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STUDIES OF LARGE AND SMALL BARBS (GENUS *BARBUS* SENSU LATO; CYPRINIDAE; PISCES) CARRIED OUT BY FRESHWATER BIOLOGY GROUP OF JOINT ETHIO-RUSSIAN BIOLOGICAL EXPEDITION (JERBE)

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ABSTRACT: Surveys performed in all six main river basins of Ethiopia enabled describing fish species composition and distribution. One of the important results was discovery of “species flocks” (aggregations of sympatric forms) of large African barbs in several rivers whereas earlier the only such “species flock” was known from Lake Tana. In each flock there are generalized and specialized forms which differ in appearance, skull characters, and feeding habits. In a long term experiment, it was shown that both external traits and skull characters of the barbs change under influence of environmental conditions. Among progeny of specialized forms of the Lake Tana barbs, some individuals reared in aquaria were indistinguishable from the generalized form even at age of 5 years. In the coastal zone of Lake Tana, morphologically distinct groups of large barbs were found that cannot be affiliated with nominal species described from the lake. Absence of post-mating reproductive isolation between different forms (morphotypes) of the Lake Tana barbs was shown. Small barbs of Ethiopia are phylogenetically distant from large barbs. Judging from their morphology, small barbs include several distant phylogenetic lineages. The lineage of small barbs with serrated spine in the dorsal fin exhibit a noticeable evolution pattern of the parallel reduction of spine in uppermost parts of the three isolated river drainages. Molecular phylogenetic studies are needed to clarify taxonomy and relationships of most populations of small barbs found in the country.

Key words/phrases: African barbs, Reproductive isolation, Resource partitioning, Species flock.

INTRODUCTION

Members of Freshwater Biology Group of JERBE were engaged in studying fish inhabiting lakes and rivers of Ethiopia beginning from 1984 (Fig. 1). They described fish fauna of main river systems, and results of their studies are presented in a number of publications (Golubtsov *et al*., 1989;

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Golubtsov, 1993; Dgebuadze *et al*., 1994; Golubtsov *et al*., 1995; Golubtsov *et al*., 2002; Golubtsov and Mina, 2003; Golubtsov and Darkov, 2008; Mina and Dgebuadze, 2008; Golubtsov and Redeat Habteselassie, 2010; Golubtsov *et al*., 2012).

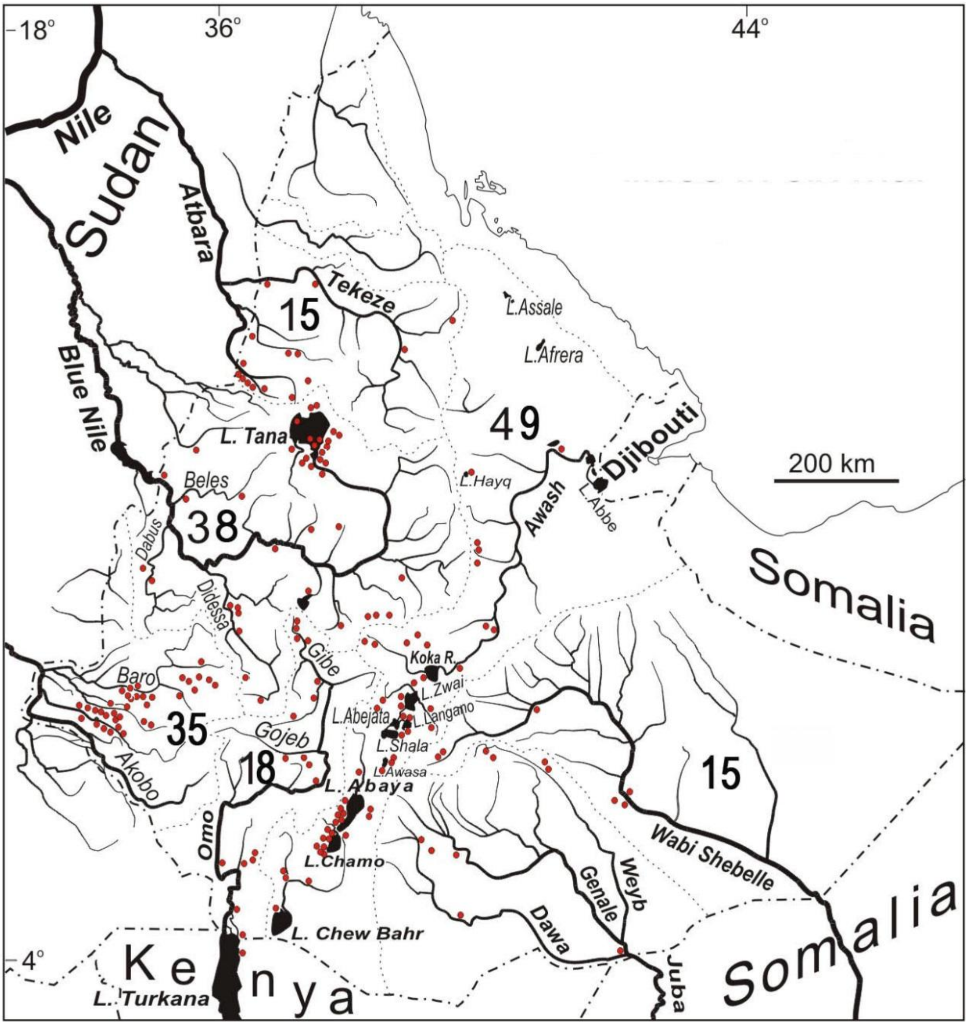

Fig. 1. Localities of sampling fish by the JERBE team. Figures indicate number of sampling sites in each of six main river basins.

Besides, special attention was paid to fish groups with complicated taxonomic and population structure which are of special interest for knowledge of consistent patterns of fish diversification and evolution. Among such groups are large and small barbs.

STUDIES OF LARGE AFRICAN BARBS (*BARBUS=LABEOBARBUS*)[1]

Large African barbs are economically important, so studies of their populations' structure and dynamics are necessary to organize their rational exploitation and protection. In several rivers of Ethiopia and in Lake Tana they are represented with several sympatric forms (morphotypes) differing in external appearance. Such sets of forms are called "species flocks", but since it is not proved that all morphotypes composing the set are biological species, we prefer the term "flock of forms".

Studies of the Lake Tana large barbs

The most known "flock of forms" is that in Lake Tana. Fourteen of these forms were recognized by Nagelkerke and Sibbing (2000) as different species. Differing from this assertion, we have suspended our judgment concerning species status of the morphotypes until degree of their reproductive isolation is assessed and irreversibility of differences between them is proven. It should be stressed that authors describing species of the Lake Tana barbs considered them as "biological species *sensu* Mayr" that is, reproductively isolated populations. At the same time, they did not claim that the isolation was complete and reported finding hybrids between barbs and *Varicorhinus beso* more distantly related to large barbs than different morphotypes to each other (Nagelkerke and Sibbing, 1996).

As our experimental studies have shown (Alekseyev *et al.*, 1996; Dzerzhinskii *et al.*, 2007), there was no decrease in fertilization rate or increase of mortality rate of progeny from heteronomic crossings of barbs, that is crossings of barbs of different morphotypes, in comparison with homonomic crossings, that is crossings of barbs of same morphotype, thus affirming absence of post-mating isolation between the morphotypes. At the same time, mortality of progeny from crossing barbs with *Varicorhinus beso* was very high during the earliest stages of development (Dzerzhinskii *et al.*, 2007).

Evidence of premating reproductive isolation was seen in segregation in time and place of spawning of morphotypes coming to spawn into the River Gumara, a tributary of Lake Tana. Yet, we believed (Dgebuadze *et al.*, 1999) that though temporal and spatial segregation of morphotypes could contribute to their reproductive isolation, but it hardly prevented

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[1] Large African barbs are now frequently incorrectly named *Labeobarbus* (Skelton, 2001; de Graaf *et al.*, 2008), which seems contrary to the presently accepted rules, because the innovation was not accompanied by the diagnosis of the genus as a taxon different from that described under the same name by Rüppell (1836). However, it should be noted that *Barbus* could not be assigned to entirely different groups (small barbs and large barbs).

interbreeding completely. Judging from data presented by Palstra *et al.* (2004) in the River Gumara during the spawning season, barbs of several morphotypes were always found. Whether barbs preferably mate with individuals of the same morphotype can be ascertained only by observing the process of spawning. Such observations are scarce and the only publication describing spawning of morphotypes other than "riverine intermedius sensu, Alekseyev *et al.* (1996)" is the paper by Dzerzhinskii *et al.* (2007). They observed spawning of barbs belonging to three morphotypes in the River Ducalit (a tributary of Gumara River) and found that females of "troutlike" morphotype mated extensively with "intermedius" and, probably, with males of "bigmouth small-eye" morphotype.

It was suggested that mate choice in barbs may be determined by chemoreception. Testing this hypothesis in an experiment led to the conclusion that choice of mating partners of certain morphotypes due to chemoreception might reduce the probability of interbreeding but not provide for reproductive isolation between the morphotypes (Zworykin *et al.*, 2006).

Analysis of genetic markers was expected to help describing population structure of the Lake Tana barbs, but studies of allozimic loci (Berrebi and Valiushok, 1998), mtDNA (de Graaf *et al.*, 2010; Beshera and Harris, 2014) and microsatellites (Nagelkerke *et al.*, 2015) did not reveal distinct divergences between the Lake Tana putative species (morphotypes). At the same time, analysis of the Major Histocompatibility Complex (MHC) showed no sharing of class II β chain alleles among the morphotypes (Dixon *et al.*, 1996). At first, this was accepted as an evidence of genetic isolation between them and, consequently, of their species status (Sibbing *et al.*, 1998; Nagelkerke and Sibbing, 2000; de Graaf *et al.*, 2010), but was later recognized as unconvincing (Nagelkerke *et al.*, 2015). These data do not prove reproductive isolation between the morphotypes, but should not be ignored. It is noteworthy that no sharing was observed not only among morphotypes, but also between some individuals of the same morphotype. This may be considered as an evidence of presence in the sampling locality groups of barbs partially isolated from each other, some of such groups being formed by individuals of the same morphotype. This is not surprising if one considers the large dimensions of Lake Tana (about 3 500 km^2) and the relatively large number of tributaries that barbels can use for spawning. Analysis of MHC performed on bigger samples in different seasons and localities could shed light upon nature of assortativeness in the Lake Tana barbs taking into account the role of these genes in mate choice demonstrated for many vertebrates, fish included (Penn, 2002; Milinski, 2006).

Since the revival of interest in the Lake Tana barbs in 1990s the attention was concentrated mainly on fish caught in the offshore part of the lake and in the spawning rivers. Just these fish were classified into morphotypes and species. Barbs inhabiting the coastal zone were considered as "variable shore complex" that constitutes a morphological continuum (Nagelkerke *et al.*, 1995). However, principal component analysis of 28 skull characters performed on samples taken in 2010 and representing catches from the coastal area of the lake (Bahar Dar Gulf) revealed discrete clusters of individuals in coordinates PC1 and PC2 (Mina *et al.*, 2013) (Fig. 2). Barbs of many morphotypes described in the 1990s were absent in the sample under study, and there were individuals that could not be affiliated with the previously described morphotypes (Fig. 3). It was suggested that some of these fish represented morphotypes which did not occur in the offshore part of the lake, and some were hybrids of the described morphotypes or originated from homonomic crossings but did not have diagnostic characters of the parental morphotype. What remains to be explained is the discreteness of the clusters. Do they represent populations polymorphic in external characters but similar in skull proportions and are they comparable with morphotypes described from the offshore part of the lake? The answer could be found if samples of ripe and running fish from spawning grounds were available, but to get such samples is difficult because neither time nor localities of spawning are known. It is evident that structure of the Lake Tana barbs population system is more complicated and variable than it is customarily thought.

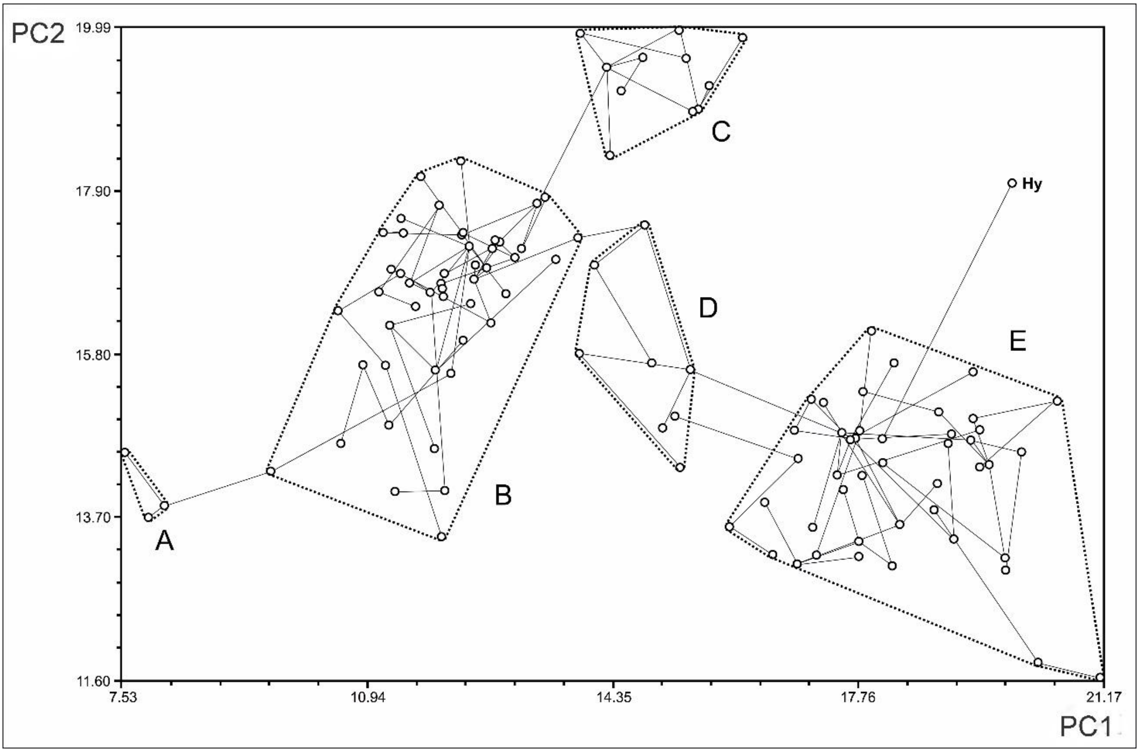

Fig. 2. Scatterplot of studied Lake Tana large barbs and a hybrid (Hy) between a barb and *Varicorhinus beso* from the coastal zone of Lake Tana in the space of the PC1 and PC2. 28 skull indices. Minimum spanning tree superimposed. A, B, C, D, E – discerned clusters.

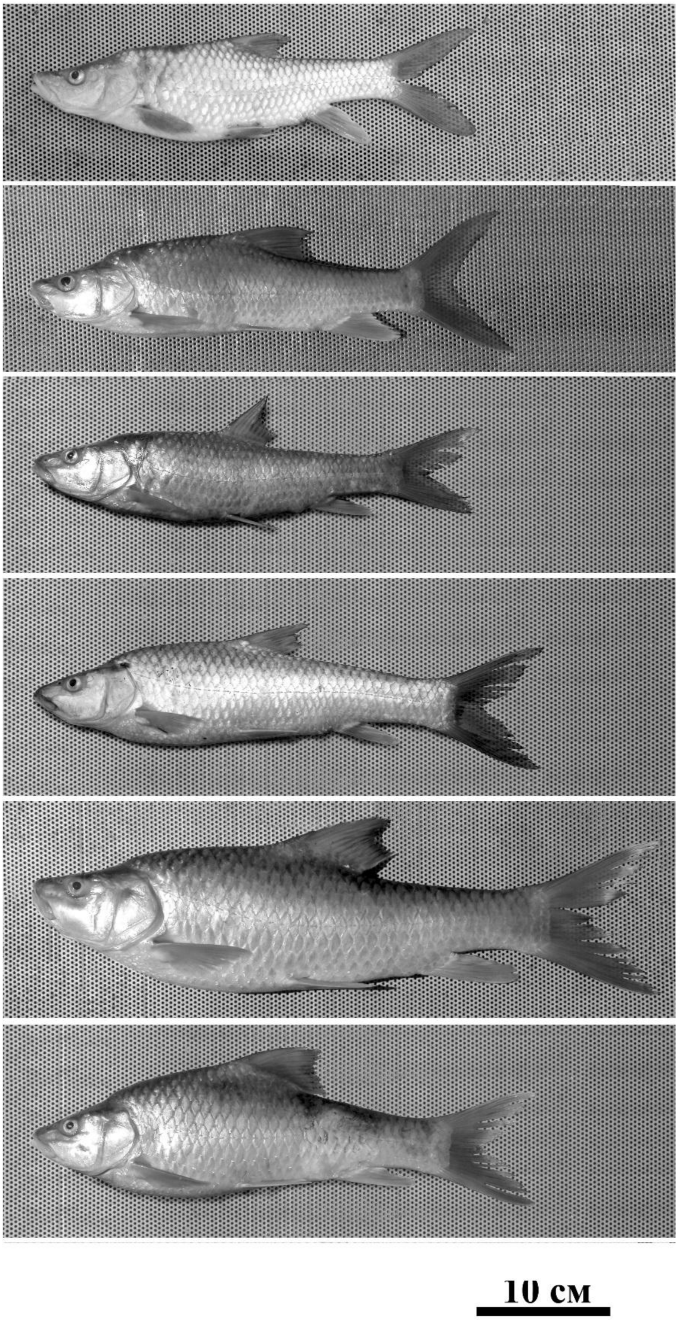

Fig. 3. Large barbs from the coastal zone of Lake Tana which cannot be affiliated with nominal species described from the lake.

Another issue requiring consideration is the role of developmental plasticity as a factor determining phenotype diversity of the Lake Tana barbs. In the absence of specific genetic markers of morphotypes, the only way to estimate this role is rearing barbs of different morphotypes in the same conditions and barbs of the same morphotype in different conditions. It requires certain facilities and time expenditure since the barbs should be under observation during several years. Such an experiment was performed and its results are described by Mina *et al.* (2012). Progeny from both homonomic and heteronomic crossings of barbs representing several morphotypes were kept in aquaria for six years (2005–2011). Besides, progeny from the homonomic crossing bigmouth small-eye X bigmouth small-eye was reared in a pond. The authors warn that their inferences should be cautiously extrapolated to the natural situation especially dealing with morphotypes that were not represented in the experiment but, nevertheless, find it possible to state that (1) Siblings from both homonomic and heteronomic crossings living in the same conditions considerably differ both in external and in skull characters, (2) Progeny from homonomic crossings of large mouthed barbs (bigmouth small-eye, bigmouth big-eye, and troutlike) acquire diagnostic traits of their parental morphotypes at different age, and some of them do not acquire such traits even at the age 5+. This corroborates the previously made suggestion on late divergence of morphotypes in ontogeny (Mina *et al.*, 1996), (3) Among progeny from both homonomic and heteronomic crossings, some males which did not display the diagnostic traits of their parental morphotype (s) reached sexual maturity and were fertile, (4) identification of offspring from heteronomic crossings and backcrosses by external appearance is difficult if not impossible, (5) Siblings from crossing bigmouth small-eye X bigmouth small-eye living in different environmental conditions substantially differed both in external and skull characters, and differences between them were equivalent to the differences between morphotypes (Fig. 4).

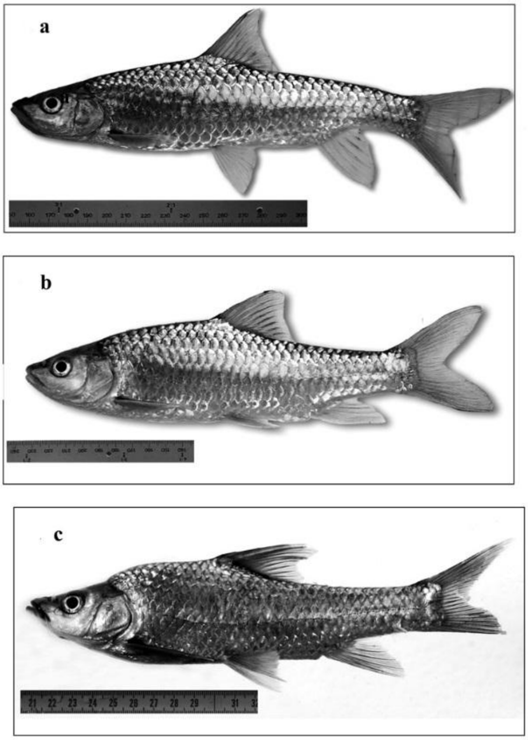

Fig.4. c and d - offspring from the crossing Se X Se at the age 5+ that lived in aquaria (a,b) and their sibling from the pond at the age 3+ (c).

Thus, the question, are differences between the morphotypes of the Lake Tana barbs genetically determined or environmentally induced, in our view, should be considered with regard to concrete morphotype, since there is no reason to believe that all the differences between morphotypes are of the same nature, and relative importance of genetic and environmental factors is equal.

Of a special interest are morphological differences between siblings living in the same environment. This allows us to suppose that divergence of morphotypes may begin not because different members of an ancestor population got into different environmental conditions, but because some change in environmental conditions entailed differences in response to this change between individuals. For example, it was found that the siblings from homonomic crossing “intermedius” × “intermedius” differed in their response to change in the level of the thyroid hormone: some of them displayed obvious morphological transformations acquiring some traits of big-mouthed morphotypes whereas some others did not (Shkil *et al.*, 2010).

It is impossible to say whether progeny of barbs which in changed environment maintained specific traits of their parents would maintain these traits in next generations in the same changed environment. Yet, the fact that although in natural conditions among progeny from a homonomic crossing fish may appear having diagnostic characters of morphotype other than the parental one, prompts us to doubt the species status of the parental morphotype.

Studies of large barbs beyond Lake Tana

While carrying out survey of Ethiopian fish fauna, quite a few un-described forms (morphotypes) of large barbs were detected (Mina *et al.*, 1998; Golubtsov, 2010). It was shown that the “flock of forms” in Lake Tana is not unique. In several rivers large barbs seemed to be represented with more than one morphotype. Commonly, individuals of generalized form (similar with “intermedius” from Lake Tana) and individuals with enlarged lips (similar with “lip” morphotype from Lake Tana) dwell together. Besides, “flocks of forms” composed of both generalized and specialized forms distinctly differing in appearance and skull characters were found in the Didessa River (the Blue Nile basin), the Genale River (the Wabe Shebele basin), the Sor River (the White Nile basin), the Gibe and Gojeb rivers (the Omo basin) (Golubtsov, 2010). Some morphotypes from these flocks resemble morphotypes from Lake Tana but are not identical to them, whereas some other have no analogues to the Lake Tana flock.

For example, there are six forms of large barbs in the Genale River which are distinguished by external morphology and feeding habits. These are: “generalized form” – typical *Barbus* (=*Labeobarbus*) *intermedius* (GF), “largemouth piscivorous” (LMP), “deep-bodied form” (SH), “largemouth scraper” (LMS), “smallmouth scraper” - probable hybrid *B. intermedius* × *V. jubae* (SMS), “form with swollen lips” (LIP) (Fig. 5). The taxonomic status of different morphotypes from the Genale as well as that of *V. jubae* is uncertain (Golubtsov, 2010).

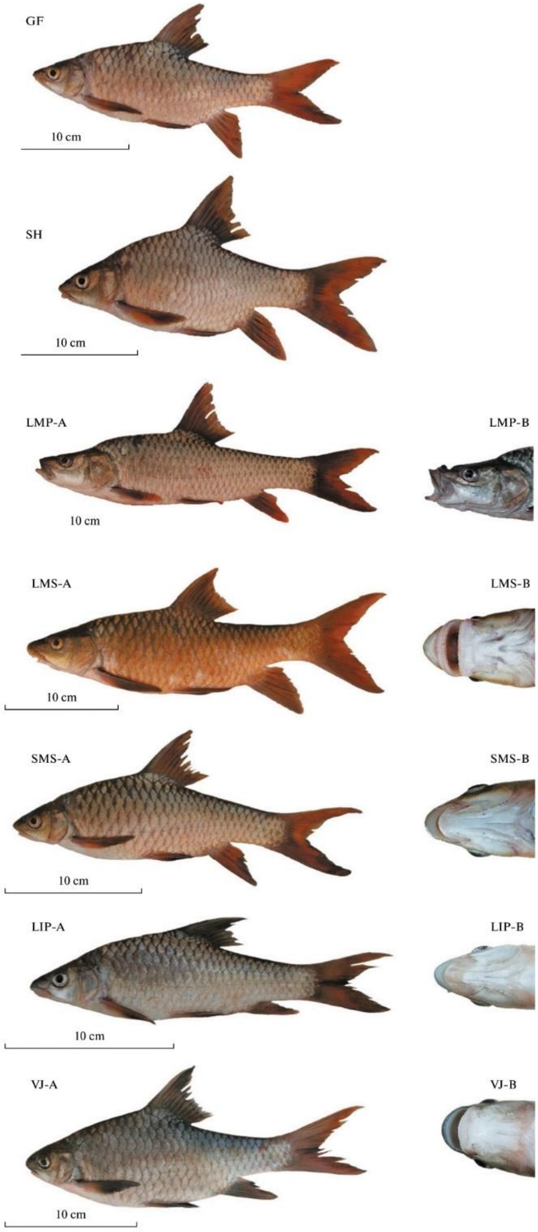

Fig. 5. Typical representatives of forms of the large African barbs *Barbus* (=*Labeobarbus*) *intermedius* and *Varicorhinus jubae* from the Genale River. GF—"generalized form"—typical *Barbus* (=*Labeobarbus*) *intermedius*; LMP—"largemouth piscivorous"; SH—"deep-bodied form"; LMS—"largemouth scraper"; SMS—"smallmouth scraper"—probable hybrid *B. intermedius V. jubae*; LIP—"form with enlarged lips"; VJ—*Varicorhinus jubae*. A—fish as a whole, B—head of the fish.

Bearing in mind that fish scale morphology in many times is successfully used in fish taxonomy, we have investigated scale structure in morphotypes from the Genale River using light and scan electron microscopy (Dgebuadze and Chernova, 2012). The utility of scanning electron microscopy for specific identification has been shown for such genus as *Labeo* (Cypriniformes) (Kaur and Dua, 2004), *Pomoxis*, *Sander*, *Morone* (Perciformes) and *Esox* (Salmoniformes) (Oates *et al*., 1993). It was found that macrostructural scale parameters (shape and lateral line scales number) cannot be used for identification of forms of the Genale barbs and *V. jubae* (Dgebuadze and Chernova, 2012). Scan electron microscopy analysis of scale microstructure of large barbs, *V. jubae* and *V. beso* has shown that the relief of the caudal field of the scales is not uniform and four main zones may be distinguished. The differences between forms and species in the relief details are weakly expressed, however, they can be arranged in succession according to the development of specific characters in transitional zone II: *B. intermedius* (5 forms: GF, LMP, SH, LMS, LIP) → "smallmouth scraper" form (probable hybrid *B. intermedius* × *V. jubae*) (SMS) → *V. jubae* → *V. beso*. By the development of granulation zone III, the following series are suggested: *B. intermedius* (5 forms: GF, LMP, SH, LMS, LIP), *V. jubae* → "smallmouth scraper" form (SMS) → *V. beso*. By the degree of founded "trabecular" structure development, the following series can be arranged according to the character reduction: *B. intermedius* (GF, LMP, SH, LMS, LIP) → "smallmouth scraper" form - (SMS) → *V. jubae* → *V. beso*. Thus, in accordance to scale microstructure *Varicorhinus jubae* is closer to *Barbus* (=*Labeobarbus*) *intermedius* than to *V. beso* (Dgebuadze and Chernova, 2012).

Up to now, the published data on "flocks of forms" beyond Lake Tana are scarce especially concerning their genetic relationships and reproductive isolation. The only communication is that of Dimmick *et al*. (2001) who analyzed mtDNA of three morphotypes from the Genale flock. They found substantial difference of the large-mouthed form from the generalized and "lipped" forms but not between the latter two and inferred that the large-mouthed morphotype represented an un-described species.

An interesting situation was detected in Rift Valley lakes Hawassa and Langeno (Mina *et al*., 2016). In both lakes, barbs are represented with a generalized form displaying no external traits characteristic to specialized morphotypes. However, it is shown that in each of the lakes there are groups of barbs whose individual ontogenetic trajectories are situated within separated ontogenetic channels in the space of skull characters (Fig. 6).

Separation of the channels is by far less distinct than that of the channels of generalized and specialized forms of barbs from Lake Tana. We believe that the revealed polymorphism relates to food resource partitioning and might serve as a prerequisite to further divergence of sympatric forms of large African barbs. Earlier, Demeke Admassu and Elias Dadebo (1997) suggested that there were two forms in Lake Hawassa, one of them piscivorous and another feeding mostly on mollusks and larvae of aquatic insects. This suggestion was corroborated by Zerihun Desta *et al*. (2006), who combined studies of gut contents with analysis of stable isotopes. We suppose that both in Hawassa and Langeno ontogenetic trajectories of piscivorous and omnivorous forms are located in different ontogenetic channels.

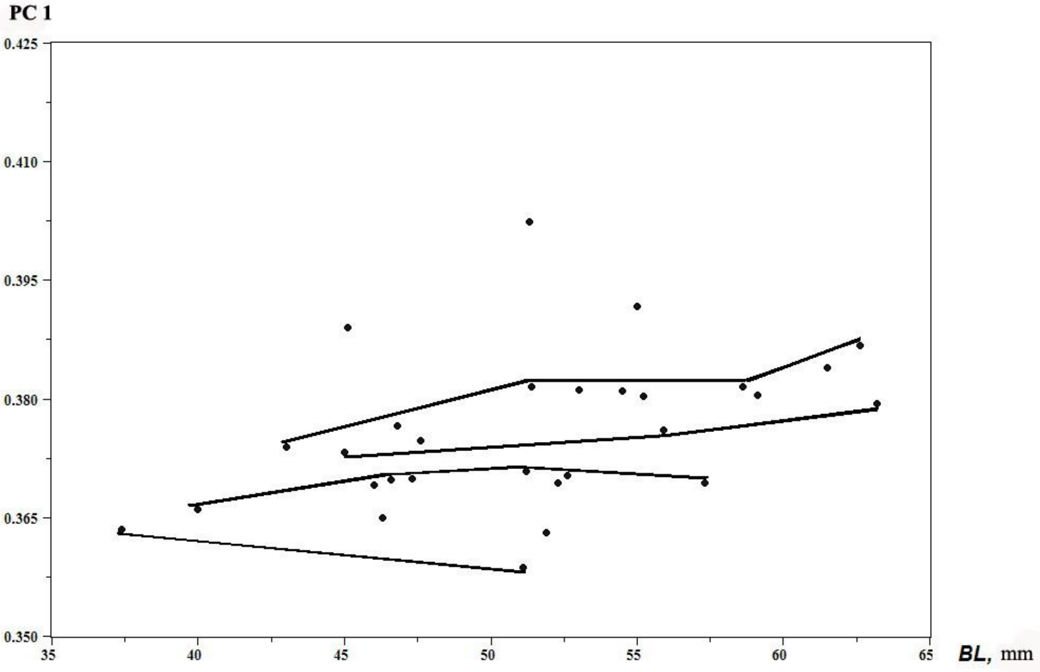

Fig. 6. Distribution of barbs from Lake Hawassa in coordinates *BL* (basal length of the skull) and PC1 13 characters (indices), n=28.

It is noteworthy that ontogenetic channels of barbs from Lake Hawassa are already divided when individuals reach the size at which fish become main component of their food. Thus, it seems that not transition to feeding on fish is the cause of morphological peculiarities of piscivorous barbs, but morphological peculiarities of young individuals predetermine their future diet.

The fact that divergences in skull proportions during ontogeny of barbs from lakes Hawassa and Langeno are not correlated with development of differences in external traits similar to those observed between morphotypes composing “flocks of forms” indicates that in the process of a flock formation, divergence in skull proportions preceded divergence in external traits.

Urgent tasks of studying Large African barbs in Ethiopia

There are many unanswered questions concerning population structure and evolution even of the best studied Lake Tana barbs, to say the least of barbs from other regions. It is an urgent task to find out when and where barbs of different morphotypes spawn and whether their mating is assortative. Importance of studying barbs from different localities should be emphasized since hopefully comparative analysis of local situations will help to understand general patterns of population structure dynamics and evolution. The real challenge is to figure out whether in nature, like in the experiment described above, offspring can belong to a morphotype other than the morphotype of parents. To go some way toward solving this problem is to carry out experiments in conditions as possible akin to natural, in big aquaria or in ponds. Such experiments could allow to follow development of progeny from various homonomic and heteronomic crossings, to study behavior of fish and, with any luck, their spawning and mating preferences. By varying living conditions of fish it would be possible to evaluate their developmental plasticity and its role in evolution of the barbs. However hard it is to provide facilities for this experiment, the task is executable if Ethiopian authorities support such a project and scientists from other countries are engaged.

It should be emphasized that the situation with Large African barbs in the territory of Ethiopia is unique, as it allows to study the process of diversification of fish both in lakes and in rivers. There is every reason to believe that this process is reversible and can be severely disrupted due to anthropogenic effects, primarily associated with fishing. In this regard, studies of distribution, population structure and reproduction of the Large African barbs have not only theoretical but also applied significance.

Studies of Small African barbs

Small barbs of Ethiopia are phylogenetically distant from large barbs (Golubtsov and Krysanov, 1993; Tsigenopoulos *et al.*, 2002; Yang *et al.*, 2015) and, as it is typical for small commercially not important fishes, have been studied less than large barbs. Formally, their countrywide taxonomic diversity (approximately 15 species) is twice lower than that of large barbs (26−30 species as it was estimated by Golubtsov and Darkov, 2008). The diversity of large barbs, however, is formed to the great extent by the lacustrine and riverine species/form flocks including the Lake Tana flock (14 nominal species). Among the Ethiopian small barbs, only few lacustrine endemics are known: *B. tanapelagius* described by de Graaf *et al*. (2000), *Barbus turkanae* Hopson and Hopson (1982) and probably un-described species from Lake Abaya mentioned by Golubtsov *et al*. (2002). *Barbus trispilopleura* described by Boulenger, 1902 from Lake Tana or closely related form has been found by us in the Dura River, the northern tributary of the Blue Nile (unpublished data). Phylogenetic relationships of *B. pleurogramma* Boulenger, 1902, another presumptive endemic of Lake Tana, is discussed below. In general, we believe that taxonomic diversity of the Ethiopian small barbs is greatly underestimated and application of the molecular methods may reveal hidden diversity, as has happened with the Kenyan small barbs (Schmidt *et al*., 2017).

Below we briefly review the diversity of Ethiopian small barbs based on morphological and distributional data. First, based on structure of the last unbranched ray in the dorsal fin and number of the lateral line scales, Ethiopian small barbs may be divided into three groups: (1) barbs with enlarged serrated last unbranched ray in the dorsal fin and small number (23−27) of the lateral line scales, (2) barbs with enlarged serrated last unbranched ray in the dorsal fin and high number (32−38) of the lateral line scales and (3) barbs with not enlarged and not serrated unbranched last ray in the dorsal fin.

The barbs of the group (1) were found in the Chamo-Abaya lake basin and identified as *Barbus kerstenii* Peters, 1868 (Golubtsov *et al*., 2002; Golubtsov and Berendzen, 2005). A molecular phylogenetic study by Schmidt *et al*. (2017) demonstrated that in Kenya the populations of small barbs identified as *B. kerstenii* represent quite distinct phylogenetic lineages. The phylogenetic relationships of the Chamo-Abaya populations of *Barbus* cf. *kerstenii* (Fig. 7) need to be clarified with molecular methods. Obtaining new samples of this barb for molecular studies is, however, problematic because of the human-caused alteration of its habitat. The swampy areas along the western shore of Lake Chamo and the lower reaches of the Darse (Hare) River, a tributary of Lake Abaya, where we sampled this barb previously, are greatly transformed by extension of agricultural lands and irrigation. We failed to re-sample it after 2005.

Fig. 7. *Barbus* cf. *kerstenii*, small barbs with enlarged serrated last unbranched ray in the dorsal fin and low number of the lateral line scales from the lower reaches of the Darse (Hare) River, a tributary of Lake Abaya (photo in aquarium).

The barbs of the group (2) are relatively well studied (Golubtsov *et al*., 2002; Golubtsov and Krysanov, 2003; Golubtsov and Berendzen, 2005). Following Boulenger (1911) and Greenwood (1962), we identified them as *Barbus paludinosus* Peters, 1852, but the molecular phylogenetic study by Schmidt *et al*., (2017) demonstrated that Ethiopian populations of these barbs are phylogenetically distant from *B. paludinosus* from South Africa and *B*.cf. *paludinosus* from Kenya and Tanzania. Thus, until the phylogenetic structure of the Ethiopian barbs with enlarged serrated last unbranched ray in the dorsal fin and high number (32−38) of the lateral line scales will be solved with the molecular methods, it is reasonable to designate this group as *B. pleurogramma* complex.

According to Golubtsov and Berendzen (2005) and our unpublished data, the barbs of this group are distributed in the central part of the Ethiopian Rift Valley (the Zwai, Langano and Hawassa lake basins), in the headwaters of the Omo-Turkana system (the Gibe and Gojeb rivers), in the headwaters of the White Nile system (the upper reaches of the Baro River and the middle reaches of the Sore River and its tributaries) and in the headwaters of the Blue Nile system (the Lake Tana basin, the middle reaches of the Dura, Didessa and Dabus drainages). Previously barbs of this group occurred also in the upper reaches of the Awash drainage (Boulenger, 1906; Greenwood, 1962), but we failed to sample them there during the whole period of the JERBE activity.

These barbs exhibited a very interesting evolutionary trend, the parallel reduction of the enlarged serrated last unbranched ray in their dorsal fin. As was described by Golubtsov and Berendzen (2005), these phenomena take place in the uppermost parts of their distributional ranges in the Gibe (the Omo-Turkana basin) and Sore (the White Nile basin) drainages. Recently, we found similar situation in the Dura River (the Blue Nile basin). The latter situation is presented in Fig. 8. In all three cases, the border between the spined and spineless populations of the small barbs coincide with the upper distributional limit of the large barbs in the particular river drainage. Thus, we suggested that the absence of a predator determines the parallel reduction of the dorsal spine in the three isolated parts of the group range.

The barbs of the group (3) (with not enlarged and not serrated last unbranched ray in the dorsal fin) apparently include the representatives of quite distant phylogenetic lineages. The main diverse of this group is found in the lowland waters of the White Nile system within the limits of Ethiopia, the Gambela region. Just few species of this group occurring in this region can be reliably identified based on their morphological characters. These are *Barbus anema*, *B. perince* and *Barbus pumilis* (Fig. 9). The bulk of the species of group (3) are characterized with black sports (sometimes fusing in a black line) along the mid-lateral line of their body. These spotted barbs are distributed in the Gambela region, in the middle and upper reaches of the Blue Nile system (including *B. trispilopleura* from the Lake Tana basin), in the lower reaches of the Omo-Turkana system and in the southern portion of the Ethiopian Rift valley (the Chamo-Abaya and Chew Bahir basins). A spotted barb was obtained by us also from the middle reaches of the Genale River (the Juba system in the Indian ocean basin in south-eastern Ethiopia). The taxonomy and phylogeny of these spotted barbs, as well as the whole group (3), could be reliably solved only with molecular methods.

In general, the small barbs are narrowly distributed in Ethiopia compared to the large barbs. They have not yet been found in the Atbara-Tekeze system and the Wabi Shebele drainage, while in the Awash system they seem to be extinct.

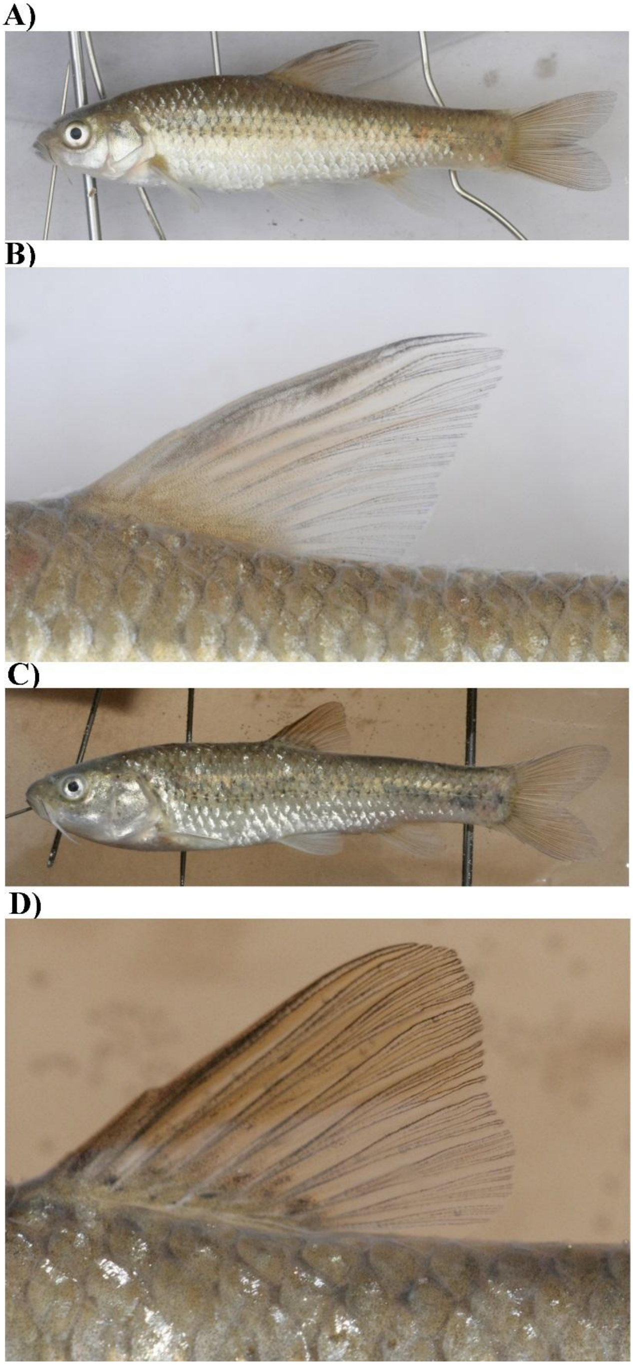

Fig. 8. Reduction of the dorsal spine in *Barbus pleurogramma* complex from the Dura River, a tributary of the Blue Nile: A) and B) a specimen from the upper reaches, standard length (SL) 61 mm; C) and D) a specimen from the middle reaches, SL 81 mm; B) and D) side-view of the dorsal fin.

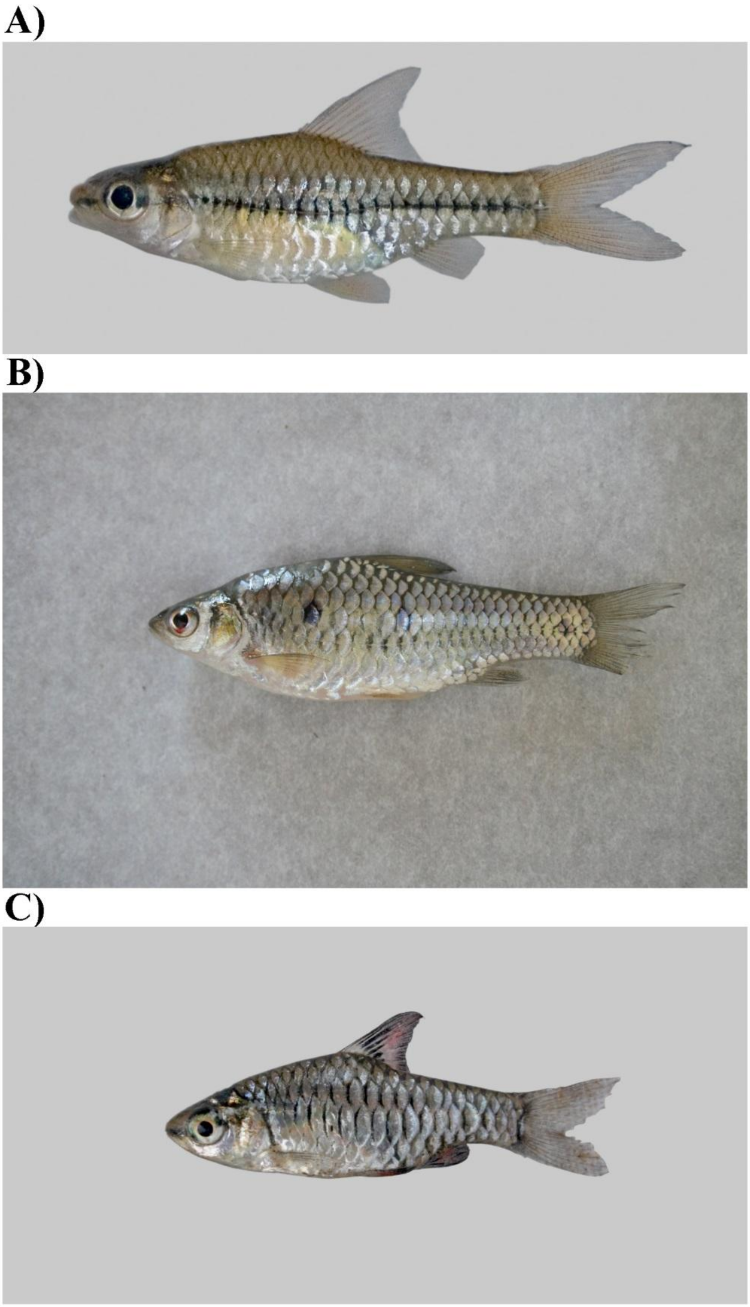

Fig. 9. Three species of easily identifiable small barbs with not enlarged last unbranched ray in the dorsal fin from the White Nile basin in Ethiopia: A) *Barbus anema*, standard length (SL) 28 mm; B) *B. perince*, SL 67 mm and C) *B. pumilis*, SL 25 mm.

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