Longitudinal zonation of fish assemblages in a tropical river: Awash river basin, central Ethiopia

With taxonomic and ecological considerations on the genus *Garra* (Teleostei: Cyprinidae)

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by

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ABSTRACT

The present study aimed to clarify the fish diversity in the upper and middle reaches of the Awash river. Patterns of fish assemblages along the longitudinal gradient were studied and the phenotypical variability within the most abundant genus *Garra* was outlined. Therefore, the first 650 km of the river, from the headwaters in the Chilimo forest (2389 m a.s.l.) to the lowland zone in the Afar region (570 m a.s.l.) were investigated. During November 2017 and January 2018 (dry season) the reaches of interest were sampled 3 times along 12 sites. These sampling sites were selected based on habitat criteria, characteristics of river morphology and low anthropogenic impact. A combination of fishing gears was used (e.g. electrofishing, beach seine, gill nets) to sample a variety of mesohabitats. Physical and chemical water parameter were recorded at each site. Microhabitats and river morphological characteristics were quantitatively estimated along with human activities observed. Representatives of the genus *Garra* were preserved in 96% ethanol and morphometric and meristic characteristics recorded. Water temperature (ºC) and conductivity (µS cm^{-1}) significantly increased from the source region (S1, max. 17.9ºC, max. 269 µS cm^{-1}) to the lowland zone (S12, max. 26.2ºC, max. 993 µS cm^{-1}) but showed unusual gradients possibly related to human impacts. The complex geomorphological setting and the river gradient determined the sediment composition. Fish diversity increased from the rhithron (S1, 2 taxa) to the potamon (S12, 7 taxa), but was highest at site 8 (8 taxa). *Garra dembeensis* and *Garra* aff. *makiensis* were characteristic for the upper reaches, whereas *Garra* sp. and *Micropanchax* cf. *antinorii* were frequent taxa in potamal stretches. *Labeobarbus* cf. *intermedius* was most widespread in the Awash river. The impact of the Koka reservoir was detectable by a decline in water temperature (-2.7ºC) and conductivity (-253 µS cm^{-1}) but had no observable effect on fish biocenoeses. The alternating steep and low gradient sections of the Awash river determined the succession of fish assemblages. Two distinct transition zones were observed where fish communities clearly changed along environmental gradients. With the use of morphometric and genetic features, 3 distinct groups of *Garra* could be detected. *Garra dembeensis* was clearly identified, whereas the taxonomic placement of *Garra* aff. *makienis* and *Garra* sp. is not yet resolved. The presence of several morphotypes within each group might reflect specific adaptations to certain abiotically defined environments.

Key words: spatial variability – river gradient – fish morphology – genetic barcoding

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1. INTRODUCTION

Ethiopia is a country of diverse landscapes and characterised by sharp climatic and environmental gradients which range from the high mountain plateaus to the hot and dry Danakil Depression in the eastern part. From north-east to south-west, the Main Ethiopian rift system (MER) shapes the topography of the landscape. Although unevenly distributed, the country has abundant water resources and 12 major river basins can be identified (Habteselassie, 2012). The north, western and south-western parts are drained by tributaries of the Nile river (Atbara, Blue- and White Nile systems) leading to the Mediterranean Sea, whereas the south-eastern part drains into the Indian Ocean via the Wabi Shebele and Genale Dawa systems (Golubtsov et al., 2002). Central Ethiopia is characterised by two major endorheic drainage basins. The Omo-Gibe and the Awash river basin, the latter draining into Lake Abbe at the border to Djibouti. The topographic and climatic diversity of the country is also reflected by a high number of endemic animal and plant species. According to Froese and Pauly (2017) at least 40 fish species are restricted to the water systems within Ethiopia and the taxonomic status of several forms is not yet clarified and needs further investigation.

The first scientific records of Ethiopia’s ichthyofauna date back to the first half of the 19th century and were made by the German explorer Eduard Rüppell (Golubtsov and Mina, 2003). In the following decades the knowledge about native fish species subsequently increased especially in lentic systems. A major limitation is still the lack of complete taxa lists in most of the smaller river basins and insufficient knowledge of autecological parameters of many fish species. This was highlighted by Getahun and Stiassny (1998) who stated that little research had been done to investigate the fish diversity and their habitat demands in lotic ecosystems of Ethiopia. Since that time, several authors (e.g. Golubtsov et al., 2002, Stiassny and Getahun, 2007 and Habteselassie, 2009) contributed detailed information based on literature review, morphological descriptions and field investigations which consequently improved our understanding of fish biocoenoses in Ethiopia’s riverine systems.

So far, no comprehensive investigation of the fish fauna and especially its longitudinal distribution has been made in the Awash river basin. Existing scientific literature is often incomplete and contradictory (e.g. Wubie et al., 2017). The surveys reported in Golubtsov et al. (2002) date back nearly three decades and might not be representative any more. Human settlements and industrialisation increased rapidly and go along with adverse environmental impacts (Degefu et al., 2013). Apart from that, most sampling sites in the region are known from easily accessible river stretches, near bridges or close to towns (Golubtsov et al., 2002), which are highly impacted by human activities (e.g. car washing, laundry, water abstraction or watering cattle) and possibly do not fully represent the entire diversity.

With the rapid population growth and the progressive development and industrialisation of the region, a reliable classification of running water systems seems urgently needed. Water pollution (mainly domestic wastewater and industrial effluents) and habitat degradation (e.g. deforestation, bank erosion and subsequent sedimentation) lead to the loss of functioning aquatic ecosystems in many parts of the country (Getahun and Stiassny, 1998). This threatens biodiversity and poses serious health risks to the local populations which directly depend on the available water resources in the Awash river and the Koka reservoir (Dsikowitzky et al., 2012). Several scientific studies (e.g. Degefu et al., 2013) have stressed this aspect and pointed out the problem of nutrient loading from agriculture but also the high concentration of heavy metals, resulting from industrial effluents (e.g. soap and alcohol factories, tanneries, breweries) and the use of pesticides in plant production (Benti, 2014).

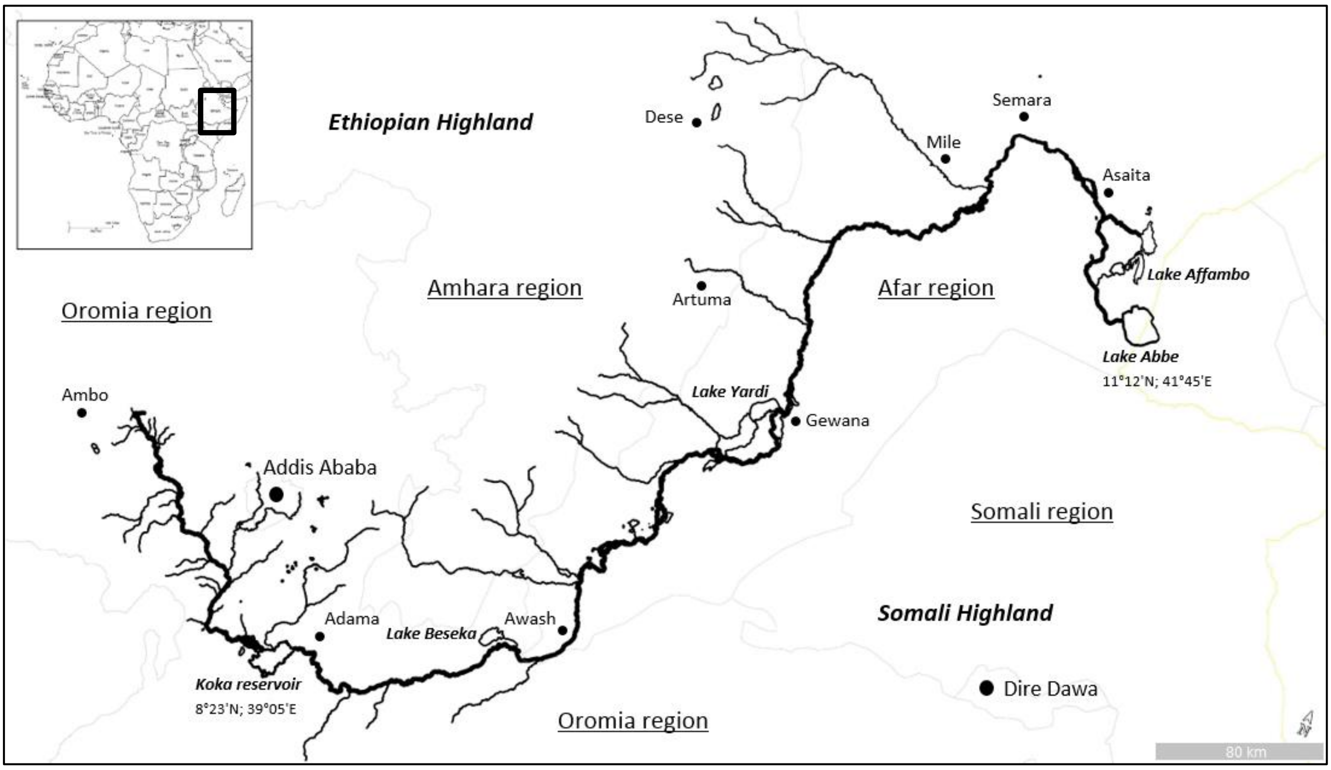

Figure 1. The Awash river basin from the source region to Lake Abbe. Important towns and villages along the river course are depicted. Names of major tributaries as well as the exact location of the Tendaho reservoir are indicated in Figures 4a and 4b. Addis Ababa city centre (8°58'49.58"N, 38°45'26.26"E). The yellow line marks the border to Djibouti. Source of information: Google Earth Pro 2017.

1.1. The Awash river basin

The Awash river basin extends from the foothills of the Ethiopian Highlands, west of Addis Ababa, to the Danakil Depression at the border to Djibouti (Figure 1). With a catchment area of about 112,000 km^2 (Tesfaye and Wolff, 2014) the endorheic basin is the fourth largest in Ethiopia and covers parts of the Oromia, Somali, Amhara and the Afar region (Koriche, 2012). Brown and Lemma (1970) who studied the molluscan fauna in the Awash river (length of approximately 1200 km), suggested a subdivision in 3 parts: ‘upper basin’ (until Awash town), ‘middle valley’ (Awash town to Dubti) and the ‘lower plains’ (Dubti to Lake Abbe). Following this classification, an engineering consultancy (Halcrow, 2006) divided the course in ‘Upper stream area’, ‘Middle valley’ and ‘Lower valley’ (Figure 2). The geographic denominations ‘Middle Awash’ and ‘Lower Awash’ are frequently used in paleontological research and refer to the Afar region around Lake Yardi and Hadar respectively (e.g. Geraads et al., 2012).

From its source in the Chilimo Forest near the village Ginchi (Figure 4a) the river flows to the south into the MER until it is dammed and forms the Koka reservoir (Lake Koka or Lake Gelila) (Figures 1 and 4a). The dam was constructed in the 1950s for hydroelectric power supply and supports an important fishery in the region (Tesfaye and Wolff, 2014). Due to insufficient agricultural practices and consequent soil erosion the sediment load of the Awash and other tributaries is high and gradually fills the reservoir (Behailu, 2004; Bishaw and Kedir, 2015).

Downstream of Lake Koka the river flows to the north-east following the rift valley into the Afar-depression. In this region, 2 run-of-the-river hydropower stations (Awash II and III) are located and irrigation agriculture (mainly sugar cane) is intensively developed with seemingly high water abstraction. At Matahara the river is connected to the largely expanding saline Lake Beseka (Figures 1 and 4b). An artificial channel was constructed in order to regulate water levels. It should be noted that the physical and chemical properties of the lake are entirely different compared to the Awash river (Olumana et al., 2009 and Belay, 2009). Further downstream the famous Awash falls (Figure 4b) are formed and the river flows along the Awash National Park, confined in a narrow valley.

At the end of the upstream area the channel slope declines and a meandering course is developed. Until the Yangudi Rassa National Park (or the Mile Serdo Wildlife Reserve – boundaries are not clear) the Awash river is lined by cultivated areas (irrigation agriculture) and wetlands. One notable exception is the area north-west of mount Hertali (Hertale) where the river character changes and a relatively steep slope shapes the riverbed morphology. At the boarder to the National Park the Awash forms an extensive wetland with several side arms and stagnant water bodies (among them Lake Yardi). The river than flows through an arid landscape developing a meandering course. Large-scale human impacts seem to be absent and the area is only inhabited by tribes of the local Afar people.

In the region of Semera (regional capital of the Afar region) the Awash is dammed by the Tendaho reservoir (completed in 2014) and heavily impacted by water abstraction and agriculture. Before it dried out in 2016, it had been stocked 3 times with *Oreochromis niloticus* ssp. In 2017 it was restocked by the National Fish and Other Aquatic Lives Research Center (NFLARC) in Sebeta, with the same taxon (Alemayehu Wubie, pers. comm., 2018). At the boarder to Djibouti the river finally empties into a series of saline lakes which ends in Lake Abbe (Figures 1 and 4b). With an average annual air temperature above 34 °C the Danakil Depression is among the hottest regions on earth.

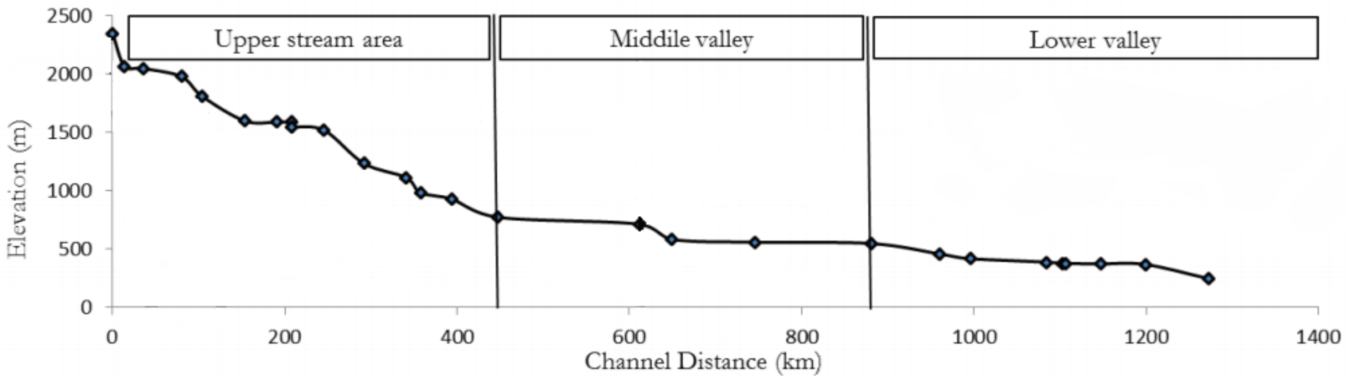

Figure 2. Longitudinal gradient of the Awash river (classification adopted from Halcrow, 2006). In the present study, the first 650 km of the upper and middle Awash were of interest. The Lower valley was not subject of the investigation. Source: adjusted from Halcrow (2006).

1.1.1. Geological background of the study area

More than any other African country, Ethiopia is characterised by elevated plains with sharp margins and deep valleys. They originated from layers of basalts erupted on a Paleozoic basement during the Oligocene era (ranging from 40 to 45 Ma), simultaneously with the establishment of the Red Sea rift. Close to this event, the MER developed, following the spread of the Gulf of Aden and connecting it with the East African rift system. Both rifts were accompanied by volcanic phases (eruption of different magma types, mainly andesites and basalts) when developing, but became nearly inactive in the present (Abbate et al., 2015). Various extinct volcanoes still bear witness to those times (Figure 3). In the north-east, the Danakil Depression is still volcanically active and Ertá'alé volcano gives insight into the ongoing rifting process.

The establishment of the MER divided the central Ethiopian highlands into two separate blocks, the larger one (Abyssinian highland) in the northwest and the smaller one (Somali highland) in the southeast of the country (Abbate et al., 2015). The former hosts the main watersheds of Ethiopia and the spring of large rivers, among them the Blue Nile. Its southern margin is drained to the MER, where rivers, such as the Awash river, enter saline lakes in basins without outlets (endorheic basins). In this area, volcanic activities caused several changes of river courses, valley geomorphology and river gradients (Figure 3).

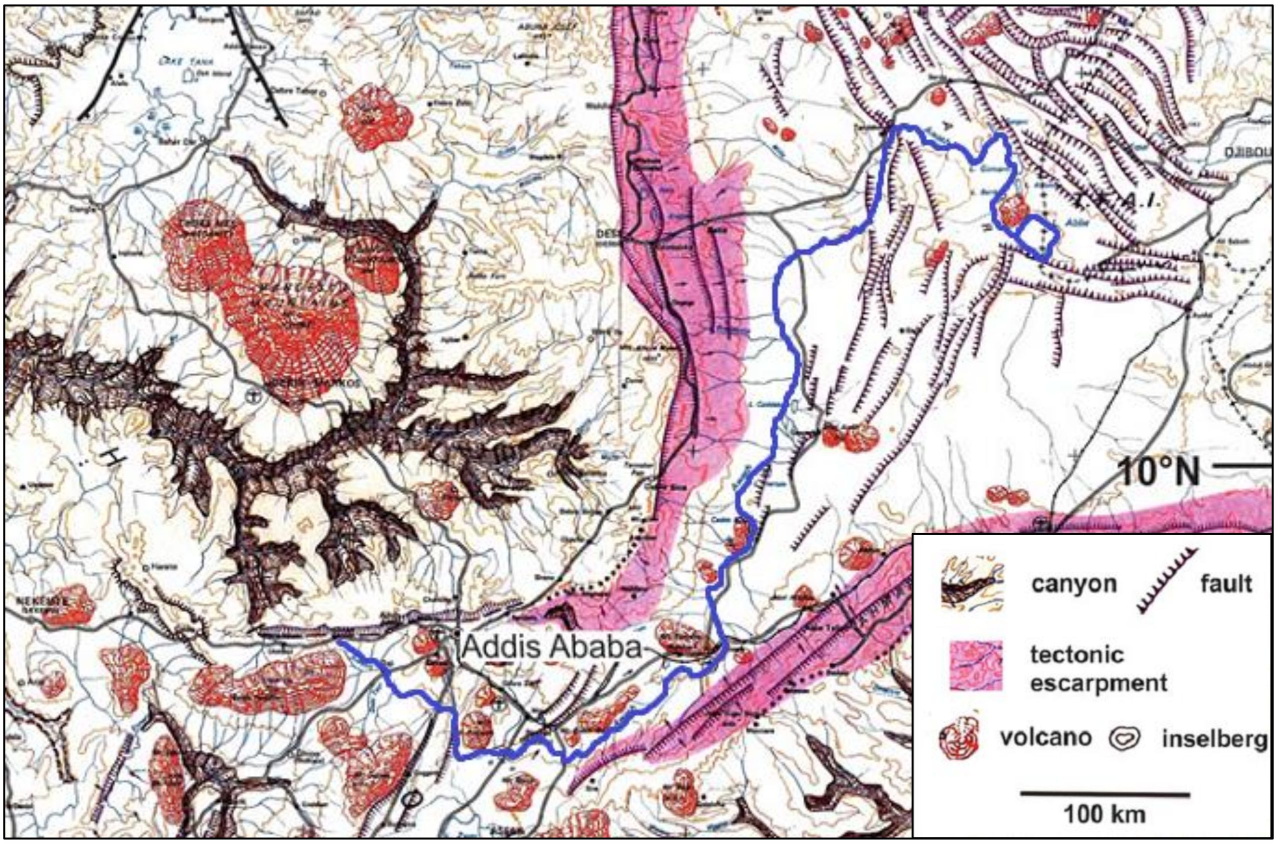

Figure 3. Morphological and geological features of the northen part of the Main Ethiopian Rift. The formation of volcanos has a visible influence on the course of the Awash river which is highlighted in blue. Based on Merla (1963) and adjusted from Merla et al. (1979).

1.2. Human impacts on Ethiopian riverine ecosystems

Human impacts in the region are manifold and only partly covered in the present thesis. Many anthropogenic stressors observed in the Awash river basin are related to industrialisation and urbanisation but also the fast-growing population and a high livestock density pose specific threats to functioning ecosystems. Apart from that, the longitudinal continuum of the river is interrupted by several technical structures (dams and weirs). Similar patterns of adverse impacts can be observed in other major river systems of Ethiopia as well which was pointed out by Habteselassie (2009).

In the present investigation, sampling sites were chosen on the basis of habitat quality and morphologically unimpaired sites (if feasible). This implies to avoid large-scale direct human impacts. However, various human activities are present along the whole course of the Awash river but vary in intensity. An overview of environmental challenges in the upper Awash river was given by Wubetu (2013), Degefu et al. (2013) or Benti (2014). Additional information is added based on the observations of Getahun and Stiassny (1998) and Habteselassie (2009) in other river systems. According to their conclusions the following impacts are prevailing:

- **Sand mining from the riverbed**: Supply of local markets as construction material. Causes an alteration of the river bed (instability of river banks) and increased sedimentation.
- **Urbanisation**: Settlements spread and roads are built as a result of a rapid population growth and the development of infrastructure. Causes soil sealing which prevents infiltration (higher surface runoff – higher discharge and increased erosion) and changes in land cover and land use.
- **Agriculture and livestock farming**: Extension and intensification (also greenhouses) of agriculture to increase food production – irrigation systems seem to be well developed in the river basin (which may lead to lower water levels). Causes high nutrient loads (from livestock farming and application of fertilizers) and the input of heavy metals (application of pesticides) in the adjacent water bodies.
- **Deforestation**: Supply of local markets as construction material and firewood. Causes a change in land cover and land use. Soil stability is lost and the land is increasingly prone to erosion (causing a higher sediment load in rivers). Farmers extend their fields to the edge of the river (no buffer strips). As a result, riparian vegetation and floodplain ecosystems (lateral interaction) are lost; reduced shading could increase water temperature.
- **Industrial effluents**: Industrialization of the region is promoted by the government to generate jobs, especially in the upper basin around Sebeta, Awash Melka and Mojo (alcohol, soap and oil factories, tanneries and breweries). Causes degradation in water quality, change in chemical and physical parameters (e.g. pH, conductivity, temperature), increased nutrient loads and a high concentration of heavy metals (here especially tanneries and oil factories).

- **Domestic pollution**: Rivers are used as public dumping grounds for all kind of domestic waste (biological and non-biological). Discharge of domestic waste water is seemingly high in the area of Addis Ababa (Akaki river). Causes degradation in water quality (high nutrient content), change in chemical and physical parameters.
- **Hydropower**: According to Tedesse et al. (2005) and personal observations, there are 3 hydropower stations: Awash I (Koka reservoir, 43.2 MW, constructed in the 1950s), Awash II (run-of-the-river power plant, 32 MW, constructed in 1966) and Awash III (run-of-the-river power plant, 32 MW, constructed in 1971). Awash II and III are located at the cascades downstream of the village Melkasa. Sediments are flushed twice a year (at the beginning and end of the rainy season). Occasionally the stretch between Awash II and Awash III falls dry when all water is used for power generation (during the dry season). The engineering structures cause an interruption of the longitudinal continuum and impoundments change chemical- and physical properties of the water.

Increased industrialisation and human activities subsequently lead to adverse environmental impacts and the loss of functioning ecosystems (e.g. habitat degradation, change in physical-, chemical parameters) and their unique biocoenoses (outlined in Getahun and Stiassny, 1998). Moreover, the subsistence of the local populations is threatened as they directly depend on the water resources (e.g. drinking water, irrigation of agricultural fields).

1.3. Ichthyofauna of Ethiopia’s river systems

The MER separates the drainage basins of the country and the east African region in two major biogeographic units. In the northern part of the rift valley the rivers drain over the Nile system into the Mediterranean Sea. This portion belongs to the Nilo-Sudan Ichthyofauna, equally as the south-western part of the rift system (Roberts, 1975). The southern regions on the other hand drain into the Indian Ocean and belong to the East Coast Ichthyofauna (mostly river systems within Kenya). It is important to note, that the Wabi Shebele-Juba basin (draining into the Indian Ocean) was not included as part of the coastal zone by Roberts (1975) and Skelton (1994). Instead it is recognized as the most eastern portion of the Nilo-Sudan Ichthyofaunal Province as summarized by Golubtsov et al. (2002). In their work they compared the affiliation of taxa to the major faunal provinces and indicated a transitional zone (Wabi Shebele-Juba system) which shares an equal number of species from both regions. However, it seems that uncertainties still persist and several groups need detailed taxonomic revision.

The upper and middle reaches of the Awash river system belong to the Abyssinian Highlands Ichthyofaunal Province as first described by Roberts (1975). Similarities between the headwaters of the Nile (including Lake Tana) and the Omo-Turkana basin should exist. Limitations of this differentiation and the unclear boundaries are highlighted in Golubtsov et al. (2002). In addition, they discussed the impact of physical barriers (in particular the Tis Issat Falls) in the separation of biogeographic units.

A comprehensive investigation of the species diversity in the main drainage systems of Ethiopia (White Nile, Blue Nile, Atbara-Tekeze, Omo-Turkana, Rift Valley and the Wabi Shebele-Juba system) was conducted by Golubtsov and Mina (2003). For the White Nile system, they indicated the highest diversity with more than 100 species (also stated in Golubtsov et al., 1995). The central and south-eastern drainage systems showed the lowest diversity with 31 species. However, black spots of no or little information still exist (due to difficult access) in all river basins and will probably increase the number of native and even endemic species (highlighted in Habteselassie (2009) and Habteselassie et al. (2010) with the description of *Garra chebera*). Moreover, the taxonomic status (or rank) of several taxa needs clarification. A comprehensive overview of (most) fish species inhabiting lacustrine and lotic systems of Ethiopia is presented in Habteselassie (2012).

1.3.1. Fish taxa of the Awash river basin

A first detailed description of the ichthyofauna in the MER was given by Roberts (1975). In his work he stated that the southern part of the rift valley (Omo-Turkana, Abaya, Chamo and Chew Bahir basins) belongs to the Nilo-Sudan Ichthyofaunal Province. Whereas the central part as well as the upper and middle Awash basin belong to the ichthyofauna of the Abyssinian Highlands. A clear summary of the present faunistic status (species distribution and comments on ecological aspects) in the region was given by Golubtsov et al. (2002).

Within the MER, the species distribution seems to be uneven with the highest diversity found in the southern portion (Omo-Turkana) and the lowest in the central part (Golubtsov and Mina, 2003). The species accounts for the Awash river appear to be contradictory in certain aspects. Getahun and Stiassny (1998) reported almost 30 species from literature review. A few years later Golubtsov et al. (2002) noted 10 species (without *Labeobarbus* cf. *nedgia* but considering the unclear taxon *Garra* cf. *hirticeps*). Golubtsov and Mina (2003), in their review of species diversity in the main drainage systems of Ethiopia indicated 13 – 15 species for the Awash basin and adjacent enclosed sub-basins. The difference might be explained by the unclear taxonomic status of several *Garra* and *Barbus* (*Labeobarbus* sp. and *Enteromius* sp.) species. For the upper Awash region (upstream of the Koka reservoir and tributaries of the Awash), Wubetu (2013) in an unpublished thesis, reported merely 3 species (*Garra dembecha, Garra aethiopica* and *Barbus humilis*). Wubie et al. (2017) noted the occurrence of 5 taxa in the upper most reaches (*Garra quadrimacuata*, *Garra dembecha, Garra hirticeps* and 2 unclear taxa placed in the genus *Barbus*). For Lake Koka and the adjacent floodplain, Desta (2005) reported 5 species (*Cyprinus carpio, Labeobarbus intermedius, Garra makiensis, Clarias gariepinus* and *Oreochromis niloticus*). Table 1, gives an overview of the number of taxa indicated for the rift valley (only native species) and the Awash basin (native and introduced species). *Oncorhynchus mykiss*, which is not indicted below, was introduced (Akaki reservoir, Awash basin), but never established. A more detailed list with species accounts for the Awash river in earlier years is given in Table 9.

Table 1. Fish diversity (native species) of the ‘Ethiopian Rift Valley’ (geographic denotation adopted) according to Golubtsov and Mina (2003). The taxonomic status of some *Barbus* (*Enteromius* sp. and *Labeobarbus* sp.) and *Garra* species is still unclear. Fish diversity (native and introduced (established) species) in the Awash river basin according to several authors – see Table 9.

Family	**Rift Valley**		**Awash river basin**	
	Genera	**Species**	**Genera**	**Species**
Mormyridae	3	3	0	0
Characidae	1	1	0	0
Cyprinidae	5	13-16	5	16
Poeciliidae	0	0	1	1
Bagridae	1	1	0	0
Schilbeidae	1	1	0	0
Clariidae	1	2	1	1
Mochokidae	1	1	1	1
Cyprinodontidae	2	3	1	1
Centropomidae	1	1	0	0
Cichlidae	2	2	2	3
Total	**18**	**28-31**	**11**	**22**

1.3.2. The genus *Garra* (Hamilton, 1822)

The taxonomic status of the Afro-Asian genus *Garra* has puzzled scientists for a long time. Froese and Pauly (2018) mentioned 130 valid species distributed from central-western Africa to China and south-east Asia. A first comprehensive study with focus on the east African region (Ethiopia) was conducted in an unpublished thesis by Getahun (2000). Much of the earlier confusions according to synonyms and the taxonomic placement were clearly outlined and discussed. Based on three synapomorphies (2 unbranched anterior pectoral fin rays, a narrow and elongated cleithrum as well as a short and broad ethmoid) he stated that the genus is placed as a monophyletic group within the tribe Garraina (Sub-tribe Discorostralini). At this point it should be noted, that the feature of possessing 2 unbranched anterior pectoral fin rays seems to be a characteristic shared by African members of the genus only (according to present knowledge). Eurasian species are characterised by only 1 unbranched leading pectoral fin ray (e.g. Sayyadzadeh et al., 2015; Mousavi-Sabet and Eagderi, 2016). Menon (1964), in his revision of the genus, had seemingly ignored this characteristic as he stated the fin structure as 'not remarkable' and indicated I+17 rays for the pectoral fin.

In a later work conducted by Stiassny and Getahun (2007) detailed morphological characteristics were presented supporting the hypothesis of monophyly for the subgroup Garraina (not to confuse with the genus *Garra*). In addition, the descriptions of 5 new species and data on their geographic distribution were provided. With the latest description of *Garra chebera* (Habteselassie et al., 2010) a total of 18 valid species (8 endemic to Ethiopia) is known from the African continent so far. Considering the fact that several river basins have not yet been investigated in detail and that several species possess a wide geographic distribution (e.g. *G. ornata*, *G. dembeensis*), the number might increase.

Apart from a detailed taxonomic description of the genus, nearly no reliable information exists on the biology and ecology of African *Garra*. Getahun (2000) presented detailed information on habitat preferences and shortly summarized aspects on feeding and reproduction. Based on his observations of Ethiopian species, a variety of habitats, ranging from 3000 m – 1500 m a.s.l., seem to be inhabited. A preference for pool sections with low flow velocity, sand substrate and abundant riparian vegetation (in particular long grass) was noted. This aspect was mentioned by Habteselassie et al. (2010) as well, while they investigated the distribution of *G. chebera* in the Dildil stream. It should be noted that certain species (e.g. *G. congoensis*) show specific adaptations to fast flowing water and rocky substrate as stated by Roberts and Stewart (1976).

The inferior mouth position and the often well-developed disc (see Figure 25, Appendix 2) give first indication of a bottom dwelling habit. Getahun (2000) reported that the diet mainly consists of phytoplankton and small invertebrates which are scraped off the substrate. This was mentioned earlier by Sibbing (1991) and suggested by Reid

(1978). A detailed feeding analysis was conducted by Gudeta (2016) in the upper reaches of the Awash river which supported earlier observations.

There is almost no information on the spawning ecology and larval habitats of African *Garra*. It is assumed that lacustrine species migrate to rivers for spawning (Skelton et al., 1991). Desta (2005) who conducted a study on distribution and feeding ecology of commercially important fish in Lake Koka, noted the high abundance of *Garra makiensis* in the inshore areas of the Koka floodplain during the rainy season. This may give a possible hint of migration patterns and habitat preferences.

More information exists on *Garra rufa*, a Eurasian species which seems to be among the few members of the genus which are artificially propagated. In this case predominantly for aquarium trade and used to treat skin diseases. According to an ongoing research project, eggs of this species do not show any adhesive properties and are solely deposited at the bottom (Susana Ferreira, pers. comm., 2018). A possible sexual dimorphism where ripe females could be more robust and males tend to develop prominent nuchal tubercles on the snout is not yet confirmed as stated in Stiassny and Getahun (2007). Asian representatives of the genus (especially from the Mekong river basin) are well studied in terms of larval development. Detailed descriptions of colouration and pigmentation patterns of larvae and juveniles exist for 3 species found in Thailand (Termvidchakorn et al., 2016).

1.4. Theoretical concepts of stream ecology

Rivers are dynamic aquatic systems with changing physical and chemical characteristics. From the headwaters to the lower reaches, biological communities change and adapt or shift in response to the prevailing abiotic factors. Several theoretical concepts exist to classify riverine ecosystems and describe the changing environmental gradients. Ward et al. (2002) highlighted different frameworks and their relation to the four dimensions in lotic systems (longitudinal, lateral, vertical and temporal). The following concepts briefly introduce the idea of river zonation based on ecological, morphological, physical and hydrological aspects.

Fluvial systems were first classified according to the distribution of fish species in European waters. These investigations date back to the first half of the 19th century (Borne, 1877; Nowichi, 1889). Among the best-known examples of **Longitudinal Fish Zonation (Fish Regions)** are the concepts by Thienemann (1925) and Huet (1949) which were introduced a few decades later. However, the classification (from up- to downstream) in ‘Trout region’, ‘Grayling region’, ‘Barbel region’, ‘Bream region’ and ‘Flunder region’ is generally seen as too simplistic. Illies and Botosaneanu (1963) introduced the **Stream Zonation Concept** which is based on fish, benthic invertebrates and environmental gradients. The headwaters start with the Crenal (source region) which can be further divided in Eucrenal and Hypocrenal (source rivulets). Followed by the Rhithral (upper course) which is further divided in Epi-, Meta- and Hyporhithral. Characteristic for this section is the high oxygen saturation as a result of the turbulent and high flow velocity. Downstream the gradients further decline and the river is classified as Potamal (Epi-, Meta- and Hypopotamal). The above stated concepts as well as river morphological classifications can be interlinked.

One of the best studied theoretical approaches to describe biological changes along the longitudinal gradient of a river is the **River Continuum Concept (RCC)** (Vannote et al., 1980). It is based on the assumption that an unidirectional flow is the defining feature of rivers and processes change along environmental gradients (the same applies to the ideas of Illies and Botosaneanu, 1963). From the headwaters to the lower reaches the main source of energy changes from allochthonous (input of coarse particulate organic matter (CPOM)) to predominantly autochthonous (autotrophic, nutrients from upstream) production. River morphology, hydrologic aspects and the importance of riparian vegetation change along the upstream-downstream gradient and shape the biologic communities. The feeding guilds of benthic invertebrates characteristically shift from shredders to grazers and further to collectors. A comparable shift of ecological guilds can be observed in fish assemblages as well (link between fish regions and RCC). However, it should be noted that the RCC has specific limitations and is not suitable to describe anthropogenic impacts (e.g. longitudinal interruptions), therefore several authors (e.g. Statzner and Higler, 1985) suggested modifications.

Based on the consideration that disturbance is a key factor in natural ecosystems, Ward and Stanford (1983) defined the idea of the **Serial Discontinuity Concept**. It applies to morphologically altered rivers where natural dynamics have been suppressed. In 1995, Ward and Stanford reviewed their model and included the lateral dimension (interaction with the alluvial flood plains) to achieve a more realistic approach. A further concept which is based on predictable disturbance and alternating dry and wet phases is the **Flood Pulse Concept** (Junk et al., 1989). Especially in large tropical lowland rivers with extended floodplains it explains the importance of the lateral and temporal dimension for biodiversity and productivity (input of nutrients) of the systems. The reliable periodic fluctuations of water levels enable the biota to specifically adapt to the changing environment. For temperate rivers, Tockner et al. (2000) revised the idea and presented and extension of the Flood Pulse Concept.

1.5. Longitudinal fish zonation in tropical rivers

From the above stated models, especially the Flood Pulse Concept is a suitable approach to characterise biocoenoses in tropical lowland rivers with a distinct rainy season and a high degree of lateral interaction with the adjacent floodplains. However, the applicability of other concepts depends on river morphological, hydrological and ecological aspects, which require a detailed study of the prevailing characteristics.

Investigations of the spatial distribution of fish assemblages are known from several tropical river systems in South America, Africa and Asia. Payne et al. (2010) conducted a study along the Rokel/Seli river (a lowland river) in Sierra Leone (West Africa). In their work they identified 3 distinct fish zones: a ‘small cyprinid zone’ in the headwaters, a ‘large cyprinid zone’ in the mid-section and a third zone in the lower sections, dominated by cichlids and catfish. A major change in taxa diversity was recognised at the Bumbuna Falls which seem to mark a migration barrier for several species. Sara et al. (2012) investigated fish assemblages in the Vunduzi river from its headwaters to the lower reaches in the Gorongosa National Park, Mozambique. Cyprinids were found to be the most dominant family among all sampling sites. Interestingly, a member of the family Amphiliidae (*Amphilius laticaudatus*) dominated the headwaters. An increase in species diversity was noted for the intermediate (characterised by a high diversity in cichlid fishes) and lower zones. Morphological adaptations of taxa, according to the prevailing abiotic environment were noted. Balon and Stewart (1983) conducted a survey along the Luongo river in Zambia (part of the upper catchment in the Congo basin) and described an unusual longitudinal gradient and a high species richness. In Ethiopia, a detailed investigation of the Weyto River was conducted by Habteselassie (2009). He assessed the anthropogenic impact (irrigation weir) on the spatial distribution of fish assemblages in the river system.

In South America, Ibarra and Stewart (1989) investigated the longitudinal zonation of fishes on sandy beaches in the Napo river basin in Ecuador (a lowland river). Environmental factors were correlated with fish assemblages and resulted in 4 distinct groups: an ‘upland clearwater’, an ‘upland whitewater’, a ‘lowland whitewater’ and a ‘lowland blackwater’. They concluded, that turbidity, substrate and pH had the greatest influence on fish assemblages. A long-term project to reveal the species richness and the distribution of fish assemblages was conducted in streams of the Ivinhema River basin (Brazil) by Súarez et al. (2011). Supporting theoretical concepts, the species diversity increased from the upper reaches to the lowlands and altitude was found as the key factor. They pointed out, that the distribution of the 4 most characteristic species was widespread throughout the basin.

1.6. Genetic barcoding

The systematic description of organisms and their taxonomic placement in a seemingly (or literally) ever growing tree of life is by no means an easy endeavour. For centuries, the morphological diagnosis and description was the only method to create a structure and hierarchy in the diversity of life. A revolutionary concept began to rise with the discovery of the DNA (deoxyribonucleic acid) structure by Watson and Crick in 1953 (based on earlier work by Rosalind Franklin and Maurice Wilkins). A long sequence of base pairs (based on 4 bases only) which codes for all the information essential to life and passed on to the next generation. It took decades until the technical progress made replication and sequencing of DNA possible to illustrate the differences (position of bases) between organisms. The first who suggested a method of using this molecular information in identifying organisms were Hebert et al. (2003). Based on the observation that variation between taxa exists on relatively short DNA sequences, these taxa can be easily distinguished. In their initial work they proposed a specific gene region (cytochrome c oxidase I (COI or cox1), 648 base pairs) on the mitochondrial DNA for reliable 'species identification' among animals. Several DNA sequence libraries (e.g. GenBank, National Center for Biotechnology Information, Barcode of Life Database) have been established since then and DNA barcoding became a common tool in biological science.

The theoretical concept of 'genetic barcoding' which enables accurate 'species identification' would simplify studies of biodiversity. However, the concept is controversially discussed among taxonomists and faces specific limitation outlined by several authors (e.g. Ebach and Holdrege, 2005; Taylor and Harris, 2010 or Collins and Cruickshank, 2012).

1.7. Problem description

The present thesis attempts to clarify the species diversity (with taxonomic notes on the genus *Garra*) in the upper and middle Awash river and comment on previous investigations and the impact of human activities on the fish biocoenoses. The investigation of a longitudinal distribution of fish assemblages is an interesting field of ecology, where questions about species distribution and functional guilds can be stressed and contribute to a better understanding of tropical riverine ecosystems. Furthermore, the species-specific response to changes in habitat characteristics and water quality will be discussed.

This directly leads to a broader relevance of the topic with the focus on a bio-indicator based assessment of aquatic ecosystems. The rapid population growth and the progressive development and industrialisation of the region is associated with a variety of environmental challenges. Water pollution and habitat degradation lead to the loss of functioning ecosystem which threatens biodiversity and poses serious health risks to the local populations. The measurement of chemical and physical quality parameters has a long tradition in aquatic ecology but cannot characterise the overall functionality of these systems alone.

1.8. Objectives and research questions

The present concept was designed as a preliminary survey of a follow-up project and aimed to investigate the fish fauna of the upper and middle Awash river in central Ethiopia. Emphasis was put on the longitudinal zonation of fish assemblages and the question how the biocoenoses react to environmental changes. The knowledge can ultimately help to assess the applicability of fish as bio-indicators in riverine ecosystems. To get a realistic picture of the fish communities, the sampling sites were selected based on habitat criteria and morphological characteristics. This is an important aspect since most previous sampling sites in this area were located at bridges and easy accessible sites (high anthropogenic impacts), which may lead to a distorted picture of the fish fauna.

The following specific **objectives** ought to be covered in the present investigation.

- Planning and conducting 3 excursions (duration of 1 week each) along the Awash, with focus on logistics and quality of sampling sites.
- Investigation of the longitudinal zonation patterns of fish assemblages in the upper and middle Awash river.
- Detailed description (morphometric and meristic features) of morphotypes within the genus *Garra*, supported by mitochondrial DNA sequence analysis (genetic barcoding).

Specific **research questions** were developed to address the above stated research aims. In detail:

- Which fish species occur in the upper and middle Awash river basin and how reliable is existing literature?
- How do fish assemblages change (in terms of species richness) from upstream to downstream sections?
- Do changing habitat parameters influence fish assemblages?

General **working hypotheses** were developed, based on scientific literature and discussed in the present study. In detail:

- Based on theoretical concepts (e.g. River Continuum Concept (RCC) (Vannote et al. 1980), Serial Discontinuity Concept (Ward and Stanford, 1983 and 1995)), it is hypothesized that abiotic characteristics but also fish assemblages will change as a response to the most noticeable human impacts observed (e.g. deforestation, livestock farming, interruption of the longitudinal continuum).
- In compliance with previous investigations (Roberts, 1975; Golubtsov et al., 2002) it is expected that faunistic elements of the Abyssinian Highlands Ichthyofaunal Province will dominate. Following theoretical concepts of river zonation (e.g. Stream zonation concept (Illies and Botosaneanu, 1963), RCC (Vannote et al. 1980)) it is hypothesised that species richness and diversity will change and gradually increase from upstream to downstream reaches.
- With an increase in species diversity from the headwaters to the lowland reaches, it is expected to observe faunistic changes between the rhithron and the potamon along transition zones, where fish assemblages change due to environmental gradients (Illies and Botosaneanu, 1963; Ibanez et al., 2007).
- Based on the concepts of ecological tolerance (Shelford, 1913) and niches (Whittaker and Levin, 1975) as well as the fundamental idea of natural selection (Darwin, 1859), it is expected that populations occurring in a wide range of environments (covering different habitats e.g. flow velocity, substrate) show specific adaptations and (slight) phenotypical variation. These differences are a consequence of natural selection where better adaptations are favoured.

2. MATERIALS AND METHODS

2.1. Study area and Sampling sites

From the headwaters of the Awash river near Ginchi (2389 m a.s.l.) to the Afar region, downstream of Lake Yardi (570 m a.s.l.), 12 sampling sites were set, covering more than 650 km of the main river. The following maps give an overview of the study area.

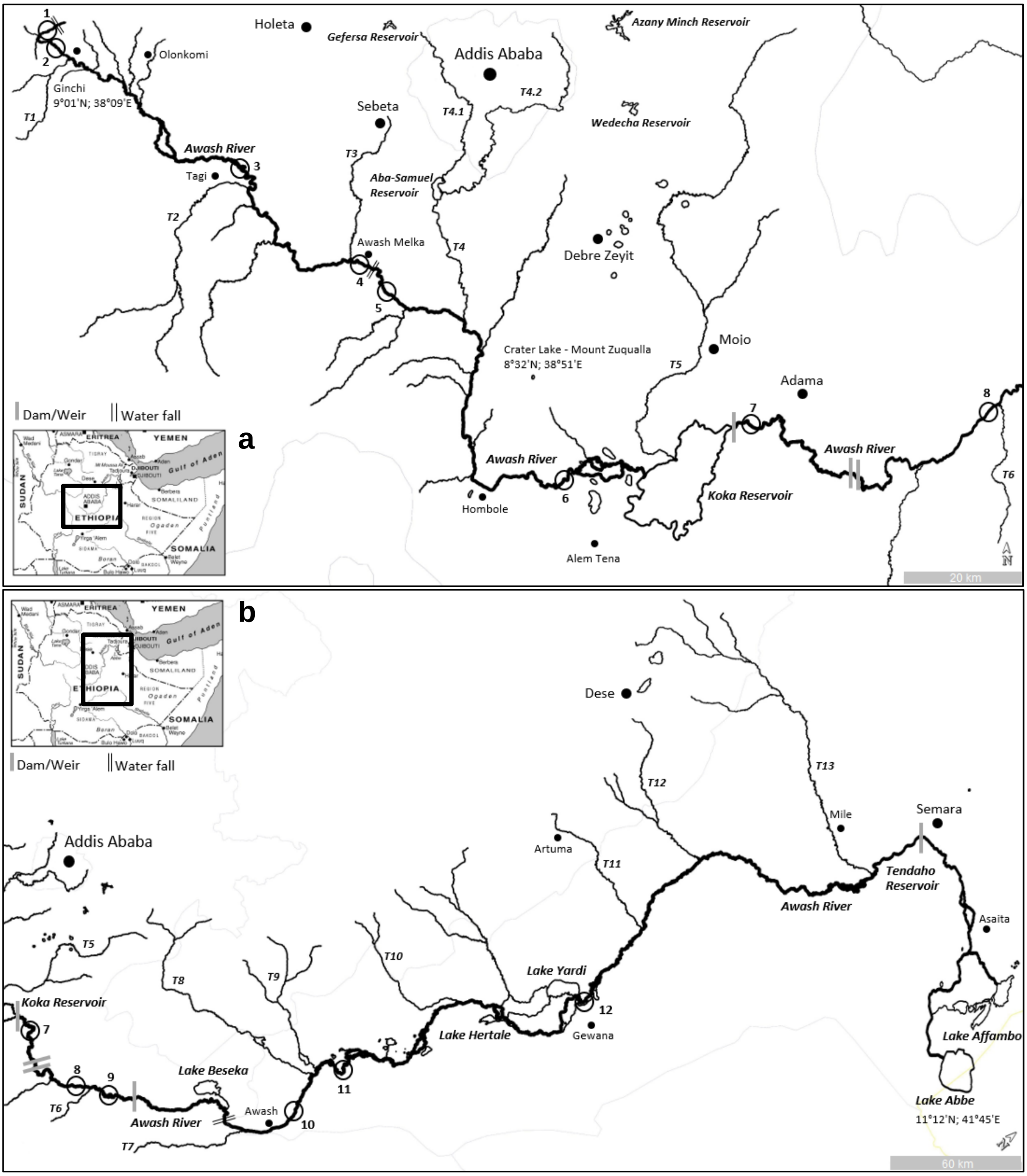

Figure 4. (a) and (b), upper, middle and lower basin of the Awash river. Sampling sites (1-12) and physical barriers are depicted. Important tributaries: T1 Debelo stream, T2 Teji river, T3 Sebeta river, T4 Akaki river, T5 Mojo river, T6 Bolo Shet, T7 Arba river, T8 Kesem river, T9 Kabena Shet, T10 Hawadi river, T11 Jona Shet, T12 Cheleka Shet, T13 Mille river. Note, that names and spelling of tributaries may differ. Source of information: Google Earth Pro 2017.

Site 1 (S1) – Chilimo forest (sampled on 06.11.2017 and 04.12.2017)

Figure 5a. Alternating pool-riffle sections in the upper reaches. Chilimo forest, 06.11.2017

Figure 5b. A cascade, marking a possible (partial) migration barrier for fish. Chilimo forest, 06.11.2017

Figure 5c. Dense riparian vegetation characterises the source region, Chilimo forest, 04.12.2017

Figure 5d. Various small streams join and form the Awash river. Chilimo forest, 04.12.2017

The Awash river drains the foothills of the Ethiopian Highlands at altitudes of 2200-2900 m.a.s.l., where the Chilimo Gaji forest complex extends over an area of about 3500 ha (Kebebew, 2012) and constitutes a major source of water. It is one of the last remaining Dry Afromontane forests (Tamrat, 1994) and harbouring several endemic plant species (Ensermu et al., 1992). Although the area is exposed to various human threats (e.g. deforestation) most river stretches are still in a near pristine condition. The 1st sampling site was set in the headwaters of the Awash at an altitude of 2389 m a.s.l. (9° 4'1.05''N, 38° 8'9.02''E, accessible from Ginchi). Surrounded by abundant riparian vegetation the small brook forms alternating pool-riffle sections. Flowing partly over bedrock, the substrate is mainly made up of boulders and coarse gravel. Banks of pools are often covered with fine gravel and patches of grass. The input of CPOM (in particular leaves and branches) is high. A notable feature of this first steep gradient section is a small (about 2 m in height) cataract (Figure 5b, approximately at: 9° 4'9.45''N, 38° 8'15.62''E), which marks a possible (partial) migration barrier for fish.

Site 2 (S2) – Gare Arera (sampled on 06.11.2017 and 05.12.2017)

Figure 6a. Deforestation and agriculture shape the character of the landscape. Gare Arera, 06.11.2017

Figure 6b. Steep river banks with scarce vegetation are prone to soil erosion. Gare Arera, 05.12.2017

Figure 6c. Deeply eroded stretches without shading are a common feature. Gare Arera, 06.11.2017

Figure 6d. Fine organic substrate and filamentous algae during dry season. Gare Arera, 05.12.2017

A few kilometres downstream of the first site, the land cover and land use change dramatically. Where the natural vegetation is cleared, pastures and fields predominate. Human impacts are manifold and not only indirect trough increased soil erosion and nutrient input from agriculture or livestock farming. Especially the nearly complete loss of riparian forest vegetation and the subsequent low shading are striking characteristics. Patches of grass and few herbaceous plants (primarily *Polygonum* sp.) dominate along the river banks. The 2nd sampling site was located in this agricultural environment, which still belongs to the uppermost reaches of the Awash at an altitude of 2244 m a.s.l. (9° 2'23.42"N, 38° 6'58.49"E, accessible from Ginchi). Alternating pool-riffle sections are still the most common morphological feature as the river bed gets wider and the discharge increases. Boulders and coarse gravel characterise the substrate composition. However, especially in deep pool sections the proportion of fine sediment can be high. The input of CPOM is rather low or nearly absent.

Site 3 (S3) – Awash Belo (sampled on 17.11.2017)

Figure 7a. The floodplain of the first low gradient section. Awash Belo, 28.10.2017

Figure 7b. A typical mesohabitat, fine substrate and scarce riparian vegetation. Awash Belo, 17.11.2017

Figure 7c. A short riffle stretch in an otherwise low gradient section. Awash Belo, 17.11.2017

Figure 7d. Livestock farming, a major anthropogenic impact in the area. Awash Belo, 28.10.2017

After the first steep gradient section in the Chilimo forest, the Awash river forms a wide floodplain at more than 2000 m a.s.l. In this region the 3rd sampling site was located upstream of the village Awash Belo at an altitude of 2065 m a.s.l. (8°51'39.12"N, 38°23'44.25"E). As the river gradient decreases, morphological characteristics of a lowland river are developed (e.g. meanders, deposition of fine sediment, increasing floodplain width). During the rainy season an extensive area is flooded and fine sediment is transported into the surrounding farmland. When the water levels retreat (dry season), the fertile fields are tilled and the river shrinks to a small water body. Water abstraction for irrigation seems to impair the situation. The pristine state of this environment is unknown since the natural vegetation had been entirely cleared and the area transformed into farmland. Predominantly non-native species (e.g. *Eucalyptus* sp.) were reforested. The banks are characterised by fine substrate (sand and fine gravel) and low vegetation cover. Coarse material is only found in riffle sections and covers parts of the riverbed.

Site 4 (S4)– Awash Kunture (sampled on 07.11.2017 and 06.12.2017)

Figure 8a. The last fragment of a near natural forest along the river. Awash Kunture, 06.12.2017

Figure 8b. Long pool section with low flow velocity and fine substrate. Awash Kunture, 06.12.2017

Figure 8c. Livestock farming and consequent nutrient enrichment. Awash Kunture, 07.11.2017

Figure 8d. Several cascades mark the transition to the gorge section. Awash Kunture, 28.10.2017

The 4th sampling site was set around the paleoanthropological site of Awash Kunture at an altitude of 2003 m a.s.l. (8°42'21.94''N, 38°36'18.78''E, accessible from Awash Melka). This locality is noteworthy in two aspects. Firstly, a last remaining part of a near natural forest (in this area of interest) exists along the river in the protected property of the former paleoanthropological excavation site and forms a dense riparian vegetation. Secondly, it marks the transition between the first low gradient section and the following second steep gradient section. Both morphological features are expressed although the anthropogenic impact (livestock farming, washing and bathing) is rather high. Deep pools are characterised by slow flow velocity and fine sediment. The input of CPOM is relatively high, this however accounts only for a rather short distance (about 1 km). More impacted stretches are heavily loaded with organic nutrients (manure). In contrast, the second half of the site which is characterised by high flow velocity and predominantly bedrock or large boulders. The shore is scarcely covered with grass (Poaceae and Cyperacae) and shrubs.

Site 5 (S5) – Sulula (sampled on 07.11.2017 and 06.12.2017)


Figure 9a. View on the gorge section downstream of Awash Kunture. Sulula, 07.11.2017


Figure 9b. Alternating pool-riffle sections in a largely unimpacted river course. Sulula, 07.11.2017


Figure 9c. If the river corridor gets wider, sediment is deposited (braiding character). Sulula, 07.11.2017


Figure 9d. Mesohabitats are characterised by predominantly coarse substrate. Sulula, 07.11.2017

A series of rapid cascades and falls characterise the beginning of the second steep gradient section which extends over a length of approximately 120 km. The falls mark a natural interruption of the longitudinal continuum and may act as a migration barrier for some fish species. Confined in a deep gorge, characteristics of a constrained river with erosion and degradation predominate. Where the valley widens, a partially braiding character (with stable islands) is developed. The lateral dimension is otherwise insignificant. The 5th sampling site was located at an altitude of 1916 m a.s.l. (8°39'56.83"N, 38°37'58.81"E, accessible from Awash Melka). The most notable features are large boulders which dominate the sediment composition and shape the character of the river stretch. Deep pools alternate with riffles (partly with very high flow velocity) and runs. The riparian vegetation is rather sparse which seems to be a natural characteristic and not only altered by human impacts. Livestock farming, washing and bathing are common anthropogenic stressors. Where the river is frequently accessed, the banks are prone to erosion during the rainy season.

Site 6 (S6) – Lafessa (sampled on 08.11.2017 and 08.12.2017)

Figure 10a. The surrounding landscape, affected by deforestation and overgrazing. Lafessa, 08.11.2017

Figure 10b. Remaining riparian vegetation along the river course. Lafessa, 08.11.2017

Figure 10c. Easily accessible sites are often heavily affected by livestock. Lafessa, 08.11.2017

Figure 10d. Sandbanks and deep pool sections are common characteristics. Lafessa, 08.11.2017

Upstream of Lake Koka, the channel slope declines again and the second low gradient section is formed. Typical physical elements of a lowland river (e.g. deposition of fine sediment) prevail, and wide passive meanders with sand banks and deep pools shape the character. The runoff increases considerably since the Akaki river (a major tributary coming from Addis Ababa) joins the Awash. Parts of the area belong to a wide floodplain where the reservoir extends during the rainy season. At an altitude of 1608 m a.s.l. the 6th site (8°23'16.34''N, 38°54'30.62''E, accessible from Alem Tena) was located at the edge of the floodplain. Deforestation, livestock farming and partly water abstraction were predominant human stressors along the sampling segments. Although most of the riparian vegetation was cleared, resulting in a destabilisation of river banks and decreased shading, the proportion of woody debris is worth mentioning. Different habitat types (e.g. sandbanks, shallow backwaters) which were not encountered upstream, characterise the site. The presence of crocodiles (most likely *Crocodylus niloticus*) indicate an increase in water temperature.

Site 7 (S7) – Wonji (sampled on 09.11.2017 and 26.01.2018)

Figure 11a. Wide and flat terrain downstream of the Koka reservoir. Wonji, 26.01.2018

Figure 11b. Abundant semiaquatic vegetation along the shore of the Awash river. Wonji, 26.01.2018

Figure 11c. Different habitat types (woody debris and large boulders). Wonji, 09.11.2017

Figure 11d. Shallow parapotamon, an ideal habitat for juvenile fish and amphibians. Wonji, 26.01.2018

To assess a possible impact of the Koka reservoir on physical and chemical water properties and the biocenoses, the 7th sampling site (8°28'23.83''N, 39°12'43.83''E, accessible from Wonji) was located 6.3 km downstream of the dam at an altitude of 1552 m a.s.l. The geomorphological character of the Awash is slightly different compared to the previous site. Notable characteristics are the low height of the river embankment and coarse bedload in short sections where riffles and runs are formed. Where the river corridor widens, sediment is deposited and (partially) stable islands develop, which add ideal habitat structures for juvenile fish (shallow parapotamon). Abundant riparian and semiaquatic vegetation (mainly *Polygonum* sp. and *Phragmites* sp.) characterise sites with low flow velocity where fine sediment is deposited. The impact of deforestation is less severe compared to S6 and a narrow remnant of trees and shrubs lines the river (shading, input of CPOM). The floodplain however is transformed into an agricultural landscape where the natural vegetation had been cleared. Water abstraction for irrigation was observed at several sites.

Site 8 (S8) – Korkada (sampled on 10.11.2017 and 09.12.2017)


Figure 12a. Seasonal agriculture and livestock farming characterise the site. Korkada, 10.11.2017


Figure 12b. A wide and largely bedrock confined river section. Korkada, 10.11.2017


Figure 12c. A connected side channel which offers different habitat structures. Korkada, 10.11.2017


Figure 12d. High flow velocity habitats are difficult to access. Korkada, 10.11.2017

After the second low gradient section (S6 and S7), which is interrupted by the Koka reservoir, a series of cascades and a drop in elevation (190 m over approximately 9.5 km) characterise the Awash. Two hydropower stations (Awash II and III) are located downstream of Melkasa and heavily impair the river stretch (interruption of the longitudinal continuum, flushing of sediment and low residual water during the dry season). The Awash then develops a constrained river course surrounded by a range of hills of volcanic origin. The 8th sampling site was located upstream of the village Doni at an altitude of 1260 m a.s.l. (8°30'2.78"N, 39°33'7.41"E, accessible from the road to Sodere). Compared to the upstream sites, the riverbed is wide and characterised by bedrock and large boulders. The main channel is very difficult to access due to the high flow velocity. Connected side channels (natural and for irrigation purpose) and stable islands are occasionally developed and increase habitat diversity (low flow velocity, fine substrate, riparian vegetation). Apart from washing and bathing, livestock farming and seasonal agriculture (water abstraction), direct human impacts are low.

Site 9 (S9) – Nur Sada (sampled on 31.01.2018)


Figure 13a. Fine sediment (sand in particular) and coarse substrate (volcanic origin). Nur Sada, 31.01.2018 (Image by Herwig Waidbacher)


Figure 13b. Constrained river section (cataract) with high flow velocity and bedrock. Low riparian vegetation. Nur Sada, 31.01.2018


Figure 13c. Potamal section with fine sediment and woody debris. Stable islands are formed. Nur Sada, 31.01.2018 (Image by Herwig Waidbacher)


Figure 13d. Seasonal agriculture and livestock farming, the most common stressors. Nur Sada, 31.01.2018 (Image by Herwig Waidbacher)

In the area of Nur Sada, the 9th sampling sites was located at an altitude of 1214 m a.s.l. (8°33'9.32''N, 39°38'9.77''E, accessible from Harbona (main road) and possibly Doni – see previous site description). The section is interesting as morphological characteristics of both, intermediate and steep gradients are developed. Short cataracts (bedrock, fast flow velocity) alternate with deep pools and runs where abundant fine sediment and woody debris are deposited. Occasionally, stable islands are developed. The main channel is difficult to access due to water depth and high flow velocity. Connected side channels offer different habitat structures but are often heavily affected by nutrient input (manure). The surrounding landscape is shaped by human activities (e.g. seasonal agriculture and livestock farming) and the natural riparian vegetation was cleared in most parts. Irrigation channels which divert water from the Awash to crop plantations in the former floodplain are a common feature. A short distance upstream, greenhouses are located close to the river.

Site 10 (S10) – Yimre (sampled on 30.01.2018)

Figure 14a. The Awash river is confined in a deep valley and lined by a corridor of trees and shrubs. Yimre, 30.01.2018 (Image by Herwig Waidbacher)

Figure 14b. Coarse gravel banks are a common feature and visible during the dry season. Yimre, 30.01.2018 (Image by Herwig Waidbacher)

Figure 14c. Deposition of abundant fine sediment is an unusual characteristic for this site. Yimre, 30.01.2018 (Image by Herwig Waidbacher)

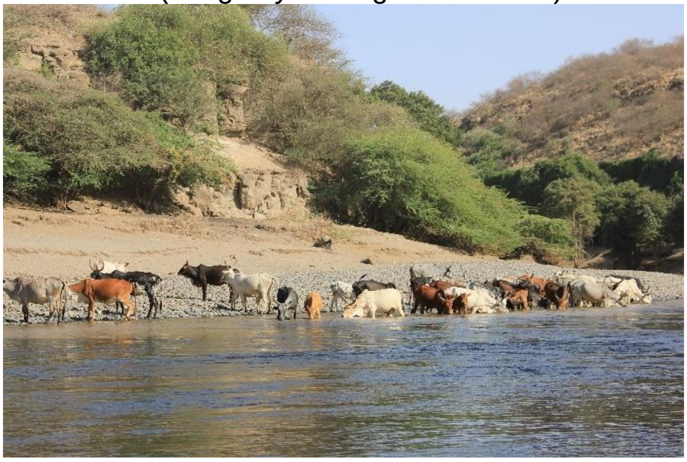

Figure 14d. Livestock farming is the basis of subsistence for the Afar people and constitutes one of the few direct human impacts. Yimre, 30.01.2018

Downstream of Metahara, where Lake Beseka is artificially connected with the river, the channel slope increases again and the Awash falls are formed. The river is then confined in a deep valley (for approximately 20 km) where coarse gravel (partly bedrock) prevails. Characteristics of a constrained river (e.g. a narrow river channel, high flow velocity) predominate. The 10th sampling site was set at the lower part of the gorge at an altitude of 797 m a.s.l. (9°4'59.08''N, 40°10'3.33''E, accessible from the main road (heading to the Afar region) downstream of the village Awash). Alternating pool-riffle-run sections shape the character. Habitats with low flow velocity and small stretches of parapotamon with abundant woody debris can be found as well. A notable observation is the relatively high proportion of fine sediment (sand) along the banks, which seem to be deposited when the water level retreats at the beginning of the dry season. The only noticeable human impact in an otherwise near natural river stretch is livestock farming, which constitutes the basis of subsistence for the local Afar people.

Site 11 (S11) – Worer (sampled on 29.01.2018)

Figure 15a. Lowland character (upstream view). Note the high river embankment of the right shore. Worer, 29.01.2018 (Image by Herwig Waidbacher)

Figure 15b. The very high proportion of woody debris in the river channel is a notable characteristic of the sampling site. Worer, 29.01.2018

Figure 15c. The riparian vegetation (partly cleared) is dominated by shrubs (especially *Prosopis* sp.) and herbaceous plants. Worer, 29.01.2018

Figure 15d. A dry side channel in the high floodplain which might be seasonally connected when the water level is high. Worer, 29.01.2018

The morphology and character of the Awash change once more about 195 km downstream of the Koka reservoir. As the channel slope and flow velocity decline, the river forms meanders, side channels and backwaters in a wide floodplain where fine sediment is deposited. Especially along the left shore, abundant vegetation and several small lakes and wetlands characterise the landscape. Due to the difficult access of the area, the 11th sampling site was located downstream of Amibara along the right shore of the Awash (9°20'6.98''N, 40°10'19.50''E, 743 m a.s.l., accessible via the “Agriculture Research Center in Amibara Wereda”). The natural floodplain was entirely transformed into an agricultural landscape and is partly decoupled from the river by an earth dam. Minor morphological alterations (stabilization of the shoreline) were observed. Water abstraction for irrigation purpose is widespread and seems to decrease the water level of the Awash considerably during the dry season. Deep pools, point bars and very abundant woody debris characterise mesohabitats at this site.

Site 12 (S12) – Kada Bada (sampled on 28.01.2018)

Figure 16a. A near natural site characterised by abundant riparian vegetation and an extended floodplain. Kada Bada, 28.01.2018

Figure 16b. Rare alluvial forest along the Awash river, note the low river embankment. Kada Bada, 28.01.2018 (Image by Herwig Waidbacher).

Figure 16c. Trees, shrubs and lianas dominate the riparian zone. The accessibility of most stretches is limited. Kada Bada, 28.01.2018

Figure 16d. A connected side channel offering diverse habitat structures. Kada Bada, 28.01.2018 (Image by Herwig Waidbacher)

Downstream of Lake Yardi, the 12th sampling site (10°13'53.49"N, 40°34'43.09"E) was located at an altitude of 570 m a.s.l. The area is accessible from Gewana but only accompanied by members of the local Afar community. Between Lake Hertale and the site, the Awash forms a large floodplain (wetland) with side channels and lakes (e.g. Lake Hertale, Yardi, Caddabassa and Dalay). Part of the land is seasonally used for agriculture. Wide areas are covered with Papyrus (*Cyperus* sp.) and a non-native shrub (*Prosopis* sp.). The locality is unique among all sites in many respects. It represents a near natural tropical lowland river with an intact alluvial forest, side channels and highly diverse habitat structures. The main channel (Eupotamon) is characterised by abundant woody debris and a relatively low river embankment. However, most stretches are difficult to access due to the thick riparian vegetation and a high number of crocodiles. Adverse human impacts (deforestation and partly channelization) were observed along the right bank downstream of the bridge.

Table 2. Overview of sampling sites along the Awash river. Altitude was recorded using a GPS-system (Garmin VISTA etrex) and verified with a simple geographic information system (GIS) software (Google Earth Pro 2017). Distance from source is based on the same GIS software.

Site name	Geographic Coordinates	Altitude (m a.s.l.)	Distance from source (km)
S1 - Chilimo forest	9° 4'1.05"N, 38° 8'9.02"E	2389	5.3
S2 - Gare Arera	9° 2'23.42"N, 38° 6'58.49"E	2244	13.0
S3 - Awash Belo	8°51'39.12"N, 38°23'44.25"E	2065	73.3
S4 - Awash Kunture	8°42'21.94"N, 38°36'18.78"E	2003	116.3
S5 - Sulula	8°39'56.83"N, 38°37'58.81"E	1916	123.8
S6 - Lafessa	8°23'16.34"N, 38°54'30.62"E	1608	194.5
S7 - Wonji	8°28'23.83"N, 39°12'43.83"E	1552	243.3
S8 - Korkada	8°30'2.78"N, 39°33'7.41"E	1260	301.8
S9 - Nur Sada	8°33'9.32"N, 39°38'9.77"E	1214	317.1
S10 - Yimre	9°4'59.08"N, 40°10'3.33"E	797	416.8
S11 - Worer	9°20'6.98"N, 40°10'19.50"E	743	468.1
S12 - Kada Bada	10°13'53.49"N, 40°34'43.09"E	570	658.4

2.2. Field work

Between November 2017 and January 2018 (dry season), 3 excursions along the Awash river were planned and conducted. Based on habitat criteria (e.g. riparian vegetation, natural river embankment, diverse meso- and microhabitats), morphological characteristics (e.g. geomorphological setting, longitudinal gradient) and accessibility (by car or by foot, less than 60 min of walking), 12 sampling sites were selected along the longitudinal gradient. In total, more than 650 km of the river stretch, ranging from the Chilimo forest to Kada Bada were covered (1819 m altitudinal difference). All study sites upstream of Lake Koka (with the exception of S3) and 2 sites downstream (S7 and S8) were sampled twice. Fish sampling and habitat assessment were conducted for 1 day in each location (except of S4, S5 and S6, where gillnets and longlines were set over night).

2.2.1. Fish sampling

In the present investigation, a combination of several fishing gears (electrofishing, beach seine (mosquito net), frame net, gillnets, cast net as well as longlines) were used. Depending on the character of the site (e.g. water depth, flow velocity and substrate), the best suitable methods available were chosen. In headwaters and wade able shallow habitats, point abundance sampling (according to Copp, 2010) was carried out using a back-pack electrofishing unit (Honda GXV 50, direct current, 1.5 kW, 300/580 V). This method was only used during the first excursion (06.11-10.11.2017, S1-S6). Each section was fished against the water flow (downstream to upstream) for a maximum of 15 min., including the time for walking and handling fishes (time increased with increasing wetted width). For an efficient procedure at least 3 people were needed. The first person fishing with the anode (length of pole: 2 m), a second following with a hand-net (width: 40 cm, length: 25 cm, mesh size: 5 mm, length of pole: 1.5 m) and a third with a bucket where fish were stored.

Two standard mosquito nets (polyethylene, without chemical treatment, mesh size: 1.5 mm), purchased from local markets, were used to construct 2 beach seins. At each side 2 poles (bamboo or hardwood) were fixed for better handling. The bottom was stabilized using a sinking line (lead), whereas the top was supported by floaters (final dimensions, width: 2.1 m and height: 1 m). Constructed to be used by 2 persons, this method was applied from the headwaters to the lowland region. In the uppermost sites (S1, S2) the complete wetted width was covered, and the net was dragged against the flow direction (low water level during the dry season). With increasing channel width, fish were captured especially along the shore and to a maximum water depth of 1 m by dragging the net downstream (this requires walking faster than the current). In pool sections or side channels with low flow velocity, fast walking was avoided in order not to disturb the sediment and chase away fish. Sampling segments were usually between 5 and 20 m in length. In rough riffle sections (fast flow velocity) and over coarse substrate (crevices) the method was limited.

Figure 17a. Electrofishing in a shallow side channel. Lafessa, 09.11.2017

Figure 17b. Dragging the ‘mosquito net’. Yimre, 30.01.2018 (Image by Herwig Waidbacher).

For vegetated shore lines and side channels a frame net (width: 0.9 m, height: 1 m, mesh size: 1.5 mm) was used which could be handled by one person only. The applicability was restricted to rather shallow water depths. However, the method was suitable to sample smaller fish along the shore and applied at S10, S11 and S12.

In deep pool sections, where other methods were limited, gillnets were used. For this purpose, two nets with different mesh size were prepared (1st: 25 m long, 1.5 m in height, stretched mesh size: 80 mm; 2nd: 50 m long, 2 m in height, stretched mesh size: 60 mm). Gillnets were set in the late afternoon and collected in the following morning. Additionally, these mesohabitats were sampled using longlines (hooks: size 8 and 4, and lines: monofilament 0.18 and 0.25 mm (diameter), 6.0 and 8.8 lbs (straight tension), each 3 m long). At each pool section 10-15 hooks (bait: meat or soap) were placed along the shoreline and checked every 30 minutes or left over night. Both methods were applied during the second excursion (04.12.-10.12.2017, S4-S6).

Slow moving pools and runs in the main channel were fished using a cast net (radius: 1 m, stretched mesh size: 15 mm). The method was applied at S9, S10, S11 and S12.

2.2.2. Species identification

Prior to field work, a comprehensive pictorial guide for species identification was developed (available at: University for Natural Resources and Life Sciences (BOKU), Institute of Hydrobiology and Aquatic Ecosystem Management (IHG), Austria and the National Fish and other Aquatic Lives Research Centre (NFLARC), Sebeta, Ethiopia). In addition, identification keys for several families (e.g. Cyprinidae), genera and species (e.g. *Garra* sp.), presented in Habteselassie (2012), Froese and Pauly (2017) and Stiassny and Getahun (2007) were used. All fish not clearly identifiable in the field (with focus on the genus *Garra*) were preserved in 96% ethanol solution for further analysis (ethanol was changed at least 3 times in each sampling container to ensure a high concentration and an optimal preservation – especially for DNA analysis). Natural characteristics (e.g. colour of the skin and fins in life) were recorded and photographs of specific details taken (digital camera, Olympus Stylus TG-4).

2.2.3. Habitat assessment and water parameter

Qualitative habitat parameter (substrate composition, microhabitats, riparian and aquatic vegetation and human impacts) and river morphological characteristics (see below) were recorded for each sampling site. Substrate fractions (pelal: < 6 µm, psammal: > 6 µm – 2 mm, akal: > 0.2 – 2 cm, mikrolithal: > 2 – 6 cm, mesolithal: > 6 – 20 cm, makrolithal: > 20 – 40 cm and megalithal: > 40 cm) were estimated in percentage (%) for each mesohabitat (verification by at least 2 persons). Microhabitats (xylal, leaves, roots of trees and lithal) vegetation (submerged plants (refer also to semiaquatic plants), trees, shrubs, herbaceous plants and grass (Poaceae and Cyperaceae) and human impacts (agriculture, livestock farming, settlements, solid waste, washing/bathing, industry, sand mining, water abstraction, deforestation and channelization) were recorded according to observations during the field work. The following categories were assigned: abundant (‘major’ for human impacts), present, scarce (‘minor’ for human impacts) and absent. Morphological features of the river (e.g. height of river embankment, width of the active channel) and general characteristics of the sampling sites (e.g. fished water depth) are based on measurements (measuring tape, length of 50 m) or estimations (verification by at least 2 persons).

At each sampling site, water quality parameters were measured using a portable HACH-multimeter (HQ40d). The focus was put on dissolved oxygen concentration (probe: LDO 101), electric conductivity (probe: CDC 401) pH-value (probe: PHC 301) and temperature. If possible, measurements (3 for each parameter) were conducted at noon (sun at zenith).

2.3. Laboratory work

About 1500 specimens of *Garra* were collected from all sampling sites along the river course and preserved in 96% ethanol solution for detailed analysis. Most specimens were stored at NFLARC in Sebeta, Ethiopia and few specimens were brought to Austria (BOKU). In the first step, material was screened and morphotypes were identified. For each morphotype, 30 specimens (representing different mesohabitats and size classes) were selected and morphologic, morphometric and meristic data were recorded.

2.3.1. Morphometric measurements and meristic counts of *Garra*

Measurements and counts follow Getahun (2000) (Figure 24, Appendix 2) and were conducted at NFLARC, Sebeta, Ethiopia and BOKU, Austria using a stereo microscope (Novex-RZ and Nikon-Type 102 with LED illumination) and a digital caliper to the nearest 0.1 mm. All morphometric measures are given in percentages (proportion to standard length (SL), head length (HL), orbit diameter (OD) or distance between anal fin and pelvic fin insertion). The classification and designation of the suctorial discs (disc types A, B and C) follow Stiassny and Getahun (2007) (Figure 25, Appendix 2). Counts of fin rays (branched and unbranched) were conducted using a stereo microscope (with transmitted-light illuminator) and therefore could be less accurate (the first small spines are nearly invisible) compared to radiographs or stained and cleared specimens. The presence of the first unbranched rays of dorsal and anal fin were challenging to confirm. Uncertainty may exist in the number of branched and unbranched rays of the pectoral fin (especially in posterior position). The high number of unbranched pectoral fin rays (4 – 5) stated in Stiassny and Getahun (2007) could not be clarified. In the present study, counts of unbranched rays always refer to the anterior position. Postpelvic scales were counted in one continuous row between pelvic fins and vent. All measures refer to the left side of the body. Photographs of each taxon and morphotype (lateral-, dorsal-, ventral side, predorsal region, lateral- and ventral side of head and snout from lateral- and dorsal side) were taken using a digital camera (Olympus Stylus TG-4).

2.3.2. Genetic analysis of *Garra*

Since reference material (DNA sequences) for African representatives of the genus *Garra* is rare, the specific objective was to support and compare to morphometric and meristic data (obtained in this investigation). Reference sequences of selected congeners from Africa, the Arabian Peninsula and Asia was obtained from GenBank (library for DNA barcodes). A total of 100 representatives of *Garra* (representing all morphotypes, mesohabitats and sites) was selected for genetic barcoding (mtDNA). Fin clips (in most specimens the right pectoral fin, only in few small specimens the caudal fin or muscle tissue) of all specimens were preserved in 96% ethanol and stored at room temperature until analysis. Extraction of DNA and PCR (polymerase chain reaction) were conducted in the Institute of Forest Entomology, Forest Pathology and Forest Protection at BOKU, Vienna, Austria. Sequencing of the selected gene region was conducted by Eurofins Genomics (Ebersberg Germany).

DNA extraction

Genomic DNA was isolated using the GenElute Mammalian Genomic DNA Miniprep Kit for tissue preparation (Sigma-Aldrich, St. Louis, USA), according to the enclosed User Guide. The following steps were either slightly adapted or are essential to be considered:

Only a small part of the fin clip was used for DNA extraction. Before adding ‘Lysis Solution T’ tissue has to be dry (evaporation of ethanol) and cut in small pieces (to simplify digestion). Working devices must be flamed after each individual sample to avoid contamination. Samples were incubated for 3 hours at 55 ºC. To obtain RNA-free DNA, ‘RNase A Solution’ was added. Absolut ethanol (99%, undenatured) was added to facilitate binding of the DNA strands to the membrane. The ‘Column Preparation Solution’ improves binding of DNA to the membrane (using GenElute Miniprep Binding Column). After washing (2 times, using Wash Solution) the clean DNA remains on the membrane and can now be eluted. Samples were then stored at 4 ºC for further procedure. Proper labelling of all vials during different analysis steps and accurate working is a prerequisite.

Polymerase chain reaction (PCR)

The procedure was carried out according to PeqGOLD Taq-DNA-Polymerase (peqlab/VWR, Erlangen, Germany). Two pairs of primers were used: **Fish-COI-F** (5'-TCAACYAATCAYAAAGATATYGGCAC-3'), **Fish-COI-R** (5'-ACTTCYGGGTGRCC RAARAATCA-3') and **KAI-F** (5'-GAAGAACCACCGTTGTTATTC-3'), **KAI-R** (5'-ACCTCCRAYCTYCGGATTACA-3'). Note that Y = C +T and R = A + G (following the technical datasheet of Sigma-Aldrich, 2015).

The following steps were either slightly adapted or are essential to be considered: To determine the volumes needed, a 'mastermix' of all components was compiled (see Table 3). Each tube finally contained 9 µL of the 'mastermix' and 1 µL of extracted DNA. In total, 35 cycles of PCR were run to amplify DNA. Temperature setting during PCR was according to Meulenbroek et al. (2018). Additionally, DNA concentration can be measured using NanoDrop 2000c (before sequencing). In the present study the mean concentration was 20 ng μL^{-1}.

Table 3. Example of the volumetric composition (in total 10 µL – representing 1 tube) for all compounds (mastermix) to conduct a PCR.

Component	**Fish-COI F/R**	**Component**	**Kai F/R**
sterile H_2O dest.	6.1	sterile H_2O dest.	5.1
puffer solution (Y-P)	1.0	puffer solution (Y-P)	1.0
bovine serum albumin (BSA)	1.0	enhancer solution P	2.0
dNTP-Mix	0.2	dNTP-Mix	0.2
upstream Primer	0.3	upstream Primer	0.3
downstream Primer	0.3	downstream Primer	0.3
taq-DNA-Polymerase	0.1	taq-DNA-Polymerase	0.1
template DNA	1.0	template DNA	1.0
Total volume	10.0		10.0

Sequencing

A volume of 15 µl concentrated DNA was separated and sent to Eurofins Analytik GmbH, Germany where purification and sequencing was carried out. Results were made available as text files and chromatograms.

2.4. Statistical analysis

All data recorded on field protocols were immediately transferred and organized using a spreadsheet (MS Excel, 2016). For further statistical analysis, specialised software packages were used (**R:** RStudio Open Source License, 2017; **SPSS:** IBM SPSS Statistics 21).

2.4.1. Water parameter

Arithmetic mean and standard deviation for all sampling sites were computed. To point out relationships between water parameters (temperature (ºC), conductivity (µS cm^{-1}), dissolved oxygen (mg L^{-1}) and pH) and river morphological characteristics (active channel width (m) and height of river embankment (m)), scatterplots were used. This method also enables to show changes of variables along the longitudinal gradient. A more precise picture of the relation was obtained by performing a correlation analysis (Person's correlation). A p-value of < 0.01 was considered as significant.

To emphasise patterns in a multidimensional data set, a standard eigenvector based method (principle component analysis (PCA)) was conducted (based on the descriptions by Borcard et al., 2011). Variables were centred and scaled (divided by the standard deviation) to enable comparison. A scree plot, showing the variances of each principal component (PC), was plotted to see which PC accounts for most of the variation within the data. Eigenvectors were graphically displayed and calculated. PC were correlated with original variables to interpret results (correlation coefficients 'r' are given for each variable). In the present study, the R function **prcomp ()** (package **stats**) was used to compute PC. For graphical illustration the R functions **ggplot ()** (package **ggplot2**) and **fviz_pca_biplot ()** (package **factoextra**) were applied.

2.4.2. Species distribution and zonation assessment

Absolute number of specimens for each taxon (all specimens recorded at each site, single morphotypes were not considered) was used to calculate diversity indices (Table 4). Several indices were used in order to see advantages and limitations of each (with regard to different fishing methods used at each site (sampling effort) and the resulting difficult comparability). Relative abundance (in %) for all taxa (at each sampling site and mesohabitat) was calculated. Abundance data of the 5 most frequent taxa were plotted along all sampling sites and possible transition zones indicated.

Table 4. Indices used in the present analysis. S = number of species (taxa), N = total number of individuals per site, ni = number of specimens per taxon, pi = (ni/N)*(ni/N) for each taxon.

Diversity indices	Formula	Reference
Margalef diversity index	$D_{Mg} = (S-1)/\log N$	Margalef (1958)
Menhinick diversity index	$D_{Mn} = S/$squared root of(N)	Menhinick (1964)
Simpson diversity index	$D_1 = (N*(N-1))/(\Sigma\ ni(ni-1))$	Boenigk and Wodniok (2014)
Simpson index	$D_2 = \Sigma(pi^2)$	Boenigk and Wodniok (2014)
Gini-Simpson-index	$D_{1-D2} = 1-\Sigma(pi^2)$	Guiasu and Guiasu (2010)
Shannon diversity index	$H' = -\Sigma(ni/N)*\ln(ni/N)$	Lampert and Sommer (2007)
Evenness or Equitability	$E = H'/\ln(S)$	Begon et al. (2006)

A common method in ecological science to analyse data and indicate patterns or similarities (especially in the context of abundances) is the correspondence analysis (CA). In the present study a method summarized by Borcard et al. (2011) was followed to outline and determine which sites do have a similar species (taxa) composition. Relative abundance data of each taxon (single morphotypes were not considered) were used and variables reduced to two axes as this method best represents the observations. Like the PCA, the CA is an eigenvector based tool. However, instead of the Euclidian distance it is based on Chi-square distances. As suggested for proper interpretation, two scalings of the results were visualized (see further explanation and differences in Figures 20a and 20b). Eigenvalues for each axis were plotted. The R function **cca ()** in the package **vegan** was used.

To describe how communities change along environmental gradients, Ter Braak (1986) introduced an extension of the CA, the canonical correspondence analysis (CCA). In addition, the method may allow to explain taxa occurrence as a result of their optimal ecological tolerance (if sampled throughout their entire range) as indicated in Borcrad et al. (2011). A set of environmental variables (temperature (ºC), conductivity (µS cm^{-1}), dissolved oxygen (mg L^{-1}) and pH) was used to explain fish communities (based on their absolute abundance, single morphotypes were not considered) and similarities between sampling sites along the longitudinal gradient. River morphological characteristics were not included in the data set. Absolute abundance data of fish were log-transformed (to reduce the influence of very rare or very abundant taxa). Variance inflation factors (VIF) were computed (R function **vif.cca ()**) to outline linear dependences between environmental variables (VIF > 10 was avoided). Permutation tests (ANOVA) were conducted to test for significance of the main components in the model (Tables 12a, 12b and 12c, Appendix 1). A p-value of < 0.05 was considered as significant. For CCA the R function **cca ()** in the package **vegan** was used.

2.4.3. Morphometric analysis of *Garra*

A set of 19 characteristics (see Tables 14 – 18, Appendix 1), including all morphometric measurements plus lateral line scales and predorsal scales, was used to conduct a PCA (following Borcard et al., 2011). Variables were centred and scaled (divided by the standard deviation). A scree plot, showing the variances of each PC, was plotted to select the first 2 PC that account for most of the variation within the data. For proper interpretation, eigenvectors were displayed and PC correlated with original variables. The R function **prcomp ()** in package **stats** was used to compute PC. For graphical illustration the R functions **ggplot ()** (package **ggplot2**) and **fviz_pca_biplot ()** (package **factoextra**) were applied. Habitat preferences of taxa were graphically displayed by calculating the relative abundance (%) for each taxon (per sampling site and habitat) and plotting it for all mesohabitats observed (Figures 31 – 33, Appendix 2).

2.4.4. Genetic analysis of *Garra*

Raw data were formatted using Chromas 2.6.5 (Technelysium DNA sequencing software). Further analysis steps were conducted using MEGA 5 (Molecular Evolutionary Genetics Analysis). In total, 500 base pairs (for each sample) were used for comparison. Following Saitou and Nei (1987), the relationships between taxa were inferred using the Neighbour-Joining cluster method. Evolutionary distances were computed using the Tamura-Nei method (Tamura and Nei, 1993).

The following species (based on GenBank) were included in the analysis to compare with taxa from the Awash river (all COI): HQ235945.1 *Garra tana*; KF 929909.1 *Garra dembeensis*; KT193003.1 *Garra dembeensis*; KT192819.1 *Garra dembeensis*; JX074202 *Garra ornata*; HM418166.1 *Garra congoensis*; JF915613.1 *Garra gotyla*; JX074157.1 *Garra lamta*; JX074219.1 *Garra nasuta*; JX074214.1 *Garra cyrano*; JQ864606.1 *Garra orientalis*; KM214729.1 *Garra buettikerii*; KM214748.1 *Garra tibanica*; KJ553483.1 *Garra caudomaculatus*; KJ553348.1 *Garra ghorensis*; KM214798.1 *Garra ghorensis*; KM214807.1 *Garra persica*; KM214743.1 *Garra rufa*; JF416296.1 *Garra rufa*; JQ677110.1 *Labeobarbus intermedius* (outgroup).

3. RESULTS

3.1. Habitat characteristics

The spatial variation of river morphological characteristics along the Awash is summarized in Table 5 and Figures 26d – 26f (Appendix 2). Mean active channel width (estimated) increased from the headwaters (S1, 7 m, n = 12) to the downstream reaches (S12, 175 m, n = 4). An interruption was observed for site 5 (39 m, n = 10) and site 10 (57 m, n = 5). The separation of the headwaters (S1, S2) and the lowland reaches (S11, S12), explained by the channel width (r = 0.74, PCA) and other characteristics is clearly indicated in Figure 19 along PC1 (Dim1, 43%).

The highest mean river embankment (estimated) was encountered at site 6 (4.0 m, n = 10) and 11 (3.5 m, n = 3). Whereas the lowest heights were observed in the source region (S1, 0.5 m, n = 12) and in the lowland floodplain (S12, 0.5 m, n =4). The influence of this morphological measure (r = 0.53, PCA) is depicted along PC1 in Figure 19. Mean fished water depth (estimated) increased along the longitudinal gradient, indicating a general increase in water volume. Shading (estimated) of the main channel was low among all sites, except for the Chilimo forest (S1, 50 - 70 %, n = 12), the gorge section at Yimre (S10, 10 - 30 %, n = 5) and the lowland site at Kada Bada (S12, 10 - 30 %, n = 4).

Table 5. Summary of topographical and morphological characteristics of all sampling sites. Altitude was recorded using a GPS-system (Garmin VISTA etrex) and verified with a simple geographic information system (GIS) software (Google Earth Pro 2017). Distance from source is based on the same GIS software. Other values depicted are based on estimations in the field for each mesohabitat (a mean for the sampling site is given). The values for shading refer to the mean shading of all sampling points at zenith and bright sky.

Site	Altitude (m a.s.l.)	Distance from source (km)	Shading (%)	Active channel width (m)	Height of river embankment (m)	Fished water depth (cm)
S1	2389	5.3	50-70	7	0.5	25
S2	2244	13.0	0-10	21	0.9	35
S3	2065	73.3	0-10	33	1.9	23
S4	2003	116.3	0-10	57	2.3	49
S5	1916	123.8	0-10	39	3.0	55
S6	1608	194.5	0-10	47	4.0	54
S7	1552	243.3	0-10	77	1.2	47
S8	1260	301.8	0-10	90	2.0	35
S9	1214	317.1	0-10	74	2.0	64
S10	797	416.8	10-30	57	2.1	60
S11	743	468.1	0-10	68	3.5	74
S12	570	658.4	10-30	175	0.5	56

General characteristics (substrate, microhabitats, vegetation and human impacts) observed from all sampling sites are given in Table 10 (Appendix 1). The source region of the Awash river was characterised by abundant coarse particulate organic matter (CPOM) (especially leaves) and dense riparian vegetation. Aquatic or semi-aquatic plants were missing. Coarse substrate (26% mesilithal and 26% makrolithal, n = 12) dominated the sediment composition and constituted a major microhabitat. Direct human impacts (deforestation and livestock farming) were relatively low.

Site 2, still in the first steep gradient section, showed a much higher intensity of human impacts (agriculture, livestock farming and deforestation). Riparian vegetation and the input of CPOM (dead wood and leaves) were low. During the dry season, filamentous algae covered stones and shallow shoreline habitats. Mesolithal (36%, n = 12) dominated the substrate composition. A small percentage of very fine organic substrate (2% pelal, n = 12, covering coarse fractions and accumulating in pools) is notable and was observed during the dry season (05.12.2017).

The first low gradient section (S3, Awash Belo) was characterised by a high abundance of mikrolithal and akal (31% and 28% respectively, n = 6). The proportion of the finest fraction (pelal) was 4% (n = 6). Deforestation, agriculture and water abstraction were predominant human activities which shaped the character of the river. Input of CPOM was not observed. Patches of grass and herbaceous plants (partly semiaquatic e.g. *Polygonum* sp.) were the only noticeable habitat elements. Filamentous algae were missing.

Site 4 marked a transition to the second steep gradient section, and a high percentage of megalithal (57%, n = 5) was recorded. Parts of the site were still characterised by relatively slow flow velocity and the proportion of psammal was relatively high (13%, n = 3) in these stretches. Fine organic particles (1% pelal, n = 3) covered coarse substrate during the dry season (06.12.2017). Different microhabitats (e.g. leaves, xylal) were present but in low abundance and restricted to small areas (see also site description in 2.1.) Livestock farming was the major human impact observed. Patches of grass (partly submerged) and shrubs characterised the shoreline. Filamentous algae were restricted to shallow water, attached to coarse substrate.

In the gorge section (S5), makrolithal (46%, n = 9) and megalithal (35%, n = 9) dominated and made up the most abundant habitat structure (CPOM was nearly missing). The finest fraction (pelal, 1%, n = 5) was observed to cover lithal during the dry season. Riparian vegetation was rather scarce with the exception of shrubs along the shore. Livestock farming and the subsequent input of nutrients (manure) was the predominant human impact observed.

With a declining gradient, the sediment composition changed and site 6 showed a high percentage of psammal (63%, n = 10), predominating the habitat structure. Deforestation and livestock farming were the most prevailing human impacts. Woody debris was an apparent microhabitat observed in deep pool sections. Riparian vegetation was sparse, no submerged or semiaquatic plants were recognised. Filamentous algae were missing.

Downstream of Lake Koka (S7), fine sediment (psammal 41% and pelal 32%, n = 6) dominated the substrate composition. The proportion of pelal which was found especially in the shallow shoreline, was the second highest observed among all sites. Agriculture and deforestation (except on hillsides) shaped the character of the river and the surrounding floodplain areas. Riparian vegetation (mainly grass and herbaceous plants) was thick and semiaquatic plants (mainly *Polygonum* sp.) abundant. Xylal was an important microhabitat observed in the deeper parts of the main channel.

The geomorphology of the Awash river changed and site 8 was dominated by megalithal (73%, n = 6). Fine substrate (psammal 10%, n = 6) was only found in the shallow shoreline and in side channels with less flow velocity. The active channel was wide and lined by grass and scarce trees or shrubs. Filamentous algae were missing. Woody debris was found along the shore and in deep cataract sections (but rather scarce). Livestock farming and water abstraction (through irrigation channels) were characteristic human impacts.

Site 9 (Nur Sada) showed potamal elements where fine substrate dominated (psammal 25%, n = 3), but also bedrock confined sections (megalithal 14%, n = 2) were present. The abundance of xylal in few segments (potamal character) is noteworth but generally rare. Riparian vegetation was scarce with few exceptions (stable islands) where shrubs dominated. Patches of grass lined most mesohabitats (partly submerged). Agriculture, livestock farming and water abstraction were predominant human impacts.

The gorge section at Yimre (S10) was dominated by mikrolithal (28%, n = 5) but showed elements form pelal (5%, n = 2) to megalithal (7%, n = 3) as well. Lithal was the most dominant habitat structure. The input of CPOM along all sampling segments was present but generally rather scarce. Riparian vegetation was shaped by trees and shrubs. Filamentous algae were observed in the shallow waters of riffle sections. Livestock farming (and the consequent input of manure) was the only notable direct human impact.

In the lowland sections of the Awash around Worer (S11), the finest sediment fraction was most abundant (pelal 50%, n = 4). Psammal made up 32% (n = 4) and one undercut bank was stabilized by large boulders (megalithal 5%, n = 1). The most remarkable characteristic was the high abundance of xylal and leaves. In some mesohabitats the entire bottom of the river was covered with woody debris. Trees and shrubs dominated the riparian zone. Semi-aquatic plants and filamentous algae were missing. Agriculture, livestock farming, water abstraction (for irrigation) and partly deforestation (especially in the floodplain along the right shore) were the most predominant human impacts.

The last sampling site downstream of Lake Yardi was characterised by psammal (50%, n = 6) and to a minor extend pelal (22%, n = 6) and akal (21%, n = 6). Abundant riparian vegetation (trees, shrubs, lianas, herbaceous plants and grass) lined the main river and side channels. Filamentous algae were missing, but free floating hydrophytes (*Azolla* sp.) were observed in connected side channels (stagnant or low flow velocity). The input of CPOM was relatively high (dead wood and leaves). Deforestation and livestock farming were characteristic human impacts. Some sections were clearly altered, others in a near natural state.

3.2. Water parameter

An overview of physical and chemical water parameters along all sampling sites and their correlation with topographical and geomorphological characteristics is given in Table 6 and Table 11 (Appendix 1), Figures 18a – 18b and Figures 26a – 26c (Appendix 2). Similarities and differences between sites, based on the above stated features, are outlined by PCA in Figure 19. Water temperature (during the dry season) significantly ($p < 0.01$, n = 57) increased with distance from source and declining altitude. The lowest temperature was recorded in the headwaters (S1, 15.9 ± 1.8 ºC, n = 6), whereas the highest temperature was observed in the lowland floodplain around Kada Bada (S12, 26.1 ± 0.5 ºC, n = 3). A rapid increase in water temperature was recorded between site 1 and 2 (+4.5 ºC) as well as site 5 and 6 (+3.1 ºC). A clear decrease was noted after the Koka reservoir between site 6 and 7 (-2.7 ºC). The spatial variation and rapid changes in temperature are outlined in Figure 18a and Figure 26a

(Appendix 2). As illustrated in Figure 19, water temperature (r = 0.9, PCA) clearly separated sampling sites 6, 10, 11 and 12 from all others along PC1 (Dim1, 43%). These localities had a mean temperature above 24 ºC.

A similar pattern of significant increase ($p < 0.01$, n = 57) from the headwaters (S1, 244 ± 15.3 µS cm^{-1}, n = 6) to the lowland reaches (S11, 1206 ± 12.4 µS cm^{-1}, n = 3) was observed for conductivity. A notable rise was recognized between site 1 and 2 (+ 101 µS cm^{-1}) as well as site 5 and 6 (+ 180 µS cm^{-1}) (Figure 18b). The highest gradient was noted after site 9, where the value increased from 350 ± 5.1 µS cm^{-1} (n = 3) to 941 ± 11.2 µS cm^{-1} (n = 3). By far the highest value was recorded at site 11 (max. 1219 µS cm^{-1}). After Lake Koka, the conductivity decreased form 540 ± 75.2 µS cm^{-1} (n = 6) to 287 ± 26.8 µS cm^{-1} (n = 6). Conductivity was significantly correlated ($p < 0.01$, n = 57) with temperature (p = 0.65, n = 57) and dissolved oxygen (p = -0.41, n = 57). Like in temperature, sites 6, 10, 11 and 12 are clearly separated from others along PC1 (conductivity, r = 0.83, PCA). The mean conductivity was above 500 µS cm^{-1} for these sites with a clear maximum at S11.

The variation of dissolved oxygen concentration (mg L^{-1}) along the river course is given in Table 6 and Figure 26b (Appendix 2). A slight significant decline (p = -0.37, n = 57) was observed with distance from source. A positive correlation with the pH value was noted (p = 0.52, n = 57). The lowest oxygen concentration was recorded at site 11 (4.90 ± 0.0 mg L^{-1}, 65.1 ± 0.6%, n = 3), whereas the highest concentration was observed at site 2 (8.72 ± 0.7 mg L^{-1}, 126.3 ± 0.8%, n = 6). No significant correlation with temperature (p = 0.15, n = 57) could be detected. A rapid increase was observed between site 1 and 2 (+ 1.44 mg L^{-1}), whereas a decline in dissolved oxygen was noted between site 3 and 4 (-1.37 mg L^{-1}), site 6 and 7 (-1.31 mg L^{-1}), as well as site 10 and 11 (-3.18 mg L^{-1}). The separation of sites with low (S11, S12) and high (S2, S6) oxygen concentration (r = -0.87, PCA) is depicted in Figure 19 along PC2 (Dim2, 27. 2%).

Like the dissolved oxygen concentration, the pH value showed a similar variation. A slight negative correlation with altitude (p = -0.34, n = 57) was identified. Highest values were recorded at site 10 (8.83 ± 0.0, n = 3) and site 9 (8.80 ± 0.0, n = 3), whereas the lowest pH was observed in the source region (S1, 8.42 ± 0.1, n = 6). Along PC2 (Figure 19) differences between sites, explained by the variation in pH (r = -0.81, PCA) can be seen.

Table 6. Physical and chemical water parameter for all sampling sites (measured during the dry season between November 2017 and January 2018). Date and time of measurements are depicted. At each locality and date 3 measurements were taken for each parameter. Mean value and standard deviation are depicted for each parameter.

Site	**Date**	**Time**	**Temperature (°C)**	**Conductivity (µS cm^{-1})**	**DO (%)**	**DO (mg L^{-1})**	**pH**
S1	06.11.17 04.12.17	13:05 16:03	15.9±1.8	244±15.3	95.7±2.2	7.28±0.1	8.42±0.1
S2	06.11.17 05.12.17	16:00 11:10	20.4±3.6	345±22.5	126.3±0.8	8.72±0.7	8.76±0.1
S3	17.11.17	14:30	20.6±0.6	285±3.2	107.8±0.2	7.54±0.0	8.69±0.2
S4	07.11.17 06.12.17	13:00 09:17	20.3±1.0	346±31.8	85.7±18.0	6.17±1.1	8.45±0.0
S5	07.11.17 06.12.17	19:07 15.45	21.1±0.4	360±37.0	103.4±6.4	7.31±0.4	8.68±0.1
S6	08.11.17 08.12.17	13:30 14:06	24.2±0.4	540±75.2	124.1±2.6	8.59±0.1	8.73±0.1
S7	09.11.17 26.01.18	17:00 17:10	21.1±2.1	287±26.8	97.7±1.7	7.28±0.4	8.56±0.2
S8	10.11.17 09.12.17	13:00 16:00	21.5±1.1	309±8.2	103.4±1.2	7.85±0.1	8.72±0.1
S9	31.01.18	14:45	21.5±0.1	350±5.1	109.8±0.2	8.33±0.1	8.80±0.0
S10	30.01.18	13:10	24.6±0.2	941±11.2	106.4±0.5	8.08±0.0	8.83±0.0
S11	29.01.18	16:30	24.9±0.1	1206±12.4	65.1±0.6	4.90±0.0	8.53±0.0
S12	28.01.18	12:45	26.1±0.5	975±23.2	75.0±0.1	5.64±0.1	8.67±0.1

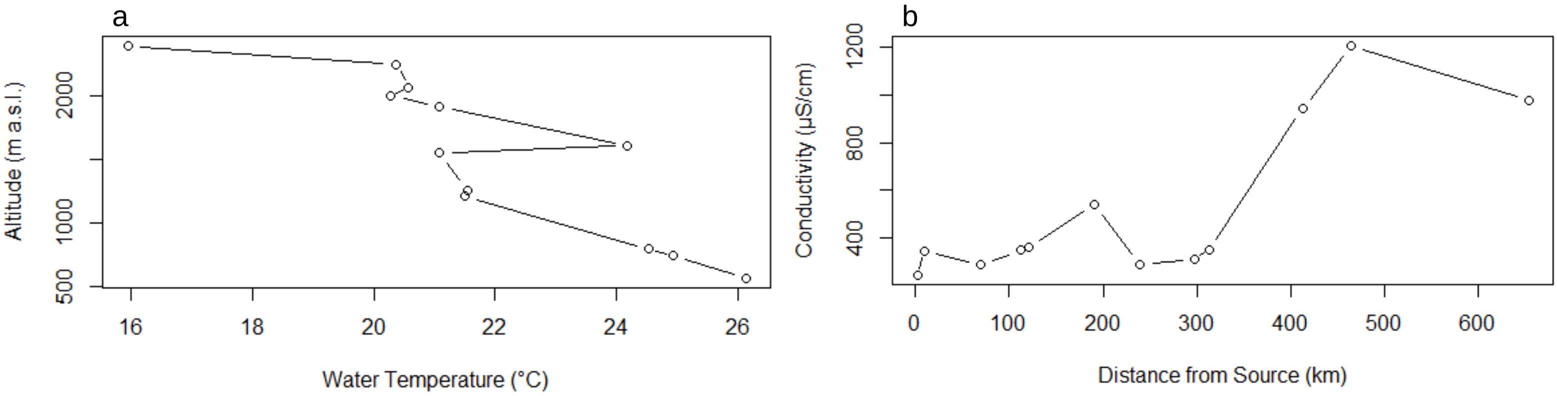

Figure 18. (a) Scatterplot of water temperature with declining altitude. Note the sharp increase between S1 and S2 (distance of 7.7 km between these sites) as well as between S5 and S6 (distance of 70.7 km between these sites). The temperature decrease between S6 and S7 is remarkable. (b) Scatterplot of conductivity with distance from source. Note the sharp increase after approximately 300 km. the highest conductibity was measured at S11. Each point represents a sampling site.

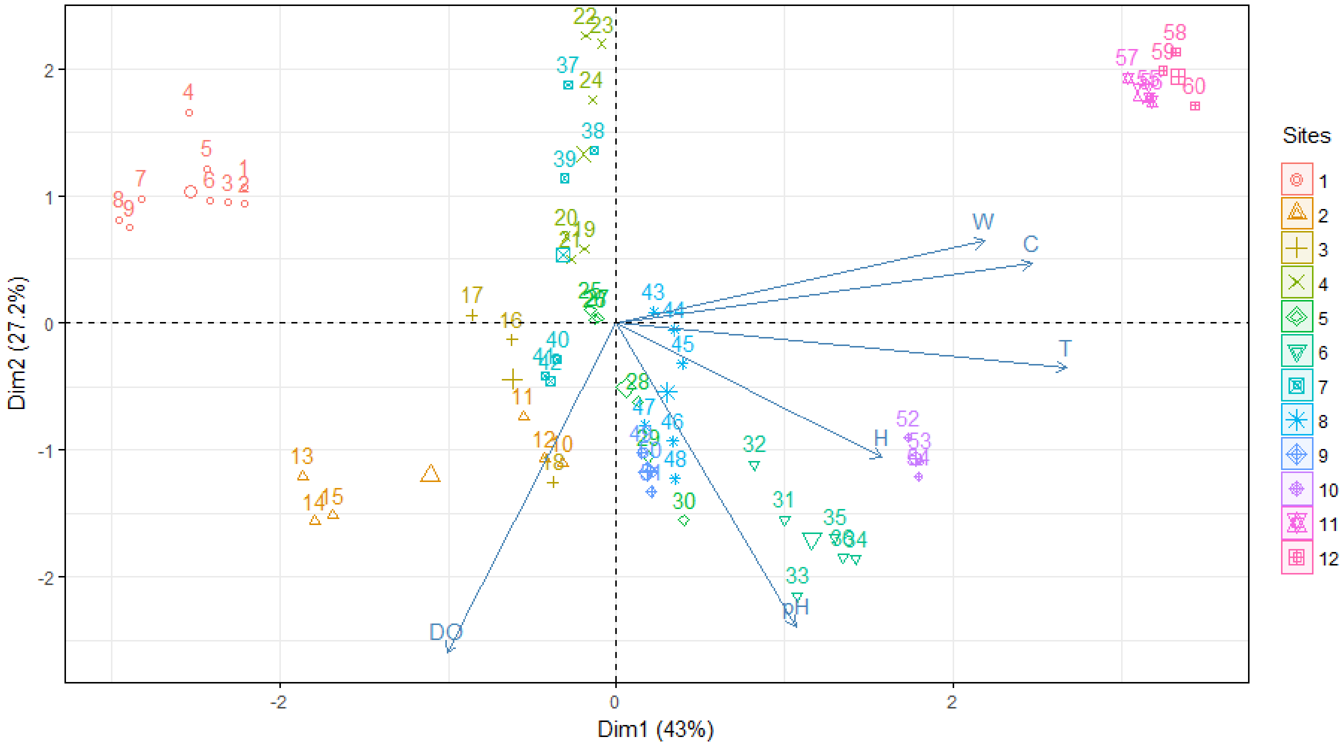

Figure 19. Principle component analysis for river morphological characteristics (W: mean river bed width, H: height of river embankment) and physical and chemical water parameters (C: conductivity, T: temperature, DO: dissolved oxygen and pH). The first 2 dimensions depicted, represent 70% of the variance. Along the first dimension the highest correlation with PC1 was observed for T (r = 0.90). Highest correlation with PC2 was observed for DO (r = -0.87). Numbers indicated above the symbols are related to measurements at the sampling sites.

3.3. Taxa accounts and distribution

A total of 11 taxa (based on morphometric and genetic analysis but excluding 8 morphotypes of the genus *Garra*) were characterised in the present research (Table 7). The relative abundance (%) per sampling site and taxon is depicted in Table 13 (Appendix 1). Figures 31 – 33 (Appendix 2) show relative abundances (%) for each mesohabitat and taxon.

Most of the investigated taxa belong to the family of Cyprinidae (8). Among them the non-native species *Cyprinus carpio* which was found downstream of Lake Koka. It was not abundant at any site (highest rel. abundance 3.8% at S8, n = 3) and was found only in the eupotamon (main channel at S7, S8 and S12, connected side arm (slow flow velocity) at S12) (Figures 32c-d and 33d, Appendix 2).

Enteromius sp. (not closer described in the present thesis) was solely found in S12 (rel. abundance 8.8%, n = 120). It was abundant in the eupotamon but exclusively in connected side channels (rel. abundance in deep parts 17.1%, n = 57 and in shallow sections 7.6%, n = 22). Two specimens were captured in a short parapotamon (connected to the main channel only at the downstream end). In stagnant side waters (plesiopotamon, not connected to the main channel during the dry season) the rel. abundance was 15.1% (n = 39) (Figure 33d, Appendix 2).

The genus *Garra* and all morphotypes considered in this investigation are closer described in 3.5. At this stage it should only be mentioned that the genus was present from the headwaters in the Chilimo forest (2389 m a.s.l.) to the lowland reaches (570 m a.s.l.). *Garra dembeensis* was found to be a very abundant taxon between S1 and S9 (except of the low gradient sections at S3, S6 and S7). The taxon *Garra* sp. was characteristic for all sites downstream the second steep gradient section (S6 – S12).

The genus *Labeobarbus* was represented by 3 taxa. *Labeobarbus* cf. *intermedius* had the widest distributional range (S5 – S12) but occurred only downstream of the cascades at Awash Kunture (Figure 22). The taxon was very abundant at site 10 (rel. abundance 86.5%, n = 336) and site 11 (rel. abundance 47.5%, n = 48). In the gorge section of S5, the highest rel. abundance during the dry season was observed in pools (27.4%, n = 40). Few specimens were captured in runs (rel. abundance 1.1%, n = 2) and the shoreline of riffles (rel. abundance 1.1%, n = 1). In high flow velocity habitats (riffles) *L.* cf. *intermedius* was not found. In the second low gradient section, the taxon was recorded primarily from pool habitats (S6, rel. abundance 80.0%, n = 20) and riffles (S6, rel. abundance 15.3%, n = 13 and S7, rel. abundance 28.6%, n = 2). Smaller individuals were found to stay close to the shoreline (with and without vegetation) in more shallow water (S6, rel. abundance 21.4%, n = 3 and S7, rel. abundance 4.4%, n = 17). Late juveniles were very abundant in stagnant side waters (parapotamon S7, rel. abundance 31.3%, n = 120). Downstream of the floodplain, *L.* cf. *intermedius* became increasingly abundant and inhabited predominantly the main channel (S8, rel. abundance 55.2%, n = 37, S9, rel. abundance 87.5%, n = 14). Pools, riffles, runs and shoreline habitats were dominated in the gorge section around Yimre (S10). Larger specimens were found in the deeper parts whereas juveniles predominated the shallow shoreline of running water stretches (rel. abundance 93.6%, n = 102) and short parapotamon habitats (rel. abundance 95.5%, n = 42). The same pattern was observed for the lowland sites, but overall abundance of the taxon was reduced there.

Labeobarbus cf. *nedgia* was recorded at site 5 (upstream of the Koka reservoir) and sites 9 – 10, but never occurred in high abundances (highest rel. abundance in S10, 6.2%). The taxon was predominately found in pool sections of the main channel (rel. abundance, S5, 3.4%, n = 5; S9, 12.5%, n = 2; S10, 8.8%, n = 10). All localities were characterised by (at least partly) coarse substrate (macrolithal, megalithal or bedrock) and a steep gradient (Table 10, Appendix 1 and Figure 22).

Labeobarbus beso was the only representative of the genus which occurred upstream of the cascades at Awash Kunture (Figure 22). Like *L.* cf. *nedgia*, the species inhabited steep gradient sections and was bound to course substrate (S2, S4, S5 and S8). Note that the taxon was always found together with *G. dembeensis*. The highest rel. abundance of the species was observed at S5 (4.9%, n = 24) and S8 (3.8%, n = 1). However, most specimens where captured at site 2 (n = 29). Pool habitats were preferred in S2 (rel. abundance 1.1%, n = 25) and S5 (rel. abundance 8.2%, n = 12). Unlike *L*. cf *intermedius* and *L.* cf. *nedgia* the species was captured in riffle sections at S5 (rel. abundance 1.3%, n = 1).

Among non-cyprinid fishes, *Micropanchax* cf. *antinorii* (fam. Poeciliidae) was a very abundant taxon and captured from S6 to S12 (with the exception of S9). The taxon was very characteristic at site 7 (rel. abundance 70.3%, n = 666) and site 12 (rel. abundance 51.0%, n = 692). Especially in vegetated low flow velocity habitats it occurred in high numbers. Vegetated (relative abundance 89.4%, n = 110) and non-vegetated (rel. abundance 78.1%, n = 299) shoreline habitats were preferred at S7. Where those habitat structures were not available (S8 – S11) the taxon occurred only in small numbers restricted to side channels or pools. In the lowland site (S12), *M.* cf. *antinorrii* was found in similar habitats as *Enteromius* sp. but occurred in higher abundances (Figure 33d, Appendix 2). It is interesting that the taxon also inhabited shallow shoreline habitats and small backwaters in the main channel (S12, rel. abundance 98,4%, n = 63).

Oreochromis niloticus ssp. (fam. Cichlidae) occurred in 2 different types (based on mtDNA barcoding, see Figure 49 in Appendix 2) and was found in most sites but was absent in the headwaters. The highest relative abundance was observed at S12 (10.3%, n = 139). *O. niloticus* ssp. ‘a’ was only found in the first low gradient section (S3, total rel. abundance 2.1%, n = 12) and inhabited predominantly pool sections (rel. abundance 5.0%, n = 11), whereas *O. niloticus* ssp. ‘b’ was recorded between S4 and S12 (with the exception of S5, S9 and S11). The highest abundance was recorded for the lowland site (S12, rel. abundance 10.3%, n = 139). In its distribution range a variety of mesohabitats were inhabited with a preference for pools (S6, rel. abundance 12.0%, n = 3) and low flow velocity habitats (parapotamon S12, rel. abundance 14.4%, n = 54). However, the taxon was also present in the main channel (in proximity to the shoreline) at S12 (rel. abundance 14%, n = 16). The difference between the types of *O. niloticus* is not closer described in the present thesis.

The only representative of the family Clariidae found in the Awash river was *Clarias gariepinus*. A distributional range like *M.* cf. *antinorii* was observed (Figure 22) and the species occurred at all sites between S6 and S12. It was most abundant in site 8 (rel. abundance 11.5%, n = 3) and the highest number of specimens was caught in S6, S8 and S12 (n = 8). *C. gariepinus* inhabited a wide range of habitats (e.g. deep pools, backwaters, shoreline, xylal) but was not observed to be abundant in any (Figures 32b – 33d, Appendix 2). In river stretches where the gradient and subsequently the flow velocity increased, the species was mainly found in side channels (S8, side channel, rel. abundance 15.4%, n = 2) (Figure 32d, Appendix 2).

Diversity indices were used to compare the community structure between sampling sites (Table 8). Margalef's diversity index (D_{Mg}), accounting for sampling size and effort, indicated the highest diversity for S8 (4.95) and the lowest diversity for S1 (0.37). At the same time these sites showed the highest (8) and lowest (2) number of taxa respectively. Menhinick diversity index (D_{Mn}) showed the same pattern with the highest diversity for S8 (1.57) and the lowest for S1 (0.09). For localities with an equal number of taxa both indices assigned the higher value to the one where less specimens were captured.

Following the Simpson diversity index (D_1), sampling site 8 (4.11) showed the highest diversity whereas site 1 (1.04) was characterised by the lowest diversity. The Simpson index (D_2) on the other hand resulted in high values for the headwaters (S1, 0.96 and S3, 0.92) with a small number of taxa and low values for S8 (0.27) with the highest taxa richness. Using the Shannon diversity index (H’) the highest diversity was observed for S8 (1.59) and S12 (1.35). Site 1 (0.10) and site 3 (0.20) resulted in the lowest values. If comparing two communities based on the evenness (E) or equitability (quantified between 0 and 1), S9 (0.80) and S8 (0.77) resulted in the highest values. Lowe values were observed for S1 (0.15) and S3 (0.18).

Based on the above stated indices, a general increase in diversity was observed from the headwaters in the Chilimo forest until site 8 (Korkada), where the highest number of taxa was observed (8 taxa). Further downstream, diversity seemed to decrease (especially S10) until S11, followed by a slight increase in the floodplain area of S12.

Table 7. Taxa list with remarks on length range (TL = total length, SL = standard length) observed (early juveniles are not considered) and distribution (S = sampling site) along the Awash river. Sites indicated with (*) are based on reports (e.g. local fishermen). *G. dembeensis* was identified based on morphological characteristics (see 3.5). *G.* aff. *makiensis* is the sum of all morphotypes. The specimens of *Oreochromis niloticus* ssp. ‘a’ which were sampled in Awash Belo (S3) seem to be different from specimens captured further downstream (Figure 49, Appendix 2). *Oreochromis niloticus* ssp. ‘b’ seems to be the most common form in the Awash river, most likely *Oreochromis niloticus cancellatus* (Trewavas, 1983).

Taxa	N	Length range (mm)	Distribution
Cyprinidae			
Cyprinus carpio	11	51.0-220.0 (TL)	(S6*), S7, S8, S12
Enteromius sp.	120	20.4-50.3 (TL)	S12
Garra dembeensis	803	45.0-112.0 (SL)	S1-S9
• *G. dembeensis* morph. ‘a’	860	48.7-116.5 (SL)	S1-S5
Garra aff. *makiensis*	1906	34.7-125.3 (SL)	S1-S5
• *Garra* aff. *makiensis* morph. ‘a’	141	34.7-125.3 (SL)	S4, S5
• *Garra* aff. *makiensis* morph. ‘b’	1195	45.5-89.3 (SL)	S1, S2, S4
• *Garra* aff. *makiensis* morph. ‘c’	570	34.7-75.9 (SL)	S3, S4
Garra sp. morph. ‘slender’	717	49.5-117.4 (SL)	S6-S12
• *Garra* sp. morph. ‘large’			
• *Garra* sp. morph. ‘tubercles’			
Labeobarbus beso	56	57.9-300.0 (TL)	S2, (S3*), S4, S5, S8
Labeobarbus cf. *intermedius*	652	45.0-360.0 (TL)	S5-S12
Labeobarbus cf. *nedgia*	30	70.0-320.0 (TL)	S5, S9, S10
Poeciliidae			
Micropanchax cf. *antinorii*	1402	13.0-43.0 (TL)	S6-S8, S10-S12
Cichlidae			
Oreochromis niloticus ssp.	202	18.5-275.0 (TL)	S3, S4, S6-S8, S10-S12
• *Oreochromis niloticus* ssp. ‘a’	12	27.7-180.0 (TL)	S3
• *Oreochromis niloticus* ssp. ‘b’	190	18.5-275.0 (TL)	S4, S6-S8, S10, (S11*), S12
Clariidae			
Clarias gariepinus	31	41.0-550.0 (TL)	S6-S12

Table 8. Diversity indices for all sampling sites. N (total number of specimens per sampling site), T (number of taxa). Abbreviations: D_{Mg} = Margalef diversity index, D_{Mn} = Menhinick diversity index, D1 = Simpson diversity index, D2 = Simpson index, D_{1-D2} = Gini-Simpson-index, H' = Shannon diversity index, E = Evenness or Equitability. S8 (highest diversity) and S1 (lowest diversity) are highlighted. Note the small number of specimens caught in S8.

Diversity index	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12
D_{Mg}	0.37	0.58	0.72	1.32	1.49	2.06	2.02	4.95	2.08	1.98	1.50	1.92
D_{Mn}	0.09	0.06	0.13	0.29	0.23	0.37	0.23	1.57	0.55	0.33	0.40	0.19
D_1	1.04	1.61	1.09	1.87	2.19	2.05	1.90	4.11	3.33	1.33	2.32	2.98
D_2	0.96	0.62	0.92	0.54	0.46	0.49	0.53	0.27	0.31	0.75	0.44	0.34
D_{1-D2}	0.04	0.38	0.08	0.46	0.54	0.51	0.47	0.73	0.69	0.25	0.56	0.66
H'	0.10	0.61	0.20	0.72	1.04	1.08	0.96	1.59	1.28	0.56	0.93	1.35
E	0.15	0.55	0.18	0.52	0.64	0.60	0.49	0.77	0.80	0.32	0.67	0.69
N	521	2632	575	190	486	265	948	26	84	340	101	1356
T(S)	2	3	3	4	5	6	7	8	5	6	4	7

3.4. Zonation assessment

Similarities between sampling localities (taxa composition) are depicted in Figure 20a-b. The influence of environmental variables on sampling stretches and taxa is illustrated in Figure 21a-b. The longitudinal distribution of taxa is given in Figure 22. The first axis (CA1, eigenvalue 0.83, CA) in Figure 20a broadly separates two groups of sites. On the left side, the upper sections of the Awash river (S1 – S5) and on the right side S6 (still upstream of the Koka reservoir) and all sites downstream of Lake Koka. Only 3 taxa (*G. dembeensis*, *G*. aff. *makiensis* and *L. beso*) seem to be linked to the uppermost stretches. *G*. aff. *makiensis* was found to be the most characteristic taxon for these sites (species score -1.33, CA). The majority of taxa is related to sites 6 – 12. Along the second axis (CA2, eigenvalue 0.53, CA), sites seem to be opposed according to their inclination (with 2 notable exceptions: S2 and S11). Sites 1, 2, 5, 8, 9 and 10 are characterised by steep gradients. The most characteristic taxa for these stretches are *L*. cf. *nedgia* (species score -1.08, CA) and *L.* cf. *intermedius* (species score -0.70, CA), whereas sites 3, 6, 7, 11 and 12 represent low gradient sections of the river. *E.* sp. (species score 1.44, CA) and *M.* cf. *antinorii* (species score 1.15, CA) were found to be most characteristic for these sites. Note that both axes considered at the same time separate the localities in 4 relatively distinct groups with characteristic taxa for each of them.

This aspect is further highlighted in Figure 20b which shows how groups of taxa are related and distributed along the longitudinal gradient. *L. beso* only occurred together with *G. dembeensis*, and both taxa are closely linked to steep gradient sections in the upper reaches of the river (until S8). Note that taxa which are plotted closer to the centre (e.g. *G*. sp.) are more widespread and equally distributed.

If environmental variables are considered in a CCA ($p < 0.05$, ANOVA), the distribution of fish communities and the similarities between sites can be seen from a different perspective (Figure 21a-b). Tow relatively clear groups are separated by water temperature ($p < 0.01$, ANOVA) and conductivity ($p = 0.39$, ANOVA) along CCA1 ($p < 0.05$, ANOVA). Sites 1 – 5 and 7 – 8 are characterised by lower values for both variables. Three taxa (*G. dembeensis*, *G*. aff. *makiensis* and *L. beso*) are associated to this group. On the other hand, site 6 and sites 10 – 12 are related to higher water temperature and increased conductivity. More taxa are associated here. The effects of dissolved oxygen and the pH value are less distinct and do not clearly separate localities along CCA2 ($p = 0.43$, ANOVA).

The association of taxa to specific environmental variables is depicted in Figure 21b. Two distinct groups of taxa can be identified. *G. dembeensis*, *G*. aff. *makiensis* and *L. beso* which seem to prefer lower water temperatures and lower conductivity. The taxa are not ultimately linked to steep gradients since *G.* aff. *makiensis* (*G*. aff. *makiensis* morphotype ‘c’) dominated the first low gradient section. The second group is less demarcated and shows variation along CCA2 as well. *G.* sp., *M*. cf. *antinorii* and *O. niloticus* ssp. seem to be linked to a similar environment. The temperature tolerance of *L.* cf. *intermedius* in contrast to *L. beso* is noteworth. *L*. cf. *nedgia* seems to prefer habitats with high oxygen concentration, whereas the oxygen demand of *E*. sp. seems to be much lower.

Possible transition zones (TZ) between fish communities are depicted in Figure 22 and Figure 27 (Appendix 2). A first clear change (TZ1) was observed between site 5 and 6 (upstream of Lake Koka). With *L.* cf. *intermedius*, *C. gariepinus*, *G*. sp. and *M.* cf. *antinorii* 4 additional taxa occurred at site 6. Likewise, the abundance of *G. dembeensis* and *G*. aff. *makiensis* declined. The second transition zone (TZ2) was less clear and located between site 9 and 11. *G. dembeensis* was not found downstream of site 9 and the increasing abundance of *L*. cf. *intermedius* (as well as typical potamal forms like *G*. sp. and *M*. cf. *antinorii*) indicate a possible transition.

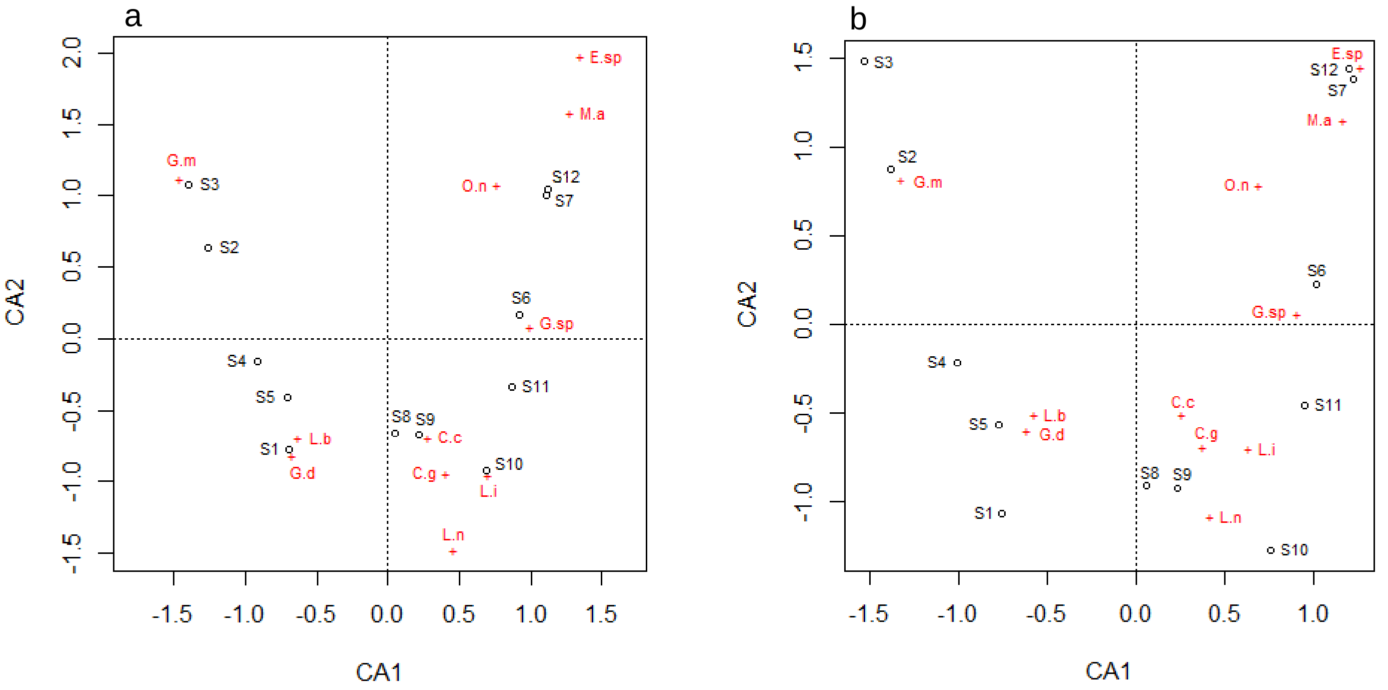

Figure 20. Correspondence Analysis biplot. (a) (scale 1) of taxa (morphotypes assigned to the closest related taxon) and sampling sites. Site proximities (groups) and gradients between localities can be interpreted. (b) (scale 2) reveals groups of taxa closely related. The closer a taxon is placed to the origin of the graph, the more widespread and uniformly distributed it is. The numbers above the symbol corresponds to the sampling site (S1 – S12). Abbreviations relate to taxa (see Table 7).

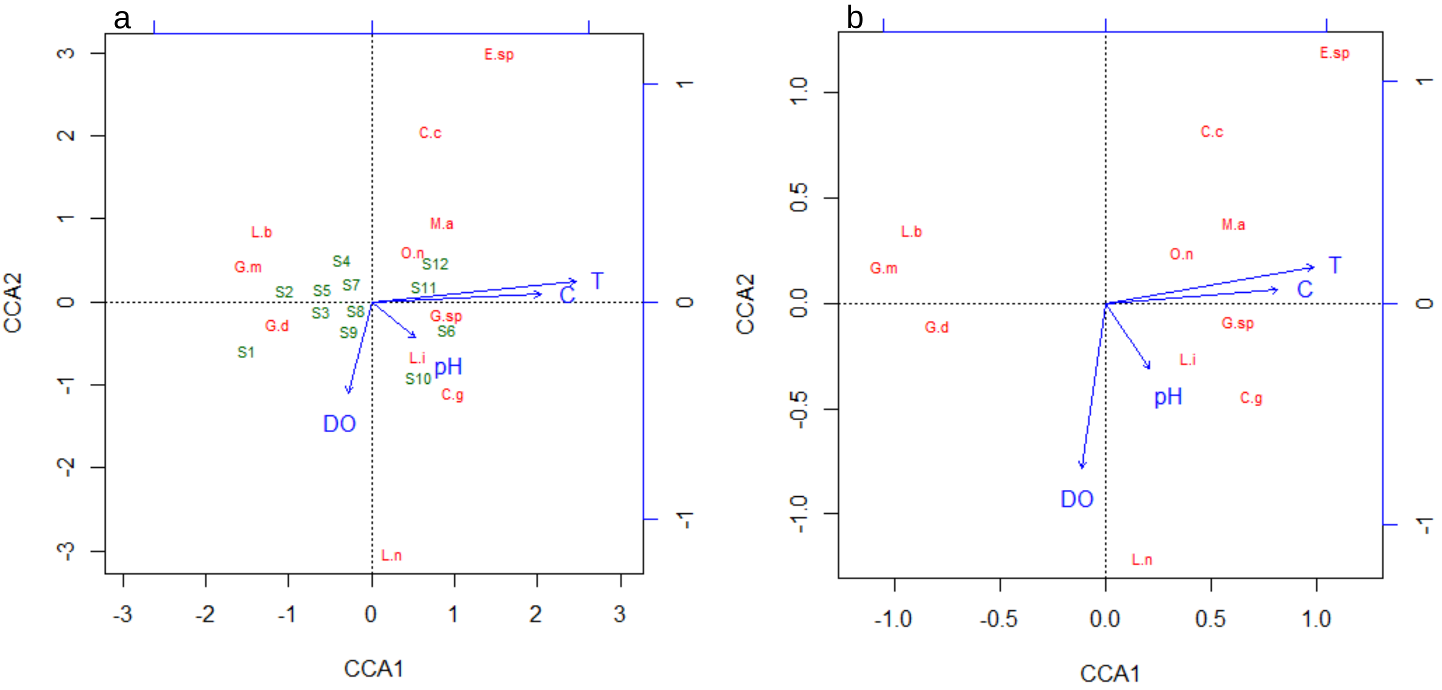

Figure 21. Canonical Correspondence Analysis triplot. (a) (scale 1) for taxa (morphotypes assigned to the closest related taxon), sampling sites and water parameters. Similarities between sites and taxa explained by environmental variables. Note that rare species (*E*. sp.) make an interpretation difficult. (b) (scale 2) only for taxa. Possible preferences for war certain environmental conditions could be deduced. Note that data were only taken during the dry season. The numbers above the symbol correspond to the sampling sites (S1 – S12). Abbreviations relate to taxa (see Table 7).

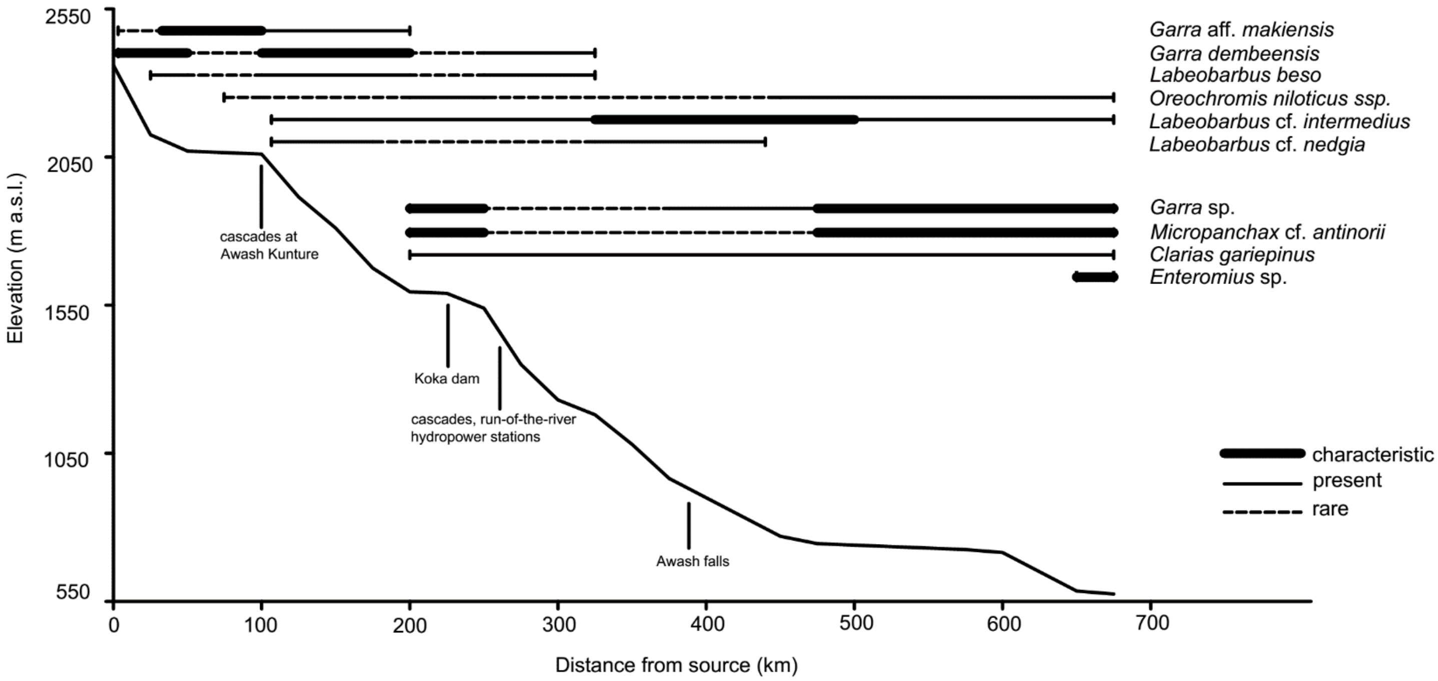

Figure 22. Longitudinal distribution of fish taxa. Only the first 680 km of the Awash river are depicted. Note the sequence of alternating steep and low gradients. Different line types indicate the relative abundance per site (*Garra dembeensis* was dominant at S8 and S9 but only few fish were caught in general). A natural distribution of *Oreochromis niloticus* ssp. upstream the cascades of Awash Kunture is not clear. *G. dembeensis* and *G.* aff. *makiensis* are characteristic for the upper zone, *G.* sp. and *Micropanchax* cf. *antinorii* for the potamal stretches. *Labeobarbus* cf. *intermedius* seems to be the most widespread taxon (cascades at Awash Kunture a possible migration barrier). The graph was generated with AutoCAD, 2016.

3.5. Morphometric analysis of *Garra*

3.5.1. ***Garra dembeensis*** s. str. (Rüppell, 1836)

Diagnostic-, morphometric- and meristic characteristics are depicted in Table 14 and 15 (Appendix 1); lateral, dorsal and ventral view of specimens is given in Figure 34 – 38 (Appendix 2). Figure 28 (Appendix 2) gives a graphical illustration of differences to *G. dembeensis* morph. 'a'.

Material examined: In total, 803 specimens (adults and late juvenile stages) were collected from the source region in the Chilimo forest (S1) to downstream of the Koka reservoir at Nur Sada (S9). Larvae and early juveniles are not included here but did not occur at S1 and downstream of S9. Thirty specimens (45.0 – 112.0 mm SL) were analysed in detail (all sampling sites and mesohabitats considered) with focus on external morphometric and meristic features. A comparison to data (range and mean ± SD) of Stiassny and Getahun (2007) is given in Table 14 (Appendix 1). For genetic analysis 16 individuals were randomly selected, covering all sampling stations. The species was identified based on diagnostic features and the detailed description in Stiassny and Getahun (2007).

Characteristics: In most specimens, disc well developed (type C) with abundant papillae on disc periphery. Some specimens (especially in the upstream reaches) with intermediate (type B) disc but all with free posterior and lateral margins. Note that disc development seems to vary strongly ontogenetically, juveniles often tend to develop a type A disc with a free posterior margin first, this characteristic persists in few adult specimens. The rostral margin is well developed and invecked (few specimens smoothly invecked). Tubercles on snout are small (but not present in all individuals). Predorsal region rarely asquamate, instead with 0-8 scales; chest and belly asquamate. Postpelvic region rarely asquamate instead with 0-4 scales (distinction to *G.* aff*. dembeensis* morph. 'a'); lateral line scales 36 – 39 (mean 37). Intermediate body depth (15.2 – 23.5% of SL), with greatest depth in advance of dorsal fin insertion. Head (length 22.3 – 25.6% of SL) somewhat depressed (depth 49.8 – 63.6% of HL) and far wider than deep. Eyes positioned middle to posterior on head and interorbital width 41.5 – 49.0% of HL. Orbit diameter relatively small (15.9 – 24.0% of HL), caudal peduncle short (length 9.7 – 14.6% of SL) and deep (depth 9.9 – 13.3% SL). Vent is situated far away from anal fin (27.0 – 35.3% mean 32.2%).

Habitat: Pool (rel. abundance 23.8%, n = 115) and riffle (rel. abundance 26.3%, n = 10) habitats were populated in the headwaters (Figure 31a, Appendix 2). With changing character of the river (S2), habitats with higher flow velocity were preferred (riffle, rel. abundance 29.4%, n = 144), only *G*. aff. *dembeensis* morph. 'a' occurred in higher numbers (218). In the first low gradient section the species was rare (only 9 specimens were caught) and showed a preference for riffle sections (rel. abundance 3.8%, n = 3) Site 5 (Figure 32a, Appendix 2) supported the observations from upstream reaches: *G*. *dembeensis* s. str. was dominant in riffle (rel. abundance 90.0%, n = 72) and run (rel. abundance 53.3%, n = 96) sections. A shallow side channel was preferred in the second low gradient section (S6, rel. abundance 65.8%, n = 75). Note that only juveniles were caught from this mesohabitat. Based on observations of their distributional range (Figure 20 – Figure 22), the species seems to be associated with cooler water temperatures (max. observed mean temperature during the dry season 24.2 ± 0.4 ºC) and lower conductivity (max observed mean conductivity during the dry season 540 ± 75.2 µS cm^{-1}).

3.5.2. *Garra* aff. *dembeensis* morphotype 'a'

Diagnostic-, morphometric- and meristic characteristics are depicted in Table 15 (Appendix 1); lateral, dorsal and ventral view of *G*. aff. *dembeensis* morph. 'a' is given in Figure 39 (Appendix 2). Figure 28 (Appendix 2) gives a graphical illustration of differences and similarities to *G. dembeensis*.

Material examined: In total, 860 specimens (adults and late juvenile stages) were collected from the source region in the Chilimo forest (S1) to Sulula (S5). Larvae and early juveniles are not included here (the distinction from *G. dembeensis* s. str. seems to be impossible at this stage of development). Thirty specimens (48.7 – 116.5 mm SL) were analysed in detail (all sampling sites and mesohabitats considered) with focus on external morphometric and meristic features. A comparison to *G. dembeensis* s. str. from the Awash river (range and mean ± SD) is given in Table 15 (Appendix 1). For genetic analysis 10 individuals were randomly selected, covering all sampling stations.

Characteristics: Disc often rather small (intermediate type B) and only in few specimens well developed (type C), but free posterior and lateral margins always present. Abundant papillation on disc periphery is rare. The disc development seems to vary strongly ontogenetically (see *G. dembeensis* s. str.). Rostral margin is well developed and clearly invecked, tubercles on snout small (but not present in all individuals). Predorsal region only in very few specimens asquamate, most specimens with 0 – 14 scales (scattered). Chest asquamate, belly often with few scales (0 – 6) but solely in the lower region. Postpelvic region scaled 4 – 6 scales (distinction to *G. dembeensis* s. str.) and 37 – 40 lateral line scales (mean 38). Intermediate body depth (16.3 – 24.0% of SL), with greatest depth in advance of dorsal fin insertion. Head (length 22.1 – 25.3% of SL) only slightly depressed (depth 54.0 – 74.6% of HL) and rather blunt. Eyes in middle position on head. Interorbital width 40.0 – 50.0% of HL and orbit diameter relatively small (11.9 – 23.1% of HL). Caudal peduncle relatively short (length 11.2 – 14.6% of SL) and deep (depth 10.0 – 12.8% SL). Vent positioned far away from anal fin (26.7 – 35.5% mean 31.2%).

Habitat: Similar to *G. dembeensis* s. str., the morphotype inhabited pool (re. abundance 73.9%, n = 357) and riffle (rel. abundance 73.7%, n = 28) sections in the headwaters but was more abundant in both habitats (Figure 31a, Appendix 2). The preference for high flow velocity was observed in S2 as well (riffle rel. abundance 44.6%, n = 218). In site 4 and 5 the taxon was still present, especially in riffle (S4, rel. abundance 34.1%, n = 15) and run (S5, rel. abundance 9.4%, n = 17) sections. Further downstream, the morphotype was not captured. The highest abundance of *G.* aff. *dembeensis* morph. 'a' was observed in site 1 and 2. Highest mean water temperature recorded during the dry season was 20.4 ± 3.6 ºC (S2).

3.5.3. *Garra* aff. *makiensis* morphotype 'a'

Diagnostic-, morphometric- and meristic characteristics are depicted in Table 16 (Appendix 1); lateral, dorsal and ventral view of *G*. aff. *makiensis* morph. 'a' is given in Figure 40 and Figure 47 (Appendix 2). Figure 29 (Appendix 2) gives a graphical illustration of differences and similarities between all morphotypes assigned to *G. makiensis*.

Material examined: In total, 141 specimens (adults and juveniles) were collected from Awash Kunture (S4) and Sulula (S5). Larvae and early juveniles were not present among samples. Few juvenile specimens (based on DNA analysis) were captured in S6 (only in a shallow side channel). Thirty specimens (45.5 – 125.3 mm SL) were analysed in detail (all sampling sites (except S6) and mesohabitats considered) with focus on external morphometric and meristic features. A comparison to *G. makiensis* s. str. (data of Stiassny and Getahun (2007), range and mean ± SD) is given in Table 16 (Appendix 1). For genetic analysis 14 individuals were randomly selected, covering all sampling sites.

Characteristics: Disc very well developed (large type C) in all specimens (also juveniles) with wide free posterior and lateral margins, abundant papillae on disc periphery. Rostral margin is well developed and clearly invecked. Tubercles on snout large and horny (with 2 prominent tubercles at the tip of the snout – above rostral barbels), present in all specimens collected. Predorsal region fully scaled (10 – 18 scales), chest and belly often asquamate or with only few deeply embedded scales – characteristic is difficult to observe! Postpelvic region scaled, and lateral line with 36-38 scales (mean 36). Body dorso-ventrally flattened (body depth 15.2 – 22.3% of SL), with greatest depth in advance of dorsal fin insertion. Head (length 20.8 – 23.4% of SL) somewhat depressed (depth 53.9 – 67.4% of HL) and wider than deep. Eyes in posterior position on head. Interorbital width 40.0 – 48.1% of HL and orbit diameter 16.4 – 22.9% of HL. Caudal peduncle relatively short (length 10.7 – 17.4% of SL) and intermediate in depth (depth 9.1 – 11.9% SL). Vent relatively close to anal fin (16.8 – 25.0% mean 21.5%).

Habitat: The morphotype occurred solely in S4 and S5 (few juveniles in S6). Coarse substrate seems to be preferred. High flow velocity habitats in riffles might be avoided (S5, rel. abundance 6.3%, n = 5). In contrast, mesohabitats of intermediate flow velocity (S5, run, 29.4%, n = 53; S5, shoreline of riffle, 26.4%, n = 23) seem to be favoured. Based on observations during dry season, the taxon (*G*. aff. *makiensis*) seems to be associated with cooler water temperatures (highest observed mean temperature 21.1 ± 0.4 ºC) (Figure 21a).

3.5.4. *Garra* aff*. makiensis* morphotype ‘b’

Diagnostic-, morphometric- and meristic characteristics are depicted in Table 17 (Appendix 1); lateral, dorsal and ventral view of *G*. aff. *makiensis* morph. ‘b’ is given in Figure 41 and Figure 47 (Appendix 2). Figure 29 (Appendix 2) gives a graphical illustration of differences and similarities between all morphotypes assigned to *G. makiensis*.

Material examined: In total, 1195 specimens (adults and late juveniles) were collected from Chilimo forest (S1), Gare Arera (S2) and Awash Kunture (S4). Early juvenile stages (very abundant in S2) were not considered due to uncertainty in identification. Most specimens were caught in December 2018 in S2 (counted and released). Thirty specimens (45.5 – 89.3 mm SL) were analysed in detail (all sampling sites and mesohabitats considered) with focus on external morphometric and meristic features.

A comparison to *G.* aff. *makiensis* morph. ‘c’ (range, median and mean ± SD) is given in Table 17 (Appendix 1). For genetic analysis 10 individuals were randomly selected, covering all sampling sites.

Characteristics: Disc in all specimens well developed (large type C) and with wide free posterior and lateral margins, abundant papillae on disc periphery. Rostral margin is well developed and smoothly invecked. Some specimens with few variously sized tubercles on snout, others without tubercles. Predorsal region fully scaled (12 – 18 scales), chest asquamate and belly with small scattered scales deeply embedded in skin – characteristic is difficult to observe! Postpelvic region scaled, lateral line scales 35 – 39 (mean 36). Body robust (depth 19.8 – 25.0% of SL), with greatest depth in advance of dorsal fin insertion. Head (length 21.5 – 24.3% of SL) moderately depressed (depth 57.8 – 67.6% of HL) and wider than deep. Eyes positioned medially on head. Interorbital width 42.9 – 48.2% of HL and orbit diameter 18.3 – 24.0% of HL. Caudal peduncle relatively short (length 10.8 – 14.3% of SL) and intermediate in depth (depth 11.4 – 13.2% SL). Vent relatively close to anal fin (16.3 – 29.6% mean 20.8%).

Habitat: The morphotype was rare in the headwaters (11 specimens) and only found in pool sections (rel. abundance 2.3%, n = 11). In site 2 (still the first steep gradient section) it was the most abundant taxon and dominating pool sections (rel. abundance 83.9%, n > 1000). Riffle sections were less preferred (rel. abundance 24.7%, n = 121). In S4 the morphotype was recorded particularly from pool sections (rel. abundance 13.8%, n = 8). The highest mean temperature (during the dry season) recorded within the distribution range was 20.4 ± 3.6 ºC (S2).

3.5.5. *Garra* aff. *makiensis* morphotype ‘c’

Diagnostic-, morphometric- and meristic characteristics are depicted in Table 17 (Appendix 1); lateral, dorsal and ventral view of *G*. aff. *makiensis* morph. ‘c’ is given in Figure 42 and Figure 47 (Appendix 2). Figure 29 (Appendix 2) gives a graphical illustration of differences and similarities between all morphotypes assigned to *G. makiensis*.

Material examined: In total, 570 specimens (adults and juveniles) were collected from Awash Belo (S3) and Awash Kunture (S4). Most specimens were caught in November 2017 in S3. Thirty specimens (34.7 – 75.9 mm SL) were analysed in detail (all sampling sites and mesohabitats considered) with focus on external morphometric and meristic features. A comparison to *G. aff. makiensis* morph. ‘b’ (range, median and mean ± SD) is given in Table 17 (Appendix 1). For genetic analysis 10 individuals were randomly selected, covering all sampling stations.

Characteristics: Disc development shows considerable variation. In few (especially large) specimens, disc well developed (type C) with wide free posterior and lateral margins (abundant papillae on disc periphery), others with intermediate disc (type B) and narrow free posterior and lateral margins (papillation generally missing or inconspicuous). Rostral margin is well developed and smoothly invecked. Some specimens with few variously sized tubercles on snout, but most without tubercles. Predorsal region fully scaled (14 – 18 scales), chest asquamate (in few individuals scattered – small deeply embedded scales) and belly with rather small scattered scales deeply embedded in skin – characteristic is difficult to observe! Post pelvic region scaled, lateral line scales 34 – 38 (mean 36). Body robust (depth 20.9 – 25.8% of SL), with greatest depth in advance of dorsal fin insertion. Head (length 21.6 – 24.7% of SL) moderately robust (depth 62.1 – 71.1% of HL) and slightly wider than deep. Eyes positioned medially to anteriorly on head. Interorbital width 43.2 – 50.0% of HL and orbit diameter 17.6 – 23.9% of HL. Caudal peduncle relatively short (length 11.0 – 14.3% of SL) and intermediate in depth (depth 11.3 – 14.1% SL). Vent relatively close to anal fin (15.6 – 32.0% mean 22.2%).

Habitat: The taxon was found in site 3 and site 4. All mesohabitats in site 3 were dominated by this morphotype (rel. abundance: pool 92.8%, n = 205; riffle 91.3%, n = 73 and run 98.2%, n = 273). In S4, only pool sections were inhabited (rel. abundance 32.8%, n = 19). Highest mean temperature (during the dry season) recorded within the distribution range was 20.6 ± 0.6 ºC (S3).

3.5.6. *Garra* sp. morphotype ‘slender’

Diagnostic-, morphometric- and meristic characteristics are depicted in Table 18 (Appendix 1); lateral, dorsal and ventral view of *G*. sp. (represented by 3 morphotypes) is given in Figure 43 – Figure 46 and Figure 48 (all Appendix 2). Figure 28 and Figure 30 (both Appendix 2) give a graphical illustration of differences and similarities between *G*. sp. and congeners found in the Awash river and in Africa.

Material examined: In total, 717 specimens (adults and late juveniles) were collected from Lafessa (S6) to Kada Bada (S12). Only 1 specimen was sampled in S8 (Korkada). Larvae and early juveniles were not present among samples. Thirty specimens (49.5-117.4 mm SL) were analysed in detail (all mesohabitats but only 2 sampling sites (S6 and S7) were considered) with focus on external morphometric and meristic features. A summary of all characteristics is given in Table 18 (Appendix 1). For genetic analysis 38 individuals (covering all sampling sites) were randomly selected (with focus on phenotypical differences observed). Two morphotypes within this taxon (differing in size and tuberculation) are not closer described here but depicted in Figures 45 – 46 and Figure 48 (Appendix 2).

Characteristics: Disc development shows variation, especially in large specimens the disc is often well developed (type C) with wide free posterior and lateral margins, others with a rather intermediate disc (type B) and narrow free posterior and lateral margins. Papillation on lower lip and disc periphery generally present (in some abundant). Rostral margin is well developed and invecked. Most specimens with variously sized tubercles on snout (tuberculation seems to vary considerably). Predorsal region fully scaled (12 – 16 scales), chest in few specimens asquamate, in others scattered – scales small deeply embedded in skin. Belly fully scaled (scales large and not deeply embedded). Post pelvic region scaled and lateral line with 37 – 40 scales (mean 39). Body moderately robust (depth 16.9 – 22.5% of SL), with greatest depth in advance of dorsal fin insertion. Head short (length 17.1 – 22.2% of SL) and moderately robust (depth 61.7 – 69.8% of HL), slightly wider than deep (width 65.1 – 77.1% of HL). Eyes large (orbit diameter 20.1 – 26.4%, mean 23.5 ± 1.6% of HL) and positioned medially on head. Interorbital width (44.9 – 53.1% of HL) and caudal peduncle relatively long (length 14.3 – 18.8% of SL) and narrow (depth 8.2 - 10.7% SL). Vent close to anal fin (11.0 – 19.6% mean 15.2%). Dorsal fin long (length 23.9 – 28.2% of SL), with III-IV unbranched and 7 branched rays. Anal fin (length 16.9 – 20.6% of SL) rays III-IV and 5-6. Pelvic fin (length 18.1 – 22.1% of SL) rays II and 7. Pectoral fin (length 17.4 – 22.6% of SL) rays I and 12 – 14.

Habitat: The taxon has a wide distributional range and was found from the second low gradient section (S6 and S7) to the lowland reaches (Figures 32b and 33d, Appendix 2). *G.* sp. inhabited a variety of mesohabitats (e.g. main channel, shorelines, parapotamon, plesiopotamon) with a possible preference for sandy substrate. It was especially abundant in shoreline habitats without riparian vegetation (S6, shoreline without vegetation, rel. abundance 81.9%, n = 68) but also in backwaters and connected side arms (S12, shallow side channel, rel. abundance 25.2%, n = 73). Shallow shoreline habitats with abundant semiaquatic vegetation were less preferred (S7, rel. abundance 1.6%, n = 2). Even high flow velocity habitats were inhabited (S10, riffle, rel. abundance 15.2%, n = 5). Within the area of distribution, temperature (during the dry season) varied between 19 ºC (S7) and 26.6 ºC (S12). Highest conductivity was recorded at site 11 (1206 ± 12.4 µS cm^{-1}). Oxygen concentration varied between 64.9% (4.89 mg L^{-1}) at site 11 and 127.0% (8.75 mg L^{-1}) at site 6. A pH range from 8.24 (S7) to 8.87 (S10) was observed.

Differences to other African congeners: Figure 30 (Appendix 2) gives an overview of all valid African species (except *G. chebera*) in comparison to *G*. sp. The separation along PC1 (Dim1 34%) is relatively clear. Highest correlation with PC1 was observed for head length (r = 0.88, PCA), predorsal length (r = 0.81, PCA) and vent distance (r = 0.79, PCA) which separates taxa on the right side of the centre. *G*. sp. (on the left side of the centre) is distinguished by dorsal (r = -0.83, PCA), anal (r = -0.77, PCA) and pelvic (r = -0.64, PCA) fin length, head depth (r = -0.73, PCA) and interorbital width (r = -0.82, PCA). The most conspicuous feature of *G*. sp., by which it seems to be readily distinguished from other African congeners, is only 1 unbranched anterior pectoral fin ray.

3.6. Genetic analysis of taxa and morphotypes within the genus *Garra*

Evolutionary relationships between taxa of the genus *Garra* found in the Awash river and selected congeners from Africa, Arabia and Asia are depicted in Figure 23. Based on morphometric and meristic characteristics 3 distinct groups were identified. These groups could be verified with genetic data. Two of them fitting to the African line (76/100). The third fitting closer to the Asian populations (59/100) with the next possible relatives on the Arabian Peninsula (e.g. *G. tibanica*). Members of *G. dembeensis* found in other river basins of Ethiopia seem to show remarkable difference to the Awash population.

However, within these groups, morphotypes can be distinguished based on diagnostic characteristics, but not on the gen region under consideration (cytochrome c oxidase I (COI)). *G. dembeensis* s. str. and *G. dembeensis* morph. ‘a’ do not show any difference on the COI region (500 base pairs). The same result was obtained for morphotypes assigned to *G. makiensis* and *G.* sp*.*

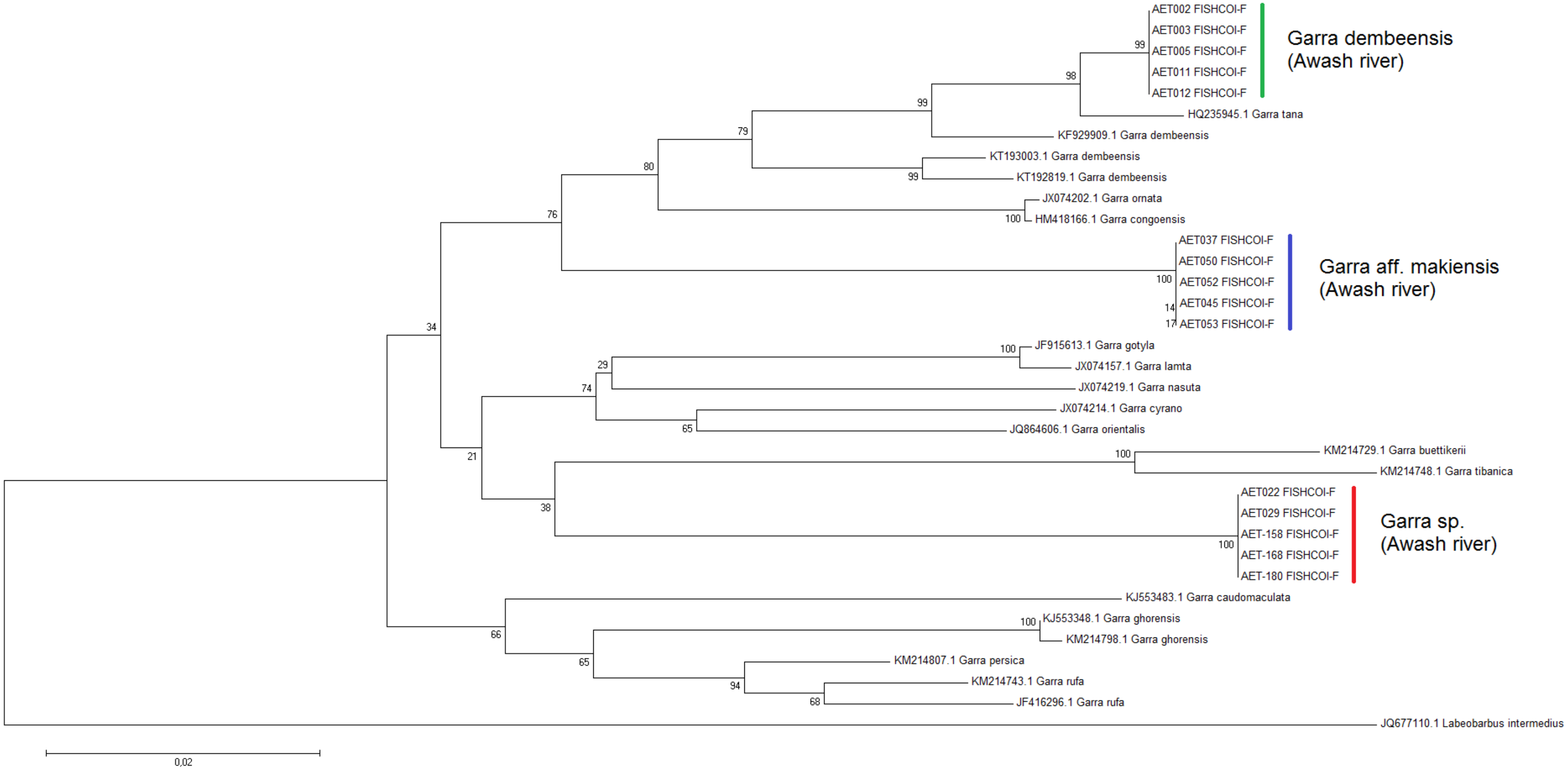

Figure 23. Evolutionary relationships of taxa (genus *Garra*) from the Awash river and other river basins (based on literature). The relationships were inferred using the Neighbor-Joining cluster method. The optimal tree with the sum of branch length = 0,78855111 is shown. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (10000 replicates) are shown next to the branches. The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The evolutionary distances were computed using the Tamura-Nei method and are in the units of the number of base substitutions per site. The analysis involved 35 nucleotide sequences. All ambiguous positions were removed for each sequence pair. *Labeobarbus intermedius* is included as an outgroup. For further explanation see text.

4. DISCUSSION

In the following chapter, the different morphotypes of the genus *Garra* are assigned to the closest taxon and sufficiently discussed in 4.4 and 4.5.

4.1. Implications of major human impacts along the river course

- Based on theoretical concepts (e.g. River Continuum Concept (RCC) (Vannote et al. 1980), Serial Discontinuity Concept (Ward and Stanford, 1983 and 1995)), it was hypothesized that abiotic characteristics but also fish assemblages will change as a response to the most noticeable human impacts observed (e.g. deforestation, livestock farming, interruption of the longitudinal continuum).

The observed water parameters and river morphological characteristics along the first 650 km of the Awash river show conspicuous changes with distance from source and decreasing elevation. At the first glance, this would support theoretical concepts (e.g. RCC) based on the unidirectional flow as the only defining feature (Vannote et al., 1980). However, considering the unusual gradients observed for water temperature (ºC) and conductivity (µS cm^{-1}) this conclusion seems too simple.

Comparing the first two sampling sites (distance of only 7.7 km between S1 and S2, and both sites above 2200 m s.l.), the near complete loss of natural vegetation and the high density of livestock farming along Gare Arera (S2) are notable. Water temperature and conductivity clearly increase between the source region in the Chilimo forest (S1) and the river stretches along S2. Winemiller et al. (2008) reasonable argued, that not only physical characteristics such as the water temperature, but also biological processes (and biocoenoses) depending on the input of allochthonous organic material will ultimately change if the riparian vegetation is lost. Lampert and Sommer (2007) further concluded that nutrient enrichment in combination with improved light availability will favour filamentous algae. This is in line with field observations at S2 (during the dry season), where a high concentration of dissolved oxygen (> 100%) may indicate this trophic change (Begon et al., 2006). A notable difference between the two sites was also recorded for the fish bioceonoses. While *Garra dembeensis* was most characteristic for the near natural site upstream, *Garra* aff. *makiensis* was found to dominate the impaired site a few kilometres downstream. For *Labeobarbus beso* the area might be the uppermost limit of its natural distribution in the Awash river (see also Golubtsov et al. 2002).

Between Lafessa (S6) and Wonji (S7) the Koka reservoir interrupts the natural succession and turns the lotic system into a lacustrine environment. The decrease in water temperature and conductivity, recorded at S7, is striking and seems to affect the Awash more than 100 km downstream (S8 and S9). This may indicate a thermal stratification of Lake Koka, partially during the dry season or diurnal. Degefu et al. (2011) indicated a much higher surface water temperature (0 – 50 cm, 25 – 26 ºC) compared to the deeper layers (> 100 cm, 23 ºC) of the reservoir (October to March) but concluded that the lake would mix continuously. A diurnal turnover as observed in many shallow tropical lakes and proposed by Baxter et al. (1965) seems more plausible but does not fully match with the observed differences. In general, the noticed characteristics are well explained by Ward and Stanford (1983) and their proposed Serial Discontinuity Concept. In the present study, measurements were not taken continuously (over 24 hours) and therefore only represent a short period of time. Other water parameters recorded (dissolved oxygen (% and mg L^{-1}) and pH) show indistinct variations between sampling sites and are better explained by the different time of measurement (Begon et al., 2006).

Although the construction of the Koka dam seems to pose a clear upstream migration barrier for all fish species, the structure of the fish biocoenoses did not explicitly change between S6 and S7. This seems to be in contrast with general considerations from the tropics and temperate climates (Agostinho et al., 2008; Dugan et al., 2010). Habteselassie (2009) pointed out significant differences when studying the up- and downstream reaches of a diversion weir in the Weyto river. Apart from a lower species richness in the upstream segments, he also reported a less heterogenous habitat structure, related to anthropogenic modifications. This however was not true for the present investigation. Both study reaches showed similar river morphological characteristics (low gradient) with common habitat structures. The difference between the most dominant taxon (*G*. sp in S6 and *Micropanchax*. cf. *antinorii* in S7) might be best explained by different sampling effort and accessibility of mesohabitats. *Cyprinus carpio* was only caught in S7 but seems to occur in S6 as well (based on reports by local fishermen). A similar observation was reported by Golubtsov et al. (2002) who mentioned 6 species as possibly occurring in Lake Koka: *Clarias gariepinus*, *Oreochromis niloticus*, *Coptodon zillii* (*Tilapia zillii*), *M. antinorii* (*Aplocheilichthys antinorii*), *C. carpio* and *G. makiensis*. Note that *G. dembeensis* seems to be the only taxon not capable to inhabit the lacustrine environment. The preference of this species for a higher flow velocity and coarse substrate was previously mentioned by different authors (e.g. Bailey, 1994; Habteselassie, 2009) and can be supported here.

Further downstream of Lake Koka, a rapid increase in conductivity between Nur Sada (S9) and Yimre (S10) was noticed. The most likely explanation is an artificial connection of the currently expanding saline Lake Beseka with the Awash river (based on orthophotos, outlet at: 8°53'16.49"N, 39°55'7.34"E). According to Belay (2009), the conductivity in the lake can reach to a maximum of 7400 µS cm^{-1}. A possible natural connection with the Awash river in the future was argued by Dinka (2012), if the lake will continue to expand. The disappearance of *G. dembeensis* and *L. beso* might be related to the high conductivity. Both taxa occur upstream but cannot be found in S10, although the habitat structure seems to be favourable (course substrate, high flow velocity). This, however, can only be assumed here and needs detailed clarification.

4.2. Species distribution and diversity

- In compliance with previous investigations (Roberts, 1975; Golubtsov et al., 2002) it was expected that faunistic elements of the Abyssinian Highlands Ichthyofaunal Province will dominate. Following theoretical concepts of river zonation (e.g. Stream zonation concept (Illies and Botosaneanu, 1963), RCC (Vannote et al. 1980)) it was hypothesised that species richness and diversity will change and gradually increase from upstream to downstream reaches.

With the exception of *C. carpio*, all taxa identified from the Awash river were native. *O. niloticus*, *C. gariepinus* and *M.* cf. *antinorii* are widespread in the Main Ethiopian Rift system and East Africa (Golubtsov et al., 2002). The genus *Labeobarbus* and *G. dembeensis* are characteristic taxa of the Abyssinian Highlands Ichthyofaunal Province (Roberts 1975). *G.* aff. *makiensis* seems to be shared with the adjacent Meki river basin, Lake Langano and possibly the upper reaches of the Gibe-Omo system (Stiassny and Getahun, 2007). *G.* sp. seems not closer related to congeners found in the Awash river, but the taxonomic classification is unclear (see 4.4.). *Enteromius* sp. shares common characteristics with *E. paludinosus* (Habteselassie, 2012), a group of small African barbs where the last spine of the dorsal fin is serrated but could not be clearly identified.

Fish continuously inhabit the Awash river from the headwaters in the Chilimo forest to the lowland plains of the Afar region. Even upstream of the first sampling site (S1) fish seem to populate the small source rivulets (Yonas Terefe and Olyad Dereje, pers.

comm., 2018). The dominance of the genera *Garra* and *Labeobarbus* supports previous observations, that common characteristics are shared with the headwaters of the Blue Nile and the Omo river (see above). In consistence with theoretical concepts (e.g. Vannote et al., 1980), species (taxa) diversity changed along the longitudinal gradient from the headwaters (S1, 2 taxa) to the downstream reaches (S12, 7 taxa). However, a constant gradual increase with the highest number of taxa in the lowland sites (Araùjo et al. 2009) was not recognized. All biodiversity indices used, support this observation and result in the highest diversity for S8 (8 taxa). It should be considered that a high diversity index does not necessarily account for a higher overall diversity or a better habitat quality. Depending on the index used, different variables are taken into account and therefore need to be reflected critically (Boenigk and Wodniok, 2014).

A possible decrease in taxa richness in the lowland reaches of the Awash river is an interesting observation as it seems contrasting to theoretical concepts (e.g. Illies and Botosaneanu, 1963; Vannote et al., 1980) and practical studies (Golubtsov and Mina 2003). Based on the argumentations of Lowe-McConnell (1975) and Winemiller et al. (2008), the number of species in any system is related to diversity, size and stability of mesohabitats (availability of niches). These aspects are usually developed in larger productive lowland river systems (Vannote et al., 1980). This however cannot be fully answered for the Awash in the present study as too little information exists on further downstream reaches (see Getahun and Stiassny, 1998; Golubtsov et al. 2002) and the importance of the lateral interaction during rainy season (Junk et al., 1989). From the present study it can only be noted that habitat diversity was low at S11 where only 4 taxa were found.

4.3. Zonation of fish assemblages

- With an increase in species diversity from the headwaters to the lowland reaches, it was expected to observe faunistic changes between the rhithron and the potamon along transition zones, where fish assemblages change due to environmental gradients (Illies and Botosaneanu, 1963; Ibanez et al., 2007).

Theoretical concepts have been suggesting gradual changes of biotic communities along the longitudinal dimension for a long time (Illies and Botosaneanu (1963), Vannote et al. (1980)). Especially for fish communities this became evident in river systems all over the world (Thieneman (1925), Balon and Stewart (1983), Ibarra and Stewart (1989), Payne et al. (2010), Chakrabart and Homechaudhuri (2013)). The results of the present study give good reason to suggest a similar zonation pattern in the Awash river. However, the complex geomorphological setting seems to determine a variety of environmental aspects (e.g. river gradient, sediment composition) and ultimately seems to shape the structure of the biocoenoses (Balon and Stewart, 1983; Winemiller et al. 2008).

In general, the **upland zone** (S1 – S5) was found to be clearly different from river reaches further downstream. This is not only visible in fish assemblages but also clearly seen from abiotic parameters (e.g. water temperature) (Ibarra and Stewart, 1989; Allan and Castillo, 2007). Cyprinids where dominating (see Golubtsov et al., 2002) and the genus *Garra* was most characteristic. A closer view on the observed biocenoses makes clear that the rhithron is not an entirely homogeneous entity but reflects external control mechanisms (e.g. geological setting). Montgomery and Bolton (2003) clearly highlighted these mechanisms and pointed out interrelations between organisms, instream habitat structures and the catchment scale. While *G. dembeensis* was dominating the steep gradients and swift waters (Bailey, 1994) *G*. aff. *makiensis* was abundant in low gradient reaches. The presence of *O. niloticus* in the floodplain of Awash Belo could not be resolved in the present study. However, due to the clear genetic difference from downstream populations (Figure 49, Appendix 2) and the fact that it has never been caught from these sites (Wubetu, 2013), an anthropogenic introduction might be assumed.

In accordance with previous studies conducted in Ethiopia and the African continent (Habteselassie, 2009; Payne et al., 2010), species richness increased with distance from source. However, in the example of the Awash river, it appears that the alternating river gradient (steep and low gradient sections) seems to determine biotic characteristics. Balon and Stewart (1983) found similar patterns while investigating fish assemblages along the Luongo river in Zambia. It became clear that faunistic elements seem to change where the natural characteristic of a homogenous river is interrupted. Theoretical concepts (e.g. Thienemann, 1925) often seem to pretend that river systems are characterised by sharp transitions of faunal regions. However, natural systems rarely appear to change rapidly (Ferreira and Petrere-Júnior, 2009) along the longitudinal gradient. Only physical interruptions may appear to clearly separate fish faunas. This aspect was highlighted by Golubtsov et al. (2002) who stated the separation of biogeographic units along the Tis Issat Falls (Blue Nile Basin). In the Awash river, the cascades downstream of Awash Kunture might prevent upstream migration of certain species (e.g. *L*. cf. *intermedius*, *O. niloticus*).

Two clear **transition zones** (TZ), separating the upper rhithron zone from the lowland potamon were observed along the first 650 km of the Awash river. The first relatively sharp faunistic change (**TZ1**) was noted along a decline in river gradient at an altitude of 1608 m a.s.l. (S6). The potamal character (habitat structure) and a higher water temperature seem to affect the fish community (Bone and More, 2008). An influence of the Koka reservoir may be assumed as Desta (2005) mentioned a migration of fish in the adjacent floodplain during the rainy season. *G. dembeensis*, a typical highland element (Getahun et al., 2008) and dominating the upper reaches, was only found in few numbers restricted to shallow side channels and few riffle sections. According to Baensch and Riehl (1991) is may be assumed that the species can tolerate a maximum water temperature of 26 ºC. At the same time the presence of *C. gariepinus*, *O. niloticus*, *M*. cf. *antinorii* and *G*. sp. seem to reflect the change of environmental characteristics and the structure of the biocenosis.

The second transition (**TZ2**) appears to be between S9 and S11 but is less pronounced and does not seem clearly related to the river gradient. It might be assumed that the sharp increase in conductivity (see above) may alter the faunistic composition (Bone and More, 2008). As mentioned above, *G. dembeensis* and *L. beso* were not found further downstream although habitat characteristics seem favourable. This, however, needs further clarification as little specific information on autecological parameters of both species exist (Froese and Pauly, 2018). The increasing abundance of *L*. cf. *intermedius* is interesting but needs detailed clarification especially as mainly small (juveniles) specimens were caught. According to Palstra et al. (2004) the substrate composition (at S10) might be a favourable spawning ground for *Labeobarbus* sp. The presence of *L*. cf. *nediga* (S9 and S10) is notable as well and supports earlier observations (Nagelkerke, 1997; de Graaf et al., 2008) which pointed out the preference of this taxon for coarse substrate.

Between these transition zones a sequence of both, rhithral (e.g. high flow velocity, coarse substrate) and potamal (e.g. sediment deposition, point bars) elements was observed. Especially the aspect of **natural rhithralisation** (Balon and Stewart, 1983) downstream of Lake Koka is interesting, since the temperature was recorded to decline (Ward and Stanford, 1983), but fish assemblages seem closer related to the river gradient. The sampling sites downstream of the reservoir (S7, S8, S9) seem to be more similar to the upper reaches (S1 – S5) and would support the Serial Discontinuity Concept (Ward and Stanford, 1983) in the specific aspect of abiotic parameters. Note that the taxa composition of S7 closely resembles the lowland reaches (S12). This might be best explained by similar habitat characteristics (Whittaker and Levin, 1975). The higher diversity observed between the 2 TZ is not necessarily explained by a higher habitat diversity (Habteselassie, 2009) but rather by the presence of typical potamal elements upstream (S6). The most characteristic taxa are *G. dembeensis* and *L*. cf. *intermedius*. Typical potamal elements like *O. niloticus* or *M*. cf. *antinorii* are rare and restricted to few habitats.

The **lowland reaches** of the Awash were only partially covered in the present investigation and little information is available on their fish communities (e.g. Getahun and Stiassny, 1998; Golubtsov et al. 2002). The sampling site downstream of Lake Yardi represents a typical potamal river where an increasing importance of the lateral dimension became apparent (Junk et al., 1989). *O. niloticus*, *M*. cf. *antinorii*, *G*. sp. and *E*. sp. were most characteristic. Especially the presence of *E*. sp. seems to support the increasing importance of the lateral interaction since the taxon was exclusively found in connected side arms and plesiopotamon but not in the main channel.

It is worth mentioning, that the zonation observed in the present study does not confirm previous classifications of the Awash river (e.g. Brown and Lemma, 1970; Halcrow, 2006). The rhithrion (upland zone) seems much shorter than proposed by Brown and Lemma (1970) (see 1.1) and would support general condideratins by Illis (1961).

4.4. The genus *Garra* – morphology

- Based on the concepts of ecological tolerance (Shelford, 1913) and niches (Whittaker and Levin, 1975) as well as the fundamental idea of natural selection (Darwin, 1859), it was expected that populations occurring in a wide range of environments (covering different habitats e.g. flow velocity, substrate) show specific adaptations and (slight) phenotypical variation. These differences are a consequence of natural selection where better adaptations are favoured.

In the following, the most important characteristics are discussed and related to environmental factors. In addition, observations by several authors need to be addressed (e.g. interpretation of chest and belly scales in *G. makiensis*, *G. aethiopiaca* and *G. quadrimaculata* by Menon (1964), Golubtsov et al. (2002), Stiassny and Getahun (2007)) which are often inconsistent and complicate determination of some taxa.

***G. dembeensis* s. str.** is clearly identified and easily distinguished from congeners in the Awash river by external diagnostic characteristics (Table 14, Appendix 1). In comparison with data presented by Stiassny and Getahun (2007), the head seems much wider and flatter. This variation would indicate a more pronounced bottom dwelling habit over coarse substrate and fast flowing water as suggested by Menon (1964) and Winemiller et al. (2008). The distribution within the Awash river and the preference for swift currents (Bailey, 1994) can support this observation. At the same time, the snout is more elongated which is well explained by the smaller orbit diameter observed, as the overall head length seems equal.

Considerable variation between specimens was observed in disc type and papillation. No consistent opinion exists on the function of the different forms of suctorial discs in *Garra*. While Goren (1974) could not find any relation between flow velocity and disc size, Zhou et al. (2005) noted the disc as an important adhesive structure. Getahun (2000) suggested a possible relation to feeding habits. Based on the observations in the Awash river it is conclusive that the disc size might not be necessarily related to high flow velocity but papillae on disc periphery, lower lip and ventral side of rostral cap were more pronounced in high flow velocity sites.

***G. dembeensis* morphotype ‘a’** showed similar habitat preferences as *G. dembeensis* s. str. but was only found in the upper river reaches. It is primarily distinguished from *G. dembeensis* s. str. by possessing more scales on the predorsal and postpelvic regions and a slightly higher number of lateral line scales. This is an interesting aspect since Menon (1964) described *G. dembeensis* s. str. as possessing 38 – 42 lateral line scales, 4 – 10 predorsal scales and indicated the postpelvic region as ‘scaly’. On the other hand, Stiassny and Getahun (2007) mentioned 36 – 38 lateral line scales, 0 – 4 predorsal scales and a maximum of 2 deeply embedded scales (usually asquamate) in the postpelvic region. Note that these descriptions are not consistent and may indicate great variability between geographically separated populations. It should be considered that Menon (1964) did not only include specimens from Ethiopia but also from the East African region. Examining material of *G. dembeensis* in the National Museum of Kenya, the presence of a completely scaled postpelvic region can be confirmed (Figure 39i).

Based on the descriptions presented in Stiassny and Getahun (2007), the taxon ***G. aff. makiensis*** found in the Awash river seems closely related to *G. makiensis* s. str. However, considering the description of the holotype *Discognathus makiensis*

Boulenger 1903, considerable variation seems to exist. Boulenger (1903) studied 6 specimens from the ‘Maki’ (Meki) river and reported 39 – 42 lateral line scales. Golubtsov et al. (2002), most likely following the description of Menon (1964), stated 38 – 42 scales. Stiassny and Getahun (2007) on the other hand, mentioned only 35 – 37 lateral line scales, although specimens from the same geographic area were examined. Some confusion exists considering scales on chest and belly. Menon (1964) reported the region as ‘scaly’ while the description of Stiassny and Getahun (2007) seem to be inconsistent. On page 77 they stated both regions with few scales, but on page 78 they reported the chest region as asquamate and the belly with few embedded scales. Note that *G*. aff. *makiensis* is classified here according to the descriptions of Stiassny and Getahun (2007).

Specimens from the Awash basin described as *G. makiensis* by Golubtsov et al. (2002) seem to resemble *G. sp*. in the present work. Their conclusions could not be followed here mainly due to the fully scaled belly (see above) and the presence of only 1 unbranched anterior pectoral fin ray as observed in *G*. sp. in this study. These characteristics (among others) seem to be in contrast with the data on *G. makiensis* presented in Stiassny and Getahun (2007).

Furthermore, a similar confusion may exist for *G. quadrimaculata*. Rüppell (1836) described the holotype (*Gobio quadrimaculatus*) from the Abyssinian Highlands and reported 35 lateral line scales. This was confirmed by Menon (1964) who stated the regions of chest and belly as fully scaled (scales not overlapping). Stiassny and Getahun (2007) added that scales are small and deeply embedded. In this perspective the difference to *G. makiensis* seems not clear anymore, especially when considering the geographic distribution of both taxa. Golubtsov et al. (2002) reported *G.* cf. *quadrimaculata* and *G*. cf. *hirticeps* from the Awash river mainly based on the absence or presence of a small red spot on the upper margin of the gill cover. Those with a red spot were identified as *G*. cf. *hirticeps*. Note that Golubtsov et al. (2002) synonymized *G. dembeensis* with *G. hirticeps*. This only adds some more confusion since Stiassny and Getahun (2007) synonymized *G. hirticeps* with *G. quadrimaculata*. Their conclusion, however, seems to be more reasonable (see Rüppell, 1836) and is followed here.

***G*. aff. *makiensis* morphotype ‘a’** was mainly characterised by prominent tubercles on the snout and a depressed body shape. The dorso-ventrally flattened body might be an adaptation to high flow velocities as explained by Getahun (2000) and Winemiller et al. (2008). This conclusion seems reasonable since morphotype 'a' was exclusively found in a steep gradient section of the Awash river. Additionally, the elongated pectoral fin is in line with observations by Getahun (2000). The characteristic tuberculation was present in all specimens observed (during the dry season) and supports observations by Krupp (1983) and Cambray and Stuart (1985). So far there is no reliable evidence that this characteristic may express sexual dimorphism in *Garra*. Getahun (2000) only noted that males may have more prominent conical (breeding) tubercles than females. The assumption by Reid (1978), who stated a possible hydrodynamic function of these structures, is interesting. This may be supported by observations in other organism groups (Statzner, 2008; Mills and Leighton, 2008) where different attachments are supposed to have a hydrodynamic advantage. Note that morphological differences between *G*. aff. *makiensis* morph. 'a' and *G. ignestii* are not entirely clear.

***G*. aff. *makiensis* morphotype 'b'** was predominantly found in the headwaters (Chilimo forest area) of the Awash river. It shows a much more robust head and body shape with a relatively short and deep caudal peduncle. The same was observed for ***G*. aff. *makiensis* morphotype 'c'** which was solely found in the first low gradient section (Awash Belo). Both morphotypes differ in disc size, tuberculation and colouration (preserved specimens). The robust shape of head and body, which is especially remarkable in comparison to *G*. aff. *makiensis* morph. 'a', might be related to habitat characteristics (Getahun, 2000). Considering the headwaters of the Awash river with low discharge and the extensive floodplain where fish can avoid physical stress during the rainy season by lateral migration, this explanation seems reasonable. The same explanation may be reliable for the caudal peduncle (depth and length).

In river sections where abiotic stressors (e.g. high flow velocity) cannot be avoided, it seems that specific adaptations are favoured and become apparent in the phenotypes observed (Darwin, 1859; Winemiller et al., 2008). Note that morphological differences between *G*. aff. *makiensis* morph. 'c' and *G. aethiopica* are not entirely clear and need clarification. It is interesting that the presence of *G. aethiopica* in the Awash river, as reported by Stiassny and Getahun (2007), could not be confirmed in the present study.

***Garra* sp.** was present from upstream of Lake Koka to the lowland sites. As stated above, it can be assumed that Golubtsov et al. (2002) identified this taxon as *G. makiensis*. Based on the descriptions of Stiassny and Getahun (2007), this view is not followed as the taxon presented here is characterised by a fully scaled belly (large scales, not embedded) and only 1 unbranched anterior pectoral fin ray (see above). The latter characteristic is (according to present knowledge) not described for any African representative of the genus. Stiassny and Getahun (2007) reported a range of 4 – 5 unbranched pectoral fin rays for all African species, with at least 2 unbranched in anterior position (see also Lundberg and Marsh, 1976; Getahun, 2000). Eurasian representatives of the genus seem to be characterized by only 1 unbranched anterior pectoral fin ray (e.g. Menon, 1964; Mousavi-Sabet and Eagderi, 2016).

Note that the holotype specimen of *D. makiensis* Boulenger 1903, could not be examined in the present study. This, however, seems necessary to clarify the inconsistent descriptions of *G. makiensis* (see above). Considering only the number of lateral line scales and the long and slim caudal peduncle (Boulenger, 1903), *G*. sp. seems to show similarities with *G. makiensis* as Golubtsov et al. (2002) stated.

Due to the reasons stated above, this taxon could not be clearly assigned. Based on the diagnostic characteristics it can be assumed that the taxon is closely related to the 'tibanica' complex (Menon, 1964). Note that Stiassny and Getahun (2007) synonymized *G. tibanica* (Trewavas, 1941) with *G. quadrimaculata*. This needs to be considered in the interpretation of Figure 23.

Comparable to *G*. aff. *makiensis*, 3 different morphotypes of this taxon were recorded. The 'slender' morphotype is described in detail in Table 18 (Appendix 1). The 'large' morphotype was most likely mentioned in Golubtsov et al. (2002) from Lake Koka (and named as *G. makiensis*). In the steep gradient section downstream of the Awash National Park, a morphotype with large tubercles was found. Morphometric and meristic data of these morphotypes and their possible implications (e.g. sexual dimorphism) are not closer described and discussed in the present study. The interesting relation to environmental conditions (e.g. flow velocity and substrate) should be noted (compare to *G*. aff. *makiensis*).

4.5. The genus *Garra* – genetic analysis

The results presented above and in Figures 23 and 49, give good evidence for 3 distinct groups of *Garra* inhabiting the first 650 km of the Awash river. *G. dembeensis* and *G*. aff. *makiensis* seem to have closest relatives on the African continent (e.g. *G. tana* and *G. ornata*), whereas *G. sp.* seems to fit closer to the Eurasian group with closer relatives on the Arabian Peninsula (e.g. *G. quadrimaculata (*including the synonym G. *tibanica* as stated above).

These results of the present study are difficult to be interpreted, as not all African and Eurasian species could be included and therefore the true relationships are not necessarily reflected. Menon (1964) stated a close relationship of *G. dembeensis*, *G. makiensis*, *G. ornata* and *G. quadrimaculata* as all of them were assigned to the 'tibanica' complex. This is not necessarily in contrast to the present findings as all of them are clearly separated from *G. rufa* ('rufa' complex). It becomes more difficult in the case of *G. nasuta* and *G. gotyla* which were assigned to the 'gotyla' complex (Menon, 1964) but appear closer related to *G. quadrimaculata*.

On the other hand, Getahun (2000) stated that African members of the genus do not inevitably show a greater relationship to each other than to Eurasian congeners. He supported this view with an extensive cladistic study (based on osteological characteristics) where he concluded that *G. makiensis* and *G. quadrimaculata* are possibly closer related to *G. rufa* than to *G. dembeensis*. This cannot be clarified by the present analysis. More data would be needed to support the evolutionary relationships between African and Eurasian members of the genus.

Previous molecular phylogenetic studies (e.g. Yang et al., 2012) have not included many African species but the close relationship between *G. ornata* and *G. congoensis* was confirmed. The clear distance between *G. makiensis* and other African congeners included in their study is interesting and supports the cladistic results of Getahun (2000). Hashemzadeh Segherloo et al. (2016) outlined the closer relationship between *G. dembeensis*, *G. congoensis* and *G. ornata,* which was found in the present study as well. Behrens-Chapuis et al. (2015) did not include African members of the genus but found no difference between *G. buettikerii* and *G. tibanica* (*G. quadrimaculata*). These taxa were found closely related to *G*. sp. in the present study.

The observed phenotypical variability within the 3 groups could not be confirmed by genetic data (mtDNA, cytochrome c oxidase I sequences) in the present analysis. The different populations are therefore classified as morphotypes but not as taxa. A more detailed analysis (e.g. SSR microsatellite markers) with focus on a different genetic region would possibly reflect some of the observed phenotypical variability.

5. CONCLUSIONS AND RECOMMENDATIONS

The dynamic nature of river systems and the importance of various external and internal control mechanisms became apparent again in the present investigation. Studying such a system in detail deserves a critical reflection of the present situation but also of the geological and geomorphological history. A chain of connections between the landscape perspective, anthropogenic activities, the riverine landscapes and ultimately the organisms living in the water body can be clearly observed. Like all other ecosystems on earth, each of them cannot be seen in total separation.

However, especially from the perspective of fish, a river can be thought as an island surrounded by dry land. Moreover, considering the longitudinal perspective of these systems, it becomes apparent that they are not even homogenous islands but are influenced and even possibly interrupted by environmental and geomorphological gradients. This ultimately raises the question of mechanisms and factors influencing the distribution of fish. To address this problem, one would need to think either in geological perspectives and the connection to adjacent river basins or of vectors transporting individuals (or certain life stages like eggs) from one river to the next (e.g. water fowl).

What can actually be observe in a river system is the succession of fish species along their ecological tolerance. The biocenosis in the rhithron is usually poor in taxa and clearly different from the community structure in the lowlands. Between these separated zones, transitions exist, where the range of ecological tolerance overlaps and diversity increases. Especially in the case of the Awash river, the complex geomorphological setting becomes apparent as fish communities seem to be related to steep or low river gradients.

These stretches were found to be especially interesting in the perspective of the genus *Garra*. Instead of finding several separated taxa it is rather remarkable to observe the phenotypical plasticity represented by morphotypes specifically adapted to certain abiotically defined environments. No absolute answers can be given at this stage, as the present study was the first to highlight these patterns in the Awash river. However, it may not be far-fetched to say, that evolutionary processes in the sense of natural selection can be observed.

This preliminary study of the Awash river gives good insights into a unique tropical system that deserves a great deal of interest. It becomes apparent that much more questions are raised than can be answered in a short investigation period. However, the study provides a comprehensive overview and fills a major gap of information. This is especially important in the light of increasing adverse anthropogenic impacts that threaten the ecosystem. In the following, aspects and limitations are highlighted and meant to give an outlook for potential future research:

- It became apparent that existing knowledge on species distribution in the Awash river (especially for the genus *Garra*) is often contradictory. This might be due to sloppy species identification but also highlights a lack of reliable identification keys (especially for field work) on the level of river basins.
- The existing uncertainties of diagnostic characteristics (partially highlighted in 4.4) in members of the genus *Garra* need to be addressed in detail. Clarification on the geographic distribution and the evolutionary relationship to congeners on the Arabian Peninsula is needed.
- The widespread occurrence of the genus *Garra* within the Awash would make it an interesting organism for bioindication. A limitation is the difficult identification and a major lack of knowledge on autecological parameters (e.g. feeding- and spawning biology, habitat preferences, tolerance to environmental stressors). This is not only true for the genus *Garra* but for a lot of other groups too and would be an interesting field of further research.
- The introduction of different subspecies of *Oreochromis niloticus* (e.g. stocking of Lake Koka and the Tendaho reservoir for commercial fishing) can pose a potential threat to locally adapted (endemic) populations of *Oreochromis niloticus cancellatus*. This aspect of ‘genetic pollution’ should be considered by the responsible authorities.
- Within the present study, a large collection of fish from the Awash river was established. Most specimens (around 2500, including all taxa found in the present investigation) were stored in the National Fish and other Aquatic Lives Research Centre, Sebeta, Ethiopia. It is recommended that they are accurately stored and made available for further studies and research institutions.
- For taxonomic purpose, especially for morphometric studies, it became clear that only accurately preserved specimens (formalin fixation) can be used. For genetic analysis it is recommended to take fin clips before preservation, these can be kept in 96% ethanol (denaturated).

- The study revealed the difficult comparability between sampling sites. As the river morphology changes, a combination of different methods had to be used, often due to the difficult accessibility of river stretches (e.g. water depth, high flow velocity, crocodiles). For an extended sampling campaign, a boat is recommended.
- Planning and conduction fieldwork takes time and requires flexibility. Only 1 day for each site is not enough to cover all mesohabitats of interest, especially in the lowland reaches.
- The Awash river is an important life line for diverse cultural groups inhabiting the surrounding landscapes. Moreover, the river has a high cultural and spiritual importance to some local communities. This must be considered and local people always informed about planned research activities.
- So far, there is little scientific knowledge on the Awash river (easily) available. Especially in the perspective of land use change and the pristine state of the environment (e.g. floodplain around Awash Belo, characteristics of the river before the Koka dam was built). The knowledge of the river system by local people is impressive and therefore local communities can play a crucial role in future conservation aspects.
- The (industrial) anthropogenic impact along the Awash river and its tributaries (especially Sebeta river, Akaki river) is dramatic. Not only does it threaten the biotic communities (e.g. benthic invertebrates, fish), furthermore it poses serious risks to the local inhabitants. Legal frameworks are urgently needed to restrict an uncontrolled discharge of pollutants from industrial factories (e.g. alcohol- and textile factories, or tanneries).

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7. APPENDIX 1

Table 9. A total of 23 fish species (native and introduced) was reported from the Awash river basin (based on literature review in the present study). The taxonomic status of several species is unclear and needs clarification. Several taxa recorded in the basin are most likely based on misidentifications. Remarks on taxonomy and possible distribution within the basin are indicted.

Family	**Species**	**Remarks and distribution in the Awash basin**
Cyprinidae	*Enteromius paludinosus*	Awash and Rift lakes (Roberts, 1975), Akaki River (Boulenger, 1906; Boulenger, 1911; Tedla, 1973).
	Enteromius humilis	Awash River and Teji River (Wubetu, 2013). Otherwise only known from the Abaya basin (Lake Tana) (Lévêque and Daget, 1984).
	Garra aethiopica	Only known from the Awash River basin (Getahun, 2007; Stiassny and Getahun, 2007), Teji River (Wubetu, 2013).
	Garra blanfordii	Awash basin (Boulenger, 1909).
	Garra chebera	Akaki river (Habteselassie, 2009).
	Garra dembecha	Known from the upper Awash River basin (Wubetu, 2013).
	Garra dembeensis	Known from Awash River (Getahun, 2007; Stiassny and Getahun, 2007), Synonym for *Garra* cf. *hiticeps* (Golubtsov et al., 2002)?
	Garra cf. *hirticeps*	Awash basin (Golubtsov *et al*., 2002), NOT a valid species, synonymized with G. quadrimaculata!
	Garra ignestii	Tributary of Awash on Dessie road (Stiassny and Getahun, 2007).
	Garra quadrimaculata	Upper reaches of Awash River (Golubtsov *et al*., 2002), Akaki River (Boulenger, 1906), Awash basin (Boulenger, 1909; Tedla, 1973).
	Garra makiensis	Middle reaches of Awash River and Koka Reservoir (Golubtsov *et al*., 2002), Gota River (Menon, 1964; Lévêque and Daget, 1984).
	Labeobarbus beso	Rivers in the Awash basin: Gota River and Akaki River (Pellegrin, 1905), Awash River and tributaries (Boulenger, 1909; Tedla, 1973; Lévêque and Daget, 1984; Golubtsov *et al*., 2002).
	Labeobarbus gorguari	Awash basin (Parenzan, 1940) Synonym of *Labeobarbus intermedius* (Banister, 1973)
	Labeobarbus nedgia	Akaki River and Gota River (Pellegrin, 1905), (Banister,1973), Synonym of *Labeobarbus intermedius* (Golubtsov *et al*., 2002)
	Labeobarbus intermedius	Entire Awash basin (Tedla, 1973), Gota River (Boulenger, 1902), Kassam and Awash River (Pellegrin, 1905; Beadle, 1981), Hurso River (Boulenger, 1902), Akaki River (Pellegrin, 1905), Errer River (Boulenger, 1902).
	Cyprinus carpio	Introduced: Aba Samuel Reservoir on the Akaki River (Tedla and Meskel 1981), Lake Koka (Tesfaye and Wolff, 2015).
Cyprinodontidae	*Aphanius dispar*	Awash basin, Lakes Abba and Abaytou (Golubtsov et al., 2002).
Poeciliidae	*Micropanchax antinorii*	Koka Reservoir (Golubtsov et al., 2002), taxonomic status unclear.
Cichlidae	*Oreochromis niloticus cancellatus*	Awash basin (Boulenger, 1904; Tedla, 1973), Lake Koka (Tesfaye and Wolff, 2015).
	Oreochromis niloticus filoa	Endemic to hot alkaline springs in the Awash National Park (Trewavas, 1983).
	Coptodon zillii	Introduced: Koka Reservoir (Abebe and Teferra,1992).
Clariidae	*Clarias gariepinus*	Kassam River (Boulenger, 1902), Awash River (Boulenger, 1904), Lake Koka (Tedla, 1973).
Salmonidae	*Oncorhynchus mykiss*	Introduced: Aba Samuel Reservoir – but never established there (Tedla and Meskel, 1981).

Table 10. Substrate (mean, estimated), microhabitats, vegetation and human impacts for all sampling sites (S1 – S12) during the dry season 2017/ 2018. ++ abundant (++ major for human impacts); + present; ± scarce (± minor for human impacts); - absent. Major characteristics are highlighted.

Parameters		**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**	**S9**	**S10**	**S11**	**S12**
Substrate (%)	• Pelal (< 6 µm)	0	2	4	1	1	1	32	0	15	5	50	22
	• Psammal (> 6 µm - 2 mm)	2	7	18	13	7	63	41	10	25	21	32	50
	• Akal (> 0.2 - 2 cm)	10	19	28	11	3	17	14	4	16	21	12	21
	• Mikrolithal (> 2 - 6 cm)	22	19	31	10	1	16	7	0	10	28	1	6
	• Mesolithal (> 6 - 20 cm)	26	36	13	3	7	2	3	0	11	15	0	1
	• Makrolithal (> 20 - 40 cm)	26	11	5	5	46	1	2	13	9	3	0	0
	• Megalithal (> 40 cm)	14	6	1	57	35	0	1	73	14	7	5	0
Microhabitat	• Xylal	+	-	-	±	-	+	+	±	±	+	++	++
	• Leaves	++	±	-	±	±	+	+	±	-	+	++	++
	• Roots of Trees	+	±	-	±	-	+	+	±	-	+	+	+
	• Lithal	++	++	±	+	++	±	+	++	+	++	±	-
Riparian and aquatic Vegetation	• Submerged plants	-	-	±	+	-	-	++	-	±	-	-	+
	• Trees	++	±	-	+	+	±	±	+	±	+	++	++
	• Shrubs	++	±	-	+	++	+	±	+	±	+	+	++
	• Herbaceous plants	++	±	±	+	±	±	++	-	-	±	+	++
	• Grass	++	+	±	++	+	+	++	++	+	-	+	++
Human impacts	• Agriculture	-	++	++	+	-	±	++	+	++	-	++	-
	• Livestock farming	+	++	+	++	++	++	+	++	++	++	++	+
	• Settlements	-	-	-	+	-	-	±	±	±	-	±	±
	• Solid waste	-	-	±	+	±	±	+	±	+	±	+	±
	• Washing/ bathing	-	+	±	+	+	±	±	+	+	+	±	±
	• Industry	-	-	-	-	-	-	-	-	-	-	-	-
	• Sand mining	-	-	-	-	-	±	±	-	-	-	-	-
	• Water abstraction	-	±	++	+	-	+	+	++	++	-	++	±
	• Deforestation	+	++	++	+	±	++	++	+	+	±	+	+
	• Channelization	-	-	±	-	-	-	-	±	±	-	-	±

Table 11. Correlation matrix (Pearson's correlation) of topographic and morphologic characteristics as well as physical- and chemical water parameters. Measured along 12 sites in the Awash river (November 2017 – January 2018). Signif. codes: * = p < 0.05; ** = p < 0.01.

Variables	**1**	**2**	**3**	**4**	**5**	**6**
1. Altitude (m a.s.l.)	1					
2. Distance from source (km)	-0.980**	1				
3. Temperature (ºC)	-0.744**	0.712**	1			
4. pH	-0.340**	0.260*	0.322*	1		
5. Dissolved Oxygen (mg/l)	0.264*	-0.365**	-0.150	0.521**	1	
6. Conductivity (µS/cm)	-0.762**	0.764**	0.646**	0.208	-0.408**	1
7. Average channel width (m)	-0.824**	0.889**	0.613**	0.199	-0.356**	0.475**

Table 12a. Results of ANOVA, permutation test for the overall model of Canonical Correspondance Analysis (CCA). Degree of freedom (df), p-value and *F*-ratio for the factor CCA Model are depicted. A p-value of < 0.05 was considered as significant.
Signif. codes for Table 12a, 12b, 12c: Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Factor	**CCA**			
	df	**Chi Square**	**p**	***F***
CCA Model	4	0.73	0.013 *	2.454
Residuals	1	0.52		

Table 12b. Results of ANOVA, permutation test for the CCA terms 'Water temperature', 'pH', 'Dissolved oxygen' and 'Conductivity'. p-value and *F*-ratio are depicted. A p-value of < 0.05 was considered as significant.

Factor	**CCA terms**			
	df	**Chi Square**	**p**	***F***
Water temperature	1	0.45	0.002 **	6.004
pH	1	0.07	0.536	0.871
Dissolved oxygen	1	0.14	0.169	1.832
Conductivity	1	0.08	0.377	1.108
Residuals	7	0.52		

Table 12c. Results of ANOVA, permutation test for the CCA axis 'CCA1', 'CCA2', 'CCA3' and 'CCA4'. p-value and *F*-ratio are depicted. A p-value of < 0.05 was considered as significant.

Factor	**CCA axis**			
	df	**Chi Square**	**p**	***F***
CCA1	1	0.50	0.031 *	6.649
CCA2	1	0.16	0.426	2.121
CCA3	1	0.06	0.870	0.844
CCA4	1	0.02	0.976	0.202
Residuals	7	0.52		

Table 13. Relative abundance per sampling site for all taxa investigated (November 2017 – January 2018). Morphotypes of the different taxa are cumulated and assigned to the closest taxon identified. *G.* aff. *dembeensis* morph. ‘a’ (N = 860), *G.* aff *makiensis* morph. ‘a’ (N = 141), *G.* aff. *makiensis* morph. ‘b’ (N = 1195), G. aff. *makiensis* morph. ‘c’ (N = 570), *Oreochromis niloticus* ssp. ‘a’ (N = 12, only in S3). Numbers indicated with (*) are based on reports and observations: S3 may be 4 species based on 1 larva (likely *L. beso*), S6 most likely 7 species, based on local people who reported *C. carpio* from this site. S11 most likely with *O. niloticus* ssp. (based on a local fisherman). The most dominat taxon (taxa) at each site is (are) highlighted.

Taxa	**N**	**Relative Abundance (%) per site**											
		S1	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**	**S9**	**S10**	**S11**	**S12**
Cyprinidae													
Cyprinus carpio	11	0.0	0.0	0.0	0.0	0.0	0.0	0.2	3.8	0.0	0.0	0.0	0.6
Enteromius sp.	120	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.8
Garra dembeensis (*G.* aff. *dembeensis* morphotype ‘a’)	1663	97.9	23.9	2.1	65.3	63.4	3.4	1.5	42.3	39.3	0.0	0.0	0.0
Garra aff. *makiensis* (*Garra* aff. *makiensis* morphotype ‘a’) (*Garra* aff. *makiensis* morphotype ‘b’) (*Garra* aff. *makiensis* morphotype ‘c’)	2706	2.1	75.0	95.8	33.2	21.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Garra sp. (all morphotypes)	717	0.0	0.0	0.0	0.0	0.0	67.9	9.2	3.8	23.8	4.1	45.5	23.5
Labeobarbus beso	56	0.0	1.1	0.0	1.1	4.9	0.0	0.0	3.8	0.0	0.0	0.0	0.0
Labeobarbus cf. *intermedius*	652	0.0	0.0	0.0	0.0	8.8	8.7	14.8	26.9	31.0	86.5	47.5	5.2
Labeobarbus cf. *nedgia*	30	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	3.6	6.2	0.0	0.0
Poeciliidae													
Micropanchax cf. *antinorii*	1402	0.0	0.0	0.0	0.0	0.0	13.6	70.3	3.8	0.0	0.3	5.9	51.0
Cichlidae													
Oreochromis niloticus ssp. (*Oreochromis niloticus* ssp. ‘a’) (*Oreochromis niloticus* ssp. ‘b’)	202	0.0	0.0	2.1	1.0	0.0	3.4	4.0	3.8	0.0	0.6	0.0	10.3
Clariidae													
Clarias gariepinus	31	0.0	0.0	0.0	0.0	0.0	3.0	0.1	11.5	2.4	2.4	1.0	0.6
Number of species:		2	3	3 (4*)	4	5	6 (7*)	7	8	5	6	4 (5*)	7
Total number of individuals:		521	3553	588	214	619	467	951	109	131	615	101	1356

Table 14. Comparison of morphometric and meristic characteristics of *Garra dembeensis* s. str. in the Awash river and the description of *G. dembeensis* s. str. by Stiassny and Getahun (2007). Specimens where collected in November 2017 and January 2018 at S1 – S9. Fin rays (unbranched and branched) were counted using stereo microscopes and may vary with different methods.

A. Morphometric measures	*Garra dembeensis* s. str. (Awash river, n=30)			*Garra dembeensis* s. str. (n=30)	
	median	**range**	**mean ± SD**	**range**	**mean ± SD**
Standard length (SL) in mm	66.6	45.0-112.0	70.7±15.9	10.7-146.1	
In percent (%) of standard length					
Body depth	20.3	15.2-23.5	20.2±1.7	15.6-23.9	20.4±1.95
Head length	23.8	22.3-25.6	23.8±0.9	19.9-27.1	23.8±162
Predorsal length	51.7	48.5-53.1	51.3±1.2	44.0-52.1	49.3±1.77
Caudal peduncle length	13.1	9.7-14.6	13.0±1.0	12.7-19.4	15.6±1.39
Caudal peduncle depth	11.6	9.9-13.3	11.6±0.8	8.3-11.6	9.9±0.86
Dorsal fin length	19.8	17.9-24.4	20.5±1.8	19.9-23.5	21.1±0.97
Anal fin length	16.5	14.3-19.8	17.0±1.6	17.0-19.7	18.3±0.82
Pelvic fin length	17.6	15.7-20.8	17.6±1.3	16.6-20.3	18.3±1.09
Pectoral fin length	20.6	18.5-24.2	20.8±1.4	15.1-23.9	19.9±1.96
In percent (%) of head length					
Head width	77.1	72.0-84.5	77.6±3.0	63.3-84.7	71.5±5.53
Head depth	57.3	49.8-63.6	58.1±5.5	50.0-68.7	59.1±4.26
Snout length	46.7	38.3-54.8	46.6±3.5	33.3-48.1	40.8±4.39
Orbit diameter	18.9	15.9-24.0	19.0±2.1	15.7-28.0	20.2±3.04
Interorbital width	44.4	41.5-49.0	45.0±2.2	36.4-48.9	41.5±2.73
In percent (%) of orbit diameter					
Rostral barbel length	47.6	34.5-65.5	50.1±9.1	33.0-68.0	54.3±10.78
Maxillary barbel length	45.0	33.3-70.0	46.6±9.8	30.1-91.0	51.1±15.19
In percent (%) of distance anal fin to pelvic fin insertion					
Vent distance	32.3	27.0-35.3	32.2±2.1	18.2–38.2	26.0
B. Meristic counts and diagnostic features					
Dorsal fin rays	III+7			III-IV+7	
Anal fin rays	III-IV+5			IV+5	
Pelvic fin rays	II-6+7			II+6	
Pectoral fin rays	II+10-12			IV+11-12	
Lateral line scales	36-39 (37)			36-38	
Scale rows lateral line–dorsal fin	4-5.5			3.5-5.5	
Scale rows lateral line–pelvic fin	4-5			3.5-4.5	
Scale rows lateral line–anal fin	4-5.5			4	
Predorsal scales	0-8			0-4	
Chest scales	asquamate			asquamate	
Belly scales	asquamate			asquamate	
Postpelvic scales	0-4			0-2	
Disc type	C - B			C - (some type B)	
Position of the eye	middle - posterior			middle	
Rostral margin	invecked (partly smoothly invecked)			weakly invecked	
Tubercles on snout	Yes - No (small)			small (circular - tubular)	
Papillae on lower lip and disc periphery	present - abundant			present - abundant	

Table 15. Comparison of morphometric and meristic characteristics of *Garra* aff. *dembeensis* morphotype ‘a’ and *G. dembeensis* s. str. in the Awash river. Specimens where collected in November and December 2017 at S1 - S5. Fin rays (unbranched and branched) were counted using stereo microscopes and may vary with different methods. Morphotype ‘a’ occured upstream of the Koka reservoir, especially in the Chilimo forest.

A. Morphometric measures	*Garra* aff. *dembeensis* morphotype a (n=30)			*Garra dembeensis* s. str. (Awash river, n=30)	
	median	**range**	**mean ± SD**	**range**	**mean ± SD**
Standard length (SL) in mm	67.5	48.7-116.5	71.7±15.9	45.0-112.0	70.7±15.9
In percent (%) of standard length					
Body depth	19.8	16.3-24.0	19.6±1.8	15.2-23.5	20.2±1.7
Head length	23.7	22.1-25.3	23.8±0.8	22.3-25.6	23.8±0.9
Predorsal length	51.0	49.2-52.5	50.9±1.0	48.5-53.1	51.3±1.2
Caudal peduncle length	13.0	11.2-14.6	13.0±0.8	9.7-14.6	13.0±1.0
Caudal peduncle depth	11.6	10.0-12.8	11.6±0.8	9.9-13.3	11.6±0.8
Dorsal fin length	20.2	17.3-21.9	20.1±1.1	17.9-24.4	20.5±1.8
Anal fin length	16.4	13.9-18.4	16.5±1.0	14.3-19.8	17.0±1.6
Pelvic fin length	17.0	15.5-19.0	17.1±0.9	15.7-20.8	17.6±1.3
Pectoral fin length	20.4	16.9-22.1	20.4±1.1	18.5-24.2	20.8±1.4
In percent (%) of head length					
Head width	76.9	72.3-84.2	77.2±2.9	72.0-84.5	77.6±3.0
Head depth	57.0	54.0-74.6	57.9±3.6	49.8-63.6	58.1±5.5
Snout length	45.6	41.3-52.4	45.4±2.6	38.3-54.8	46.6±3.5
Orbit diameter	18.6	11.9-23.1	18.4±2.0	15.9-24.0	19.0±2.1
Interorbital width	43.9	40.0-50.0	44.0±2.3	41.5-49.0	45.0±2.2
In percent (%) of orbit diameter					
Rostral barbel length	56.6	37.5-69.0	56.3±7.8	34.5-65.5	50.1±9.1
Maxillary barbel length	50.0	30.0-83.3	53.4±10.1	33.3-70.0	46.6±9.8
In percent (%) of distance anal fin to pelvic fin insertion					
Vent distance	31.3	26.7-35.5	31.2±2.5	27.0-35.3	32.2±2.1
B. Meristic counts and diagnostic features					
Dorsal fin rays	III+7			III+7	
Anal fin rays	III-(IV)+5			III-IV+5	
Pelvic fin rays	II+6			II+6-7	
Pectoral fin rays	II+10-12			II+10-12	
Lateral line scales	37-40 (38)			36-39 (37)	
Scale rows lateral line–dorsal fin	5-6			4-5.5	
Scale rows lateral line–pelvic fin	4-5			4-5	
Scale rows lateral line–anal fin	4-5			4-5.5	
Predorsal scales	0-14			0-8	
Chest scales	0			asquamate	
Belly scales	0-6			asquamate	
Postpelvic scales	4-6			0-4	
Disc type	C-B			C-B	
Position of the eye	middle			middle - posterior	
Rostral margin	invecked			invecked (partly smoothly invecked)	
Tubercles on snout	Yes - No (small)			Yes - No (small)	
Papillae on lower lip and disc periphery	present - abundant			present - abundant	

Table 16. Comparison of morphometric and meristic characteristics of *Garra* aff. *makiensis* morphotype ‘a’ in the Awash river and the description of *G. makiensis* s. str. by Stiassny and Getahun (2007). Specimens where collected in November 2017 at S4 and S5. Fin rays (unbranched and branched) were counted using stereo microscopes and may vary with different methods. The morphotype occurs only in the gorge section downstream of Awash Kunture (S4 and S5).

A. Morphometric measures	*Garra* aff. *makiensis* morphotype a (n=30)			*Garra makiensis* s.str. (n=30)	
	median	**range**	**mean ± SD**	**range**	**mean ± SD**
Standard length (SL) in mm	85.1	45.5-125.3	85.7±18.0		
In percent (%) of standard length					
Body depth	18.7	15.2-22.3	18.7±1.6	17.5-27.8	21.7±2.11
Head length	23.2	20.8-24.4	22.9±1.1	19.5-26.9	22.6±1.46
Predorsal length	48.1	44.2-51.1	47.8±1.5	43.6-50.6	46.7±1.74
Caudal peduncle length	12.3	10.7-17.4	12.5±1.3	11.1-20.1	17.1±1.85
Caudal peduncle depth	10.7	9.1-11.9	10.7±0.8	7.7-13.1	10.9±1.04
Dorsal fin length	22.4	20.7-24.7	22.5±1.0	22.8-25.6	24.1±0.79
Anal fin length	18.3	16.0-20.1	18.0±1.1	15.9-19.7	17.5±0.91
Pelvic fin length	19.1	16.4-20.8	19.2±1.1	19.0-22.7	20.6±1.06
Pectoral fin length	21.5	19.5-23.3	21.5±1.1	15.3-24.3	20.2±1.91
In percent (%) of head length					
Head width	70.8	66.1-77.6	71.2±2.3	58.7-79.0	70.3±4.31
Head depth	57.8	53.9-67.4	58.2±2.8	54.0-70.0	62.1±4.17
Snout length	48.7	44.1-53.8	48.7±2.0	26.3-50.0	41.9±5.70
Orbit diameter	18.4	16.4-22.9	18.9±1.5	14.6-31.9	21.2±4.03
Interorbital width	44.0	40.0-48.1	44.2±2.3	33.7-50.0	44.1±3.64
In percent (%) of orbit diameter					
Rostral barbel length	77.9	56.4-97.5	78.8±10.3	38.0-100.0	69.1±18.21
Maxillary barbel length	36.1	12.8-55.0	36.5±9.5	35.9-91.0	65.2±17.97
In percent (%) of distance anal fin to pelvic fin insertion					
Vent distance	21.3	16.8-25.0	21.5±2.3	10.3–16.9	13.6
B. Meristic counts and diagnostic features					
Dorsal fin rays	IV+7			IV+7	
Anal fin rays	III+5			IV-4+5	
Pelvic fin rays	II+7			III+7	
Pectoral fin rays	II+10-12			IV+11	
Lateral line scales	36-38 (36)			35-37	
Scale rows lateral line–dorsal fin	4-4.5			3.5-4.5	
Scale rows lateral line–pelvic fin	3-4.5			3-4	
Scale rows lateral line–anal fin	3-4.5			3.5-4.5	
Predorsal scales	10-18			14-15	
Chest scales	asquamate			asquamate	
Belly scales	asquamate - scattered (deeply embedded)			few non-overlapping, deeply emdedded	
Postpelvic scales	scaled			scaled	
Disc type	C (very well developed)			C (fleshy and well developed)	
Position of the eye	posterior			middle - slightly posterior	
Rostral margin	invecked			invecked	
Tubercles on snout	Yes (large horny; with 2 prominent above rostral barbels)			variously sized tubercles in both sexes	
Papillae on lower lip and disc periphery	abundant			abundant	

Table 17. Comparison of morphometric and meristic characteristics of *Garra* aff. *makiensis* morphotype ‘b’ and *Garra* aff. *makiensis* morphotype ‘c’ in the Awash river. Specimens where collected in November and December 2017 at S1, S2 and S3. Fin rays (unbranched and branched) were counted using stereo microscopes and may vary with different methods. In most specimens only the lower belly seems to be scaled (scales are generaly small and deeply embedded in skin). The difference between *G*. aff. *makiensis* morphotype ‘c’ and *G. aethiopica* needs detailed clarification (see 4.4).

A. Morphometric measures	*Garra* aff. *makiensis* morphotype b (n=30)			*Garra* aff. *makiensis* morphotype c (n=30)		
	median	**range**	**mean ± SD**	**median**	**range**	**mean ± SD**
Standard length (SL) in mm	61.0	45.5-89.3	63.0±10.9	54.1	34.7-75.9	53.7±12.2
In percent (%) of standard length						
Body depth	23.5	19.8-25.0	23.2±1.4	23.7	20.9-25.8	23.6±1.4
Head length	23.1	21.5-24.3	23.0±0.8	22.9	21.6-24.7	23.1±0.8
Predorsal length	48.8	30.6-50.9	48.5±3.4	49.1	47.0-51.3	49.2±1.1
Caudal peduncle length	12.7	10.8-14.3	12.6±0.9	12.5	11.0-14.3	12.6±0.9
Caudal peduncle depth	12.4	11.4-13.2	12.4±0.4	12.8	11.3-14.1	12.8±0.6
Dorsal fin length	20.9	19.0-23.1	21.0±1.0	21.1	19.0-25.4	21.4±1.4
Anal fin length	16.4	14.9-17.5	16.2±0.6	16.2	14.4-17.5	16.2±0.9
Pelvic fin length	17.6	15.8-19.3	17.6±0.8	17.6	14.4-19.9	17.4±1.3
Pectoral fin length	20.9	18.1-22.8	20.9±1.0	20.6	17.3-22.5	20.1±1.3
In percent (%) of head length						
Head width	73.8	66.2-79.3	74.1±2.9	75.0	67.5-80.4	74.8±2.8
Head depth	64.2	57.8-67.6	63.9±2.5	67.0	62.1-71.1	66.7±2.4
Snout length	43.0	40.6-47.8	42.9±2.1	39.7	34.5-45.0	39.4±2.7
Orbit diameter	20.5	18.3-24.0	20.6±1.4	20.5	17.6-23.9	20.5±1.6
Interorbital width	45.7	42.9-48.2	45.7±1.6	46.5	43.2-50.0	46.5±1.8
In percent (%) of orbit diameter						
Rostral barbel length	69.6	50.0-91.7	67.1±10.2	73.1	52.6-93.5	72.7±12.1
Maxillary barbel length	40.8	30.0-60.6	39.0±8.5	49.1	33.3-76.9	50.9±10.2
In percent (%) of distance anal fin to pelvic fin insertion						
Vent distance	20.5	16.3-29.6	20.8±2.9	22.1	15.6-32.0	22.2±3.0
B. Meristic counts and diagnostic features						
Dorsal fin rays		III-IV+7			III+7	
Anal fin rays		III+5			III+5	
Pelvic fin rays		II+7			II+7	
Pectoral fin rays		II+10-12			II+10-12	
Lateral line scales		35-39 (36)			34-38 (36)	
Scale rows lateral line–dorsal fin		4-5.5			4-5	
Scale rows lateral line–pelvic fin		3.5-5.5			3.5-5	
Scale rows lateral line–anal fin		4-5			4-5	
Predorsal scales		12-18			14-18	
Chest scales		asquamate			asquamate-scattered	
Belly scales		scattered			scattered	
Postpelvic scales		scaled			scaled	
Disc type		C			C - B	
Position of the eye		middle			middle - anterior	
Rostral margin		smoothly - invecked			smoothly - invecked	
Tubercles on snout		Yes - No			Yes - No	
Papillae on lower lip and disc periphery		present - abundant			present-absent	

Table 18. Morphometric and meristic characteristics of *Garra* sp. morphotype ‘slender’ in the Awash river. Specimens where collected in November 2017 and January 2018 at S6 and S7. Fin rays (unbranched and branched) were counted using stereo microscopes and may vary with different methods. The morphotypes ‘large’ and ‘tubercles’ are not included here. Possible similarities with the holotype (*Discognathus makiensis* Boulenger 1903) need clarification.

A. Morphometric measures

Character	**N**	**range**	**median**	**mean ± SD**
Standard length (SL) in mm	30	49.5-117.4	73.2	76.3±18.6
In percent (%) of standard length				
Body depth	30	16.9-22.5	20.1	20.0±1.5
Head length	30	17.1-22.2	20.0	20.1±1.1
Predorsal length	30	39.6-46.3	44.0	43.9±1.3
Caudal peduncle length	30	14.3-18.8	16.9	16.6±1.1
Caudal peduncle depth	30	8.2-10.7	9.7	9.6±0.7
Dorsal fin length	30	23.9-28.2	25.9	26.2±1.2
Anal fin length	30	16.9-20.6	18.8	18.9±0.7
Pelvic fin length	30	18.1-22.1	19.9	20.0±1.0
Pectoral fin length	30	17.4-22.6	20.1	20.1±1.0
In percent (%) of head length				
Head width	30	65.1-77.1	68.6	69.3±2.6
Head depth	30	61.7-69.8	65.7	65.6±2.4
Snout length	30	36.4-45.7	41.1	41.2±2.7
Orbit diameter	30	20.1-26.4	23.5	23.5±1.6
Interorbital width	30	44.9-53.1	49.2	49.1±2.4
In percent (%) of orbit diameter				
Rostral barbel length	30	42.9-92.9	60.5	61.7±10.8
Maxillary barbel length	30	30.2-92.9	62.1	60.0±13.0
In percent (%) of distance anal fin to pelvic fin insertion				
Vent distance	30	11.0-19.6	14.9	15.2±1.7

B. Meristic counts

Character	**N**	**range**
Dorsal fin rays	30	III-IV+7
Anal fin rays	30	III-IV+5-6
Pelvic fin rays	30	II+7
Pectoral fin rays	30	I+12-14
Lateral line scales	30	37-40 (39)
Scale rows lateral line–dorsal fin	30	4-5
Scale rows lateral line–pelvic fin	30	3.5-4
Scale rows lateral line–anal fin	30	3.5-4
Predorsal scales	30	12-16
Chest scales	30	asquamate-scattered
Belly scales	30	scaled
Postpelvic scales	30	scaled

Disc type: C-B
Position of the eye: middle
Rostral margin: invecked
Tubercles on snout: Yes
Papillae on lower lip and disc periphery: present

8. APPENDIX 2

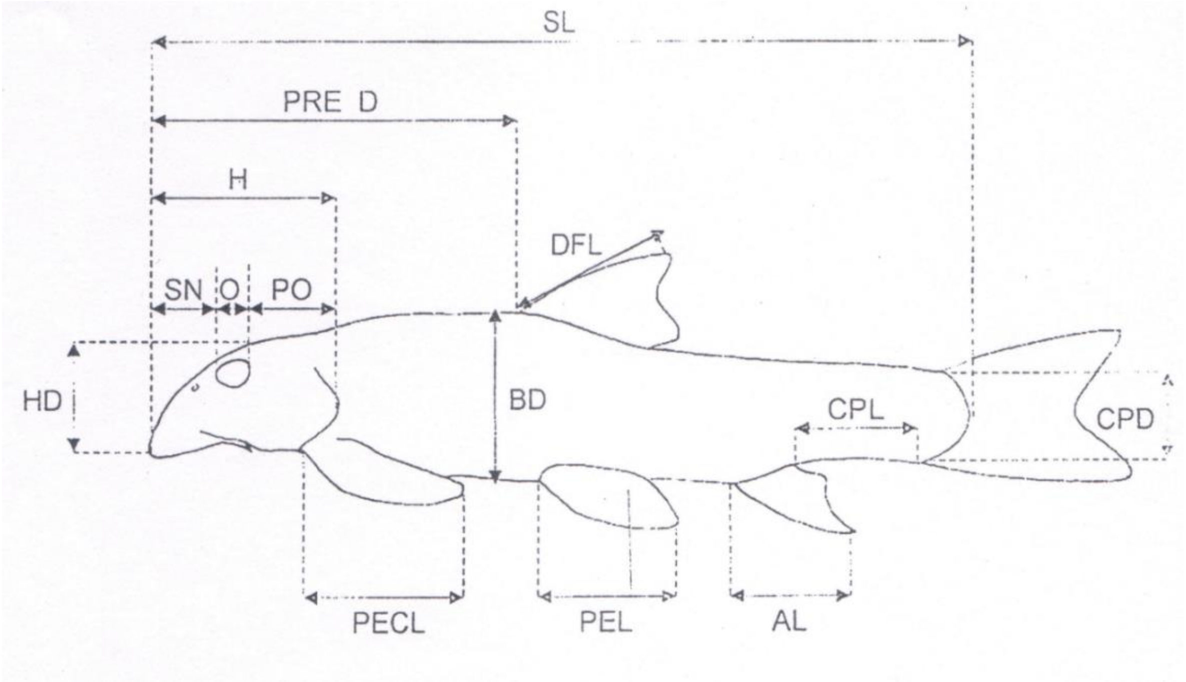


Figure 24. Morphometric measurements taken from each fish. SL = Standard length, PRE D = Predorsal length, H = Head length, SN = Snout length, O = Orbit diameter, PO = Postorbital length (not measured), DFL = Dorsal fin length, HD = Head depth, BD = Body depth, CPL = Caudal peduncle length, CPD = Caudal peduncle depth (measured at the narrowest part), PECL = Pectoral fin length, PEL = Pelvic fin length, AL = Anal fin length. Image and abbreviations according to Getahun (2000).

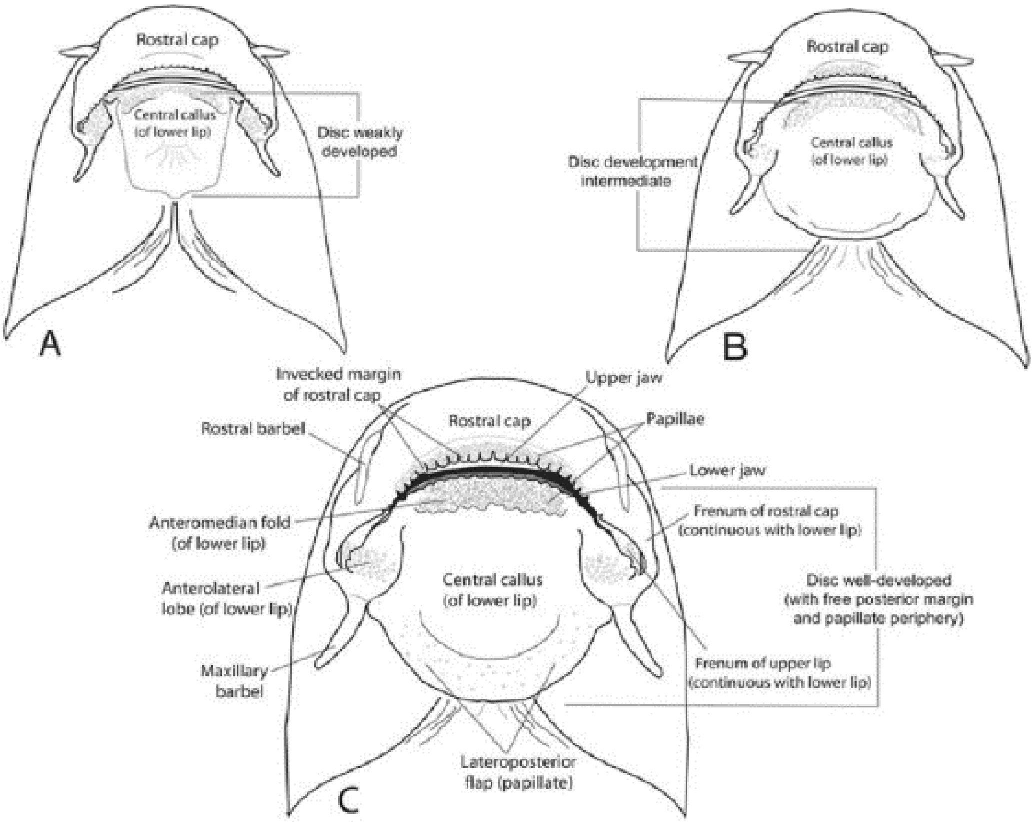


Figure 25. Range of variation in disc types among African *Garra* sp.: (A) type-A disc, weakly developed; (B) type-B disc, intermediate development; (C) type-C disc, well-developed. Source: Stiassny and Getahun (2007).

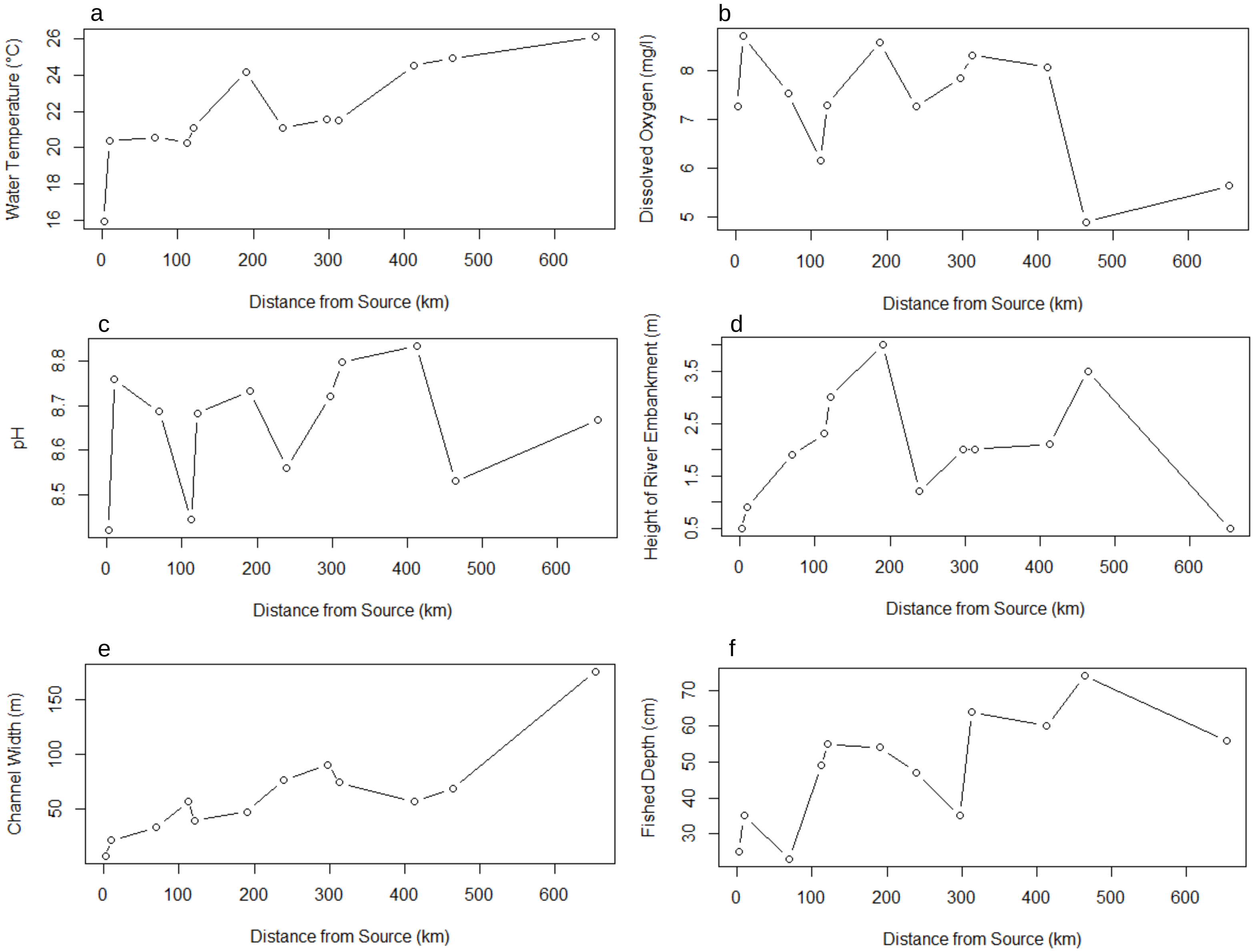


Figure 26. (a) Scatterplot of change in water temperature (ºC) with increasing distance from source (km). Note the temperature decrease after 200 km. (b) Scatterplot of variation in dissolved oxygen concentration (mg L^{-1}) with increasing distance from source (km). Note the low oxygen concentration at site 11. (c) Scatterplot of pH values with distance from source (km). (d) Scatterplot of observed average heights of river embankment (m) along the longitudinal course (km). Site 6 and 11 show the highest values. (e) Scatterplot of the variation in average active channel width (m) from the headwaters to the lowland reaches. (f) Scatterplot of average fished depth along the river course (km). Each point represents a sampling site along the longitudinal gradient.

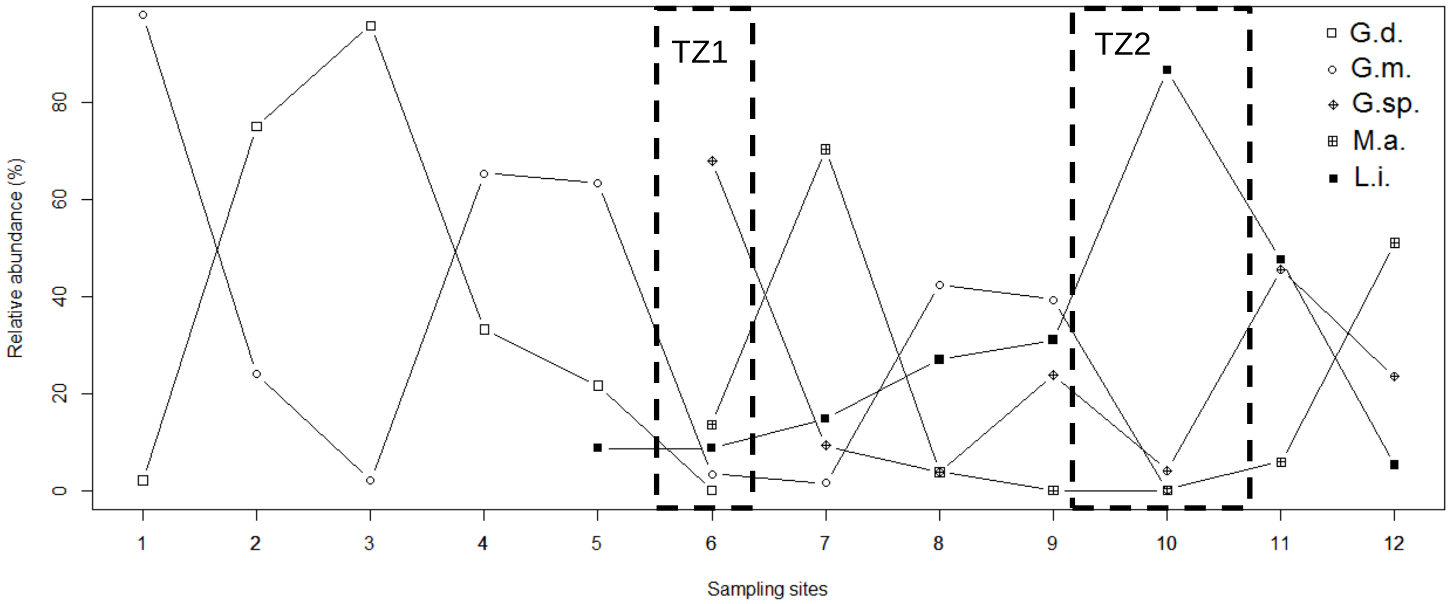
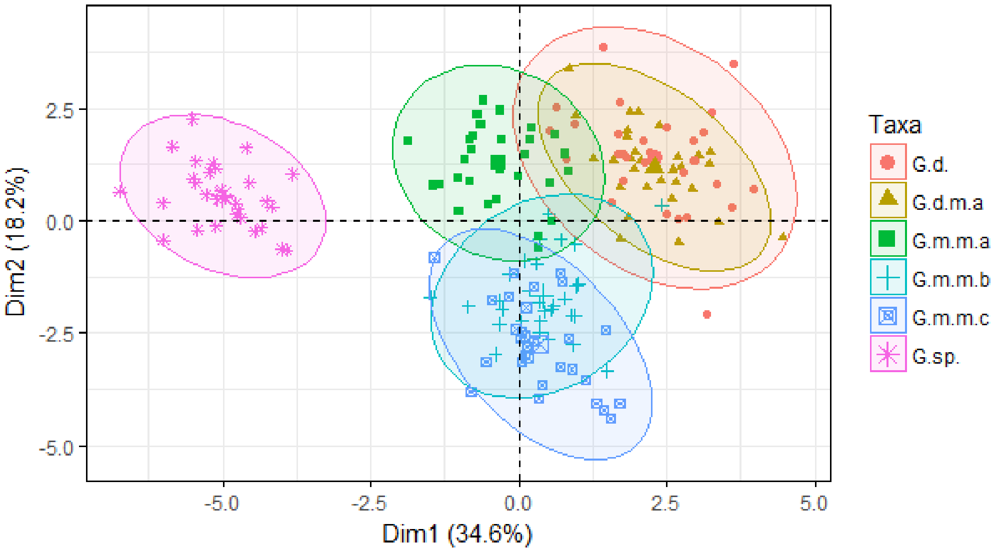
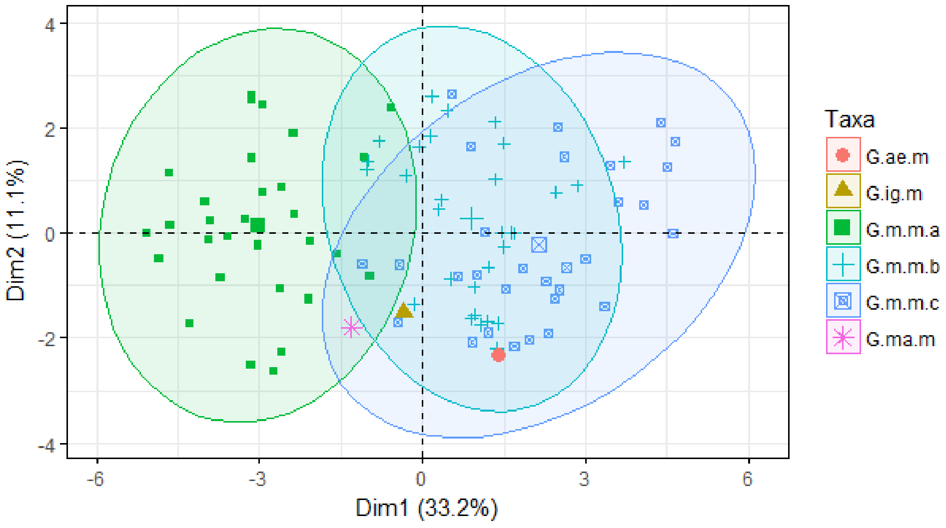


Figure 27. Diagram of the 5 most abundant (rel. abundance) taxa and their distribution along the river course (sampling sites). Two possible transition zones are depicted, based on a clear change of fish communities. G.d. (*Garra dembeensis*, morph. types included), G.m. (*G.* aff. *makiensis*, morph. types included), G. sp. (*G.* sp. – morph. types included), M.a. (*Micropanchax* cf. *antinorii*), L.i. (*Labeobarbus* cf. *intermedius*).



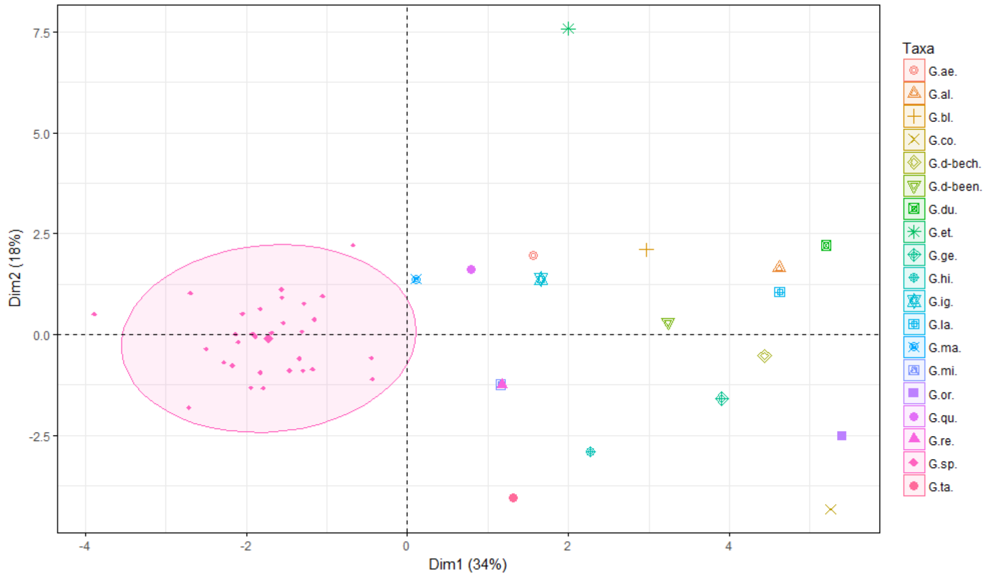
variables	**PC1**
head length	0.82
predorsal length	0.83
dorsal fin length	-0.83
pelvic fin length	-0.70
variables	**PC2**
snout length	0.60
lateral line scales	0.53
body depth	-0.83
head depth	-0.73

Figure 28. Principal Component Analysis (based on morphometric and meristic features) for all morphotypes (*Garra* sp. morph. 'large' and 'tubercles' not included). The 2 axis account for 53% of the variation. A 95% confidence ellipsoid is depicted around each taxon. Principal Components (PC) were correlated with original variables (important correlation coefficients are depicted on the right side). Highest correlation with PC1 (Dim1) was observed for head length and predorsal length (separating morphotypes of *G.* aff. *makiensis* and *G.* aff. *dembeensis* from *G.* sp.). Along the second dimension, the highest correlation with PC2 (Dim2) was observed for snout length (separating *G.* aff. *makiensis* morph 'a'). Abbreviations: G.d. (*G. dembeensis*), G.d.m.a (*G.* aff. *dembeensis* morph. 'a'), G.m.m.a (*G.* aff. *makiensis* morph. 'a'), G.m.m.b (*G.* aff. *makiensis* morph. 'b'), G.m.m.c (*G.* aff. *makiensis* morph. 'c'), G.sp. (*G.* sp).



variables	PC1
head depth	0.89
body depth	0.85
snout length	-0.85
pelvic fin length	-0.80
variables	**PC2**
head length	0.74
predorsal length	0.33
rostral barbel length	-0.64
maxillary barbel length	-0.58

Figure 29. Principal Component Analysis (based on morphometric and meristic features) for morphotypes of *Garra* aff. *makiensis*. Literature data according to Stiassny and Getahun (2007). The 2 axis account for 44.3% of the variation. A 95% confidence ellipsoid is depicted around each taxon. Principal Components (PC) were correlated with original variables (important correlation coefficients are depicted on the right side). Head depth, body depth and snout length show the highest correlation with PC1 (Dim1) (visible separation of morph. ‘a’). Mean values of *G. aethiopica*, *G. makiensis* and *G. ignestii* are depicted. Abbreviations: G.m.m.a (*G.* aff. *makiensis* morph. a), G.m.m.b (*G.* aff. *makiensis* morph. b), G.m.m.c (*G.* aff. *makiensis* morph. c), G.ae.m. (*G. aethiopica* mean based on literature), G.ig.m. (*G. ignestii* mean based on literature), G.ma.m. (*G. makiensis* mean based on literature).



variables	PC1
head length	0.88
predorsal length	0.81
dorsal fin length	-0.83
interorbital width	-0.82
variables	**PC2**
body depth	0.86
caudal peduncle depth	0.68
lateral line scales	-0.70
caudal peduncle length	-0.44

Figure 30. Principal Component Analysis (based on morphometric and meristic features) for *Garra* sp. morph. ‘slender’ and mean values of all African taxa (except *G. chebera*). Data according to Getahun (2000) and Stiassny and Getahun (2007). The 2 axis account for 52% of the variation. Principal Components (PC) were correlated with original variables (important correlation coefficients are depicted below). Dorsal fin length and interorbital width separate *G.* sp. from other African congeners along PC1. Abbreviations: G.ae. (*G. aethiopica*), G.al. (*G. allostoma*), G.bl. (*G. blanfordii*), G.co. (*G congoensis*), G.d-bech. (*G. dembecha*), G.d-been. (*G. dembeensis*), G.du. (*G. duobarbis*), G.et. (*G. ethelwynnae*), G.ge. (*G. geba*), G.hi. (*G. hindii*), G.ig. (*G. ignestii*), G.la. (*G. lancrenonensis*), G.ma. (*G. makiensis*), G.mi. (*G. microstoma* – a synonym of *G. regressus*), G.or. (*G. ornata*), G.qu. (*G. quadrimaculata*), G.re. (*G. regressus*), G.ta. (*G. tana*).

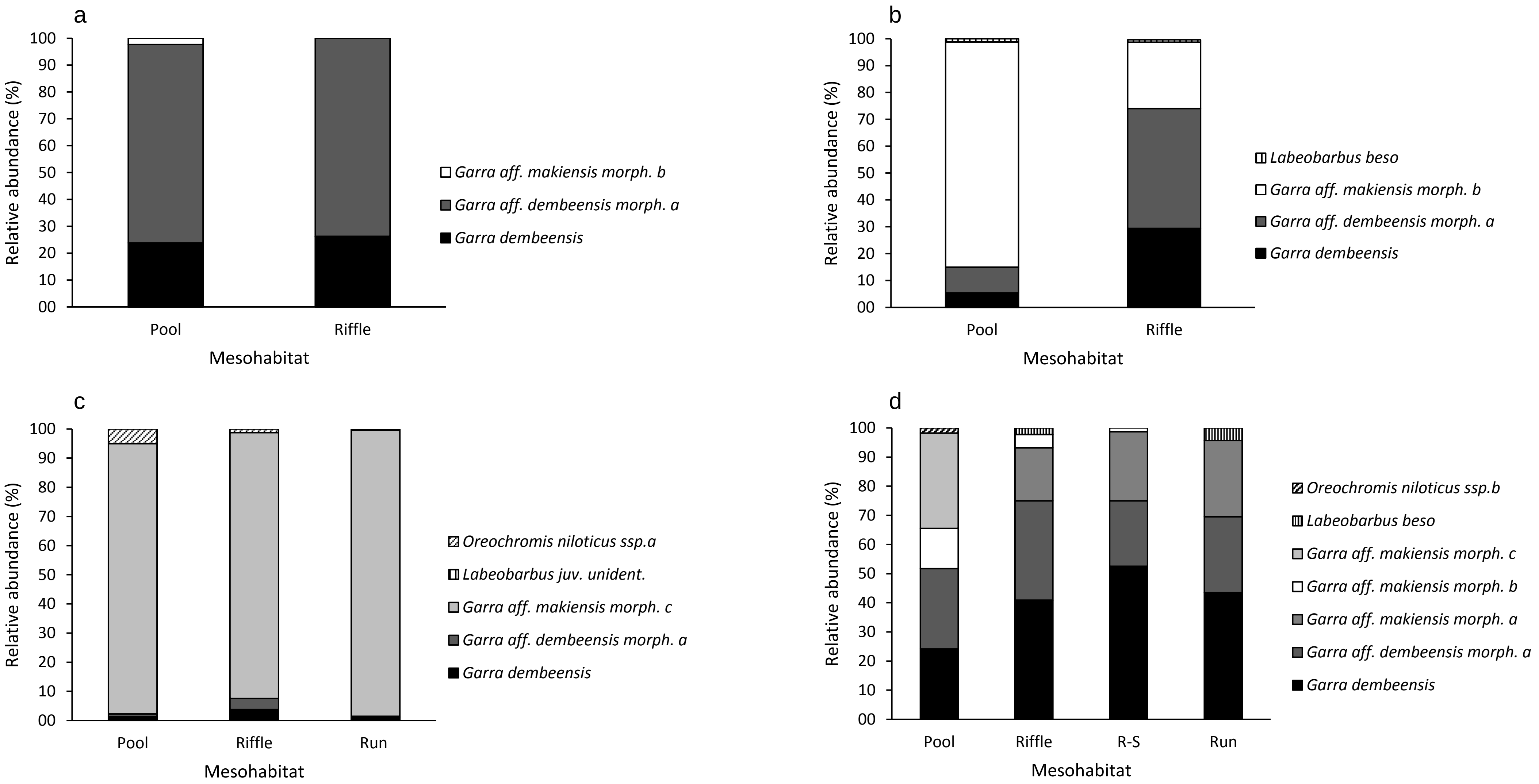


Figure 31. (a)-(d) relative abundance per taxon and mesohabitat. Note that the number of habitats also represents the availability of habitat structures at the sites. (a) S1, (b) S2, (c) S3, (d) S4. R-S = riffle + shoreline.

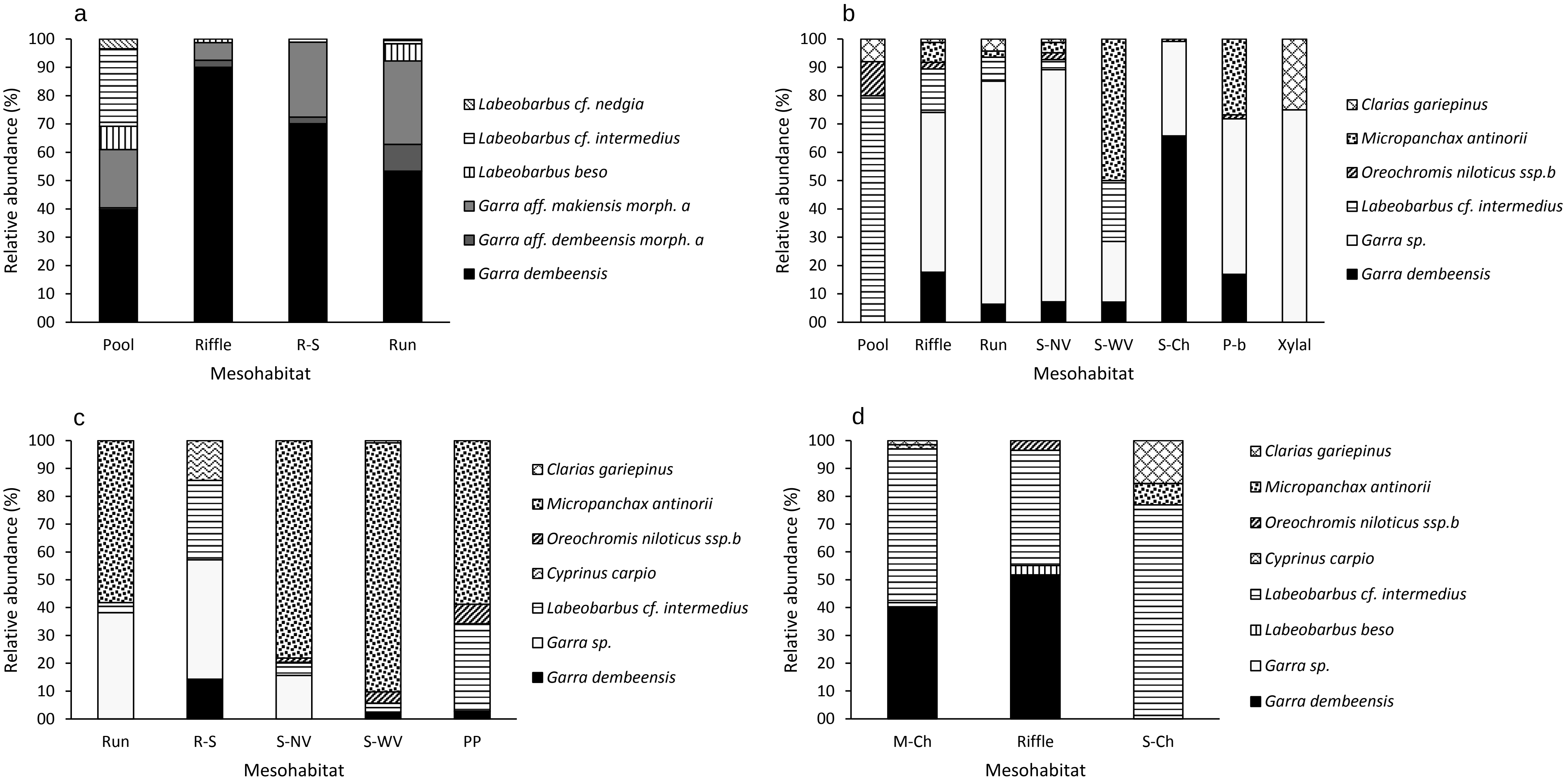


Figure 32. (a)-(d) relative abundance per taxon and mesohabitat. Note that the number of habitats also represents the availability of habitat structures at the sites. (a) S5, (b) S6, (c) S7, (d) S8. R-S = riffle + shoreline, S-NV = shoreline + no vegetation, S-WV = shoreline + with vegetation, S-Ch = side channel, P-b = point bar (shoreline + sand), PP = parapotamon, M-Ch = main channel.

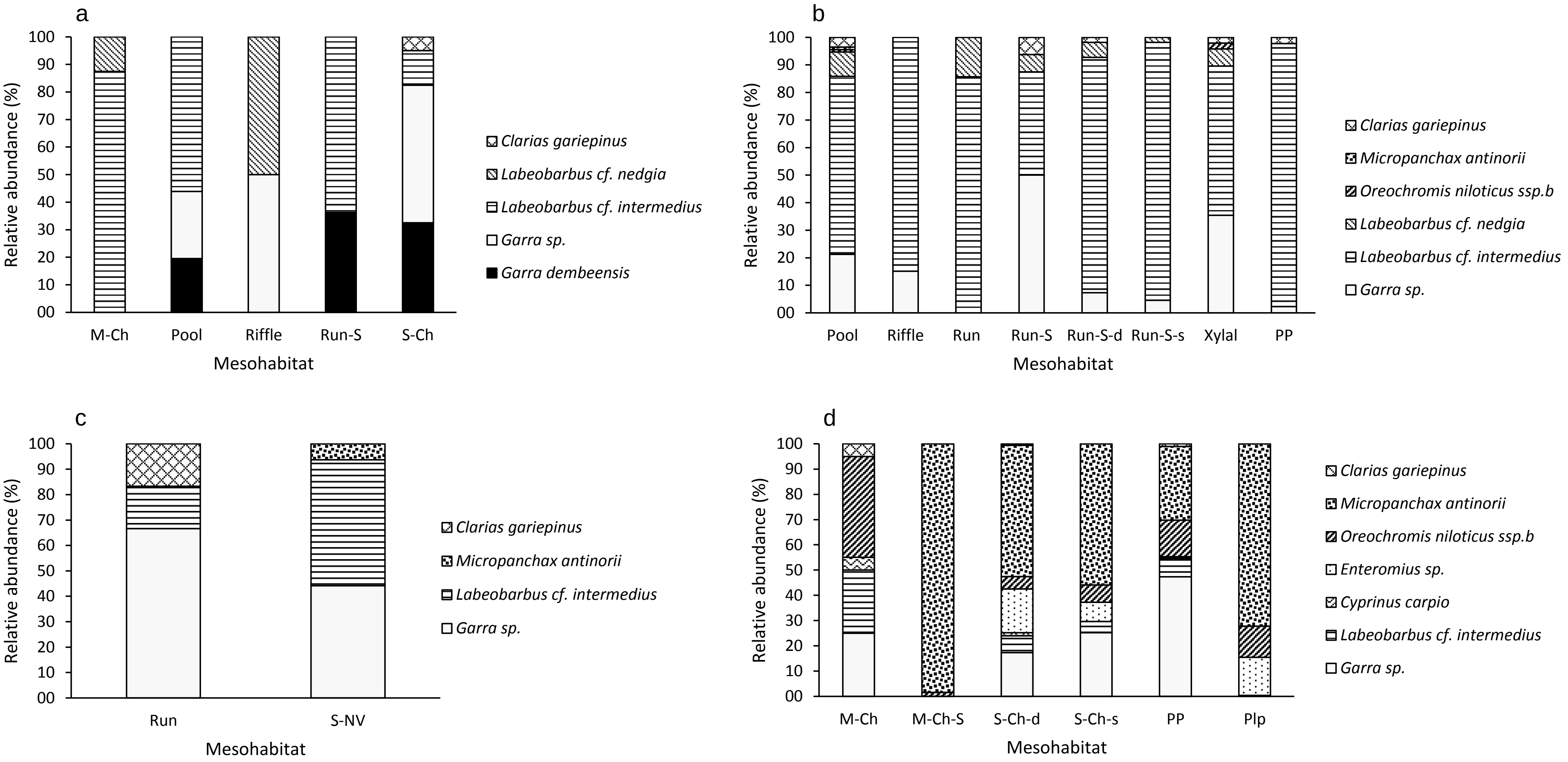


Figure 33. (a)-(d) relative abundance per taxon and mesohabitat. Note that the number of habitats also represents the availability of habitat structures at the sites. (a) S9, (b) S10, (c) S11, (d) S12. M-Ch = main channel, Run-S = run + shoreline, S-Ch = side channel, Run-S-d = run + shoreline deep, Run-S-s = run + shoreline shallow, PP = parapotamon, S-NV = shoreline + no vegetation, M-Ch-S = main channel shoreline, Plp = plesiopotamon.

Garra dembeensis s. str.

Figure 34. *Garra dembeensis* from the source region of the Awash river, note the red spot in the upper corner of the gill cover. Image by Wolfram Graf (05.11.2017).

Figure 35. (a)-(f) *Garra dembeensis* s. str. from the source region of the Awash river (S1, Pool, 04.12.2017, 59.68 mm SL). Note that the small red spot in the upper corner of the gill cover (Figure 34) vanished after preservation in 96% ethanol (a and b).

Garra aff. *dembeensis*

Figure 36. (a)-(f) *Garra* aff. *dembeensis* from the source region of the Awash river (S1, Pool, 04.12.2017, 71.20 mm SL). Note the phenotypical differences compared to Figure 35 and Figures 37 and 38. Especially the cheeks are markedly increased (different feeding habit?). The relatively small disc (type B often even clearly reduced) is a common characteristic of many specimens. This might cause a possible confusion with *G. dembecha*! – which, according to present knowledge, does not occur in the Awash river. The black spots on ventral side and fins are most likely caused by *Neascus* sp. (“Black spot disease”). Only few individuals seem to be infected in the upper reaches of the Awash. Note that sexual dimorphosm is not yet confirmed for the genus *Garra* (Stiassny and Getahun, 2007) and not discussed in the present thesis.

***Garra dembeensis* s. str.**

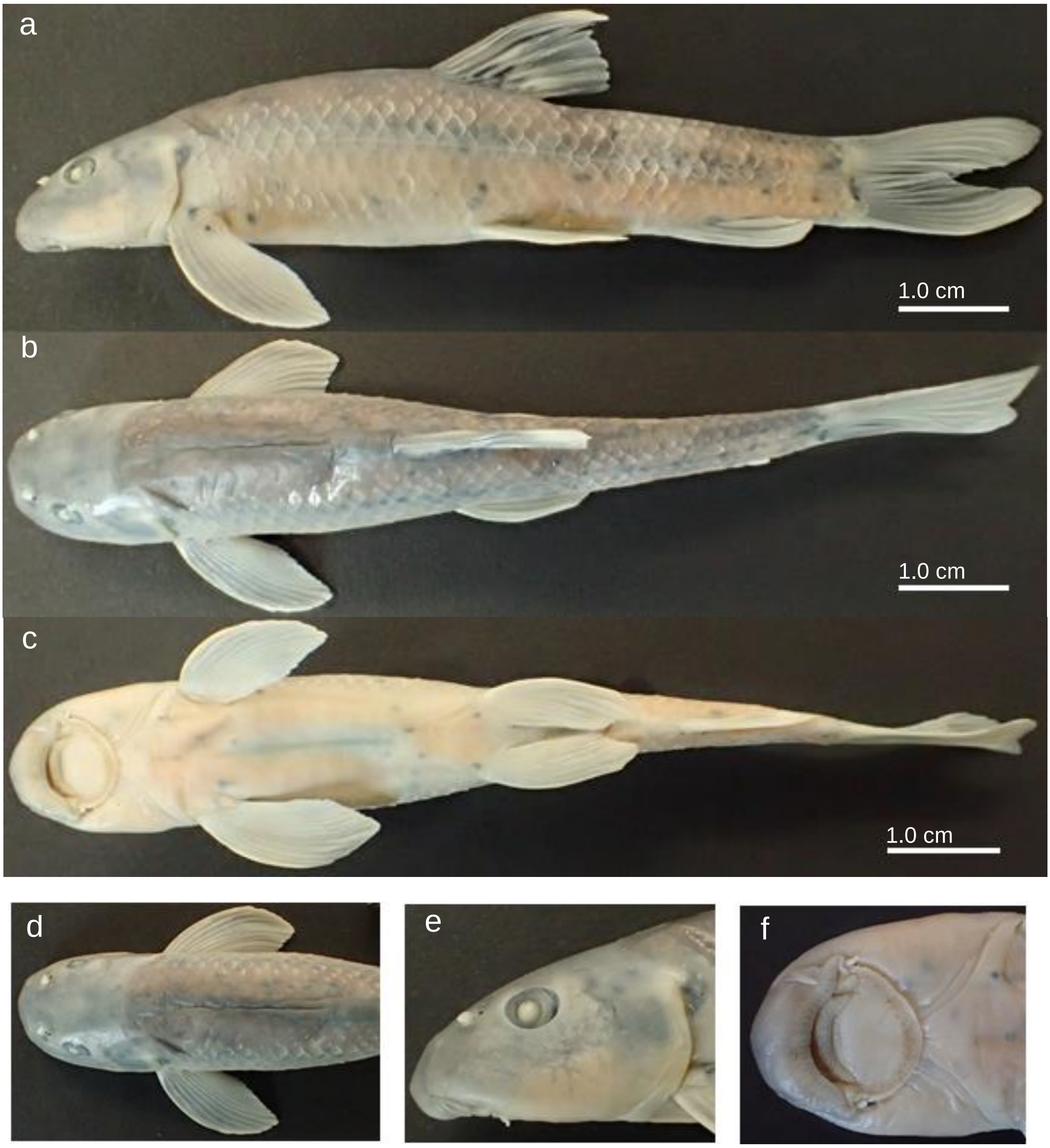


Figure 37. (a)-(f) *Garra dembeensis* s. str. from the upper Awash river (S5, Run, 07.11.2017, 76.49 mm SL). Note the phenotypical differences to Figure 35 and Figure 38. Especially the relatively flat ventral side and the well-developed disc (type C) with abundant papillae (also on ventral side of rostral cap) are striking. The black spots on ventral and lateral side are most likely caused by *Neascus* sp. ("Black spot disease"). Most specimens of *G. dembeensis* s. str. sampled from S5 showed signs of this infection.

Garra dembeensis **s. str.**

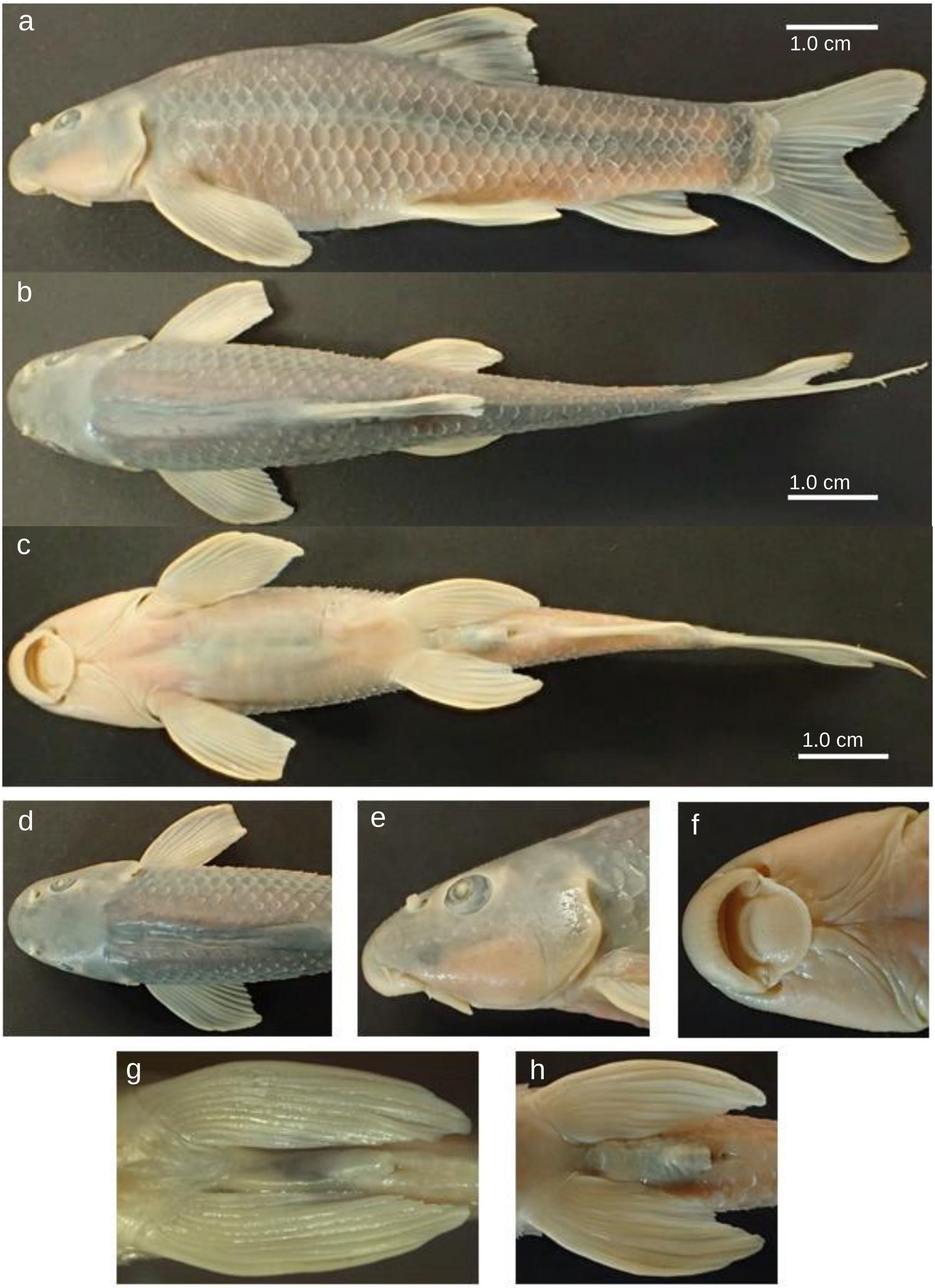


Figure 38. (a)-(h) *Garra dembeensis* s. str. from downstream of Lake Koka (S8, Riffle in main channel, 09.12.2017, 81.13 mm SL, DNA sample: AET 010– clip from right pectoral fin). Note the well-rounded disc (small type C) and the asquamate (occasionally with few – max. 4 – scales) postpelvic region. Note that sexual dimorphosm is not yet confirmed for the genus *Garra* (Stiassny and Getahun, 2007) and not discussed in the present thesis.

***Garra* aff. *dembeensis* morphotype ‘a’**

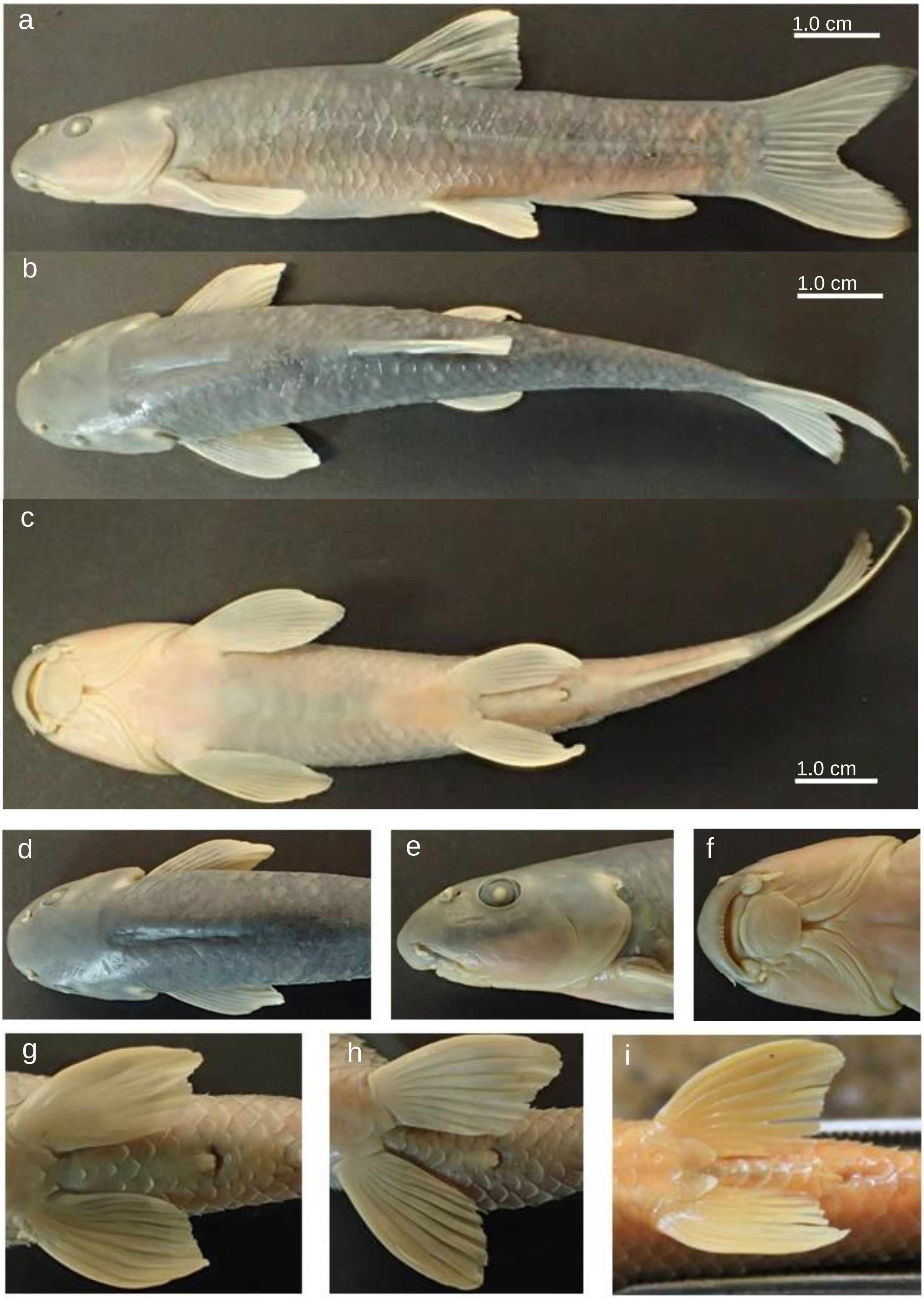


Figure 39. (a)-(h) *Garra* aff. *dembeensis* morph. ‘a’ from the source region of the Awash river (S1, Pool, 04.12.2017, 88.88 mm SL). Note the small disc (type B, nearly reduced to type A?). The postpelvic region is clearly scaled! (i) postpelfic region of *Garra dembeensis* s. str. observed in the National Museum of Kenya (Ichthyological section).

***Garra* aff. *makiensis* morphotype ‘a’**

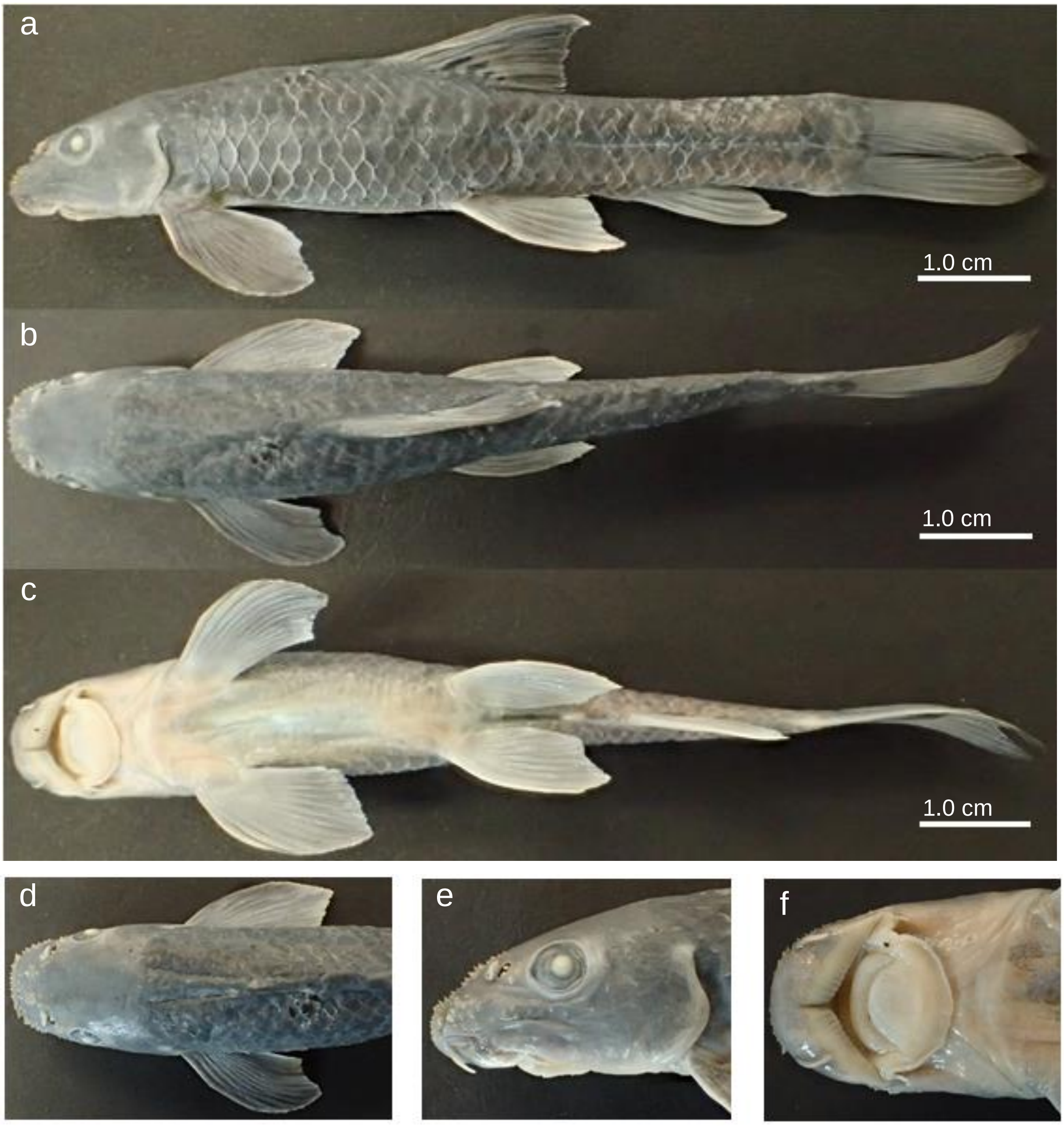


Figure 40. (a)-(f) *Garra* aff. *makiensis* morph. ‘a’ from the gorge section at Sulula (S5, Riffle, 07.11.2017, 79.20 mm SL). Note the large horny tubercles in front of and between the nostrils (see Figure 47). Pectoral fins are well developed. The disc is large (type C) with abundant papillae – observation in higher flow velocity habitats (see 4.4). The rostral fold is clearly invecked. Maxillary barbels in most specimens very short. Figure 47 shows the snout region in greater detail.

Garra aff. *makiensis* morphotype ‘b’

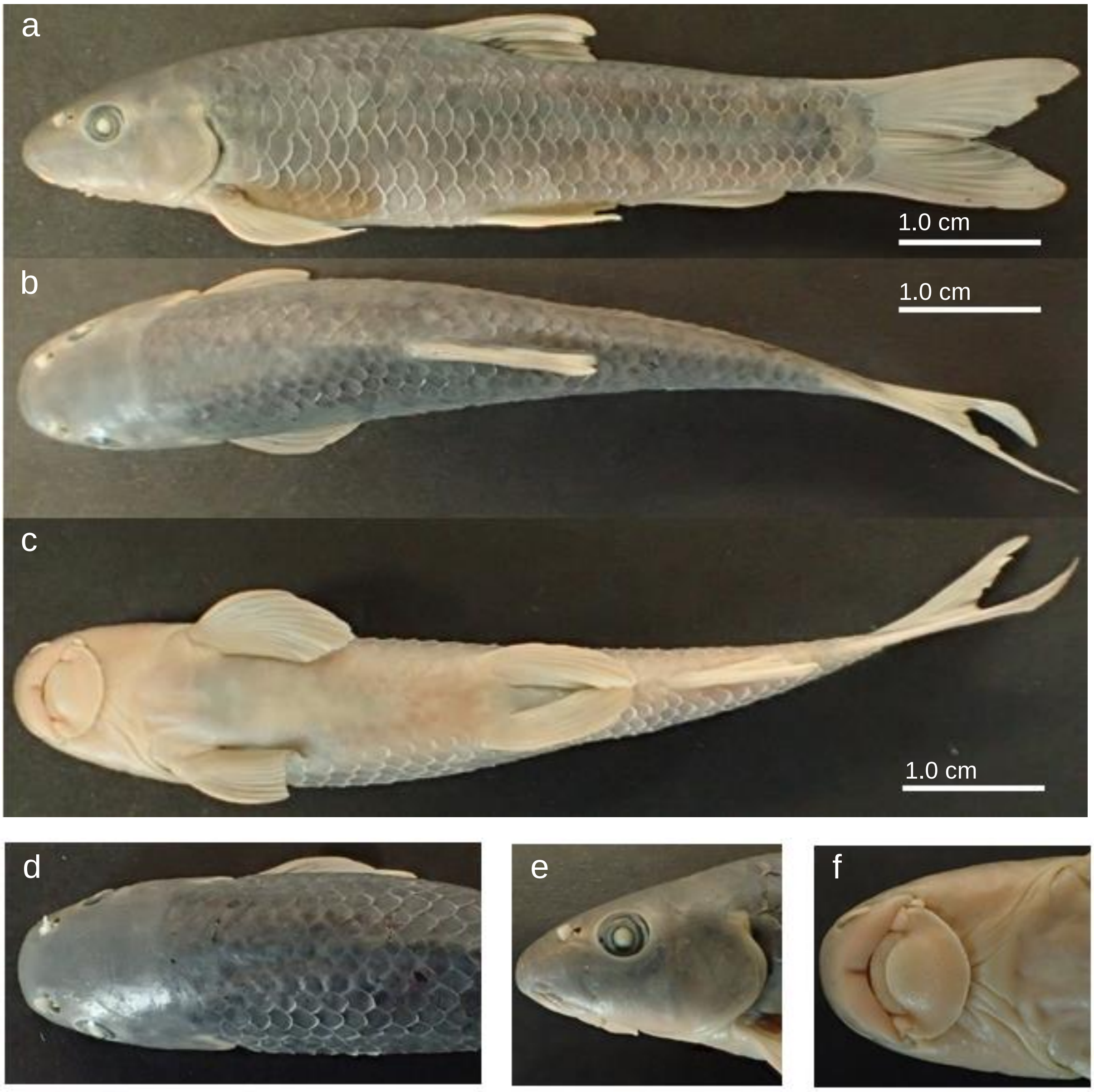


Figure 41. (a)-(f) *Garra* aff. *makiensis* morph. ‘b’ from the headwaters of the Awash river (S1, Pool, 04.12.2017, 59.43 mm SL, DNA analysis: AET033– clip from right pectoral fin). Note the relatively dark colouration of the lateral side. Small tubercles in front of nostrils (see Figure 47). Disc well developed (type C, occasionally type B), rostral margin smoothly-invecked. Figure 47 shows the snout region in greater detail.

Garra aff. *makiensis* morphotype ‘c’

Figure 42. (a)-(f) *Garra* aff. *makiensis* morph. ‘c’ from the upper Awash river (S3, Run, 17.11.2017, 52.13 mm SL). Note the relatively light colouration and the short and blunt snout. In most specimens, disc rather reduced to a type B. Few large individuals with well-developed type C disc. Papillation reduced in type B and abundant in type C. Scales on chest and belly usually difficult to see (deeply embedded in skin). Figure 47 shows the snout region in greater detail. The difference between *G*. aff. *makiensis* morph. ‘c’ and *G. aethiopica* needs detailed clarification (see 4.4).

Garra sp. morphotype 'slender'

Figure 43. *Garra* sp. from the second low gradient section at Lafessa (S6). Note the long dorsal and caudal fins as well as the large eye. Image by Wolfram Graf (09.11.2017).

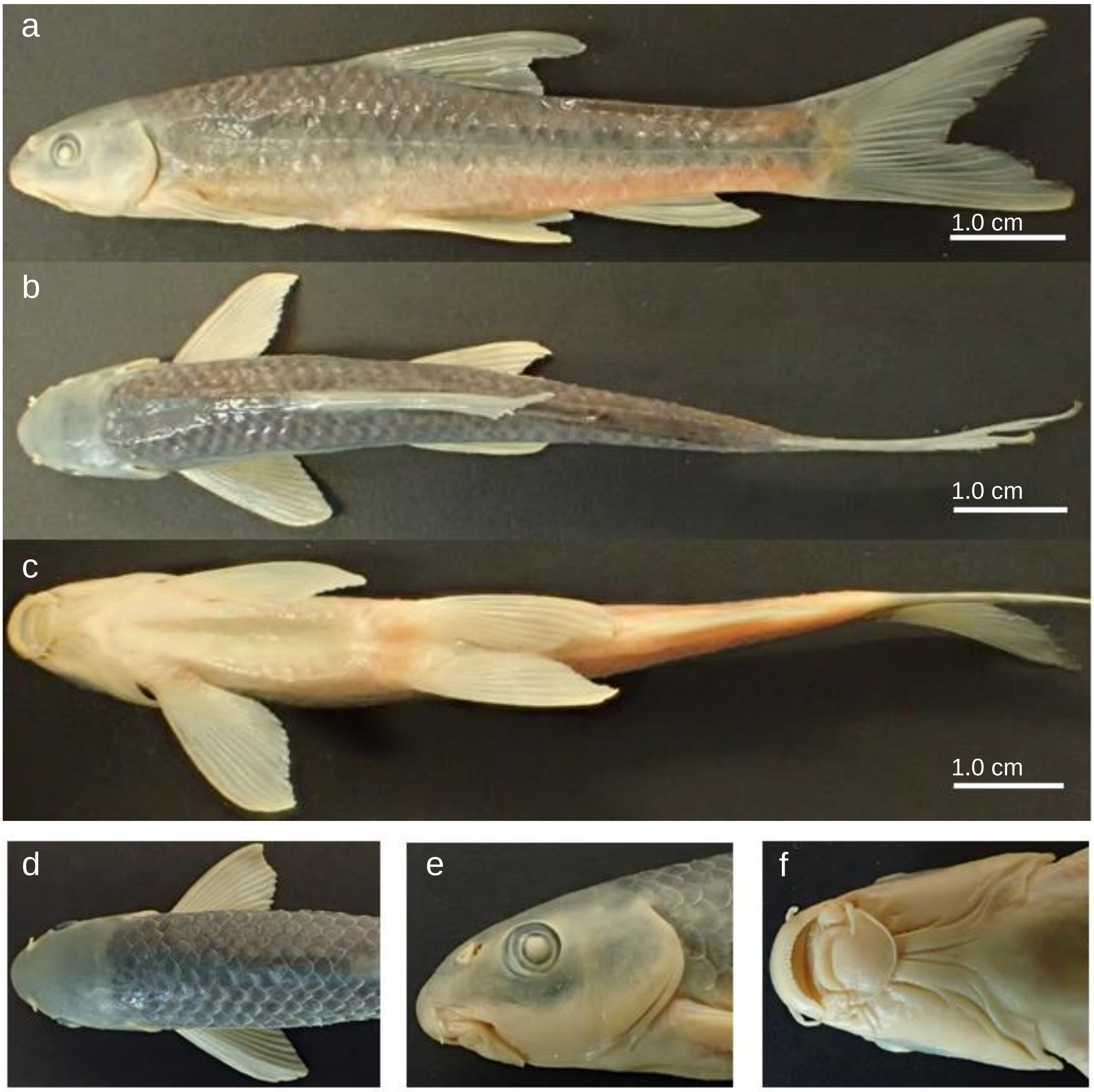


Figure 44. (a)-(f) *Garra* sp. morph. 'slender' from upstream of the Koka reservoir at Lafessa (S6, Run, 08.12.2017, 74.96 mm SL). The slender body shape and the relatively short head and snout are conspicuous characteristics. The mouth is rather small with a well- to intermediate developed disc (type B – C). Small tubercles in front of nostrils are present. Figure 48 shows the snout region in greater detail.

Garra sp. morphotype ‘tubercles’

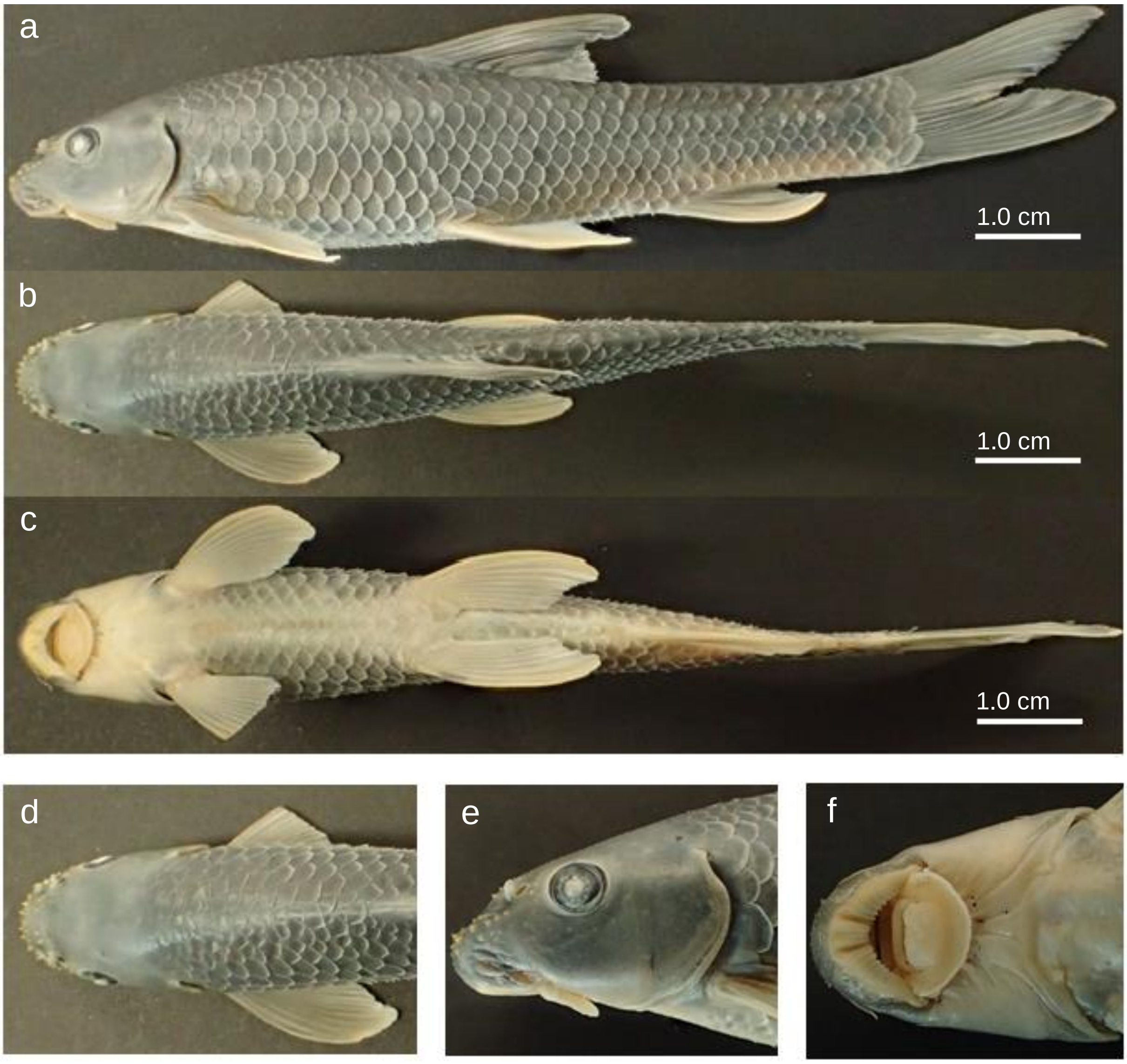


Figure 45. (a)-(f) *Garra* sp. morph. ‘tubercles’ from the gorge section at Yimre (S10, Sz4, 30.01.2018, 88.20 mm SL, DNA analysis: AET174– clip from right pectoral fin). The morphotype is not closer described here. However, the large tubercles and the well-developed rostral fold (with clearly invecked ventral margin) should be highlighted. The disc is well developed (large type C) and studded with abundant papillae – observation in higher flow velocity habitats (see 4.4). Belly completely scaled (scales large and not deeply embedded), chest with few small scales or asquamate. Pectoral fin with 1 prominent anterior unbranched ray. Figure 48 shows the snout region in greater detail. Note that sexual dimorphosm is not yet confirmed for the genus *Garra* (Stiassny and Getahun, 2007) and not discussed in the present thesis.

Garra sp. morphotype ‘large’

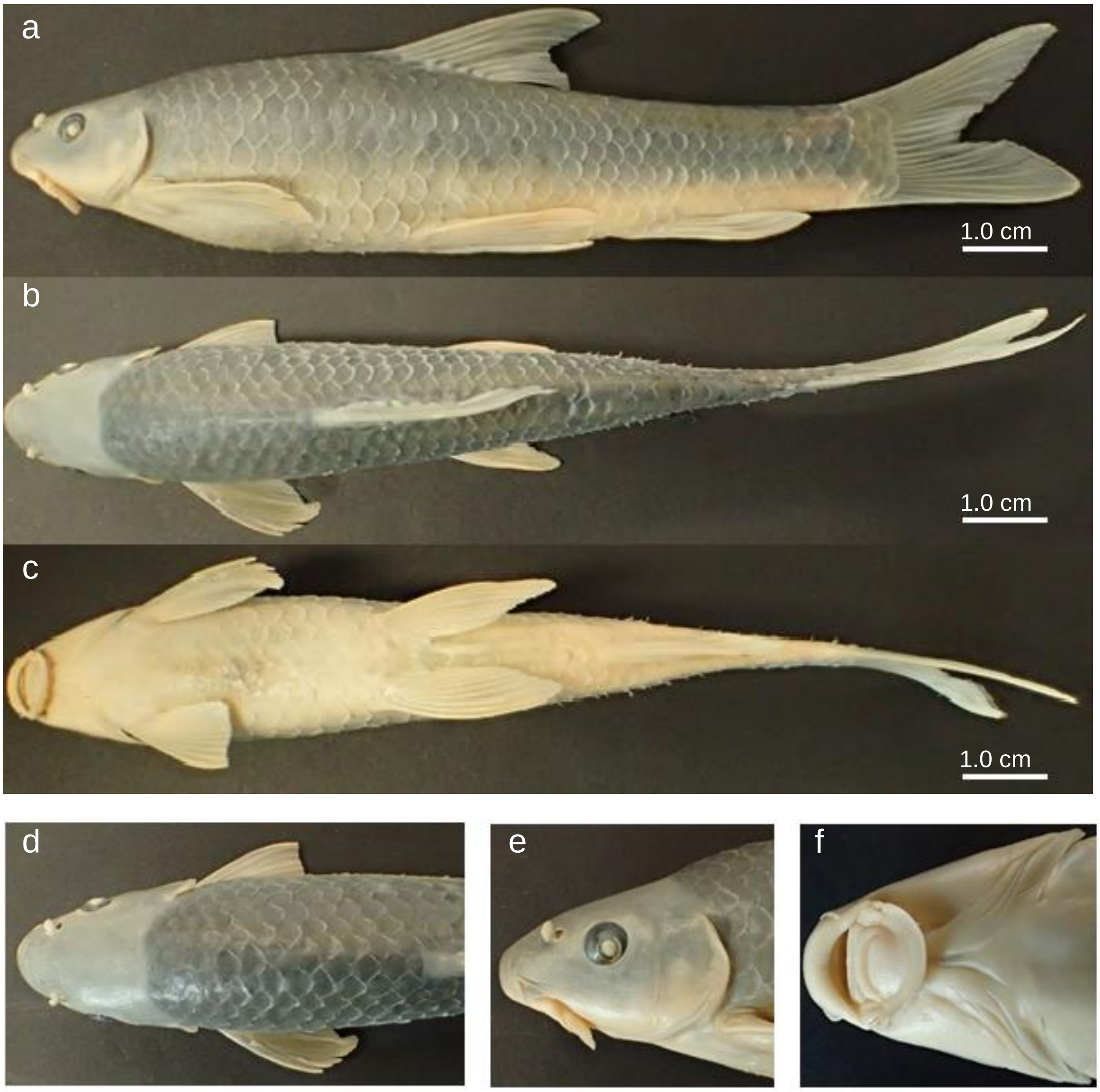


Figure 46. (a)-(f) *Garra* sp. morph. ‘large’ from the gorge section at Yimre (S10, Sz5, 30.01.2018, 118.46 mm SL, DNA analysis: AET178 – clip from right pectoral fin). The morphotype is not closer described here. However, specimens caught at S9 and S10 were exceptionally large (> 100 mm) and robust. A slight nuchal hump can be observed (e). Disc well developed and studded with abundant papillae. Margin of rostral fold smoothly-invecked. Belly completely scaled. Pectoral fin with 1 prominent anterior unbranched ray. Figure 48 shows the snout region in greater detail. Note that sexual dimorphosm is not yet confirmed for the genus *Garra* (Stiassny and Getahun, 2007) and not discussed in the present thesis.

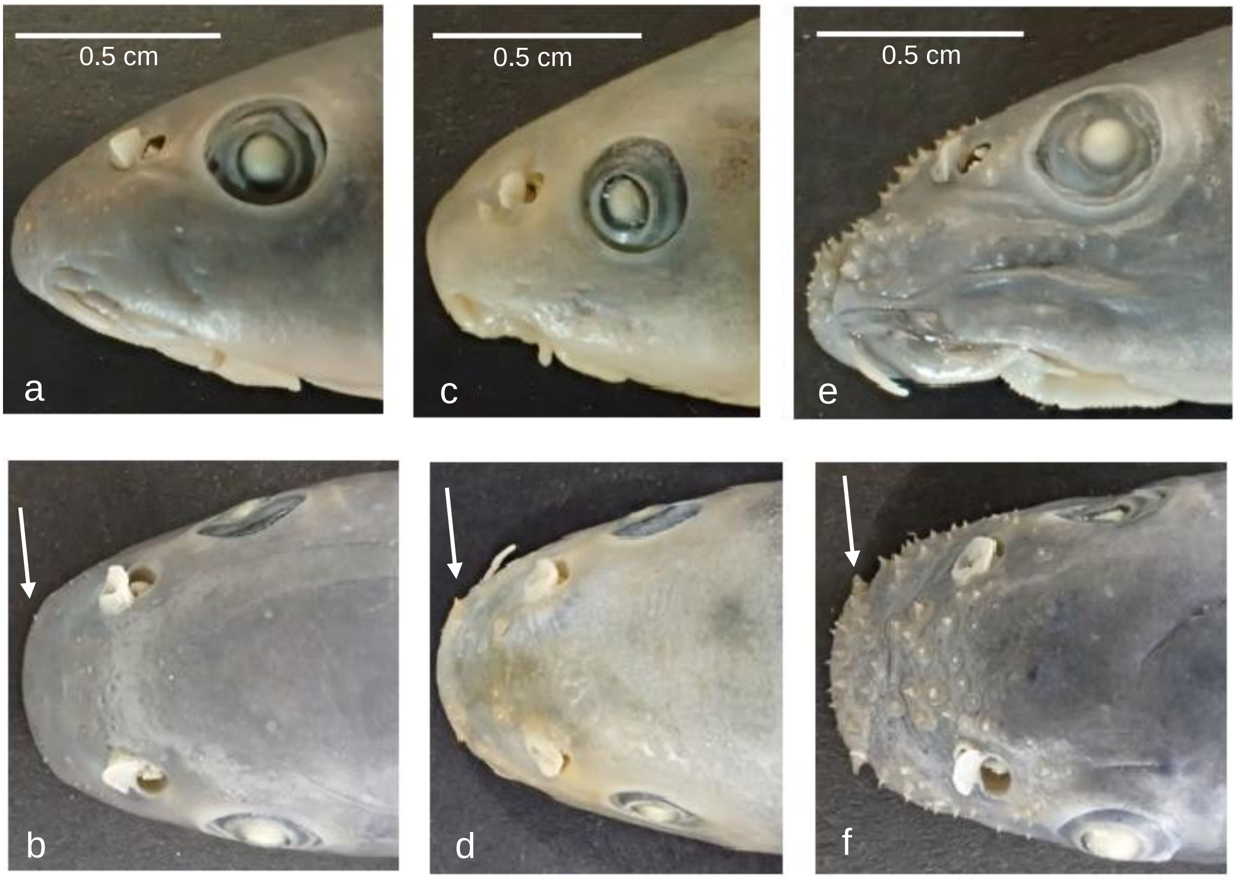


Figure 47. (a)-(f) *Garra* aff. *makiensis*, dorsal and lateral view of head and snout region. (a) and (b) *Garra* aff. *makiensis* morphotype ‘b’ with few relatively small tubercles in front of nostrils. Not all are smooth, some are relatively rigid. Note (in dorsal view) the small sharp tubercles at the tip of the snout below the nostrils (one at each side). (c) and (d) *Garra* aff. *makiensis* morphotype ‘c’, abundant in the first low gradient section (S3). Most specimens without any tubercles, some (rather large individuals) with few roundish and horny tubercles in front of nostrils. Like in b (dorsal view), note the 2 larger prominent tubercles pointing sideward at the tip of the snout. (e) and (f) *Garra* aff. *makiensis* morphotype ‘a’, specimens only captured from site 4 (few) and site 5. Rostral fold well developed, snout studded with large horny tubercles (breeding tubercles?). On tip of snout 2 very prominent tubercles pointing sideward (dorsal view). Tubercles only on snout, not reaching to the occiput. The different mouth position is an interesting feature (see also Figure 48) an may relate to different feeding habits (niches). Note that sexual dimorphosm is not yet confirmed for the genus *Garra* (Stiassny and Getahun, 2007) and not discussed in the present thesis.

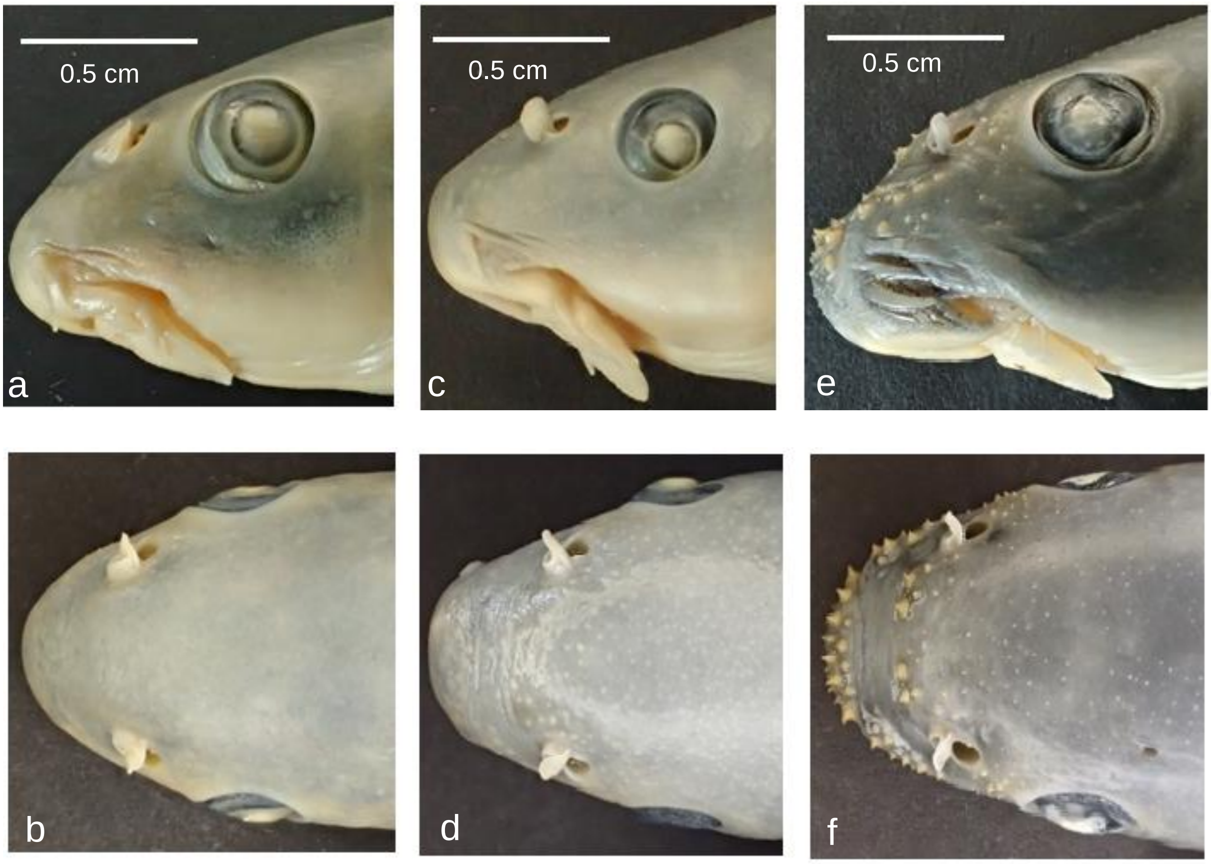


Figure 48. (a)-(f) *Garra* sp., dorsal and lateral view of head and snout region. (a) and (b) usual phenotypical appearance: ‘slender’. Small roundish and relatively flat tubercles in front and between nostrils. Note the large eye and the pointed snout region (dorsal view). (c) and (d) the ‘large’ morphotype. Specimens were captured from site 9 and 10. Tubercles in front and between nostrils like in a and b, but between eyes and along entire occiput covered with abundant small tubercles. Note the short and blunt snout (lateral view). (e) and (f) morphotype with abundant tubercles. Specimens only captured in site 10. Rostral fold very well developed, covered with large horny tubercles (conical in shape – breeding tubercles in males?). Between eyes and on occiput few small and somehow rigid tubercles. Note that tubercles are curved and only those on the tip of the snout point forward. The different mouth position is an interesting feature (see also Figure 47) an may relate to different feeding habits (niches?). Note that sexual dimorphosm is not yet confirmed for the genus *Garra* (Stiassny and Getahun, 2007) and not discussed in the present thesis.

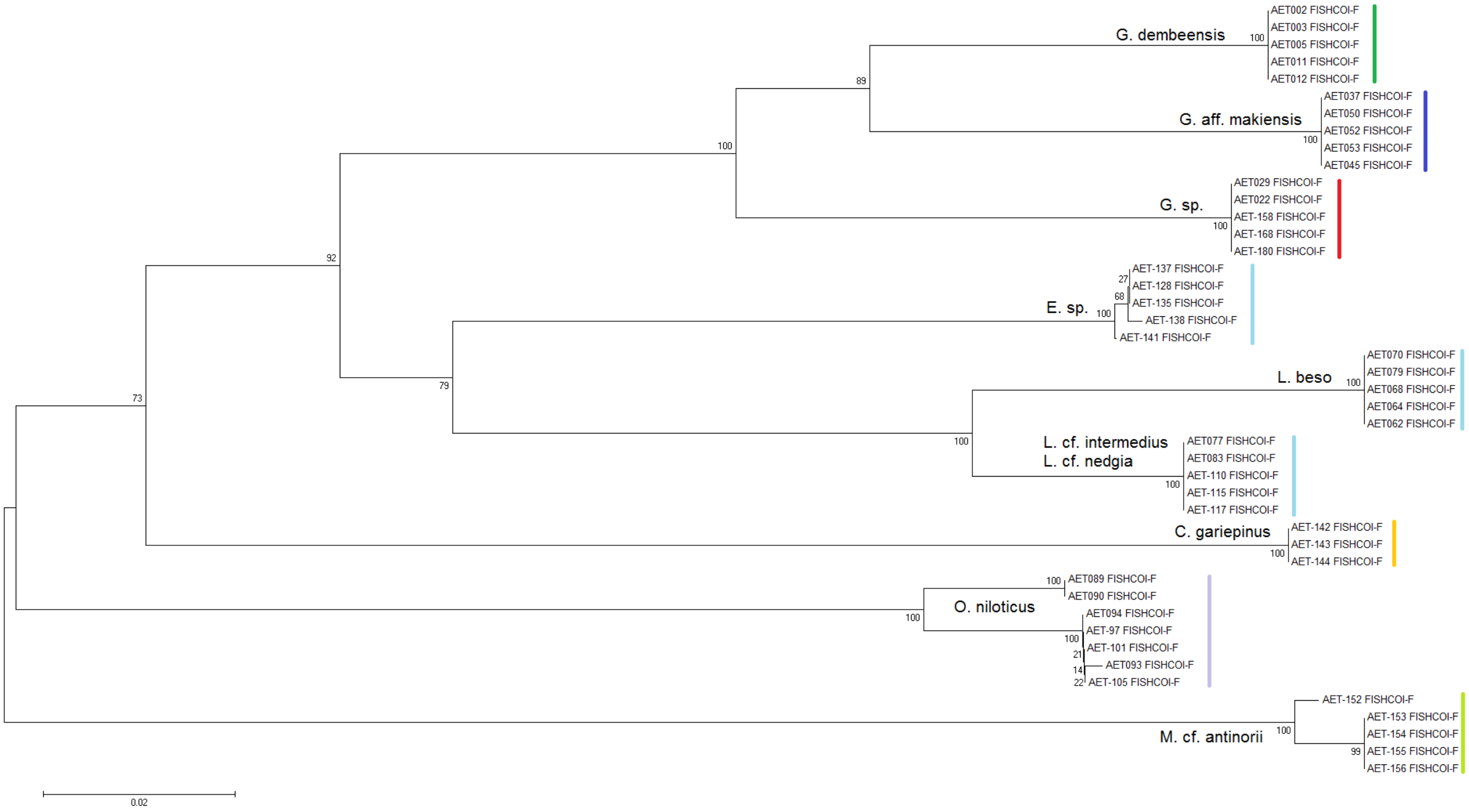


Figure 49. Preliminary study of the evolutionary relationships of taxa from the Awash river. The relationships were inferred using the Neighbor-Joining method. The optimal tree with the sum of branch length = 0.82290002 is shown. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) are shown next to the branches. The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The evolutionary distances were computed using the Tamura-Nei method and are in the units of the number of base substitutions per site. The analysis involved 45 nucleotide sequences. All ambiguous positions were removed for each sequence pair. Abbreviations: G. = *Garra*, E. = *Enteromius*, L. = *Labeobarbus*, C. = *Clarias*, O. = *Oreochromis*, M = *Michropanchax*.