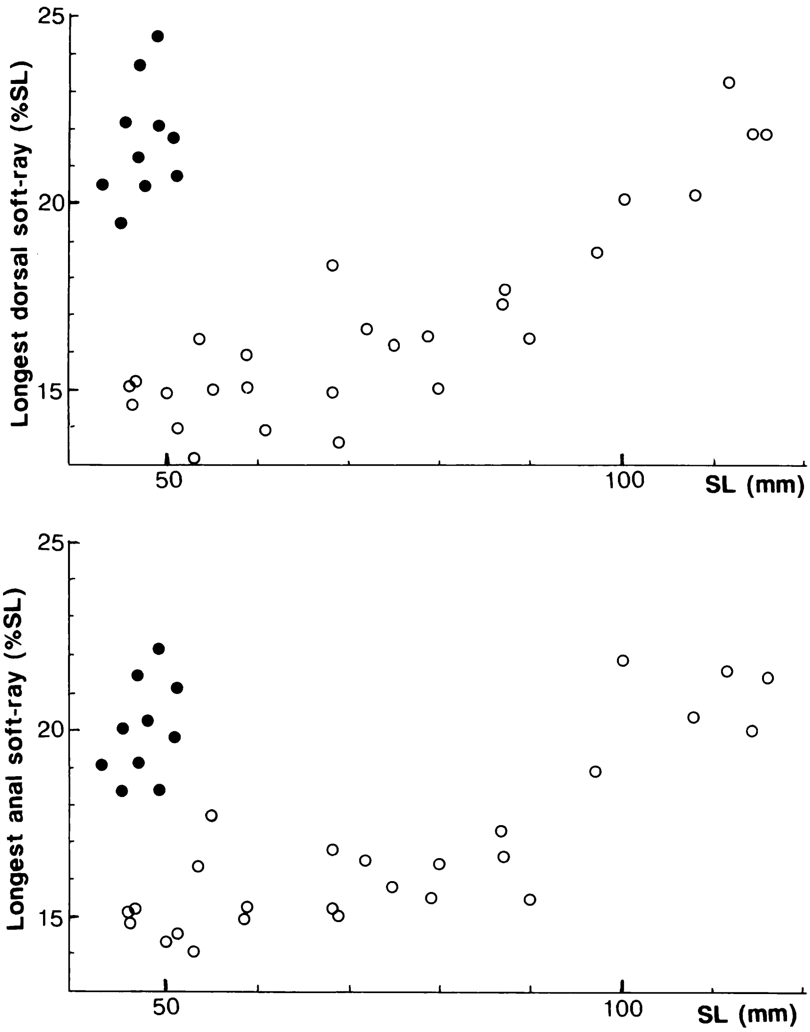

Fig. 5. Longest soft-ray of dorsal fin (*above*) and anal fin (*below*) against SL in *Lamprologus*. RB specimens (●), *L. callipterus* from other localities (○).

Neolamprologus **specimens from Rumonge (RC specimens)**

The genus *Neolamprologus* Colombe and Allgayer, 1985 is endemic to Lake Tanganyika. Specimens from Rumonge (RC specimens) are closest to *Neolamprologus mondabu* (Boulenger, 1906) in having 19 dorsal spines, 5 anal spines, and a truncate or slightly emarginate caudal fin.

Mature male and female RC specimens (Fig. 6, top and second) are much smaller than those of *N. mondabu* (Fig. 6, third and bottom). Maximum sizes of males and females were 48.2 mm SL and 41.2 mm SL for RC specimens, and 84.1 mm SL and 68.9 mm SL for *N. mondabu*, respectively. Gashagaza (1991) reported the sizes of mature *N. mondabu* as ranging from 65 to 95 mm SL (males), and from 55 to 90 mm SL (females).

Most of the meristic counts and measurements of RC specimens coincide with those for *N. mondabu* (Table 4). However, longitudinal scales are 42–46 in the type specimens (Boulenger, 1906), whereas RC and *N. mondabu* specimens examined here have 34–35 and 33–36 scales, respectively. The lower lateral line scales are 4–9 in the RC specimens, while the type specimens have 9–14 scales (Boulenger, 1906).

Morphological differences are not evident between them, except for a significantly shorter dorsal fin base

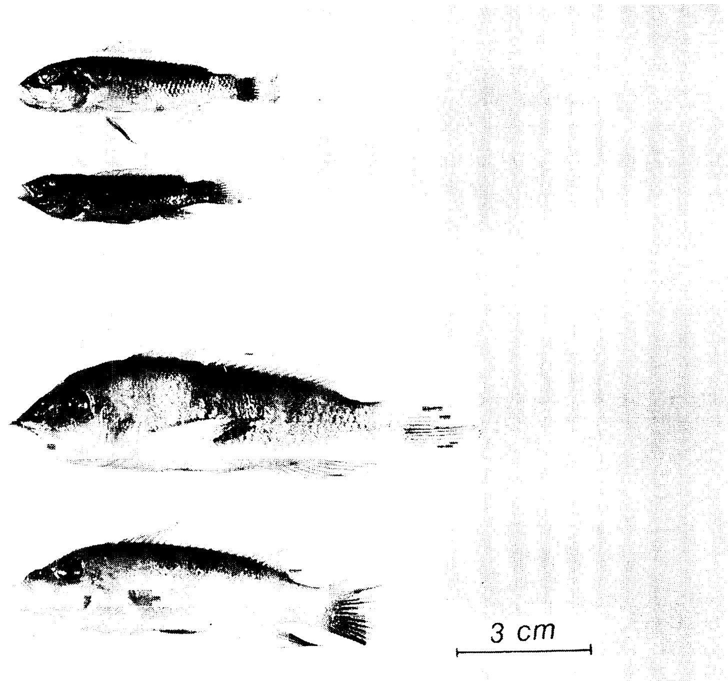

Fig. 6. RC specimens from Rumonge (*top two*) and *Neolamprologus mondabu* from Pemba (*bottom two*). From top to bottom: HUMZ 127269 (male, 48.2 mm SL), HUMZ 127101 (female, 41.2 mm SL), HUMZ 118096 (male, 84.1 mm SL), HUMZ 116422 (female, 70.7 mm SL).

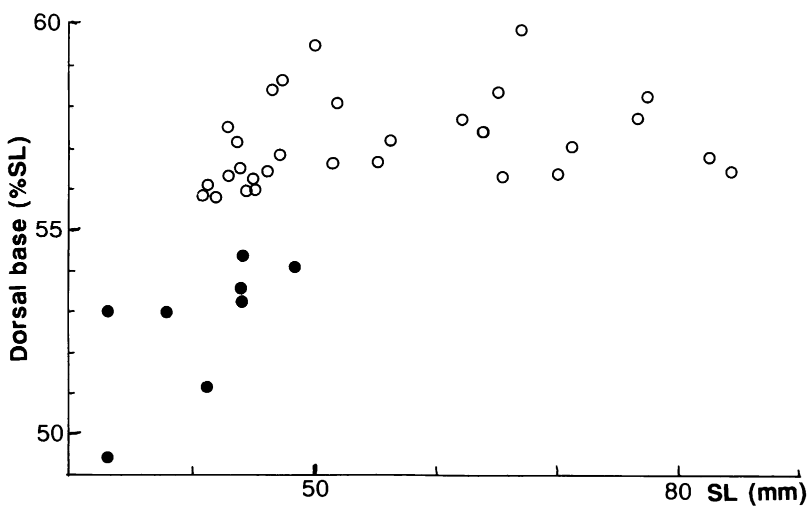

Fig. 7. Dorsal fin base length against SL in *Neolamprologus.* RC specimens (●), *N. mondabu* from other localities (○).

in RC specimens (Fig. 7).

RC females dig a small, vertical hole among shells, 60–70 mm deep, with an entrance diameter of about 30 mm. They spawn eggs on the outer surfaces of small *Neothauma tanganicense* shells in the deeper part of the hole. The hole is used by the female both as a spawning site and a shelter. Wrigglers are guarded in the shell or at the bottom of the hole by the female, which sometimes enters the shell containing wrigglers, possibly to ventilate them. Territorial males control 2 or 3 females, using shells as shelters. Wandering males and females also take refuge in shells of various sizes when chased. In sandy areas at other localities, female *N. mondabu* digs a large tunnel under the stone, usually deeper than 100 mm (Gashagaza, 1991), for use as a breeding site and shelter. Territorial males defend a large territory, encompassing several breeding sites of females. They flee along the sandy floor or hide under nearby rocks when chased.

Discussion

Morphological comparisons showed that *Altolamprologus* specimens (RA specimens), *Lamprologus* specimens (RB specimens) and *Neolamprologus* specimens (RC specimens) from Rumonge were almost identical with *A. compressiceps*, *L. callipterus* and *N. mondabu*, respectively. However, lower lateral line scales numbered 3–9 in RA specimens, whereas the type specimens of *A. compressiceps* have 9–10 scales (Boulenger, 1898). The lower lateral line scales of RC specimens were 4–9, whereas the type specimens

Table 4. Counts and measurements of RC specimens from Rumonge and *Neolamprologus mondabu*

Characters	RC specimens	*N. mondabu*	
	$n=8$	$n=27$	$(n=2)$*
Total length (mm)	——	——	(105.0)
Standard length (SL, mm)	32.8–48.2	40.9–84.1	——
Counts			
Dorsal spines	19	18–20	(19)
Dorsal softrays	8–9	8–10	(9)
Anal spines	5	5	(5)
Anal softrays	6	6–7	(7)
Pectoral fin rays	14	13–14	——
Pelvic fin rays	I, 5	I, 5	——
Caudal fin rays	14	14	——
Longitudinal scales	34–35	33–36	(42–46)
Upper lateral line scales	23–27	21–28	(25–27)
Lower lateral line scales	4–9	6–13	(9–14)
Scales below lateral line	12–13	12–15	(13–14)
Gill rakers	5–7	5–7	(7–8)
Canine teeth (upper jaw)	6	5–6	(6)
Canine teeth (lower jaw)	5–6	4–6	(6)
Vertebrae	32–33	32–34	
Measurements (% SL)			
Body depth	25.7–27.4	25.8–29.3	
Head length	33.5–38.7	31.7–35.6	
Snout length	11.0–15.6	10.5–15.5	
Interorbital width	6.8–8.5	6.9–9.5	
Eye diameter	9.3–12.7	7.7–10.1	
Suborbital width	4.9–6.4	4.9–7.6	
Upper jaw length	10.0–12.5	10.3–13.0	
Longest dorsal spine	12.6–15.5	12.2–17.8	
Longest dorsal softray	17.5–27.1	19.1–31.1	
Longest anal spine	13.2–15.2	12.8–17.4	
Longest anal softray	21.3–24.7	20.3–28.7	
Longest pectoral ray	22.3–24.5	21.6–26.9	
Longest pelvic ray	25.1–30.2	26.5–33.9	
Dorsal fin base length	49.4–54.4	55.8–59.9	
Anal fin base length	18.5–20.2	17.6–21.2	
Caudal peduncle length	18.3–20.7	15.5–21.1	
Caudal peduncle depth	11.9–13.0	11.9–14.2	

* Numbers in parentheses are type data from Boulenger (1906).

of *N. mondabu* have 9–14 scales (Boulenger, 1906). These differences may not be important, because the lower lateral line scales are variable and often unclear, making accurate counting difficult. In fact, the lower lateral line scale counts of *A. compressiceps* examined in this study were 6–11, demonstrating the wide variation in this character. Longitudinal scales are 38–40 in the type specimens of *L. callipterus* (Boulenger, 1906), whereas RB and *L. callipterus* specimens in this study had 36–37 and 35–37 scales, respectively. The type specimens of *N. mondabu* have 42–46 longitudinal scales, whereas RC and *N. mondabu* specimens in this study had 34–35 and 33–36 scales, respectively. These differences may have resulted from different methods of counting, since 36 or 37, and 35 or 36 longitudinal scales could be determined from the original figures of *L. callipterus* and *N. mondabu*, respectively (Boulenger, 1906: pl. 36, figs. 3 and 4). Poll (1956) also gave 35–37 as longitudinal scales of *L. callipterus*, based on 55 specimens collected from various localities in the lake. Poll (1956), who temporarily treated *N. mondabu* as a synonym of *N. modestus*, gave 34–37 longitudinal scales for *N. modestus*, based on 68 specimens.

In addition to their small size, RA, RB and RC specimens from the Rumonge shell-bed had a shorter dorsal fin base than the specimens from other localities. This modification in morphology may be an adaptation allowing the fish to enter deeply into shells, along the curvature of the shell wall, in order to hide from predators. One of the authors (TS) observed a mastacembelid feeding upon a *L. callipterus* female in a shell by grabbing its caudal fin. Small water cobras (*Boulengerina annulata*) are also capable of feeding upon fishes sheltering in shells (M. Deeble and V. Stone, pers. comm.), although the cobras were not seen at the study site.

The lighter coloration of RA specimens at Rumonge may also have an anti-predator function in the monotonously bright, unbroken habitat, as suggested for other cichlid species in the lake (Mboko and Kohda, 1995). An other difference noticed was in the lengths of the soft dorsal and anal fins between RB male specimens and *Lamprologus callipterus* of similar sizes. All RB specimens examined here were fully mature, whereas the latter were all immature. However, large mature males of *L. callipterus* (territorial males) had long soft dorsal and anal fins. These facts suggest that such elongation is related to reproductive condition.

As discussed above, no taxonomically important differences were found between the small-sized specimens from the Rumonge shell-bed and corresponding species from other places, and we conclude that those Rumonge fishes are the small-sized local populations of *Altolamprologus compressiceps*, *Lamprologus callipterus* and *Neolamprologus mondabu*, species which are common in rocky or sandy areas of other localities in the lake.

The small body sizes of the Rumonge populations are considered to be an adaptation primarily to the habit of using empty shells as a brooding substrate and shelter. It is essential for females of Rumonge shell-bed to enter shells for spawning and tending eggs (*A. compressiceps* and *L. callipterus*), and for ventilating the young inside shells (all species). Female *A. compressiceps* and *L. callipterus* usually plug the shell (or hole) entrance with their bodies (Gashagaza, 1991; Sato, 1994). Such behavior is probably effective in guarding young inside the shell against potential predators. Regarding males, fertilizing eggs inside shells does not necessarily require the ability to enter the shell. Large males of many shell-brooders fertilize eggs from the outside by positioning their genital area at the shell entrance, while females are spawning inside the shell (e.g., Sato, 1994). This behavior was observed in *A. compressiceps* and *L. callipterus* at Rumonge during the present study.

On the other hand, the shells are the only available shelters for adult cichlids on the shell-bed. At least three species of potential predators on adult cichlids were observed at the study site (two large piscivorous cichlids, *Lepidiolamprologus cunningtoni* and *Boulengerochromis microlepis*, and a spiny eel, *Afromastacembelus* sp.). Small body sizes, enabling them to enter shells, would therefore be advantageous for both males and females in the shell-bed environment, not only during the daytime but also at night when *Afromastacembelus* spp. and large catfishes actively forage on the bottom.

This study exemplified the morphological plasticity present within a species, according to the available shelter and/or brooding sites, and calls for the comprehensive taxonomic, ecological and phylogenetic studies on geographically-separated cichlid fishes in Lake Tanganyika.

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タンガニーカ湖北部のシェルベッドに分布する小型カワスズメ科魚類の分類

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アフリカの大地溝帯にあるタンガニーカ湖の北東部ブルンジ国のルモンゲ沖には，水深 9–13 m に巻貝の 1 種 *Neothauma tanganicense* の空き殻が一面敷き詰められた平坦な地域（シェルベッド）がある．このシェルベッドには，湖の他の水域に生息する種と形態的には似るが，体の大きさが極端に小さいカワスズメ科の魚類が生息している．これらの魚類 3 タイプを分類学的に検討した結果，湖の岩場や砂泥底に分布する *Altolamprologus compressiceps*, *Lamprologus callipterus*, および *Neolamprologus mondabu* であると結論された．これらシェルベッドに生息する個体は体が極端に小さいことの他に，背鰭基底が短いなどの共通の変異がみられたが，このことはシェルベッドで巻貝の空き殻を産卵場所や避難場所として利用する形態的な適応であると考えられる．

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