Rastrineobola argentea (Teleostei, Cyprinidae), a small African rasborine with four rows of pharyngeal teeth

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Received 20 January 2006; Accepted 7 August 2006

Abstract. It is widely accepted that cyprinid fishes have not more than three rows of teeth developed on each pharyngeal jaw. In this study we describe the East African cyprinid *Rastrineobola argentea*, with typically four rows of pharyngeal teeth developed on the pharyngeal jaw, a unique feature for the Cyprinidae. Generally the fourth row of *Rastrineobola argentea* is formed by one tooth, less commonly by two teeth. In a few specimens a fifth arbitrary tooth row occurs asymmetrically either on the left or on the right half of the pharyngeal jaw.

Key words: Lake Victoria, Cyprinidae, *Rastrineobola*, pharyngeal teeth

Introduction

Rastrineobola argentea (Pellegrin, 1904) is a small, zooplanktivorous cyprinid fish from Lake Victoria and Lake Kioga, East Africa. It is one of the most abundant fish species in Lake Victoria and of high commercial interest (Wanink 1999, Mwebaza-Ndawula 1998, Wanink & Witte 2000).

In all cyprinids the ceratobranchials 5, last remnants of the fifth gill arches, are modified to tooth-bearing bones. These bones form the lower pharyngeal jaw (LPJ), an adaptation for food processing (Sibbing 1991, Nelson 1994). Generally the LPJ "chews" against a horny pad located on the pharyngeal process of the basioccipital bone on the base of the skull. Upper pharyngeal jaws are absent in cyprinid fishes.

It is widely accepted that Cyprinidae have not more than three rows of pharyngeal teeth developed on each ceratobranchial 5 (Vladykov 1934, Chu 1935, Wu et al. 1981, Sibbing 1991, Nelson 1994). A fourth row is known either as an aberrant feature of a few species of *Barbus* and of *Cyprinus carpio* Linnaeus, 1758 (Banister 1973, Eastman & Underhill 1973, Golubtsov et al. 2005) or the number of individuals with four rows of pharyngeal teeth is low and typically three rows are developed as in two species of Schizothoracinae (Terashima 1984).

In this study we describe a rasborine cyprinid species, *R. argentea*, with four rows of pharyngeal teeth typically developed on the ceratobranchials 5.

Materials and Methods

The samples were collected in 1996 and 1997 in the northern part of Lake Victoria (Uganda) by one of us (L. M.-N.) (Fig. 1). Samples were taken with a small mid-water trawl net. The conical net was approximately 6 m long with a mouth opening of 1 x 1 m and a stretched mesh size of 5 mm. The net was secured to the back of a canoe and towed through water with a 25 hp outboard motor. Fish samples were preserved in 10% formaldehyde.

The pharyngeal jaws of 42 adult specimens of *Rastrineobola argentea* from the following localities were examined: Napoleon Gulf, inshore, 19 specimens, 42.0–53.4 mm standard length (SL). Bugaia Island, inshore, 17 specimens, 39.7–46.1 mm SL. 10 km south of Bugaia Island, offshore, 6 specimens, 39.6–44.3 mm SL.

The tooth count is expressed as the pharyngeal tooth formula. For example the formula of 1.1.3-3.1.1 (*Cyprinus carpio*) indicates that each ceratobranchial 5 has one, one and three teeth in the lateral (outer), median and medial (inner) row, respectively.

Pharyngeal teeth were obtained by disarticulating cleared and stained specimens following the method of Mayden & Wiley (1984) or by dissection.

In the nomenclature of the neobolines we follow Howes (1991) who proposed monophyly for this genus group of small African cyprinids (including the monotypic genus *Rastrineobola*) within the Rasborinae.

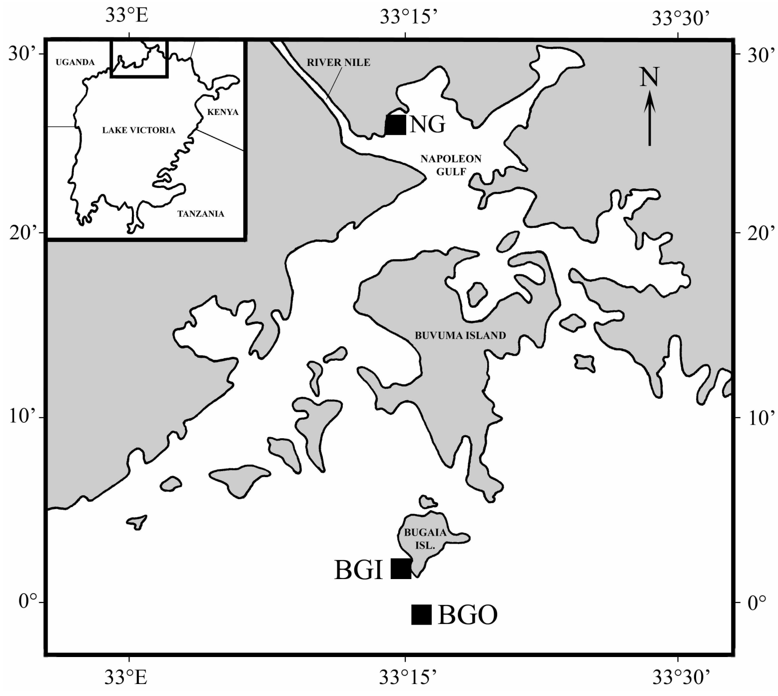

Fig. 1. Map of northern Lake Victoria showing localities for material examined. NG – Napoleon Gulf, BGI – Bugaia Island inshore, BGO – Bugaia Island offshore.

Results

The pharyngeal jaws of *Rastrineobola argentea* are well developed and the pharyngeal teeth characteristically arranged. The teeth are closely set, forming a dense patch with a large surface area, except for the first tooth of the medial (main) row which is positioned somewhat anterior to the other teeth.

The pharyngeal teeth on each half of the LPJ of all examined specimens (n = 42) are arranged in four rows (Fig. 2). Three specimens display a fifth arbitrary row: one specimen with the fifth row on the left and two specimens on the right ceratobranchial 5. These aberrant rows are represented by a single tooth (Fig. 2).

The overall number of the teeth is 10 (n = 31, 73.8%) or 11 (n = 8, 19.0%) on each ceratobranchial 5. In one specimen (2.4%) we found 12 teeth on the right ceratobranchial 5 and 11 on the left ceratobranchial 5. The two remaining specimens have either 10 teeth on the right and 11 teeth on the left ceratobranchial 5 or vice versa. Generally the number of teeth is the same on each of the LPJ (n = 39, 92.9%).

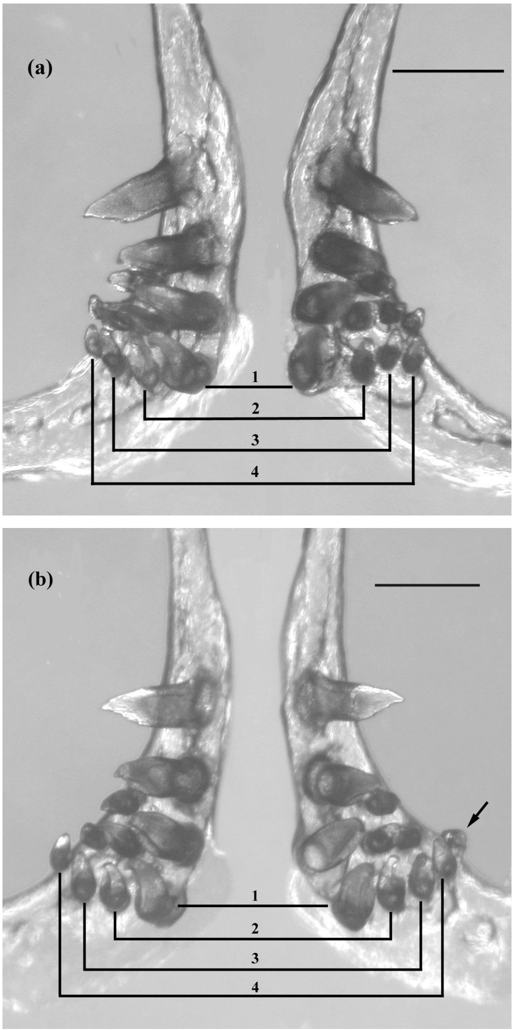

Fig. 2. *Rastrineobola argentea*; Lake Victoria, Uganda; the pharyngeal jaws of two cleared and stained specimens. 1 – 4 = the four rows of pharyngeal teeth, 1 = main row. (a): specimen with four rows of teeth on each ceratobranchial 5; tooth formula 2.2.3.4-4.3.2.2; (b): specimen with four rows of teeth on the left and five rows of teeth on the right ceratobranchial 5; tooth formula 1.2.3.4-4.3.2.1.1; arrow indicates the single tooth of the fifth arbitrary row. Scale bar = 0.5 mm.

The variability in the tooth formula is higher than it is in the number of the teeth. There is no variability in specimens with 10 teeth on one ceratobranchial 5, but there are differences in specimens with 11 teeth. In former the formula is always 1.2.3.4 in latter 1.2.3.5 or 2.2.3.4.

Most specimens have a 1.2.3.4-4.3.2.1 tooth formula (n = 31, 73.8%). In specimens with 11 teeth this formula is 1.2.3.5.-5.3.2.1 (n = 5, 11.9%) or 2.2.3.4-4.3.2.2 (n = 2, 4.8%). The formula for the single specimen with 12 teeth on the LPJ is 1.2.3.5-5.3.2.2. The typical arrangement of the pharyngeal teeth is obviously symmetrically (85.7 %, n = 36).

Generally the fourth row is represented by one tooth only and the main row by four teeth. Less frequently the fourth row is formed by two teeth and the main row by five. In the two aberrant specimens with a fifth row of pharyngeal teeth on the right ceratobranchial 5, the tooth formula is 1.2.3.4-4.3.2.1.1 or 2.2.3.4-4.3.2.1.1. For the specimen with the aberrant fifth row on the left ceratobranchial 5 the formula is 1.1.2.3.4-4.3.2.1

The first (anterior most) tooth in the main row is somewhat distant from the other teeth which are closely arranged forming a triangular patch (Fig. 2). This first tooth is larger and more robust than the others with a pointed tip, not hooked and with a narrow and shallow, concave grinding surface, serrated on the margins. The other teeth are slender, hooked at their tips and each with a concave grinding surface serrated on their margins. The teeth, longest in the medial (main) row, decrease gradually in length from medial to lateral and from anterior to posterior (Fig. 2). The grinding surfaces are elongated on the teeth of the medial row and widen gradually towards the lateral row.

Discussion

Rastrineobola argentea, a small zooplanktivorous cyprinid fish, is one of the most abundant fish species in Lake Victoria (Mwebaza-Ndawula 1994, 1998, Wanink & Witte 2000). During recent decades many publications focus on the ecology of this small cyprinid (for instance Mwebaza-Ndawula 1994, 1998, Wanink 1999, Branstrator et al. 2003, Goudswaard et al. 2004). Nevertheless, detailed anatomical studies are rare (Howes 1984, Wanink & Witte 2000) and information on the number and arrangement of the pharyngeal teeth is inconsistent: Boulenger (1911) mentioned eight teeth arranged in two rows (3.5-5.3) for *R. argentea* (as *Engraulicypris argenteus*), Howes (1984) described nine pharyngeal teeth arranged in three rows (2.3.4-4.3.2).

Wanink & Witte (2000) presented a rapid morphological adaptation following niche shift in *R. argentea*. These authors observed reduction in the number of gill rakers which they linked to the shift from pelagic to benthic feeding. This shift was possible after the depletion of the former dominant haplochromine cichlids by the Nile perch from the inshore waters of Lake Victoria in the 1980's. As a consequence *R. argentea* was able to invade benthic habitats of the sublittoral (Mwebaza-Ndawula 1998, Wanink & Witte 2000).

In our opinion it is unlikely that the fourth row of pharyngeal teeth is a new feature for *R. argentea* linked to the above mentioned habitat shift. The specimens of our study were collected inshore and offshore. Those from inshore fed on pelagic and on benthic prey, those from offshore predominantly on pelagic prey (Mwebaza-Ndawula 1998). Nevertheless, four rows of pharyngeal teeth are developed in all specimens from the inshore and the offshore samples. Possibly the fourth row of teeth has previously been overlooked.

It is widely appreciated that cyprinid fishes have their pharyngeal teeth arranged in not more than three rows on each ceratobranchial 5 (Chu 1935, Nikolski 1957, Nelson 1994, Golubtsov et al. 2005). As an abnormality a fourth row is described from a few

Cyprininae (Banister 1973, Eastman & Underhill 1973, Golubtsov et al. 2005). Such arbitrary rows do not occur symmetrically but either on the left or on the right ceratobranchial 5. Additionally, defects during tooth replacement may cause an extra row of teeth (Evans & Deubler 1955, Eastman & Underhill 1973). Possibly such a defect is the reason for the aberrant fifth tooth row on the LPJ of three specimens of *R. argentea*.

The pharyngeal dentition in two species of *Schizothorax*, *S. oconnori* Lloyd, 1908 and *S. raraensis* Terashima, 1984 is interesting. These two species are dimorphic in this feature and display symmetrically either three (2.3.5-5.3.2) or four rows (1.2.3.4-4.3.2.1 or 1.2.3.5-5.3.2.1) of teeth on the LPJ. However, the number of individuals with four rows of teeth is low and was therefore classified as a variation (Terashima 1984).

Nevertheless, there is an ongoing discussion about the plesiomorphic number of pharyngeal tooth rows in cyprinid fishes. Seemingly most authors favour the hypothesis that three rows are plesiomorphic for Cyprinidae over the one-row-hypothesis (Chu 1935, Fink & Fink 1981, Nikolski 1957, Nelson 1994, Golubtsov et al. 2005).

Two principal phyletic lineages are recognised in the Cyprinidae (Howes 1991, Nelson 1994), the basic cyprinine and the leuciscine lineages (Liu & Chen 2003). So far single specimens with more than three rows (arbitrary or as a variation) are known from the cyprinine lineage, either from Cyprininae or Schizothoracinae (Terashima 1984, Golubtsov et al. 2005). Golubtsov et al. (2005) assume that the multi-rowed condition in Cyprininae, if plesiomorphic for cyprinid fishes, is an atavism based on hidden genetic information tracing back to a common ancestor of the two cyprinid lineages.

Rastrineobola argentea is to date the only known cyprinid species with obligatory four rows of teeth on the LPJ. It is not clear if this four-rowed condition is an apomorphic or a plesiomorphic character state. For clarification it has to be investigated if the four-rowed condition of *R. argentea* is unique among the neobolines *sensu* Howes (1984) or if other species of this genus group have also a fourth row of pharyngeal teeth developed.

Nevertheless, it has to be noted that the neobolines, a monophyletic group of small African cyprinids, were placed within the Rasborinae by Howes (1991). Based on molecular data Gilles et al. (2001) classified the Rasborinae as the most basic subfamily of Cyprinidae. If this is correct, a species of this subfamily with four rows of pharyngeal teeth could support the hypothesis that the multi-rowed condition of pharyngeal dentition is the plesiomorphic state for cyprinid fishes. But recently Liu & Chen (2003) disputed the point of view of Gilles et al. (2001) and placed the Rasborinae at a basal position within the leuciscine lineage.

Acknowledgments

We thank N. G. Bogutskaya (Russian Academy of Sciences) and B. W. Coad (Canadian Museum of Nature) for commenting an earlier version of the manuscript.

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