



# The African hexaploid *Torini* (Cypriniformes: Cyprinidae): review of a tumultuous history

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A review of the tumultuous history of the alpha- and genus-level taxonomy of the hexaploid African *Torini*, i.e. *Labeobarbus s.l.* (synonym: *Varicorhinus*), as well as of the closely related monospecific genera *Acapoeta* and *Sanagia*, is provided. The main purpose of the present paper is to provide a continental framework for multidisciplinary research on this megadiverse vertebrate group. Based on the inspection of almost all relevant type specimens, a complete and fully annotated checklist of all valid species and junior synonyms is provided for each of the four nominal genera. It comprises ~275 nominal taxa, 125 of which are valid African *Labeobarbus* spp. and three of which are formally named hybrid phenotypes. Particular attention is drawn to the diversity and taxon-specific distribution of mouth phenotypes, which previously served as generic identification characters, i.e. ‘rubberlips’ with strongly developed, sometimes hypertrophied lips and a mental lobe, and ‘chiselmouths’ (former *Varicorhinus* spp.) with a cornified sharp cutting edge on their lower jaw. Interestingly, many species are polymorphic and include a large array of intermediate mouth phenotypes. The recurrent occurrence of similar mouth phenotype diversity within, but also far beyond, the borders of *Labeobarbus s.l.* is highlighted, raising numerous evolutionary questions.

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ADDITIONAL KEYWORDS: *Acapoeta* – hexaploidy – hybridization – intraspecific variation – *Labeobarbus* – mouth phenotype – mouth polymorphism – *Sanagia* – *Varicorhinus*.

‘... one of the most difficult with which it has ever been my lot to deal.’ (Boulenger, 1902f: 422)

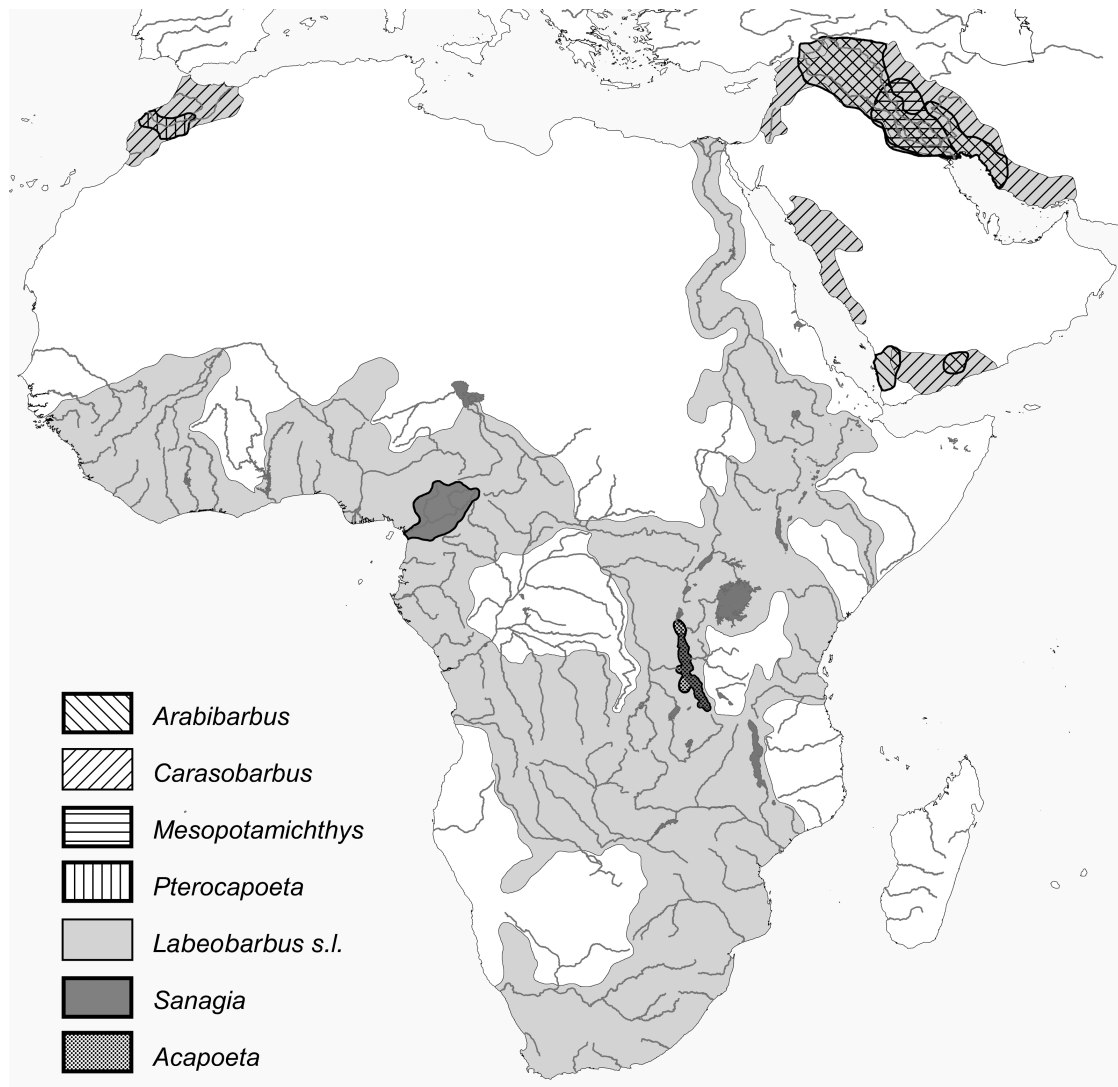
## INTRODUCTION

This paper is aimed to provide an exhaustive review of the systematics and taxonomy of all ~275 described African, large-sized, hexaploid, torine taxa (i.e. Cyprininae: see Yang *et al.*, 2015). These are members of the genus *Labeobarbus* Rüppell, 1835 *s.l.* (‘rubberlips’), including its recent junior synonym *Varicorhinus*

Rüppell, 1835 (‘chiselmouths’) (see Tsigenopoulos, Kasapidis & Berrebi, 2010; Berrebi *et al.*, 2014 and Yang *et al.*, 2015), as well as of the two monospecific genera *Acapoeta* Cockerell, 1910 and *Sanagia* Holly, 1926 [i.e. ~275(+2)]. Whereas both of the latter monospecific genera are highly restricted in distribution, i.e. endemic to Lake Tanganyika<sup>1</sup> and the Sanaga River in Cameroon, respectively, the genus *Labeobarbus s.l.* is wide-

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<sup>1</sup>*Acapoeta tanganyicae* has recently been collected from the Songwe River (Lake Rukwa basin) and reveals that the species is not endemic to the Lake Tanganyika and its immediately proximate sections of connected rivers (Genner *et al.*, 2015).



**Figure 1.** Distribution map of *Labeobarbus s.l.* *vide* Tsigenopoulos *et al.* (2010) and Berrebi *et al.* (2014), and of *Arabibarbus*, *Carasobarbus*, *Mesopotamichthys*, and *Pterocapoeta* as currently delimited by Borkenhagen (2014) and Borkenhagen & Krupp (2013). As a matter of completeness, the distribution of the monospecific African genera *Acapoeta* and *Sanagia* has been added as well.

spread and present in each of the ten African ichthyofaunal provinces as currently defined (see Snoeks, Harrison & Stiassny, 2011: fig. 3.1; modified from Roberts, 1975) (Fig. 1).

Their complicated history cannot be reviewed adequately without referring to closely related genera from the Arabian Peninsula and Asia, and without referring to three peculiarities of these Torini: (1) their chromosomal ploidy level; (2) their mouth phenotype variation; (3) the repeatedly observed occurrence of their mouth polymorphism. Whereas to date the ploidy level of *Acapoeta* and *Sanagia* remains unknown, the hexaploidy of rubberlips and chiselmouths has been established for numerous species (see Oellermann & Skelton, 1990; Krysanov, Golubtsov & Alexeev, 1991;

Golubtsov & Krysanov, 1993; Krysanov & Golubtsov, 1996; Guégan *et al.*, 1995; and Arai, 2011). The current compilation lists a total of 275 nominal African species to be included in *Labeobarbus s.l.* Of these, only 125 nominal species are still considered valid African *Labeobarbus* spp., whereas the majority, i.e. 147, are junior synonyms (including one suppressed name), and three others are formally named hybrid phenotypes. The present situation testifies already to the tumultuous taxonomic history of the group as a whole.

Originally, African chiselmouths (former *Varicorhinus* spp.) were diagnostically differentiated from rubberlips (former *Labeobarbus s.s.*) by a cornified sharp cutting edge on their lower jaw, as compared with the typically strongly developed, sometimes even hyper-

trophied lips and a mental lobe. The subsequent discovery of numerous species with several intermediate mouth phenotypes (see below), as well as the occurrence of *Labeobarbus*-like and *Varicorhinus*-like mouth phenotypes outside of Africa, have blurred that systematic pattern, however.

Apart from this African *Labeobarbus*–*Varicorhinus* (*Lab.*–*Var.*) species complex, similar patterns of polyploidy and mouth phenotype polymorphism have evolved outside of Africa and in different genera: (1) in the Middle East genus *Arabibarbus* Borkenhagen, 2014 [in *Arabibarbus grypus* (Gray, 1834) (see Roberts & Khaironizam, 2008: fig. 8; Borkenhagen, 2014)]; (2) in the Middle East and North African (sub)genus *Carasobarbus* Karaman, 1971 (synonym: *Kosswigobarbus* Karaman, 1971) [in *Carasobarbus fritschii* (Günther, 1874) see Borkenhagen & Krupp, 2013: fig. 3]; (3) as well as in the Southeast Asian genus *Neolissochilus* Rainboth, 1985 [in *Neolissochilus soroides* (Duncker, 1904) (see Roberts & Khaironizam, 2008: figs 3–6; and Khaironizam, Zakaria-Ismail & Armbruster, 2015: fig. 6B–D)]. All these genera appear closely related to *Labeobarbus* in the wider sense (see Tsigenopoulos *et al.*, 2010: fig. 1; Borkenhagen *et al.*, 2011: fig. 2; Borkenhagen, 2014: fig. 8; Yang *et al.*, 2015: figs 2, 4). Whereas *Carasobarbus* seems to be composed of hexaploid species [*Carasobarbus canis* (Valenciennes, 1842) in Cuvier & Valenciennes, 1842 (see Gorshkova, Gorshkov & Golani, 2002; Arai, 2011)], the ploidy level of *Arabibarbus* remains unknown, but several species of the very closely related southern and Southeast Asian genera *Tor* Gray, 1834 and *Neolissochilus* are all tetraploid [including the type species *Tor tor* (Hamilton, 1822), see Suzuki & Taki, 1981; Khuda-Bukhsh, 1982; Khuda-Bukhsh, Chanda & Barat, 1986; Rishi & Shashikala, 1994; Khuda-Bukhsh *et al.*, 1995; Sahoo, Nanda & Barat, 2007; Mani *et al.*, 2009; Arai, 2011; the polyploidy level of type species *Neolissochilus sumatranus* (Weber & de Beaufort, 1916) is unknown].

Interestingly, the Caucasian and western Asian (see Bănărescu, 1999) genus *Capoeta* Valenciennes, 1842 (in Cuvier & Valenciennes, 1842) is also composed of hexaploids [including the type species *Capoeta capoeta* (Gueldenstaedt, 1773); see Krysanov 1999; Safar *et al.*, 2000; Kiliç Demirok & Ünlü, 2001; Gorshkova *et al.* 2002; Arai, 2011)]. *Capoeta* is member of a distantly related mitochondrial lineage [defined as the *Barbus s.s.* lineage by Berrebi *et al.* (2014); and Cyprininae (Tribe: Barbini) in Yang *et al.* (2015: table 3)], also comprising the European, Middle Eastern, and north-west African (see Tsigenopoulos *et al.*, 2003) genus *Luciobarbus* Heckel, 1843, the European and West-Asian (see Kottelat & Freyhof, 2007) genus *Barbus s.s.*, and the Bosnia-Herzegovinan and Croatian endemic (see Kottelat & Freyhof, 2007) and monospecific genus *Aulopyge* Heckel,

1841. In contrast to *Capoeta*, all latter genera are tetraploid [including both the type species, i.e. *Barbus barbatus* (Linnaeus, 1758) and *Aulopyge huegelii* Heckel, 1843; see Collares-Pereira & Madeira, 1990; Collares-Pereira & Moreira da Costa, 1999; Arai, 2011; the polyploidy level of the type species *Luciobarbus esocinus* Heckel, 1843 is unknown]. Whereas *Capoeta* species invariably exhibit a typical chiselmouth phenotype, with a characteristic cutting edge covered by a horny sheet on the lower jaw (see Bănărescu, 1999), *Luciobarbus*, *Barbus* (see Kottelat & Freyhof, 2007: fig. 31), and *Aulopyge* instead have a rubbermouth-like or intermediate mouth phenotype. As such, and in contrast to the polymorphic African *Labeobarbus*, the mouth phenotype polymorphism in those other genera appears to covary with mitochondrial lineages.

Even for unrelated central Asian cyprinid genera, Roberts & Khaironizam (2008) pointed to the occurrence of similar mouth phenotype polymorphism in *Schizothorax* Heckel, 1838 [Cyprininae (Tribe: Schizothoracini): see Yang *et al.* (2015: table 3)], which is endemic to the Qinghai–Tibetan Plateau (Roberts & Khaironizam, 2008; see Qi *et al.*, 2012: 7, fig. 4). Although its polymorphism is slightly different (see Roberts & Khaironizam, 2008: fig. 9), it is nevertheless clearly reminiscent of the *Lab.*–*Var.* type and, interestingly, *Schizothorax* is composed of both tetraploid as well as hexaploid species (the polyploidy level of the type species *Schizothorax esocinus* Heckel, 1838 is unknown; for other species, see Zan, Song & Liu, 1986; Collares-Pereira, 1994; and Arai, 2011).

In combination, all these observations suggest a recurrent and possibly correlated pattern of polyploidy and mouth phenotype polymorphism in these cyprinid lineages. The processes that generate these patterns remain completely unexplored. Their origin may be of relevance for evolutionary biology, because the geographically widespread occurrence of this pattern across major cyprinid lineages, in combination with the enormous alpha-level diversity that has evolved in these lineages, points to a universal causal link between ploidy and phenotypic diversity, possibly expressed in one of the most famous examples for lacustrine species flocks, i.e. the *Labeobarbus* species flock of Lake Tana, Ethiopia.

Unfortunately, inter- and intrageneric phylogenetic relationships are poorly known, mainly because of the lack of phylogenetically informative morphological characters, incomplete taxon sampling, and, last but not least, because of the use of mainly mitochondrial DNA (mtDNA) as phylogenetic markers. mtDNA is a single non-recombining locus that is maternally inherited alone, and therefore only allows an incomplete view on species phylogenies to be inferred, an approach that cannot detect hybridization events with confidence, for example (Avice, 2004). With regard to the African *Labeobarbus*

and *Varicorhinus*, Levin *et al.* (2013) reported the mitochondrial paraphyly of *Varicorhinus beso* Rüppell, 1835, type species of the genus, and a chiselmouth-like taxon, *Varicorhinus jubae* Banister, 1984. Based on this observation, they concluded that the *Varicorhinus* mouth phenotype has evolved twice independently, and identified it as a case of parallel evolution. Analogously, the fact that the two hexaploid genera *Capoeta* and *Labeobarbus* are members of two non-monophyletic mitochondrial DNA lineages has been considered evidence for the independent evolution of hexaploidy (i.e. *sensu* Tsigenopoulos *et al.*, 2010 and Berrebi *et al.*, 2014). Although the single gene (*RAG1*) nuclear DNA data of Yang *et al.* (2015: fig. 4) confirm, at least partially, this hypothesis [i.e. with (1) *Cyprinion* Heckel, 1843 as paternal source (2n) for both genera, and (2) *Luciobarbus* and Torini as maternal source (4n) for *Capoeta* and *Labeobarbus*, respectively], a nuclear multigene approach will undoubtedly be needed to provide sufficient genomic coverage and statistical support to critically evaluate this hypothesis. In the same line of thought, Qi *et al.* (2012) interpreted the occurrence of similar mouth phenotypes in non-monophyletic mitochondrial lineages of Central Asian Schizothoracinae as evidence for convergent mouth phenotype evolution; however, these interpretations were not verified with recombining nuclear genetic loci, and therefore the presumed convergent occurrence of such peculiar and highly specialized mouth phenotypes in predominantly hexaploid taxa might equally be related to genomic processes, the history of which cannot be deciphered with mtDNA alone.

Incorporating our present knowledge about ploidy, mouth polymorphism, and phylogenetic relationships, this review first presents a detailed overall historic overview of our changing understanding of both these African genera, i.e. *Labeobarbus* and *Varicorhinus*, as well as both the putatively related genera *Acapoeta* and *Sanagia*. Second, a narrative history of our changing interpretation of what intraspecific variation seemingly ought to be in both these genera of hexaploid, large size, Torini is presented. Next, as a result of our almost complete inspection of type specimens, a compilation of the current species diversity in *Labeobarbus s.l.*, as well as in *Acapoeta* and *Sanagia*, is provided, with particular attention paid to the level of observed and/or recognized intraspecific mouth phenotype variation for each. Finally, in the discussion, the magnitude of the problems with regard to our current understanding of species diversity in both these genera on a pan-African scale, and beyond, are further exemplified. By providing these baseline data for the first time, we hope to smooth the path for an exhaustive exploration of the megadiversity of this fascinating group of freshwater teleosts as well as answering the challenging questions regarding their evolutionary dynamics.

## MATERIAL AND METHODS

The taxonomy, systematics, phylogeny, and intergeneric hybridization of *Labeobarbus* and related genera are reviewed here, based upon an extensive survey of the literature. This was especially needed to identify which of the many African *Barbus*, ‘large barbs’, and/or *Labeobarbus* species, should be reallocated to or removed from *Labeobarbus*. In this respect, the following pragmatic choices were made. First, the synonymy of *Varicorhinus* with *Labeobarbus*, as proposed by Tsigenopoulos *et al.* (2010), and recently applied by Berrebi *et al.* (2014) in their review paper on *Barbus s.l.*, has been fully accepted. Although Yang *et al.* (2015) still retained *Varicorhinus* as a valid genus in their mitochondrial and nuclear DNA publication on cyprinine phylogeny and classification, at least their mtDNA data also support Berrebi *et al.*’s (2014) decision. We refer to this delimitation of the genus as *Labeobarbus s.l.*, and to that pre-dating the synonymy as *Labeobarbus s.s.* We have refrained from following the recent revalidation, redefinition, and description of those genera, which would render *Labeobarbus s.l.*, in the mitochondrial DNA phylogeny of Tsigenopoulos *et al.* (2010), Berrebi *et al.* (2014), and Yang *et al.* (2015), paraphyletic. This applies to the redefinition of *Varicorhinus* as a monospecific genus by Levin *et al.* (2013), the confirmation and revalidation of *Carasobarbus* (for the first revalidation, see Bănărescu, 1997), and both monospecific genera *Mesopotamichthys* Karaman, 1971 (for the first revalidation, see Bănărescu, 1997) and *Pterocapoeta* Günther, 1902 (for *Carasobarbus*, see Borkenhagen *et al.*, 2011 and Borkenhagen & Krupp, 2013; for both *Mesopotamichthys* and *Pterocapoeta*, see Borkenhagen, 2014; for *Pterocapoeta* only, see Geiger *et al.*, 2014), and the original description of *Arabibarbus* by Borkenhagen (2014). As a result, all are here enclosed in *Labeobarbus s.l.* (i.e. the *Labeobarbus* clade of Yang *et al.* 2015: fig. 2). This decision also enabled us to avoid the use of the generic appellation ‘*Labeobarbus*’ for species that, following this recent increase of genus names used, are still of uncertain generic affiliation [see Borkenhagen, 2014 (still as ‘*Barbus*’); Yang *et al.*, 2015]. Species recognition, however, and the synonymization of taxa classified as African *Carasobarbus* species by Borkenhagen & Krupp (2013), as proposed by these authors themselves, has been followed here. Furthermore, within *Labeobarbus s.l.*, we have concentrated our efforts on compiling African species diversity for which, because of the largely persistent indiscriminate use of the generic appellation *Barbus* (see below), a proper overall delimitation of the *Labeobarbus s.l.* lineage is still lacking. We have, however, refrained from mapping *Labeobarbus s.l.* species diversity from outside Africa, as the recent work

of Borkenhagen *et al.* (2011), Borkenhagen & Krupp (2013), and Borkenhagen (2014) includes a good overview of species diversity from that region for the genera *Arabibarbus*, *Carasobarbus*, and *Mesopotamichthys*. The species list provided has further been completed with a tabulation of the observed mouth phenotype variation after the re-examination of almost all type specimens of all valid species, and, whenever available, mouth phenotype variation as currently perceived in each of the African species, the latter based on: (1) major revisions and/or faunal guides; and (2) wherever possible, a selected re-examination of type specimens of junior synonyms, in such a way as to cover the intraspecific mouth phenotype variation reported in the literature. A list of all examined (type) specimens is provided in the Appendix. Despite the actual synonymy of *Varicorhinus* with *Labeobarbus*, we have indiscriminately used the genus name *Varicorhinus*, if we: (1) refer to the genus as formerly recognized; or (2) refer to it as the highly specialized cutting-edge mouth phenotype ('exposed cornified mandibular cutting edge': see Howes, 1982: 131), and hereby discriminate it from others such as the *Labeobarbus* or intermediate mouth phenotypes (see below). We have referred to a *Varicorhinus*-like mouth phenotype in two particular cases: (1) when referring to comparable mouth phenotype(s) as found in other African *Labeobarbus* species, i.e. with a real cutting edge, but displaying a more extended lip development on the lateral sides of the lower jaw than observed in *V. beso*, where the lips are only poorly developed (for more details, see legend and notes to Table 1); (2) whenever referring to comparable mouth phenotype(s), i.e. with a real cutting edge, as found in other cyprinid genera from outside Africa (e.g. *Chondrostoma* Agassiz, 1832), irrespective of other similarities or differences.

Although it is currently well established that all African large (now *Labeobarbus*) and small *Barbus* [recently transferred to the revalidated genus *Enteromius* Cope, 1867 (see Yang *et al.*, 2015) and a few other small genera] do not belong to the genus *Barbus* s.s., i.e. the barbine lineage of tetraploid species from European and Maghreb region of north-west Africa (see Kottelat & Freyhof, 2007; Skelton, 2001; Berrebi *et al.*, 2014; Yang *et al.*, 2015), we have refrained from using '*Barbus*' (see Farm, 2000; Bamba, Vreven & Snoeks, 2011; Banyankimbona, Vreven & Snoeks, 2012b) to discriminate them from the latter lineage. This decision is motivated by the fact that the current discrimination cannot be extrapolated unequivocally into a historical context pre-dating these insights. Therefore, as a matter of convenience and when used in a historical context, all African *Barbus* (i.e. now *Labeobarbus* and *Enteromius*, and a few smaller genera) have indiscriminately been referred to as *Barbus* and not '*Barbus*' throughout the text.

Institutional abbreviations follow Fricke & Eschmeyer (2015): i.e. collections from the Natural History Museum (NHM), London, UK, and the Royal Museum for Central Africa (RMCA), Tervuren, Belgium, will be referred to as BMNH and MRAC, respectively, i.e. their well-established historical acronyms. Other abbreviations: FL, fork length; SL, standard length; TL, total length.

#### COMPILATION OF THE ANNOTATED CHECKLISTS

As a reference for further research, a full list of all valid African *Labeobarbus* s.l. species (*sensu* Tsigenopoulos *et al.*, 2010; Berrebi *et al.*, 2014; Yang *et al.*, 2015) is provided as an annotated checklist. The list is ordered alphabetically by species or subspecies name, as given in the original description. The genus name and the author(s) name(s), as given in the original description, are also provided. Museum collection abbreviations follow Fricke & Eschmeyer (2015).

The full type series, as currently identified, is listed and the number of type specimens in a record is given between brackets after the collection number, except for holo-, lecto-, and neotypes, which are single specimens by definition. Type series are based on data from the original publication and/or collection data, and have not been verified in all cases. Differences between the number of type specimens identified and the number of type specimens in the original description, if given, are mentioned in the 'Notes' section.

Type locality data have been provided in English, i.e. they may have been translated from the original sources of the original description and/or the museum label(s). Type localities only include those of the name-bearing type(s), as only those are of nomenclatural importance (ICZN, 1999: articles 61 and 72.1.2.–1.3). Whenever available, locality data have been arranged from the smallest to largest geographical units (locality, river, basin, and country), and have been complemented with other information (e.g. elevation) as provided in the original description or on the museum label(s). Unless otherwise stated, all information derives from the original description or from the museum label(s). Additional information on water bodies, drainage basin, and/or country is provided in parenthesis; country names have been adjusted to current use. Coordinates are also provided for the type locality/ies, and are based on the information as provided in the original description on the museum label(s), or as obtained from other sources. In the latter case '±' has been added to the coordinates and their reference source has also been provided. Coordinates always follow the geographical unit to which they refer.

Under the heading 'Current status', the status and current full species name, as to be used, is provided, with reference to the first generic placement of the

species in *Labeobarbus*. The list of African *Labeobarbus* species as provided by Skelton & Bills (2008) was revealed to be incomplete, beyond the fact that *Varicorhinus* spp. were not included because they were not considered a junior synonym at that time. Therefore, allocation of species to *Labeobarbus* by Skelton & Bills (2008) has been backed up with another reference or reference to the present paper. In the case of replacement names and revalidated synonyms, as provided and reinstated in the current paper, reference is made, respectively, to: (1) the allocation of the junior homonym to *Labeobarbus*; (2) the allocation of the previous senior synonym of the revalidated species to *Labeobarbus*. In both cases reference to the current paper has been included. For recent revalidations, such as that of *Labeobarbus pojeri* (Poll, 1944), reference to both the allocation of the previous senior synonym of the revalidated species to *Labeobarbus* and its allocation to *Labeobarbus* within the paper revalidating it have been provided.

Under 'synonyms', actual synonyms with their original names, including author and year of description, and with reference to the authors who first proposed the synonymization, are provided. The senior synonym of the proposed synonymization is also given, except if it is the currently valid species. In the cases concerned, the reference(s) for revalidation and/or re-synonymization are also provided. Synonyms are provided in alphabetic order. Nominal species placed in synonymy but recognized as a valid subspecies are also included in the synonyms list, as are subspecies that are not considered valid. A single reference after several synonyms refers to all preceding synonyms.

Under 'Distribution', the currently known distribution with the respective literature sources is given. The distribution of valid subspecies is given after their name, author, and year of description, together covering the total species distribution. Distribution data are merely a compilation of available information, without evaluation of the quality or correctness of the literature reports. Lévêque & Daget (1984) has been used as the main source for the basic distribution information, updated with recent literature sources whenever available; however, distribution information is based on the original sources when the distribution as given in Lévêque & Daget (1984) differs too much from what is given in these original sources. Distribution references are ordered chronologically.

Finally, a 'Notes' section is included for any additional information and discussion referring to data listed under previous headings. As we made extensive use of the CLOFFA (Lévêque & Daget, 1984) and the Catalog of Fishes (Eschmeyer, 2015), especially during the early stages of checklist compilation, the 'Notes' section also contains information on any discrepancies between both sources and between both and other

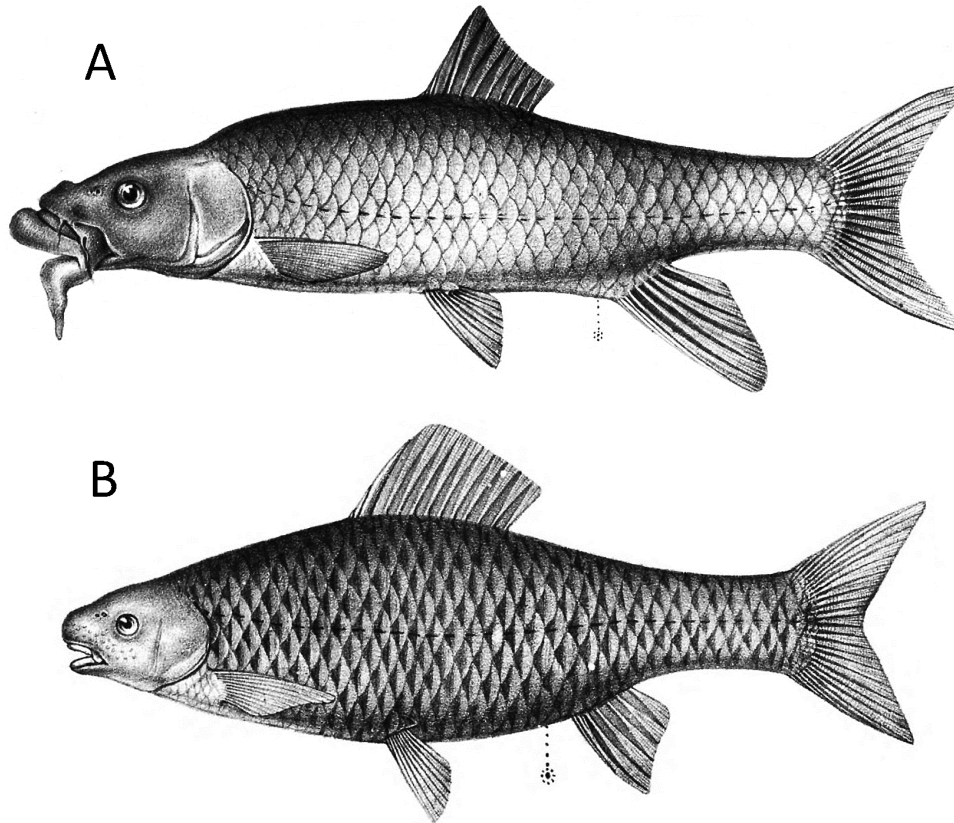
sources used. These notes should be considered an update of the information available in the CLOFFA and in the Catalog of Fishes, which, without doubt, remain baseline sources for any taxonomical study, for which they are hereby acknowledged.

Nominal species that have been identified as hybrid phenotypes are also listed in annotated checklist 1, but without further data. Full data, however, are provided in annotated checklist 2. The species of *Acapoeta* and *Sanagia* are treated as discussed above, and are listed in annotated checklist 3.

Considering the importance of the priority rule (see ICZN, 1999: article 23), whenever possible, multiple references of the same author published during the same year have also been ordered chronologically, rather than according to appearance in the text. References that we have been unable to chronologically situate have consistently been added at the end of the authors' publications for that year (i.e. Boulenger, 1907c and Pellegrin, 1935d). The printed date on a publication itself, unfortunately, does not always correspond to the actual date of publication. In those cases, as a matter of completeness, we have added (in parenthesis) the reference used to identify the latter date after the reference itself (i.e. Duncan, 1937, Banister, 1973, Roux, 1976, Bauer, Günther & Klipfel, 1995, Evenhuis, 2003, Low & Evenhuis, 2014 or Eschmeyer, 2015).

#### COMPILATION OF THE LIST OF EXAMINED (TYPE) SPECIMENS

The list provides an overview of all (type) specimens examined within the framework of the present paper. As for the compilation of the annotated checklist(s), the list is ordered alphabetically by species or subspecies name, as given in the original description, except for species for which a substitute name has been proposed and are then to be found under the latter name. Junior synonyms have been listed alphabetically under their current senior synonym, i.e. valid species name, as presented in the annotated checklists. Note that only type specimens of junior synonyms relevant to the tabulation of mouth phenotype variation within a given species, provided in Table 1, have been listed here (see Notes to Table 1). To ease the subsequent verification and/or retraction of information, the current list has been subdivided into annotated checklists: i.e. listing the African *Labeobarbus s.l.* species (annotated checklist 1); the African *Labeobarbus s.l.* species identified as hybrid phenotypes (annotated checklist 2); and the species of both the monospecific genera *Acapoeta* and *Sanagia* (annotated checklist 3), respectively. African species identified as not belonging to *Labeobarbus s.l.* have been listed separately under the heading 'non *Labeobarbus* species'.



**Figure 2.** Reproduction of the original illustration of: A, *Labeobarbus nedgia* (from Rüppell, 1835: plate 2, fig. 3); B, *Varicorhinus beso* (from Rüppell, 1835: plate 3, fig. 2) type species of *Labeobarbus* and *Varicorhinus*, respectively (both drawings flipped horizontally).

It has not always been possible to physically re-examine the type specimen(s) ourselves, either because the current loan policies of some of the relevant fish collections prevent sending primary types on loan, or because of budgetary and time constraints to visit each of the remaining fish collections, sometimes just for a single or only a few types. Therefore, some types have only been re-examined using photographs kindly sent to us by the curator(s) in charge, which are indicated by an asterisk (\*) after the collection number(s) concerned. Note that for the Lake Tana species, except for the nominal types for which the mouth phenotype data are based on photographs, extensive use has been made of the mouth phenotype data as already provided by Nagelkerke & Sibbing (1997, 2000) (see also Notes to Table 1).

## RESULTS

### PERSISTENT GENERIC PROBLEMS: MORPHOLOGICAL, CYTOGENETIC, AND MOLECULAR APPROACHES

*Labeobarbus* and *Varicorhinus* were both originally described from Lake Tana, 'Zana See' (Ethiopia) by Rüppell

(1835). The genus name *Labeobarbus*, with *Labeobarbus nedgia* Rüppell, 1835 as the type species, was chosen in reference to a barb [Latin: *barbus* (masculine)] with large fleshy lips [Latin: *labeo* (masculine)], i.e. with 'fleischige Lippen', and also possessing a mental lobe, i.e. the 'ziemlich lange fleischige Bartzaser' (see Rüppell, 1835: 14) (see Fig. 2A). The genus name *Varicorhinus*, with *Varicorhinus beso* Rüppell, 1835 as the type species, was chosen in reference to the many small tubercles, i.e. 'kleine Knorpelwarzen' [Greek: *varix* (feminine or masculine)], on the snout [Greek: *rhis* (feminine)], and the description also indicated the horny lips, i.e. 'häutigen Lippen' (see Rüppell, 1835: 20–21) (see Fig. 2B). Although there is no explicit reference to a clear cutting edge on the horny lower lip in Rüppell's (1835) original description of the genus *Varicorhinus*, this is the main diagnostic character that has subsequently been used for differentiating *Varicorhinus* from *Labeobarbus* (see below). Based on the unambiguous original description, both genera seemed well differentiable and distantly related at that time, a situation that would drastically change over time when more specimens and species became available (see below).

The history of both genera can be roughly subdivided into three major time periods. First, the ‘period of discovery’, here delimited from 1775 to approximately 1930, but well overlapping with the next period. This period is dominated by the discovery and typological naming of the overwhelming diversity in mouth phenotypes (see An overview of species diversity in African *Labeobarbus*: current state of the art). Second, the ‘period of skepsis’, starting from 1929 and lasting up to about 1987. This period is characterized by recurrent doubts with regard to the distinct generic status of *Varicorhinus*, as well as doubts about the species-level relevance of the observed mouth phenotype diversity. The latter doubts resulted in a wave of species-level synonymizations (see Phenotypic variation and/or ‘intergeneric’ hybridization). The existing generic-level classification remained unchanged, however. Finally, the 1990s marked the onset of the ‘period of multidisciplinary’, characterized by the application of new research tools that enabled the study of morphology-independent characters, i.e. enzymes, chromosomes, DNA sequences, and parasites. The potential of these methods rejuvenated the attention paid to the long-standing questions of generic delimitation and phylogenetic affinities, and facilitated the continuing step-by-step advance in their elucidation.

#### *The period of discovery*

Since Günther’s (1868) synonymization, the genus *Labeobarbus* has been a junior synonym of the genus *Barbus s.l.* Cuvier & Cloquet, 1816 (in Cuvier, 1816) – a genus that later was aptly called a ‘monstrous aggregation’ (Myers, 1960: 213) – for most of its subsequent history. The first and most striking feature that Rüppell (1835) presented in the original description of *Labeobarbus* to differentiate it from other cyprinids was the presence of the large fleshy lips (see above). Günther (1894), however, reported that large specimens of *Barbus* (now *Labeobarbus intermedius* Rüppell, 1835) have more developed lips. As such, he implicitly identified lip development as: (1) an intraspecific variable; and (2) a size-related character. Boulenger (1902f), however, refuted Günther’s (1894) interpretation of the observed mouth phenotype variation (our wording) as the holotype of *B. intermedius*, which lacks a mental lobe, is larger than the largest specimens seen by Günther (1894), which instead have a well-developed lower lip with a rounded median lobe [now syntypes of *Barbus gregorii* Boulenger, 1902: a junior synonym of *L. intermedius* (see annotated checklist 1)]. He also argued that the mouth phenotype characters presented by Rüppell (1835) in his original description of the genus *Labeobarbus* were insufficient to grant it generic separation from *Barbus* (now mainly *Enteromius* and a few smaller genera), although they are of greatest

value for species distinction (see below), and are independent of sex and age (Boulenger, 1902f).

Even so, the observed mouth phenotype variation in large barbs (now *Labeobarbus*) were revealed to be an intricate issue. Boulenger (1902a: 125), for example, had described two Moroccan species with ‘a perfectly [*Varicorhinus*-like] trenchant edge to the lower jaw’ as *Capoeta waldoii* Boulenger, 1902 and *Capoeta atlantica* Boulenger, 1902, both of which he later transferred to *Barbus* (Boulenger, 1905b: 44), now *Labeobarbus* [both are currently junior synonyms of *Labeobarbus fritschii* (Günther, 1874), see Lévêque & Daget (1984) and Borkenhagen & Krupp (2013)]. A few months later, Boulenger (1902d) described two more large *Barbus* species (now *Labeobarbus*), i.e. *Barbus (Capoeta) perplexicans* Boulenger, 1902 and *Barbus (Labeobarbus) labiatus* Boulenger, 1902, and hereby considered *Capoeta* as a junior synonym of *Barbus*. Although he had apparently based the attribution of *B. perplexicans* to the subgenus *Capoeta* on the presence of ‘a strong transverse, horny cutting-edge’ on the lower jaw, the attribution of *B. labiatus* to the subgenus *Labeobarbus* apparently was based on the ‘extremely developed’ lips, ‘each produced into a long triangular flap’ (see Boulenger, 1902d: 223). Boulenger’s struggle to come to terms with mouth phenotype variation is further exemplified by the fact that he had already abandoned his previous subgeneric classification in 1905 (see Boulenger, 1905b), but nevertheless retained species with a *Capoeta*, i.e. *Varicorhinus*-like, mouth phenotype, as large barbs (now *Labeobarbus*) within the huge genus *Barbus*, without questioning the status of *Varicorhinus* as a valid genus.

Ever since, *Varicorhinus* has never been formally synonymized, except for some early authors such as Heckel (1843), Cuvier & Valenciennes (1844), and Günther (1868), despite that its status has been much debated [e.g. by Groenewald (1958) (see below)]. Only Keilhack (1908) had described a species with a cornified real cutting edge on its lower jaw from Lake Malawi as *Barbus njassae* Keilhack, 1908 [currently a junior synonym of *Labeobarbus johnstonii* (Boulenger, 1907) (see Banister & Clarke, 1980)] although he was perfectly aware of its *Varicorhinus*-like mouth phenotype. He explicitly rejected the validity of *Varicorhinus*, and in that context referred to Boulenger (1902b) (see Keilhack, 1908: 165), who had previously attributed species with a well-identifiable *Varicorhinus* mouth (*‘Varicorhinus-Kiefer’*) to *Barbus* (see above). As a result of Keilhack’s (1908) statement, Pappenheim (in Pappenheim & Boulenger, 1914) used *Varicorhinus* as a subgenus of *Barbus*.

Notwithstanding Keilhack’s (1908) argument, the influence of Boulenger’s famous *Catalogue of African Fresh-Water Fishes in the British Museum (Natural History)* (Boulenger, 1909, 1911a, 1916a) has resulted, until recently, in a general acceptance of Boulenger’s



genus-level classification, with *Labeobarbus* as a junior synonym of *Barbus*, and with *Varicorhinus* as a valid genus. Boulenger's catalogue was also followed with regard to diagnostic morphological characters, which he used for separating all 'large barbs' (now *Labeobarbus*) from the 'small barbs' (now *Enteromius* and a few smaller genera). Both groups were mainly differentiated from each other based on the exposed surface of the scales having radiating striae in small *Barbus* (see Boulenger, 1911a: 12), in contrast to parallel or even convergent striae in large *Barbus* (see Boulenger, 1911a). In addition, Boulenger (1911a) differentiated the two groups by overlapping, branched dorsal-fin ray counts, i.e. between six and eight (rarely nine) in small *Barbus*, and between eight and 11 in large *Barbus*. Earlier, Boulenger had also provided, to some degree, the main character for diagnosing *Varicorhinus*, i.e. the lower jaw being 'completely exposed and showing a sharp cutting-edge covered with a horny layer [sheath]' (Boulenger, 1907c: 190; and 1909: 299 & 352).

Although Boulenger (1911a) did not recognize *Labeobarbus* as a separate genus or subgenus in his catalogue, he later again considered it as a subgenus of *Barbus* (see Boulenger, 1919). This classification was not adopted by subsequent authors, however, apart from a few noteworthy exceptions: Pellegrin (1921) retained it as a subgenus of *Barbus*, including the species with scales with numerous more or less parallel striae, thereby following Boulenger's (1911a) division. As a novelty, Pellegrin (1921) differentiated between several other additional subgenera, i.e. *Barbus*, *Enteromius*, and *Puntius* Hamilton, 1822 (Pellegrin, 1921, 1939), because he felt that this was necessary from a practical point of view for species identification. He further listed *Varicorhinus* as different from *Barbus*, mainly based on the absence of lips and the presence of a cornified real cutting sheath on the lower jaw. Nevertheless, Pellegrin (1926) himself described *Barbus* (*Capoeta*) *babaulti* Pellegrin, 1926 [currently a junior synonym of *Labeobarbus oxyrhynchus* (Pfeffer, 1889), see annotated checklist 1] as a new large *Barbus* (now *Labeobarbus*), although he himself reported a cornified real cutting edge on the lower jaw (our rewording) for this taxon. This also explains why he assigned this new species to the subgenus *Capoeta*, and it illustrates well his problems of coming to terms with the observed mouth phenotype variation.

#### *The period of skepsis*

The generic problems encountered would not fade away, although different authors would adopt, substantiate and promote different views. Daget (1954) also used the difference in the striation pattern of the scales and the adult size as the first dividing character in his key to the West African species of the genus *Barbus*, but

he did not recognize any (sub)division of the genus into different genera or subgenera. Instead, he explicitly stipulated the artificial nature of such a division, which, according to him, would by no means reflect the systematic arrangement. As the genus *Varicorhinus* had not been reported from West Africa at that time (see however Daget, 1962: 72), Daget (1954) did not discuss it (see below).

The subdivision of small versus large barbs as proposed by Boulenger (1911a) was also adopted by Banister (1987), who explicitly quantified the difference in adult size between the two groups, i.e. mostly much smaller than 200 mm SL for the 'small *Barbus*' (now *Enteromius* and a few smaller genera), and mostly much larger than 200 mm SL for the 'large *Barbus*' (now *Labeobarbus*) (Banister, 1987). Banister (1987) also clearly stipulated that this was a pragmatic segregation without any implication for the monophyly of either group. He further reported exceptions to the rule, such as for the large sized *Labeobarbus somereni* (Boulenger, 1911) from the Ruwenzori area, as well as the Ruzizi and Upper Malagarazi rivers (see Banister, 1973: fig. 95; Banyankimbona *et al.*, 2012a), for which he illustrated a more radiate striation pattern on the scales (Banister, 1973: fig. 93).

Berrebi (1981) was the first author to again use *Labeobarbus* as a subgenus of *Barbus* since Boulenger (1919) and Pellegrin (1921). Based on a study of three Moroccan large *Barbus*, he argued that according to his observations, and referring erroneously to Boulenger (1911a), who did not adopt a subgeneric classification of the genus *Barbus*, that in *Labeobarbus* the last dorsal spine is never serrated, whereas in the subgenus *Barbus* it always is. Along with earlier authors, he added the difference in striation pattern of the scales as a second diagnostic character. Beyond Pellegrin's (1921) subgeneric division, the absence of serrations on the last unbranched dorsal spine is, however, not fully diagnostic, as in many species of both *Labeobarbus* and *Barbus* this last unbranched ray is not spiny. If present, it lacks serrations in all large *Barbus*, now *Labeobarbus*, as well as several small *Barbus* species (see for instance in Skelton, 2001; Lévêque, 2003; De Weirtdt & Teugels, 2007). As it was unsatisfactory for many, Berrebi's suggestion was therefore not followed, and because of the lack of alternative supporting evidence, the classification with *Labeobarbus* as a junior synonym of *Barbus* remained.

The same holds true for the status of *Varicorhinus*. The problematic status of *Varicorhinus* as a separate genus became particularly apparent through the research of South African ichthyologists such as Groenewald, Crass, and Jubb. Groenewald (1958) also used the striation pattern of the scales in his key to the *Barbus* and *Varicorhinus* species of Transvaal (South Africa) to differentiate the *Varicorhinus* and large *Barbus*

(now *Labeobarbus*) – usually referred to as yellowfishes in Southern Africa, because of their golden yellowish overall colour – from the small *Barbus* (Groenewald, 1958: 268). Groenewald was also the first after Keilhack (1908) who explicitly questioned the status of *Varicorhinus* as a valid genus, because the only external difference to other yellowfishes (now *Labeobarbus*) would be the ‘square-shaped lower jaw, with its thick muscular covering and conspicuous horny cutting ridge’ (Groenewald, 1958: 273). Interestingly, he also noticed that a cornified real cutting ridge is not restricted to *Varicorhinus*, but that a weakly developed one is also present in the ‘sector’ form of another yellowfish, *Barbus brucei* Boulenger, 1907 [now *Labeobarbus marequensis* (Smith, 1841), following Jubb, 1963].

In a key for the cyprinid genera from Natal, two entries for *Barbus*, i.e. one with ‘Mouth terminal’ (small *Barbus*, now *Enteromius*) and one with ‘Mouth inferior’ were published by Crass (1964: 47). His second entry includes under the character state ‘lips undeveloped; lower jaw with exposed cutting edge’ not only *Barbus* (i.e. large *Barbus*, now *Labeobarbus*) but also *Varicorhinus*; however, he diagnosed *Varicorhinus* not by the presence of an exposed cutting edge, but by barbels being absent or reduced to a single small pair (i.e. less than half the eye diameter) versus always at least one pair of longer barbels (i.e. longer than two-thirds of the eye diameter) in *Barbus* (now *Labeobarbus*). Crass (1964) obviously considered an exposed *Varicorhinus* cutting edge alone not sufficient evidence for identifying a species as belonging to *Varicorhinus*. As a consequence, he retained only a single species in that genus, i.e. *Varicorhinus nelspruitensis* Gilchrist & Thompson, 1911, and stipulated: ‘The only difference in the jaw appears to be that the characteristic shape [i.e. exposed *Varicorhinus* cutting edge] is to be found in very young *Varicorhinus* whereas *Barbus* [now *Labeobarbus*] of less than 2 inches [i.e. 1 inch, ~25.4 mm; unclear whether TL, FL, or SL; see Crass, 1964: 17] do not have a wide jaw.’ (Crass, 1964: 70).

Three years later, Jubb (1967: 115–116) adopted and enriched Crass’ (1964) definition of *Varicorhinus*: ‘the wide square lower jaw with sharp cutting edge must be evident in the juvenile stage and not a post-juvenile adaptation. Furthermore, this form of mouth must be uniform for the species throughout its life history’. Another year later, Jubb (1968) added that the character of the lower jaw, which Boulenger (1909) described as being without lips and having a sharp cutting edge covered with a horny sheath, is of doubtful value for systematics, because this *Varicorhinus* form of mouth is also found in five large *Barbus* (now *Labeobarbus*) species (Jubb, 1968; see illustration Jubb, 1967: fig. 21). Finally, Jubb (1967, 1968) accepted the genus *Varicorhinus* only for species with the defini-

tion given above, i.e. he only recognized *Varicorhinus nasutus* Gilchrist & Thompson, 1911, *Varicorhinus nelspruitensis*, and *Varicorhinus pungweensis* Jubb, 1959 as *Varicorhinus* species among the Southern African Cyprinidae, and he excluded *B. marequensis* and *B. natalensis* de Castelnau, 1861 (now both *Labeobarbus*) specimens with a *Varicorhinus*-like mouth, because in these polymorphic mouth phenotype species, mouth phenotype differentiation would be apparent only at a minimum size of 100–150 mm FL. Instead, all specimens of less than 60 mm FL would be undifferentiated, i.e. have normal thin lips (Jubb, 1968; see also Jubb, 1967); however, Poll (1967) reported the occurrence of very similar size-related mouth phenotype changes for two *Varicorhinus* species: *Varicorhinus ansorgii* Boulenger, 1906 and *Varicorhinus macrolepidotus* Pellegrin, 1928. He found the lower lip of small (about  $\leq 125$  mm TL) *V. macrolepidotus* covered by a horny cover but without a clear cutting edge, in contrast to larger specimens, which have both. Similarly for *V. ansorgii*, Poll (1967: 333) reported a bevel (‘bissaux’), i.e. the cornified real cutting edge, only for adults (i.e. large specimens). More recently, Tweddle & Skelton (1998: 372) reported in the original description of *Varicorhinus* (now *Labeobarbus*) *dimidiatus* Tweddle & Skelton, 1998 that although adult specimens indiscriminately have a ‘keratinized scraping edge’, the mouth of juveniles is crescent-shaped, and becomes straight with round edges in larger individuals. This illustrates that in ‘true’ *Varicorhinus* mouth phenotype species, ontogenetic changes in mouth morphology also occur. As a consequence, *Varicorhinus* retained its valid status, despite the many efforts to identify stringently diagnostic characters separating *Varicorhinus* from large *Barbus* (now *Labeobarbus*).

#### *The period of multidisciplinary*

In the 1990s molecular and chromosomal characters started to be used to investigate African *Barbus* systematics. Two studies by Agnès *et al.* (1990) and Berrebi *et al.* (1990) examined enzyme polymorphism in several small and large *Barbus* species from West Africa. Both inferred that the large *Barbus* species studied (i.e. *Labeobarbus* as a subgenus of *Barbus* for Berrebi *et al.*, 1990) were tetraploid, like the European *Barbus*, whereas the small African *Barbus* (i.e. now *Enteromius*) were diploid. As such, they independently confirmed the classical morphology-based division into two major groups (e.g. see Boulenger, 1911a), i.e. small versus large African *Barbus*.

Oellermann & Skelton (1990) indirectly questioned the presumed tetraploidy of the large West African barbs, based on the direct observation of hexaploid chromosome numbers of  $2n = 148$ –150 in six of the seven South African large *Barbus* (now *Labeobarbus*). In addition, they revealed the hexaploidy of *Varicorhinus*

*nelspruitensis* (Oellermann, 1989 *vide* Oellermann & Skelton, 1990) ( $2n \sim 150$ ). Based on their shared hexaploidy, they thereby presented the first karyological evidence for a closer phylogenetic relationship of the large African barbs with *Varicorhinus*, rather than with *Barbus s.l.* This evidence was complemented by karyological studies of Krysanov *et al.* (1991), Golubtsov & Krysanov (1993), and Krysanov & Golubtsov (1996), who further found hexaploidy ( $2n = 150$ ) in some riverine Ethiopian large *Barbus* (now *Labeobarbus*) and six different *L. cf. intermedius* 'eco- and morphotypes' from the Lake Tana Basin (later described as full species by Nagelkerke & Sibbing 1997: table 5.4), as well as for the type species of *Varicorhinus*, *V. beso*.

Golubtsov & Krysanov (1993) were also the first to claim that further investigations would reveal the hexaploidy of all African 'large *Barbus*' and *Varicorhinus* species. According to them either one unique polyploidization event or two independent events might account for the origin of hexaploidy in both genera. They deemed the latter theory to agree better with the classification into two different genera, but they also acknowledged that a close morphological resemblance of some African *Varicorhinus* and large *Barbus* (now *Labeobarbus*) species had already been stressed by Banister (1976a), referring to Banister (1972), Banister & Clarke (1980), and Howes (1987: statement not found). Therefore, divergence of the hexaploid lineage into a large *Barbus* (now *Labeobarbus*) and into a *Varicorhinus* lineage might well have followed a single hexaploidization event. Within a few years, Guégan *et al.* (1995) also finally confirmed hexaploidy for three West African representatives of the large *Barbus* using karyology, and by doing so, revised the previous tetraploidy hypothesis and supported Golubtsov & Krysanov's (1993) pan-African hexaploidy hypothesis.

#### *Genus-level consequences of the new multidisciplinary studies: the revalidation of Labeobarbus*

In line with Boulenger (1919), Pellegrin (1939), Berrebi (1981), and Berrebi *et al.* (1990), and based on isoenzyme as well as monogenean Dactylogyridae parasite data for some Moroccan species, El Gharbi, Lambert & Berrebi (1993) and El Gharbi, Birgi & Lambert (1994) re-used *Labeobarbus* as a subgenus of *Barbus*. This decision was also followed by Berrebi (1995: fig. 1), in his allozyme study, including some North and West African large *Barbus* species.

After more than 125 years since Günther's (1868) first synonymization, however, Doadrio (1994) was the first to reinstate the use of *Labeobarbus* as a full generic name and, at the same time, retained *Varicorhinus* as a valid genus, including *Varicorhinus maroccanus* (Günther, 1902), the sole North African species placed within the latter genus. Despite the shared hexaploidy

of the large *Barbus*, identified as *Labeobarbus* by Doadrio (1994), with *Varicorhinus* (see Oellermann & Skelton, 1990; Golubtsov & Krysanov, 1993), he considered the hexaploidy of the former sufficient evidence to warrant it full generic status (Doadrio, 1994).

The decision to reinstate *Labeobarbus* as a subgenus or even a full genus was not followed immediately by others. Poll & Gosse (1995), for example, retained the traditional classification in their key to the African freshwater fish genera. Furthermore, Nagelkerke & Sibbing (1997), referring to Berrebi (1995) and Berrebi *et al.* (1996), who used *Labeobarbus* as a subgenus of *Barbus*, proposed the re-elevation of the subgenus *Labeobarbus* to full generic rank, but they still described their new species in the genus *Barbus*, and continued to use the genus name *Barbus* in their subsequent papers (see Nagelkerke & Sibbing, 1998: 3–7, 2000). They argued in support of Berrebi's (1995) suggestion to re-elevate *Labeobarbus* to genus level only if further and more complete evidence would confirm the monophyly of the African hexaploid barbs.

Finally, Skelton (2001) fully reinstated the genus *Labeobarbus* as a valid genus in the second edition of his *Guide to the Freshwater fishes of Southern Africa*. He hereby implemented this nomenclatural change for the first time in a major African ichthyofaunal work. As a consequence, all South African taxa that had previously been retained in *Barbus* were attributed either to *Barbus*, i.e. the African small *Barbus* (now *Enteromius*), or to *Labeobarbus*, i.e. the African large *Barbus*. Of the former diagnostic differences recognized by Boulenger (1911a), only the difference in striation pattern of the scales was retained by Skelton (2001) to differentiate both genera. Skelton (2001) also recognized the genus *Varicorhinus* (chiselmouths), mainly on the presence of the wide, straight, and inferior mouth, with a sharp and horny lower lip. He also noted that the scales in *Varicorhinus* are longitudinally or parallel striated (Skelton, 2001), as in *Labeobarbus*, and different from *Barbus*, in which they are radiately striated. Skelton's (2001) decision marked the turning point with regard to the general acceptance of *Labeobarbus* as a full genus, and subsequently several authors have accepted it and started to transfer the large African *Barbus* species, bit by bit, and depending on the geographical region of their interest, to the genus *Labeobarbus*. For example, De Weirdt & Teugels (2007) for Lower Guinea, Getahun (2007a) for Ethiopia, Banyankimbona *et al.* (2012a) for Burundi, Kullander & Roberts (2012) for the Lukuga (Democratic Republic of Congo), and Van Steenberge, Vreven & Snoeks (2014) for the Upper Luapula and adjacent regions (for full details, see annotated checklist 1) adopted *Labeobarbus* for the large *Barbus* for the region or basin under their specific attention. Although Skelton & Bills (2008) compiled a first attempt to list all African

*Labeobarbus*, prior to the proposed synonymy of *Varicorhinus*, their work has remained more or less unnoticed (see An overview of species diversity in African *Labeobarbus*: current state of the art).

*Genus-level consequences of the new multidisciplinary studies: the synonymization of Varicorhinus*

Even though *Barbus wurtzi* Pellegrin, 1908 was considered a *Varicorhinus* species at some point (see Daget, 1962: 72; Lévêque & Daget, 1984), due to the presence of a real cutting edge in some specimens at least (see Daget, 1962); Lévêque & Guégan (1990), based on a monogenean Dactylogyridae parasite study, reidentified it as a large *Barbus* and placed it back into *Barbus*, now *Labeobarbus*. As a result, the genus *Varicorhinus* has ever since been considered absent from West Africa (see Lévêque, 1990, 2003), despite the occurrence of *Varicorhinus* mouth phenotype specimens, as identified by Daget (1962; for more details, see The present overview: what is to be learned?).

Berrebi & Valiushok (1998) discussed the status of the Lake Tana (Ethiopia) *V. beso*, the type species of the genus *Varicorhinus*, in relation to *B.* (now *L.*) *intermedius*. As they found seven diagnostic loci (on 31 presumptive allozymic loci) differentiating the two taxa they considered them to be two separate species; however, with regard to the status of the genus *Varicorhinus* they referred to their own results and to the study of Nagelkerke & Sibbing (1996), which had identified 'intergeneric' hybrids and hence pointed to *Varicorhinus* as being close or even congeneric with *Barbus* (now *Labeobarbus*). Before making taxonomic changes, they asked for a large phylogenetic analysis with sufficient taxon sampling.

Machordom & Doadrio (2001) first showed on the mtDNA level that the included African hexaploid species – i.e. large *Barbus* (now *Labeobarbus*) and *V. maroccanus* (Günther, 1902), as the single included *Varicorhinus* species – form a well-supported monophyletic clade, and consequently suggested a common hexaploid ancestor for both (see Machordom & Doadrio, 2001: fig. 1). As their phylogenetic analysis was based on mitochondrial DNA only, and therefore only reflects a matrilineal phylogeny, they explicitly stated that their data are not sufficient to differentiate between different evolutionary scenarios, i.e. between dichotomous speciation by divergence or instead by introgression and/or hybridization. This remark seemed especially valid because clear morphological differences distinguish some of the species included in their mtDNA phylogeny, but which appeared as undifferentiated, according to haplotypes from the mtDNA data, a fact that might reflect either hybridization or introgression among these taxa, or incomplete mtDNA lineage sorting after very rapid dichotomous speciation.

Tsigenopoulos *et al.* (2002) also established the monophyly of large barb (now *Labeobarbus*) mtDNA haplotypes, a result based on taxon sampling of hexaploid African 'large *Barbus*' from geographically distant parts of Africa, as well as of two basally diverging taxa, the Moroccan *Barbus reinii* Günther, 1874 and the Middle Eastern *Barbus luteus* (Heckel, 1843), both with currently undetermined ploidy levels. They interpreted this monophyly as the result of a single recent origin (see below), but unfortunately, no *Varicorhinus* species had been included in this study. They were not able to assign any particular diploid or tetraploid African lineage as an African or non-African precursor lineage of these hexaploid large *Barbus* (now *Labeobarbus*). Machordom & Doadrio (2001: fig. 1) previously identified the Palaeartic tetraploids as a sister group, however, and not the African diploids and tetraploids, nor the Asian diploids, thereby clearly suggesting a non-African origin.

Durand *et al.* (2002: fig. 1) obtained highly comparable mtDNA results, supporting the monophyly of the hexaploid African large barbs (i.e. the *Carasobarbus-Varicorhinus* clade; now *Labeobarbus s.l.*), and including *V. beso*, the type species of the genus *Varicorhinus*. As such, they were the first to present genetic evidence for the possible synonymy of both genera. In addition, they identified *B. reinii* [now a *Labeobarbus* species (*s.l.* following our nomenclature), following Tsigenopoulos *et al.* (2010)] from Morocco as well as *Barbus (Tor) grypus* [now an *Arabibarbus* species, following Borkenhagen (2014), and a *Labeobarbus (s.l.)* species following Tsigenopoulos *et al.* (2010)] from Iraq, as early diverging lineages from that *Labeobarbus-Varicorhinus* clade, albeit with low statistical support. Their results also identified a poorly supported sister-group clade composed of the monospecific genus *Kossuigobarbus*, several *Carasobarbus* spp., as well as the Moroccan *Barbus paytoni* Boulenger, 1911 [now also a *Carasobarbus* species according to Borkenhagen & Krupp (2013), and a *Labeobarbus (s.l.* following our nomenclature) species following Tsigenopoulos *et al.* (2010)]. As such, they also provided evidence for a *Labeobarbus s.l.* clade, as later identified with greater taxon sampling by Tsigenopoulos *et al.* (2010), Berrebi *et al.* (2014), and Yang *et al.* (2015) (see below).

Naran, Skelton & Villet (2007) studied the karyology of three South African yellowfish [i.e. *Labeobarbus capensis* (Smith, 1841), now *Labeobarbus seeberi* (Gilchrist & Thompson, 1913), following E. Vreven, E.R. Swartz & P.H. Skelton, unpubl. data; *L. marequensis*; and *Labeobarbus polylepis* (Boulenger, 1907)] targeting, against others, the question of their hypothetical non-African origin (see Durand *et al.*, 2002). Although these were found to be hexaploid, they underscored that the species of the Asian genus *Tor* are tetraploid, a fact that, together with their biogeo-

graphical distinctiveness, in their opinion supported the taxonomic restoration of *Labeobarbus* to full generic status. mtDNA-based studies indicate, however, that *Capoeta* as another hexaploid genus (see above; see also Arai, 2011: 49), is phylogenetically nested within the tetraploid genus *Luciobarbus* (see Tsigenopoulos *et al.*, 2003: fig. 1; see also Tsigenopoulos *et al.*, 2010: fig. 1). Therefore, according to mtDNA results the evolutionary transition from tetraploidy to hexaploidy might be frequent, and hexaploid *Labeobarbus* may have arisen easily from within tetraploid *Tor*. Hence, Naran *et al.* (2007) underscored the need for a molecular phylogenetic study including both *Tor* and *Labeobarbus* to resolve their taxonomic status. The need for such a study has recently been met by Yang *et al.* (2015), who identified *Tor* (including the type species *T. tor*), at least on the mtDNA level, as the well-supported sister group of the *Labeobarbus* clade, i.e. *Labeobarbus s.l.*, comprising the *Labeobarbus*, *Carasobarbus*, and *Pterocapoeta* lineage (for distribution of different *Labeobarbus s.l.* lineages, see Fig. 1).

Tsigenopoulos *et al.* (2010: fig. 1) substantially extended the previous taxon sampling of mtDNA-based phylogenetic analyses and provided the currently most comprehensive phylogenetic data set. Their results showed that: (1) all hexaploid taxa analysed from Africa and the Middle East constitute a clear monophyletic mtDNA clade, with the tetraploid ( $2n \sim 100$ ) South-east Asian *Neolissochilus heterostomus* Chen & Yang, 1999 (in Chen, Yang & Chen, 1999) as its sister group, but excluding the hexaploid ( $2n \sim 150$ ) Middle East genus *Capoeta* as well as tetraploid ( $2n \sim 100$ ) *Luciobarbus* (cited karyological data, see Arai, 2011); (2) in the hexaploid *Labeobarbus* mtDNA clades several well-supported geographic subclades are identified; (3) *Varicorhinus*, now represented by six species, including the type species *Varicorhinus beso*, is polyphyletic. They concluded that the genus *Varicorhinus* should be considered a junior synonym of *Labeobarbus* as far as it concerns hexaploid species. In addition to their own mtDNA results, they supported this conclusion by mentioning that *Varicorhinus* is a poorly diagnosed genus, based on a limited number of morphological characters (mouth shape and lips structure), and that it had for quite a while been suspected of belonging to the genus *Labeobarbus* because of its genetic similarity (Berrebi, 1995; Durand *et al.*, 2002) and hexaploidy (Krysanov & Golubtsov, 1996). Tsigenopoulos *et al.* (2010: fig. 1) had not included the type species of *Labeobarbus* (*L. nedgia*) in their analysis, however, and their suggested synonymization was not followed.

Levin *et al.* (2013) showed that Ethiopian *Varicorhinus* are polyphyletic with respect to mtDNA clades. They interpreted their results as sufficient evidence for a homoplasious origin of the specialized scraping mouth phenotype, which would have evolved not only in *V. beso*,

the type species of the genus *Varicorhinus*, but also convergently in *V. jubae*. They further concluded that: (1) the genus *Varicorhinus* should be restricted to the type species *V. beso*, and should therefore be monospecific; whereas (2) *V. jubae*, identified as the mtDNA sister group of the *Labeobarbus gananensis* (Vinciguerra, 1895) complex, and jointly as the sister group of the *L. intermedius* complex and *Labeobarbus ethiopicus* (Zolezzi, 1939) together, should be transferred to *Labeobarbus*.

Most recently, Berrebi *et al.* (2014: fig. 1) fully incorporated the repercussions of the study of Tsigenopoulos *et al.* (2010) in their classification of *Barbus s.l.*, and considered *V. beso*, type species of the genus *Varicorhinus*, as well as several other African *Varicorhinus*, to be *Labeobarbus* species. As such, Berrebi *et al.* (2014) effectively implemented the synonymy of *Varicorhinus* with *Labeobarbus*. Although Yang *et al.* (2015: fig. 2) still referred to species with a *Varicorhinus* mouth phenotype as *Varicorhinus* spp., all sub-Saharan Torini species with either a *Labeobarbus* or a *Varicorhinus* mouth phenotype were attributed to the *Labeobarbus* lineage, which together with the *Carasobarbus* and the *Pterocapoeta* lineages make up the *Labeobarbus* clade, here referred to as *Labeobarbus s.l.*

#### *The status of Acapoeta tanganicae and Sanagia velifera*

Since its original description as a monospecific sub-genus of *Varicorhinus* by Cockerell (1910), and its synonymization with the latter genus by Boulenger (1916a), *Acapoeta* had never been considered a valid genus. Then, Fowler (1976), in his *Catalog of World Fishes* (XXV), elevated *Acapoeta* to full generic level without any justification. This was followed by Lévêque & Daget (1984) in a taxon checklist of African freshwater fishes (CLOFFA). Poll & Gosse (1995) also followed this act and distinguished the only member of *Acapoeta*, *Acapoeta tanganicae* (Boulenger, 1900), from *Varicorhinus*, mainly based on the fact that it has 60 or more lateral line scales and the eyes are in lateral position, whereas *Varicorhinus* species have less than 50 scales and the eyes are generally in superolateral position. Therefore, the status of *Acapoeta* as a genus different from *Varicorhinus*, now within *Labeobarbus s.l.*, certainly warrants further attention and confirmation. Unfortunately, karyological and/or genetic data, which would be useful to confirm its affinities within *Labeobarbus s.l.*, are currently still lacking.

The same undoubtedly holds true for the genus *Sanagia*, with *Sanagia velifera* Holly, 1926 as the single species of this monospecific genus, which was described from and is endemic to the Sanaga Basin (Cameroon). *Sanagia* has been diagnosed by Holly (1926) mainly by its unique pharyngeal teeth formula (2, 4

and 4, 2), with only two rows of teeth on each pharyngeal jaw (for an illustration, see Banister & Thys van den Audenaerde, 1973: fig. 4), versus three rows of pharyngeal teeth in *Varicorhinus* (see Banister & Poll, 1973), and by the presence of a small cornified real cutting edge on the lower jaw (for an illustration, see Banister & Thys van den Audenaerde, 1973: fig. 2). Poll (1957) found *Sanagia* to be highly similar to *Varicorhinus*, despite the two aforementioned diagnostic characters; however, although the cornified real cutting edge on the lower jaw is similar to that in *Varicorhinus*, it is clearly narrower (for an illustration, see Banister & Thys van den Audenaerde, 1973: fig. 4). Furthermore, *S. velifera* has well-developed lips on the lateral sides of the lower jaw (for an illustration, see Banister & Thys van den Audenaerde, 1973: fig. 4), a peculiar character state that is absent in the typical *Varicorhinus* mouth phenotype. Recently, Yang *et al.* (2015: 112; table 3) assessed the position of *Sanagia* based on a mitochondrial (cytochrome *c* oxidase subunit I, *COI*) fragment of *S. velifera* (GenBank accession HM418112), and found it to be a member of the '*Labeobarbus* lineage', i.e. *Labeobarbus s.s.* As the phylogenetic analysis itself has not yet been presented, however, inclusion of *Sanagia* within *Labeobarbus s.l.* is here considered pending.

The numerous problems encountered on the generic level have never been totally unrelated to the major problems encountered on the  $\alpha$ -taxonomic level. Undoubtedly important is the topic of intraspecific versus interspecific variation, and the repeated occurrence of 'intergeneric' hybridization. An introduction to both these topics is given below.

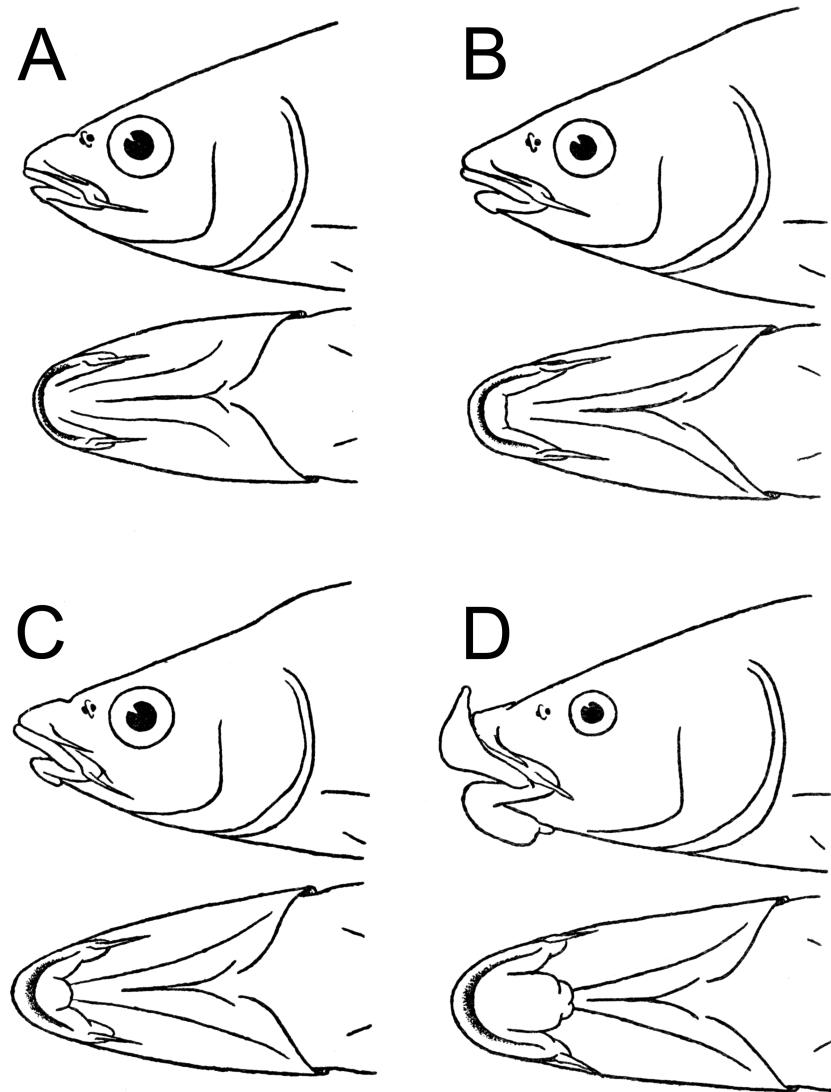
#### PHENOTYPIC VARIATION AND/OR 'INTERGENERIC' HYBRIDIZATION

The history of the problem of the genus-level categorization of the large barbs, now Torini, is intimately entwined with the efforts to find a biologically meaningful interpretation of their impressive mouth phenotype variation. Therefore, a historical overview of the gradually but profoundly changing perception of what is intra- versus interspecific mouth phenotype variation is provided here, together with the potential role and consequences of repeatedly postulated 'intergeneric' hybridization in the group.

In the second volume of his *Catalogue of the freshwater fishes of Africa in the British Museum* the major diagnostic characters used by Boulenger (1911a) to subdivide the 90 valid large *Barbus* species (now *Labeobarbus*) were: (1) the ossification of the last simple dorsal fin ray; (2) the position of the base of the ventral fins relative to the dorsal fin; and, last but not least, (3) the mouth phenotype. With regards to the mouth phenotype, he explicitly referred to: (1) the lips of the

lower jaw being either 'continuous' or 'interrupted' across the chin, which generally means with or without a mental lobe; (2) the lower jaw having a 'rounded or blunt' or instead a 'sharp' edge, with the sharp edge reminiscent of a *Varicorhinus*-like mouth phenotype. Although not apparent in his key, for ten of the valid species described in his catalogue he documented some kind of intraspecific variation of their lip phenotype. For all of these (e.g. *Barbus bynni* Forsskål, 1775; see also Boulenger, 1907c: 204) except one, this intraspecific variation fell within the boundaries of his two discrete character states, i.e. 'continuous' versus 'interrupted'. In the case of *Barbus hindii* Boulenger, 1902 (a junior synonym of *L. oxyrhynchus*, following Banister, 1973: 94), however, he noted '. . . lips moderately developed; lower continuous across chin (rarely interrupted); . . .' (emphasis ours). In this respect, *B. hindii* is an exception in crossing the boundaries between what Boulenger (1911a) generally seems to have regarded as intra- versus interspecific variation.

Based on ten newly collected large *Barbus* specimens from Lake Victoria, all of which he identified as *Barbus radcliffii* Boulenger, 1903, Norman (1928) considered *Barbus lobogenys* Boulenger, 1906, described from 'Bunkako, Buganga, Lake Victoria', a junior synonym of *B. radcliffii*, also described from 'Lake Victoria'. As such, he introduced the synonymy of two nominal large *Barbus* (now *Labeobarbus*) species, despite their very different lip morphologies, originally used by Boulenger as evidence to justify their recognition as valid species (for further details, see below). Worthington (1929), referring to Norman (1928), and based on an even larger series of specimens, redescribed *B. radcliffii*. According to Worthington (1929), the four different phenotypes all belong to one and the same species, which he referred to as *B. radcliffii* (now *Labeobarbus altianalis radcliffii*; see Worthington, 1932; and Banister, 1973): (1) specimens with a discontinuous lower lip across the chin [originally described as *Labeobarbus bayoni* (Boulenger, 1911)]; (2) specimens with continuous lower lip but without the development of a lobe (originally described as *L. radcliffii*); (3) specimens with continuous lower lip and a small lobe (identified as an intermediate form by Worthington, 1929); and finally (4) specimens with continuous and highly developed lips, i.e. including a large lobe (originally described as *L. lobogenys*; see Fig. 3; see also Worthington, 1929: legend to fig. 3). As males, females, and immature fish with large lips were found, Worthington (1929) explicitly excluded sexual dimorphism as a possible explanation for this lip polymorphism. His reinterpretation of the observed lip polymorphism in large *Barbus* (now *Labeobarbus*) also meant a radical conceptual change. Indeed, whereas before the difference between a 'continuous' versus an 'interrupted' lip morphology had generally been inter-



**Figure 3.** Illustration of four different, intraspecific, head phenotypes – in lateral and ventral view for each – as documented for *Labeobarbus radcliffii*, actually *Labeobarbus altianalis*, by Worthington (1929: 432, text to fig. 3): A, *Labeobarbus bayoni*; B, *L. radcliffii*; C, ‘intermediate’ phenotype; and D, *Labeobarbus lobogenys* (lateral views flipped horizontally). Reproduced from Worthington (1929), with permission from John Wiley and Sons.

preted as a species-specific difference (see above: Boulenger, 1911a), in the case of *B. radcliffii*, Worthington (1929) reinterpreted most if not all of it as intraspecific variation.

Later, Worthington (1932: fig. 1) illustrated and documented the same for *Labeobarbus altianalis eduardianus* (Boulenger, 1901), i.e. the Lake Edward, Lake George, and Kazinga Channel subspecies of *Labeobarbus altianalis* (Boulenger, 1900), for which he also illustrated three different mouth phenotypes similar to the ones described above for *B. radcliffii*. As an aside, he speculated that once enough specimens became available, the morphologically different endemic large barbs species from Lake Tana (Ethiopia) and the Upper Blue Nile (now *Labeobarbus*), i.e. *Barbus leptosoma* Boulenger,

1902 (actually a junior synonym of *L. intermedius*; see Banister, 1973), *Barbus degeni* Boulenger, 1902 (actually a junior synonym of *B. nedgia*; see Nagelkerke & Sibbing, 2000), and *Barbus nedgia*, might ultimately be found to be one and the same species, thereby illustrating the possible further implications of his findings.

Pellegrin (1935b), referring to Worthington (1932), reported that he found in sympatry even greater lip (‘buccal’: mouth) phenotype variation within *L. altianalis* from the Kivu and eastern tributaries of the Congo. Based on that, he recognized five different ‘varieties’, i.e. subspecies (see ICZN, 1999: article 45.6.4.), within *L. altianalis* from this region. In contrast to the Worthington (1932) case, Pellegrin also documented

non-overlapping scale counts between his subspecies. Nowadays, two of those, i.e. *Labeobarbus altianalis paucisquamatus* (Pellegrin, 1935) and *Labeobarbus altianalis longifilis* (Pellegrin, 1935), are considered full species, whereas *Labeobarbus altianalis labiosa* (Pellegrin, 1933) has been considered as a junior synonym of *L. altianalis* and *Labeobarbus altianalis lobogenysoides* (Pellegrin, 1935) has been considered as a junior synonym of *Labeobarbus paucisquamatus* (see Banister, 1972). Pellegrin's (1935b) case clearly illustrates the struggle to provide a biologically meaningful interpretation to the observed lip phenotype variation, as well as the difficulties in inferring what can and what should indeed be considered intra- versus interspecific lip phenotype variation.

A few years later, Worthington & Ricardo (1937) briefly reported that in *Labeobarbus tropidolepis* (Boulenger, 1900), endemic to the Lake Tanganyika drainage, specimens with 'interrupted' and 'continuous' lips across the chin can also be found. As a consequence, Worthington (1929, 1932) and Worthington & Ricardo (1937) concluded that lip morphology and therefore also Boulenger's key (1911a: 3, 7, 11) are of doubtful (diagnostic) value, at least for *L. a. radcliffii*, *L. a. eduardianus*, and *L. tropidolepis*. Also, Barnard (1943), referring to Worthington (1929), came to the same conclusion, i.e. that the description of new species solely on the presence of enlarged fleshy lips and labial lobes appears unwarranted. Barnard (1943: fig. 166) illustrated a similar case for *B. capensis* (now *L. seeberi*; E. Vreven, E.R. Swartz & P.H. Skelton, unpubl. data), in which both, the normal as well as the 'rubber-lip' 'varieties' are found.

Groenewald (1958: 273) further broadened the problem as he questioned the recognition of *Varicorhinus* as a valid genus different from *Barbus* (now *Labeobarbus*), by referring to the single difference between them being the 'square-shaped lower jaw, with its thick muscular covering and conspicuous horny cutting ridge'. As such, Groenewald (1958) described three different mouth phenotypes ('varieties' in his words) for *B. brucii*, which he also compared with the sympatric *Varicorhinus brucii* Boulenger, 1907: (1) a mouth phenotype without a mental lobe and with a sharp-edged lower jaw, but without a cornified real cutting edge, as found in *V. brucii* = *B. brucii* forma *sector* (= *Barbus sector* Boulenger, 1907c); (2) a mouth phenotype with a mental lobe = *B. brucii* forma *typica* (= *B. brucii*); (3) a rubberlip mouth phenotype, characterized by extremely thickened lips = *B. brucii* forma *gunningi* (= *Barbus gunningi* Gilchrist & Thompson, 1913). Groenewald (1958) also stressed that *B. brucii* as well as *V. brucii* are hardly distinguishable when seen from the side. *Barbus brucii*, *B. sector*, *B. gunningi*, as well as *V. brucii* are currently considered junior synonyms of *L. marequensis*, following Jubb (1963; for details on synonymy, see Jubb,

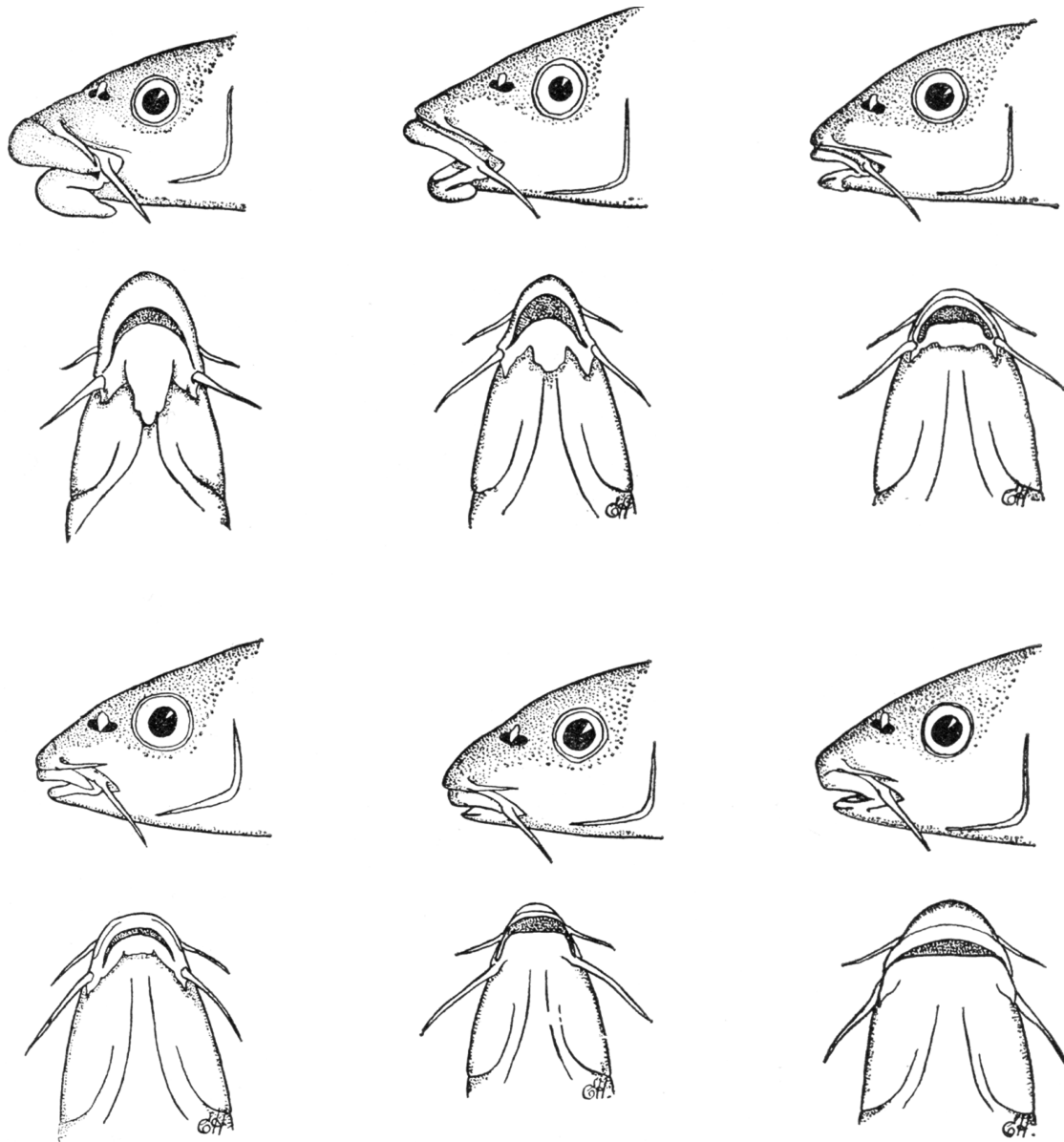
1968), with *L. marequensis* currently known from along the tropical east coast of South Africa (see Skelton, 2001: 9, 172, figs). So, although Groenewald (1958) questioned the validity of the genus *Varicorhinus*, he explicitly (see above) did not include the typical *Varicorhinus* mouth phenotype, i.e. *V. brucii*, with its cornified real cutting edge, within the intraspecific variation of *B. brucii*.

Groenewald (1958) not only documented the extreme lip polymorphism of *B. brucii* and *Barbus holubi* Steindachner, 1894 [actually a junior synonym of *Labeobarbus aeneus* (Burchell, 1822)], both with thin, normal, and thick-lipped (rubberlip) specimens, but he also provided an interesting observation for the peculiar phenomenon of lip polymorphism. He reported the case of a rubberlip specimen of *B. holubi* (now *L. aeneus*), the lips of which, after the specimen had been kept in a small pond with standing water and muddy bottom, gradually became thinner, and after a period of nearly 1 year could hardly be distinguished from the normal or thin-lipped form of the species. He concluded from this observation that no taxonomic importance can be attached to this extreme variation in lip development, because it appeared to him '... that the degree of lip development is connected with the feeding habits and method of feeding ...' (Groenewald, 1958).

In addition to *L. marequensis*, Crass (1964: fig. 7) also reported and nicely illustrated (see Fig. 4) a similar *Varicorhinus*- and *Labeobarbus*-like intraspecific mouth phenotype polymorphism ('morphs') for what is now *L. natalensis* from the tropical east coast of South Africa, i.e. KwaZulu-Natal (see Skelton, 2001). Very different from Groenewald (1958), he also regarded the typical *Varicorhinus* mouth phenotype with its clear cutting edge as part of intraspecific lip phenotype variation. Crass (1964) thereby further completed the conceptual extension of Groenewald (1958) and Jubb (1963, 1967, 1968) by including the *Varicorhinus* mouth phenotype within a single large polymorphic *Barbus* (now *Labeobarbus*) species. Considering this reinterpretation of the observed mouth phenotype polymorphism by these authors, two points should be noted: (1) their interpretation of observed strong mouth phenotype polytypy as being intraspecific variation appears to be the consequence of an apparent lack of correlation with any covarying characters that would support a species status; (2) the logical consequence of the inclusion of the typical *Varicorhinus* mouth phenotypes – i.e. with their real cutting edge – within the variation found in large *Barbus* species (now *Labeobarbus*) questioned the validity of the genus *Varicorhinus* as a distinct genus.

Gaigher (1975: 162), referring to Jubb (1967), also considered the typical *Varicorhinus* mouth phenotype as part of intraspecific variation, and speculated that

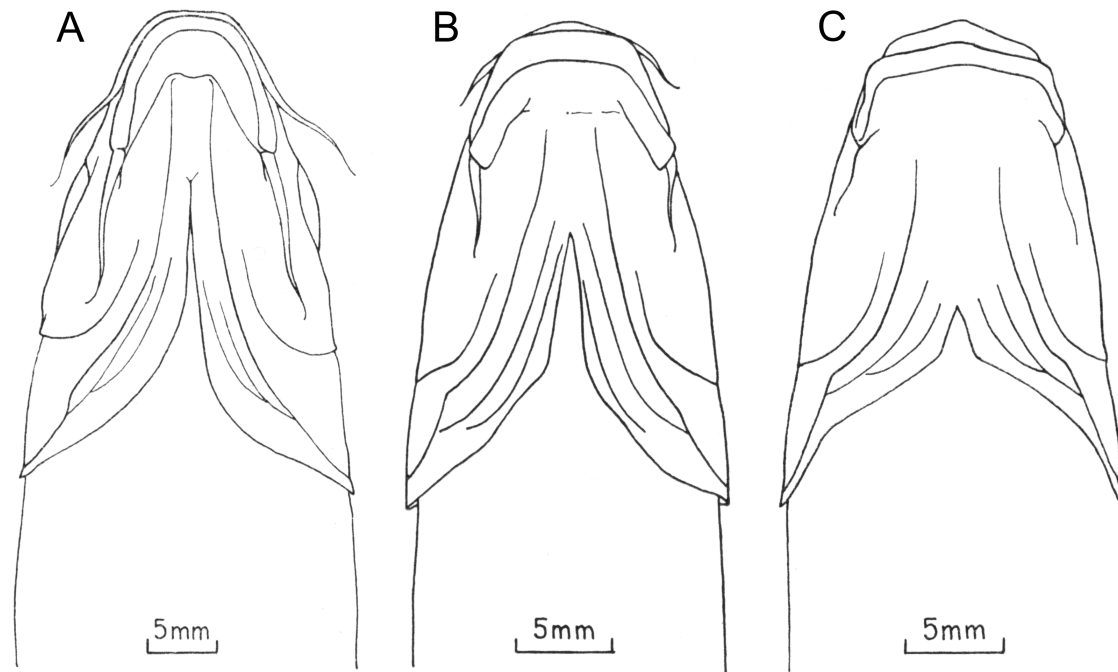




**Figure 4.** Illustration of six different, intraspecific, head phenotypes – in lateral and ventral view for each – as documented for *Labeobarbus natalensis* by Crass (1964: 53, fig. 7). Reproduced from Crass (1964), with permission from Shuter & Shooter Publishers (Pty) Ltd.

'*Varicorhinus*' and 'rubberlip' mouth forms are not genetically determined but might develop as trophic adaptations to different types of substrate. He interpreted the '*Varicorhinus*' mouth as a phenotypically plastic response to scraping epilithic algae and other food particles, whereas he considered the 'rubberlip' as a response to feeding between stones and pebbles (for the food regime, see du Plessis, 1956; Matthes, 1963). According to him, the ability to develop extreme mouth forms within a single species would be present not only in *L. marequensis*, *L. natalensis*, and *L. aeneus* (as

*B. holubi* in his paper), but in the polymorphic *L. polylepis* of the upper Elands River (Southern Africa) as well. In contrast to the Lower Elands River, *L. polylepis* in the isolated stretches are not sympatric with *L. marequensis*. Still, according to Gaigher (1975), in these stretches reduced interspecific competition could have led to the development of polymorphic mouths, because of increased ecological opportunities for *L. polylepis* as a result of little interspecific competition. Gaigher (1975) therefore was the first to explicitly correlate mouth phenotype polytypy in a *Lab.-Var.*



**Figure 5.** Schematic illustration of the ventral side of the head of: A, *Labeobarbus somereni*; B, *Labeobarbus alluaudi* – tentatively identified as an intergeneric hybrid between *L. somereni* and *Varicorhinus ruwenzorii* (now *Labeobarbus ruwenzorii*); C, *L. ruwenzorii* (from Banister, 1972: figs 2, 10, 12).

species complex with ecological opportunity, and intraspecific competition as a factor driving divergent trophic adaptation.

*Polymorphism as a result of interspecific and/or intergeneric hybridization?*

Boulenger (1902f) considered the large *Barbus* (now *Labeobarbus*) – referred to by him as the *Barbus bynni* Forsskål, 1775 group – as one of the most difficult he ever dealt with; however, he was confident that he had correctly estimated ontogenetic changes, because he had compared numerous specimens of all sizes, and therefore had not unduly multiplied the number of species. Nevertheless, he explicitly referred to the possibility that some of his species might be founded on hybrids (Boulenger, 1902f). It took decades before this idea would materialize in a concrete hypothesis or in case studies.

Almaça (1970) referred to the Moroccan *Barbus issenensis* Pellegrin, 1922 as a possible intergeneric hybrid between *Barbus massaensis* Pellegrin, 1922 [currently placed in the tetraploid *Luciobarbus* (see Arai, 2011), following Machordom & Doadrio (2001)] and *V. maroccanus*. By doing so, he was the first to suggest intergeneric hybridization between *Varicorhinus* and *Barbus* as an explanation for the occurrence of intermediate mouth phenotypes.

Banister (1972), however, was the first to thoroughly and convincingly document a first possible case of

intergeneric hybridization between large *Barbus* (now *Labeobarbus*) and *Varicorhinus* morphologically. He considered *Labeobarbus alluaudi* (Pellegrin, 1909) a possible intergeneric hybrid between two valid species, i.e. *Varicorhinus ruwenzorii* (Pellegrin, 1909) and *L. somereni*, both described from the eastern flanks of the Ruwenzori/Rwenzori mountain range (affluents of Lake George; Nile Basin) (Banister, 1972): both parental species not only differ in the typical *Labeobarbus* and *Varicorhinus* mouth phenotype characters, with an intermediate mouth phenotype found in his presumed ‘intergeneric’ hybrids (Banister, 1972: figs 2, 9, 15) (see Fig. 5), but also in selected meristics (i.e. number of lateral line scales and number of gill rakers on the first gill arch), osteological characters (e.g. the degree of development of a premaxilla ascending process; Banister, 1972: figs 6, 12, 19), and distance measurements (e.g. head length and anterior and posterior barbel lengths). It is important to point out here the differences in lateral line scales as these meristic characters are independent from the different trophic adaptations, and that this consistent but independent evidence strongly favours hybridization rather than intraspecific variation as an explanation for morphological intermediacy.

Before publishing his second case of possible intergeneric hybridization, Banister (1973) published his revision of the East and Central African large *Barbus*

(now *Labeobarbus*). In contrast to his previous publication (i.e. Banister, 1972), in this work he interpreted the observed high similarities, except in mouth phenotypes, between some large *Barbus* (now *Labeobarbus*) and *Varicorhinus* species drastically differently. For the entire Congo River Basin *s.l.* (i.e. including Lake Tanganyika and the Malagarazi Basin) he reported three large *Barbus*, now Torini species, to have specimens with both a *Labeobarbus* form (= *Labeobarbus* mouth phenotype) or a 'sector' form (= *Varicorhinus* mouth phenotype), i.e. he considered meristically and morphologically similar *Labeobarbus* and *Varicorhinus* mouth phenotypes in the Congo Basin as members of only three polymorphic species. He justified synonymizations explicitly in the first of the three cases by stating that there is '... sufficient awareness of the variability of *Barbus* [now *Labeobarbus*] species mouth parts to suggest that it is not unlikely that some African *Varicorhinus* species are highly modified individuals of various polymorphic *Barbus* [i.e. *Labeobarbus*] species' (Banister, 1972: 37). His first valid species was *Labeobarbus caudovittatus* (Boulenger, 1902) (referred to as a large *Barbus* in Banister, 1973), with *Varicorhinus stappersii* Boulenger, 1917 as a junior synonym of it. The second valid species would be *Labeobarbus trachypterus* (Boulenger, 1915), with *Varicorhinus bredoi* Poll, 1948 as a junior synonym. Interestingly in this case, Banister (1973: 120) reported for *L. trachypterus*: 'In small fishes a fleshy lower lip, often with a small mental lobe, is present, but in larger fishes the tendency is for the lower jaw to have a flat, cutting anterior margin.' By making this statement, he implicitly interpreted observed mouth phenotype variation in *L. trachypterus* as a size-related phenomenon (see *The period of discovery*). The third valid species would be *L. tropidolepis*, with *Varicorhinus chapini* Nichols & La Monte, 1950 as a full junior synonym (previously tentatively identified as a junior synonym of *L. tropidolepis* by Poll, 1953), for which he mentioned the slightly unusual mouth of the unique, small-sized holotype, and also reported the measurements as not differing from equally sized *L. tropidolepis* specimens. For the latter synonymy, however, Banister (1973) mistakenly referred to Poll (1952) instead of Poll (1953), and did not report having seen the holotype of the junior synonym himself, which does not possess a cornified cutting edge (Poll, 1953), and therefore cannot be a *Varicorhinus* mouth phenotype. In addition, in the same paper, Banister (1973) introduced two additional cases from outside the Congo Basin *s.l.*, where one or several nominal *Varicorhinus* mouth phenotype species (originally described in *Capoeta* at the genus or subgenus level) were formally synonymized with a large *Barbus* (now *Labeobarbus*) species by Banister (1973) himself (see An overview of species diversity in African *Labeobarbus*: current state of the art).

A few years later, Banister (1976a) presented his second case of possible intergeneric hybridization, this time between *V. tanganycae* (currently *Acapoeta*; see above) and *L. tropidolepis*, from Lake Tanganyika at Lunkungwe (Tanzania). Going back to his original concept of two different species (Banister, 1972), he considered these two taxa being two distinct parental species. As in the previous case (Banister, 1972), these not only differ in the typical *Labeobarbus* and *Varicorhinus* mouth phenotype characters, with an intermediate mouth phenotype found in presumed intergeneric hybrids, but also in meristics (i.e. number of lateral line scales, number of circumpeduncular scales, and number of gill rakers on the first gill arch), as well as in some distance measurements (e.g. head length, and anterior and posterior barbel lengths; %SL). As in the first case (Banister, 1972), he compared hybrids with specimens of both putative parental species, and found them not only intermediate with regards to trophic and related head morphology characters, but also in meristic characters independent of, or unrelated to, head morphology and related feeding behaviour. Banister might have justified the decision to synonymize (Banister, 1973), or not (Banister, 1972, 1976a), *Varicorhinus* with *Labeobarbus*-like taxa by his ability or disability to document any non-mouth phenotype-dependent differences: in the Congo-Basin cases (Banister, 1973), he did not find such differences, whereas he found them in the Ruwenzori and Tanganyika Basin cases (Banister, 1972, 1976a).

Banister (1976a: 184) considered Groenewald's (1958) adaptation hypothesis (our wording) unlikely, because of the apparently non-adaptive meristic differences between some sympatric *Labeobarbus* and *Varicorhinus* mouth phenotypes reported by him (see Banister, 1972, 1976a), and because of the differences in external mouth morphology between the *Labeobarbus* versus *Varicorhinus* mouth phenotypes, which he found to be correlated with structural osteological differences (for details, see Banister, 1972: figs 6–7, 12, 13).

Later, Banister & Clarke (1980) and also Banister (1984) reported two more cases of strong overall similarity between *Labeobarbus* and *Varicorhinus* forms, all from outside the Congo River Basin.

1. *Labeobarbus johnstonii* proved to be a variable species with a continuum between the *Varicorhinus* mouth phenotype (originally described as *Varicorhinus niasensis* Worthington, 1933), with a broad ventral mouth, a lower lip with a sharp, cornified real cutting edge and short barbels, and the *Labeobarbus* mouth phenotype, with a narrower and subterminal mouth, a soft lower lip, and longer barbels (Banister & Clarke, 1980; see also Tweddle, 1996). Banister & Clarke (1980: fig. 22) published a histogram of mouth widths for

*L. johnstonii* specimens from Lake Malawi showing a bimodal distribution of values for a wide-mouthed form with a cornified real cutting edge to the lower lip and a narrower-mouthed form with soft lips. Banister & Clarke (1980: plate 5) further noted that in *L. johnstonii* a horny sheath is usually associated with the broad ventral mouth, but not invariably so. A horny sheath, developed to various degrees, is present in narrow-mouthed individuals (approximately two-thirds of their sample), but may be absent from specimens with an otherwise *Varicorhinus* mouth phenotype (approximately one-third of their sample). They interpreted the bimodal distribution with comparatively few intermediates as tentative evidence for disruptive selection acting through a trophic advantage of either form for epilithic feeding or 'adventitious' feeding (Banister & Clarke, 1980). They also reported a higher frequency of wide-mouthed forms in rocky areas as compared with the equal occurrence of the generalized form in all habitats. Unfortunately, they provided no details on the size (SL) of the examined specimens, which renders it impossible to test for (probably existent) positive, allometric growth of the mouth width within *L. johnstonii*. Interestingly, in the same paper, Banister & Clarke (1980) also identified a single possible hybrid specimen between two *Labeobarbus* species, i.e. *L. johnstonii* and *L. eurystomus* (Keilhack, 1908) [= *L. brevicauda* (Keilhack, 1908), following Seegers (1995); here = *L. latirostris* (see below)].

- The second case refers to a *Varicorhinus* mouth phenotype being described as a taxonomically valid species, *V. jubae*, and to a *Labeobarbus* mouth phenotype, *L. gananensis*, both from the Juba River in Ethiopia. That the *Varicorhinus* mouth phenotype was described by Banister (1984) as a new species seems to contradict somewhat his previous decisions on synonymizations, as no obvious meristic differences were documented between the *Labeobarbus* and the *Varicorhinus* species from the Juba. According to Banister (1984) both differ only in their *Labeobarbus* versus *Varicorhinus* mouth phenotype-related head characters, i.e. gill raker counts, pharyngeal bone size, and barbel length. He even reported that both species resemble each other more closely than their congeners. He further added that the more conspicuous differences are related to feeding, and, surprisingly, added that he had '... no immediate explanation for this ...' phenomenon of 'intergeneric' siblings. Our interpretation of Banister's seemingly erratic concept is that his decision for the Juba case might well have been motivated by the absence of intermediate mouth phenotypes, which he had detected in his previous cases, in which he had synonymized meristically similar and sympatric *Labeobarbus* and *Varicorhinus*

phenotypes. Although Banister (1976a, 1984) repeatedly mentioned the need for it, and his personal work in progress, a full revision of the genus *Varicorhinus* by Banister has unfortunately never been published. Nevertheless, the synonymization of nominal species with very different mouth phenotypes has continued after Banister's work, when Lévêque & Daget (1984) synonymized two Moroccan *Capoeta* species, i.e. *C. atlantica* and *C. waldoi*, with the Moroccan *Barbus fritschii fritschii* (now *Carasobarbus*, following Borkenhagen & Krupp, 2013), both without explicit motivation, however.

Nagelkerke & Sibling (1996) identified in their Lake Tana collections four potential hybrid specimens between large *Barbus* (now *Labeobarbus*) and *Varicorhinus* (i.e. *V. beso*, the single species known from the basin). They morphologically inferred the hybrid status of these specimens based on the simultaneous presence of a horny edged, shovel-shaped lower jaw, unknown in Lake Tana *Labeobarbus*, and the presence of well-developed barbels, unknown in *V. beso*. These authors stipulated that the occurrence of hybridization does not compromise the existence of real species in Lake Tana, and that even persistent hybridization at low levels does not necessarily threaten the genetic integrity of two parent groups; however, they did not consider the possibility of a true polymorphism.

Finally, Tweddle & Skelton (1998) reported two *Varicorhinus* mouth phenotype specimens of uncertain taxonomic identity from the Ruo River, Upper Zambezi, in Malawi. Both were identified as potential hybrids between *V. dimidiatus* and *Varicorhinus xyrocheilus* (Tweddle & Skelton, 1998), although according to the authors one of them could possibly be an aberrant specimen of *V. dimidiatus*. This interesting observation strongly suggests that hybridization might not be restricted to *Labeobarbus* and *Varicorhinus* mouth phenotypes, but might also occur among similar mouth phenotype species. Indeed, this was already indirectly suggested by Banister & Clarke (1980) when they identified a large *Barbus* (now *Labeobarbus*) specimen from Lake Malawi as a hybrid between *L. eurystomus* (= *L. latirostris*, see below) and *L. johnstonii*.

Except for Banister's (1972, 1976a) two classical and groundbreaking cases, no further thorough explorations on the occurrence of this phenomenon within this group of African Torini have been made since (for a tentative identification of hybrid specimens, however, see Banister & Clarke, 1980; Nagelkerke & Sibling, 1996; Tweddle & Skelton, 1998). The repercussions of this inattention on the possible under- and/or over-recognition of species diversity within this group are manifold. To the present day a biologically sound reso-

lution of the alpha-level taxonomy of the *Lab.-Var.* species complexes is hampered by an obvious lack of elucidation of the evolutionary origin(s) and/or dynamics that have generated and maintained mouth phenotype diversity. This, however, is a prerequisite for a stable alpha- as well as the generic level taxonomy.

#### AN OVERVIEW OF SPECIES DIVERSITY IN AFRICAN *LABEOBARBUS*: CURRENT STATE OF THE ART

In light of all the aforementioned new developments in the field (see Tsigenopoulos *et al.*, 2010; Borkenhagen & Krupp, 2013; Levin *et al.*, 2013; Berrebi *et al.*, 2014; Borkenhagen, 2014), the need for a comprehensive list of all species-level taxa to be included in or excluded from *Labeobarbus s.l.* has become an important prerequisite for any further studies of the African large hexaploid Torini, in particular, and the African and Middle East ichthyofauna in general. Therefore, a table listing all currently valid African *Labeobarbus s.l.*, *Acapoeta*, and *Sanagia* species has been compiled (see Table 1). For details with regards to how data have been compiled, see the Material and methods section and the legend to Table 1.

#### *The compilation of the present overview: what, how, and why?*

Our current compilation lists a total of 125(+2) valid African *Labeobarbus s.l.* species known to date (Table 1). Mouth phenotype diversity has been tabulated with the two major hypotheses in mind: on one hand, the two morphologically well-documented cases of 'intergeneric' hybridization cited above, where Banister (1972, 1976a) illustrated intermediate mouth phenotype(s) to represent hybrid specimens; and on the other hand, the decision by Banister (1972) and others (Groenewald, 1958; Jubb, 1963, 1967, 1968; Crass, 1964) to interpret the huge observed mouth phenotype variation, encompassing both the *Labeobarbus* as well as the *Varicorhinus* mouth phenotypes, as intraspecific variation. The latter way of looking at the observed mouth phenotype diversity has also resulted in this aspect becoming somehow largely invisible, as it is presumed to be largely uninformative or even irrelevant for species diagnosis. Therefore, the current tabulation should be seen as a first effort in mapping the terrain, and has been undertaken to give a first glimpse of the current problems, questions raised, and further research needed.

#### *The present overview: details on the taxonomic decisions made*

To fully understand the extent and taxonomic conclusions of the provided list, the following points are explained in greater detail: (1) species previously explicitly allocated to *Labeobarbus* but which have been removed;

(2) the identification of implicit synonymies according to the literature; (3) a small *Barbus* revealed to be a *Labeobarbus* species; (4) *Labeobarbus* spp. identified as possible hybrid phenotypes in the literature; (5) the neotype designation for *L. beso*, previously *V. beso*, the type species of the genus *Varicorhinus*; (6) substitute names (ICZN, 1999: article 60) following the synonymization of *Varicorhinus* with *Labeobarbus*; (7) the lectotype designation for *Labeobarbus sandersi* (Boulenger, 1912), previously a *Varicorhinus* species; (8) generic level synonyms of *Labeobarbus* for Africa.

1. Six Ethiopian species reported by Getahun (2007a: 94) as belonging to the genus *Labeobarbus* were, in fact, attributed to it in error and should have remained in *Barbus* (now *Enteromius*; see Yang *et al.*, 2015). These are: *Barbus anema* Boulenger, 1903; *Barbus arambourgi* Pellegrin, 1935; *Barbus kerstenii* Peters, 1868; *Barbus neglectus* Boulenger, 1903; *Barbus stigmatopygus* Boulenger, 1903; and *Barbus wernerii* Boulenger, 1905 (actually a junior synonym of *B. stigmatopygus*: see annotated checklist 1). Indeed, all these are small *Barbus*, now *Enteromius*, with radiately striated scales and a dorsal fin formula of III7–8. One of them, i.e. *B. kerstenii*, even has a spiny, serrated, last unbranched dorsal fin ray, a character state never found in *Labeobarbus*. Also, the attribution of *Barbus litamba* Keilhack, 1908 to *Labeobarbus* by Snoeks (2004) is in error. Although this is indeed a large *Barbus* (maximum size, 315 mm SL; see Lévêque & Daget, 1984), this species also has a spiny, serrated, last unbranched dorsal fin ray, which, as stated above, is a character state that has never been documented for any of the karyotyped, hexaploid, *Labeobarbus*. Instead, the few karyotyped large African *Barbus* with a spiny, serrated, last unbranched dorsal fin ray were all shown to be diploid, as for *Barbus mattozi* Pereira Guimarães, 1884, or tetraploid, as for *B. capensis* (under *Barbus andrewi* Barnard, 1937) and *Barbus serra* Peters, 1864 (see Tsigenopoulos *et al.*, 2002). The same holds true for *Barbus rapax* Steindachner, 1894 (actually a junior synonym of *B. mattozi* following Jubb, 1963, although questioned by Skelton, 2001: 161), a sawfin *Barbus* (see Skelton, 2001) with radiating striae that has also erroneously been identified as a yellowfish (now *Labeobarbus*) by Groenewald (1958) in the past. Furthermore, following E. Vreven, E.R. Swartz & P.H. Skelton (unpubl. data), *B. capensis* has to be removed from *Labeobarbus* as a re-examination of the holotype revealed it to be a senior synonym of *B. andrewi* and hence not a *Labeobarbus* species. Therefore, in the present list, the name of *L. seeberi*, previously a junior synonym of *B. capensis*, has been used for the southern African clanwilliam yellowfish.

**Table 1.** Overview of all African (i.e. all species present on the African continent as delimited in Roberts, 1975: 266), large barbs, now Torini species, placed in *Labeobarbus s.l.*

Current name	Author & date	Mouth phenotype(s)			Notes	Max. size	References
		<i>Labeobarbus</i>	Intermediate	<i>Varicorhinus</i>			
1							
<i>Labeobarbus acuticeps</i>	(Matthes, 1959)		a & ± a <sub>h</sub>		403 TL	DeV&TvdA, 1990: 18	
<i>Labeobarbus actirostris</i>	(Bini, 1940)		a <sub>h</sub> , r & n	N1	411 FL	Na&Si, 1997: 130	
<i>Labeobarbus aeneus</i> <sup>N2</sup>	(Burchell, 1822)	h & f	x	N3	500 FL	Sk, 2001: 169	
<i>Labeobarbus altianalis</i>	(Boulenger, 1900)	f	± a <sub>h</sub> , r & n	N4	540 SL	Ec, 1992: 44	
<i>Labeobarbus altipinnis</i>	(Banister & Poll, 1973)		n <sub>h</sub>	N5	338 SL	Ba&Po, 1973: 82; Lé&Da, 1984: 336	
<i>Labeobarbus ansorgii</i>	(Boulenger, 1906)		n <sub>h</sub>		300 TL	Bo, 1906a: 111; Lé&Da, 1984: 337	
<i>Labeobarbus aspius</i>	(Boulenger, 1912)		n <sub>s</sub>		420 TL	Bo, 1912: 14; Lé&Da, 1984: 228; DeW&Te, 2007: 516–517	
<i>Labeobarbus axelrodi</i>	(Getahun, Stiassny & Teugels, 2004)				160 SL	Ge <i>et al.</i> , 2004: 160–161; Ge, 2007b: 542–543	
<i>Labeobarbus batesii</i>	(Boulenger, 1903)		± a <sub>h</sub> & n	N6	435 TL	Lé&Da, 1984: 230; Le, 2003: 367–368; DeW&Te, 2007: 520–521	
10							
<i>Labeobarbus beso</i>	(Rüppell, 1835)				360 TL	Lé&Da, 1984: 337	
<i>Labeobarbus boulengeri</i> <sup>N7</sup>	current paper				160 TL	Bo, 1910: 548; Lé&Da, 1984: 338	
<i>Labeobarbus brauni</i>	(Pellegrin, 1935)		n <sub>s</sub> ?	N8	195 SL; 245 TL	Pe, 1935: 402	
<i>Labeobarbus brevicephalus</i>	(Nagelkerke & Sibbing, 1997)		n <sub>h</sub>	N9	317 FL	Na&Si, 1997: 131; Na&Si, 2000: 192	
<i>Labeobarbus brevispinis</i>	(Holly, 1927)		a <sub>s</sub> & n <sub>s</sub>		230 TL	Lé&Da, 1984: 232; DeW&Te, 2007: 520–521	
<i>Labeobarbus bynni</i>	(Forsskål, 1775)	f, ± f <sub>h</sub>	a & n	N10	820 TL	Lé&Da, 1984: 234	
<i>Labeobarbus cardozoi</i>	(Boulenger, 1912)	f <sub>s</sub>			530 TL	Bo, 1912: 12; Lé&Da, 1984: 238; DeW&Te, 2007: 526–527	
<i>Labeobarbus caudovittatus</i>	(Boulenger, 1902)	f	a <sub>s</sub> & n	N11	800 TL	Lé&Da, 1984: 239; DeW&Te, 2007: 524 & 527; Ec, 1992: 45	
<i>Labeobarbus clarkeae</i>	(Banister, 1984)		pap <sub>h</sub>		161 SL	Ba, 1984: 277	
<i>Labeobarbus claudinae</i>	(De Vos & Thys van den Audenaerde, 1990)	f	a <sub>h</sub>		234 SL; 300 TL	DeV&TvdA, 1990: 7	
20							
<i>Labeobarbus codringtonii</i>	(Boulenger, 1908)	h & f	n <sub>h</sub>	N12	390 TL	Sk, 2001: 173	
<i>Labeobarbus compiniei</i>	(Sauvage, 1879)	h & f <sub>h</sub>		N13	730 TL	Sa, 1879: 102; Lé&Da, 1984: 241; DeW&Te, 2007: 528–529	
<i>Labeobarbus crassibarbis</i>	(Nagelkerke & Sibbing, 1997)		a, r <sub>h</sub> & n	N14	505 FL	Na&Si, 1997: 132; Na&Si, 2000: 193	
<i>Labeobarbus dainellii</i>	(Bini, 1940)	f	a, r <sub>h</sub> & n	N15	490 FL	Na&Si, 1997: 133	
<i>Labeobarbus dartvellei</i>	(Poll, 1945)		n <sub>h</sub>		117 TL	Po, 1945: 299–300; Lé&Da, 1984: 241	
<i>Labeobarbus dimidiatus</i>	(Tweedle & Skelton, 1998)		rce <sub>h</sub>	N16	245 SL	Tw&Sk, 1998: 371; Sk, 2001: 174	
<i>Labeobarbus ensifer</i>	(Boulenger, 1910)		pap <sub>s</sub>	N17	195 TL	Bo, 1910: 546; Lé&Da, 1984: 337	
<i>Labeobarbus ensis</i>	(Boulenger, 1910)		a <sub>s</sub> , r <sub>s</sub> & n <sub>s</sub>		140 TL	Bo, 1910: 550; Lé&Da, 1984: 243	
<i>Labeobarbus ethiopicus</i>	(Zolezzi, 1939)	f <sub>s</sub>	a & n	N18	258 SL	Ba, 1973: 41; Lé&Da, 1984: 243	
<i>Labeobarbus fasolt</i>	Pappenheim (in Pappenheim & Boulenger, 1914)	f <sub>h</sub>			500 TL	Pa&Bo, 1914: 241; Lé&Da, 1984: 245	

30	<i>Labeobarbus fimbriatus</i> (Holly, 1926)		<b>n<sub>s</sub></b>		213 TL	Ho, 1926: 157; Lé&Da, 1984: 338
	<i>Labeobarbus fritschii</i> (Günther, 1874)		<b>n<sub>s</sub></b>	rce (2 V. syn)	180 TL	Lé&Da, 1984: 246
	<i>Labeobarbus gananensis</i> (Vinciguerra, 1895)	<b>f<sub>h</sub></b>	<b>a &amp; n</b>		176 SL	Ba, 1973: 45; Lé&Da, 1984: 247
	<i>Labeobarbus gestetneri</i> (Banister & Bailey, 1979)		<b>n<sub>h</sub></b>		249 TL	Ba&Ba, 1979: 218; Lé&Da, 1984: 247
	<i>Labeobarbus girardi</i> (Boulenger, 1910)		<b>n<sub>s</sub></b>		300 TL	Bo, 1910: 551; Lé&Da: 1984: 247
	<i>Labeobarbus gorgovensis</i> (Bini, 1940)		<b>a, ± a<sub>h</sub>, r &amp; n</b>		618 FL	Na&Si, 1997: 134
	<i>Labeobarbus gorguari</i> (Rüppell, 1835)		<b>n</b>		532 FL	Na&Si, 1997: 135
	<i>Labeobarbus gruvelli</i> (Pellegrin, 1911)		<b>± a<sub>h</sub>, r &amp; n</b>		280 TL	Pe, 1911: 185; Lé&Da, 1984: 247; Lé&Gu, 1990: 52–54; Le, 1990: 308–309
	<i>Labeobarbus gulielmi</i> (Boulenger, 1910)		<b>a<sub>s</sub> &amp; n<sub>s</sub></b>		150 TL	Bo, 1910: 551; Lé&Da, 1984: 248
	<i>Labeobarbus habereri</i> (Steindachner, 1912)	<b>f<sub>h</sub></b>			162 TL	Ho, 1927: 141; Lé&Da, 1984: 249; DeW&Te, 2007: 518–519
40	<i>Labeobarbus harterti</i> (Günther, 1901)		<b>n<sub>s</sub></b>		285 TL	Lé&Da, 1984: 246
	<i>Labeobarbus huloti</i> (Banister, 1976)		<b>a &amp; n<sub>h</sub></b>		282 SL	Ba, 1976b: 192; Lé&Da, 1984: 250
	<i>Labeobarbus humphri</i> (Banister, 1976)		<b>a<sub>h</sub></b>		214 SL	Ba, 1976b: 198; Lé&Da, 1984: 250
	<i>Labeobarbus intermedius</i> (Rüppell, 1835)	<b>h &amp; f</b>	<b>a, r'<sub>h</sub> &amp; n</b>	rce (1 V. syn)	489 SL	Lé&Da, 1984: 255
	<i>Labeobarbus iphthimostoma</i> (Banister & Poll, 1973)			<b>rce<sub>h</sub></b>	181 SL	Ba&Po, 1973: 87; Lé&Da, 1984: 338
	<i>Labeobarbus iturii</i> (Holly, 1929)	<b>f<sub>h</sub></b>		<b>rce<sub>h</sub></b>	365 TL	Ho, 1929: 35; Lé&Da, 1984: 255
	<i>Labeobarbus jaegeri</i> (Holly, 1930)				188 TL	Ho, 1930: 199; Lé&Da, 1984: 338; Ge, 2007b: 541–542
	<i>Labeobarbus johnstonii</i> (Boulenger, 1907)		<b>a &amp; n<sub>h</sub></b>	rce (1 V. syn)	320 SL	Ba&Cl, 1980: 505–506; Lé&Da, 1984: 256; Ec, 1992: 45
	<i>Labeobarbus jubae</i> (Banister, 1984)			<b>rce<sub>h</sub></b>	135 SL	Ba, 1984: 273
	<i>Labeobarbus jubbi</i> (Poll, 1967)				166 SL; 225 TL	Po, 1967: 177; Lé&Da, 1984: 257
50	<i>Labeobarbus kimberleyensis</i> (Gilchrist & Thompson, 1913)		<b>a<sub>h</sub></b>		825 FL	Sk, 2001: 168
	<i>Labeobarbus lagensis</i> (Günther, 1868)		<b>n<sub>h</sub></b>		230 SL/255 TL	Lé&Da, 1984: 259; Lé&Gu, 1990: 49; Le, 1990: 304; Le, 2003: 363–364
	<i>Labeobarbus latirostris</i> <sup>N27</sup> (Keilhack, 1908)		<b>n<sub>l</sub></b>		370 SL	Ke, 1908: 166
	<i>Labeobarbus leleupanus</i> (Matthes, 1959)			<b>rce<sub>h</sub></b>	220 SL	Lé&Da, 1984: 338
	<i>Labeobarbus longidorsalis</i> (Pellegrin, 1935)			<b>rce<sub>h</sub></b>	260 SL; 320 TL	Pe, 1935: 403; Lé&Da, 1984: 338
	<i>Labeobarbus longifilis</i> (Pellegrin, 1935)		<b>a<sub>l</sub></b>		247 mm SL	Ba, 1973: 76
	<i>Labeobarbus longissimus</i> (Nagelkerke & Sibbing, 1997)	<b>f</b>	<b>r &amp; n<sub>h</sub></b>		548 FL	Na&Si, 1997: 135
	<i>Labeobarbus lucius</i> (Boulenger, 1910)		<b>n<sub>s</sub></b>		230 TL	Bo, 1910: 553; Lé&Da, 1984: 262; DeW&Te, 2007: 514–515
	<i>Labeobarbus lufupensis</i> (Banister & Bailey, 1979)		<b>n<sub>h</sub></b>		194 SL	Ba&Ba, 1979: 227; Lé&Da, 1984: 338
60	<i>Labeobarbus macroceps</i> (Fowler, 1936)		<b>n<sub>h</sub></b>		320 TL	Fo, 1936: 283; Lé&Da, 1984: 263
	<i>Labeobarbus macrolepidotus</i> (Pellegrin, 1928)		<b>n<sub>s</sub></b>	rce	540 TL	Lé&Da, 1984: 339
	<i>Labeobarbus macrolepis</i> (Pfeffer, 1889)		<b>n<sub>l</sub></b>		400 SL	Ec, 1992: 46
	<i>Labeobarbus macrophthalmus</i> (Bini, 1940)		<b>a, r<sub>h</sub> &amp; n</b>		425 FL	Na&Si, 1997: 136
	<i>Labeobarbus malacanthus</i> (Pappenheim, 1911)		<b>± a<sub>h</sub></b>		150 TL	Pa, 1911: 517; Lé&Da, 1984: 264; DeW&Te, 2007: 521–522

Table 1. Continued

Current name	Mouth phenotype(s)					Notes	Max. size	References
	<i>Labeobarbus</i>	Intermediate	<i>Varicorhinus</i>					
<i>Labeobarbus marequensis</i>	h & f	a <sup>2</sup> <sub>h</sub> , r & n	rce (2 V. syn)	N31	470 TL	Sk, 2001: 172		
<i>Labeobarbus mariae</i>		n <sup>2</sup> <sub>s</sub>	rce <sub>s</sub> (V.-like)	N32	300 SL	Ho, 1926: 156; Lé&Da, 1984: 339; Ge, 2007b: 543–544		
<i>Labeobarbus maroccanus</i>		a <sub>h</sub>	rce <sub>s</sub>		400 TL	Lé&Da, 1984: 339		
<i>Labeobarbus matris</i>		n <sub>h</sub>			322 TL	Ho, 1928: 4		
<i>Labeobarbus mauambi</i>		± a <sub>s</sub> & a <sub>s</sub>			150 TL	Lé&Da, 1984: 268		
<i>Labeobarbus mauambiensis</i>	f <sub>s</sub>	n <sub>h</sub>			150 TL	Lé&Da, 1984: 268		
<i>Labeobarbus mbami</i>		n <sub>h</sub>		N33	230 SL	DeW&Te, 2007: 524–525		
<i>Labeobarbus megastoma</i>		a <sub>h</sub> , r & n			824 FL	Na&Si, 1997: 137; Na&Si, 2000: 197		
<i>Labeobarbus micronema</i>		n <sub>s</sub>			340 TL	Lé&Da, 1984: 268; DeW&Te, 2007: 518–519		
<i>Labeobarbus mirabilis</i>	f	r <sub>h</sub>			353 SL	Ba, 1973: 92; Lé&Da, 1984: 270		
<i>Labeobarbus mungoensis</i>		a <sub>h</sub> & n			179 SL	Lé&Da, 1984: 271; DeW&Te, 2007: 522–523		
<i>Labeobarbus nanningsi</i>	f <sub>h</sub>	a & n	rce	N35	320 TL	Po, 1967: 157; Lé&Da, 1984: 271		
<i>Labeobarbus natalensis</i> <sup>N34</sup>	h & f			N36	638 TL	Sk, 2001: 170		
<i>Labeobarbus nedgia</i>	± h <sub>h</sub> & f			N37	707 FL	Na&Si, 1997: 138		
<i>Labeobarbus nelspruitensis</i>		a <sub>h</sub> & n	rce <sub>s</sub>		320 TL	Sk, 2001: 175		
<i>Labeobarbus nthuwa</i>		n <sub>h</sub>	rce	N38	236 SL	Tw&Sk, 2008: 29		
<i>Labeobarbus osseensis</i>	f	a, r & n <sub>h</sub>	rce (1 V. & 1 V.-like syn)	N39	264 SL	Na&Si, 2000: 190		
<i>Labeobarbus oxyrhynchus</i>	h & f	± a <sub>1</sub>		N40	400 SL	Ec, 1992: 46		
<i>Labeobarbus pagensecheri</i>				N41	350 SL	Ec, 1992: 45		
<i>Labeobarbus parauldroni</i>	h <sub>h</sub> & f			N42	230 SL	Lé <i>et al.</i> , 1987: 347; Lé&Gu, 1990: 48; Lé, 1990: 303; Lé, 2003: 363–364		
<i>Labeobarbus paucisquamatus</i>	h	a & r	rce <sup>2</sup> <sub>h</sub>	N43	248 SL	Ba, 1973: 106; Lé&Da, 1984: 279		
<i>Labeobarbus pellegrini</i>				N44	212 TL	Pe, 1932: 959; Lé&Da, 1984: 339		
<i>Labeobarbus petitjeani</i>		a <sub>s</sub> , r <sub>s</sub> & n <sub>s</sub>		N45	175 SL	Lé&Gu, 1990: 53		
<i>Labeobarbus platydorsus</i>		a, r, ± r <sub>h</sub> & n		N46	635 FL	Na&Si, 1997: 139; Na&Si, 2000: 199		
<i>Labeobarbus platyrhinus</i>		r <sub>h</sub>	rce <sub>s</sub>		400 SL	Ec, 1992: 45		
<i>Labeobarbus platystomus</i>					210 TL	Lé&Da, 1984: 339		
<i>Labeobarbus pojeri</i>		a <sub>h</sub> & n		N47	180 TL	Po, 1944: 6		
<i>Labeobarbus polylepis</i>	x?	a <sub>h</sub>	rce?		585 TL	Lé&Da, 1984: 282		
<i>Labeobarbus progenys</i>		n <sub>h</sub>			180 TL	Lé&Da, 1984: 282; Le, 2003: 366–367; DeW&Te, 2007: 516–517		
<i>Labeobarbus pungweensis</i>		a <sub>s</sub>	rce <sub>h</sub>	N48	180 SL	Sk, 2001: 176		
<i>Labeobarbus reinii</i>	f <sub>s</sub>	n <sub>h</sub>			555 TL	Pe, 1921: 136; Lé&Da, 1984: 285		
<i>Labeobarbus rhinoceros</i> <sup>N49</sup>		n <sub>h</sub>			295 TL	Ba, 1973: 83		
<i>Labeobarbus rhinophorus</i>		n <sub>s</sub>			150 TL	Lé&Da, 1984: 285		
<i>Labeobarbus robertsi</i>		pap <sub>h</sub>			220 SL	Walsh, 2010: 142		



	<i>Labeobarbus rocadasi</i>	(Boulenger, 1910)	$\pm a_s, r_s \& n_s$			350 TL	Lé&Da, 1984: 285; DeW&Te, 2007: 526–527
	<i>Labeobarbus rosae</i>	(Boulenger, 1910)	$n_s^2$	<b>rce</b> , (V.-like)	N50	95 TL	Lé&Da, 1984: 286
	<i>Labeobarbus roylii</i>	(Boulenger, 1912)	<b>h<sub>s</sub> &amp; f<sub>s</sub></b>			550 TL	DeW&Te, 2007: 523–524
100	<i>Labeobarbus ruandae</i>	Pappenheim (in Pappenheim & Boulenger, 1914)		<b>rce<sub>h</sub></b>		150 TL	Lé&Da, 1984: 340
	<i>Labeobarbus ruasae</i>	Pappenheim (in Pappenheim & Boulenger, 1914)	$\pm f_s$			430 SL;	DeV&TvdA, 1990: 19
	<i>Labeobarbus ruwenzorii</i>	(Pellegrin, 1909)	<b>a, r<sub>s</sub> &amp; n<sub>s</sub></b>	<b>rce<sub>s</sub></b>	N51	495 TL	Lé&Da, 1984: 340
	<i>Labeobarbus sacratus</i>	(Daget, 1963)	<b>f</b>		N52	231 TL	Lé&Gu, 1990: 56; Le, 1990: 307;
	<i>Labeobarbus sandersi</i>	(Boulenger, 1912)	<b>h &amp; f</b>	<b>rce<sub>1</sub></b>	N53	256 SL	Le, 2003: 367–368
	<i>Labeobarbus seebert<sup>N54</sup></i>	(Gilchrist & Thompson, 1913)	<b>a<sub>s</sub>, r<sub>s</sub> &amp; n<sub>s</sub></b>	<b>rce</b>	N55	370 TL	Bo, 1912: 12; Lé&Da, 1984: 340
	<i>Labeobarbus semireticulatus</i>	(Pellegrin, 1924)	$n_s^2$	<b>rce<sub>s</sub></b>	N56	987 TL	Sk, 2001: 171
	<i>Labeobarbus somereni</i>	(Boulenger, 1911)	$\pm n_h$			128 SL;	Pe, 1924: 287; Lé&Da, 1984:
	<i>Labeobarbus stappersii</i>	(Boulenger, 1915)	<b>a &amp; n<sub>h</sub></b>			158 TL	340; Ge, 2007b: 545–546
	<i>Labeobarbus steindachneri</i>	(Boulenger, 1910)	<b>f</b>	<b>rce<sub>s</sub></b>	N57	400 SL	Ec, 1992: 46
110	<i>Labeobarbus stenostoma</i>	(Boulenger, 1910)	<b>r &amp; n<sub>h</sub></b>	<b>rce<sub>h</sub></b>		594 SL	Ba, 1973: 119; Lé&Da, 1984: 288
	<i>Labeobarbus surkisi</i>	(Rüppell, 1835)	<b>n<sub>h</sub></b>	<b>rce<sub>h</sub></b>	N58	330 SL	Ge, 2007b: 546–547
	<i>Labeobarbus tornieri</i>	(Steindachner, 1906)	<b>a, r<sub>1</sub> &amp; n<sub>h</sub></b>			105 TL	Bo, 1910: 546; Lé&Da, 1984: 341
	<i>Labeobarbus trachipterus</i>	(Boulenger, 1915)	<b>n<sub>h</sub></b>	<b>rce</b> (1 V. syn)	N59	430 FL	Na&Si, 1997: 140
	<i>Labeobarbus tropidolepis</i>	(Boulenger, 1900)	<b>a, r<sub>1</sub> &amp; n<sub>h</sub></b>			184 SL	Ge, 2007b: 547–548
	<i>Labeobarbus truttiformis</i>	(Nagelkerke & Sibbing, 1997)	<b>a<sub>h</sub>, r &amp; n</b>		N60	239 SL	Ba, 1973: 120; Lé&Da, 1984:
	<i>Labeobarbus tsanensis</i>	(Nagelkerke & Sibbing, 1997)	<b>a<sub>h</sub>, r &amp; n</b>		N61	291–292	291–292
	<i>Labeobarbus upembensis</i>	(Banister & Bailey, 1979)	<b>rce<sub>h</sub></b>		N62	850 SL	Ec, 1992: 44
	<i>Labeobarbus urotaenia<sup>N63</sup></i>	(Boulenger, 1913)	<b>a<sub>s</sub></b>			442 FL	Na&Si, 1997: 141; Na&Si, 2000:
120	<i>Labeobarbus varicosoma</i>	(Boulenger, 1910)	<b>pap<sub>h</sub></b>			394 FL	Na&Si, 1997: 142; Na&Si, 2000:
	<i>Labeobarbus versluisii</i>	(Holly, 1929)	<b>a<sub>s</sub></b>			203 SL	202
	<i>Labeobarbus werneri</i>	(Holly, 1929)	<b>f<sub>s</sub></b>			50 TL	Ba&Bai, 1979: 229; Lé&Da,
	<i>Labeobarbus witti</i>	(Banister & Poll, 1973)				170 TL	1984: 341
	<i>Labeobarbus wurzli</i>	(Pellegrin, 1908)			N64	111 TL	Lé&Da, 1984: 295
125	<i>Labeobarbus xyrocheilus</i>	(Tweddle & Skelton, 1998)	<b>n<sub>h</sub></b>	<b>rce<sup>2</sup><sub>s</sub></b>	N65	145 TL	Bo, 1910: 547; Lé&Da, 1984: 341
	<b>Hybrids and possible hybrids</b>		<b>n<sub>h</sub></b>	<b>rce</b>	N66	375 TL	Ho, 1929: 33; DeW&Te, 2007:
	<i>Labeobarbus alluaudi</i>	(Pellegrin, 1909)	<b>n<sub>s</sub></b>			285 SL	528–529
	<i>Labeobarbus microbarbis</i>	(David & Poll, 1937)	<b>n<sub>h</sub></b>	<b>rce</b>	N67	370 TL	Ge, 2007b: 548–549
	<i>Labeobarbus microtrolepis</i>	(Boulenger, 1902)	$\pm n_h$	<b>rce<sub>h</sub></b>	N68	178 SL	Ba&Po, 1973: 91; Lé&Da, 1984:
	<b>Others</b>					198 SL	341
	<i>Acapoeta tanganiacae</i>	(Boulenger, 1900)	<b>rce<sub>1</sub></b>			230 SL;	Lé&Gu, 1990: 61
	<i>Sanagia velifera</i>	Holly, 1926	<b>rce<sub>s</sub></b> (V.-like)			270 TL	Tw&Sk, 1998: 379; Sk, 2001:
						118 SL	370
						610 TL	Ba, 1973: 89; Lé&Da, 1984: 268
						158 SL;	Lé&Da, 1984: 217
						190 T	Lé&Da, 1984: 336; DeW, 2007:
							536–537

Nominal species representing hybrid phenotypes, or suspected to be doing so, according to the literature cited, have been listed separately at the end of the table. Also both *Acapoeta* and *Sanagia* species have been added at the end as a matter of completeness (i.e. total +2). Unjustified revalidations, however, i.e. the reuse of formally synonymized species names without any explicit justification with regards to this decision, have not been followed. The same holds true for unsubstantiated proposals of possible new synonyms/fes. All species names are organized in alphabetic order.

For each species the following information is provided: current species name (Current name); author(s) and date of the original description (Author & date); maximum size (Max. size) reported (FL, fork length; SL, standard length; TL, total length; all in mm); documented mouth phenotype(s) [Mouth phenotype(s)], and as such possible mouth polymorphism; and references (References) used for the current compilation of the tabulated information with regards to the maximum reported size. Additional information has been provided under Notes, referred to in the table with superscript N, and followed by the number of the particular note. The notes themselves are to be found below the table.

Mouth phenotype(s) as well as possible mouth polymorphism have been tabulated for each of the valid species to get a first pan-African overview of this peculiar phenomenon. For this, the observed mouth phenotype diversity has been subdivided into three major categories, i.e. the *Labeebarbus* versus *Varicorhinus* mouth phenotype as the two extreme mouth phenotype categories and with a third, the intermediate category, in between these. The typical *Labeebarbus* mouth phenotype has been defined as characterized by the presence of, at least, a free mental lobe, and has been further subdivided according to the presence/absence of hypertrophied lips (i.e. the anteromedian part of the upper lip forming a flap-like extension clearly covering the anteromedian part of the snout). The typical *Varicorhinus* mouth phenotype has been restricted to species with the presence of a clear cornified cutting edge on the lower jaw. Finally, specimens with an attached or rudimentary (i.e. no real lobe, but only a discontinuous suture line demarcating a lobe-like structure) mental lobe, or without a mental lobe, have been tabulated as intermediate. Priority has been given to tabulate the mouth phenotype(s) of the type(s) with special attention in differentiating the mouth phenotype(s) as found in the name-bearing type(s), which is/are the only one(s) with nomenclatural standing (see ICZN, 1999: articles 72.1.2. and 72.1.3.). Whenever available, and based on sound, reliable, revisionary evidence [see Nagelkerke & Sibbing (1997, 2000) for the Lake Tana (Ethiopia) species and Skelton (2001) for the Southern African species], mouth phenotype polymorphism as reported for the species as a whole, i.e. including non-types, has been included.

The abbreviations used to characterize these mouth phenotypes are as follows: a, attached [equals continuous lower lip development (LLD) of Nagelkerke & Sibbing (2000: fig. 2)]; f, free; h, hypertrophied; n, no [equals interrupted LLD of Nagelkerke & Sibbing (2000: fig. 2)]; and r, rudimentary mental lobe. A few *Labeebarbus* species have papillae (pap) on the lower as well as the upper jaw instead. These have explicitly been reported as such under the intermediate mouth phenotype, although, in these cases, this does not imply the intermediacy of this character state. A question mark (?) has been used when, unfortunately: (1) the detailed mouth phenotype remains undocumented [i.e. not stipulated in the literature and the name-bearing/nominal type(s) are lost or have not been examined]; (2) the present character state is doubtful, this most often because of damage or due to the actual state of preservation of the type(s) (see Notes). Whenever personal observation of the mouth phenotype character state on the name-bearing/nominal type(s) of the valid species has been possible, reference is made to these results. The character state as found in the name-bearing/nominal type(s) is made explicit by using bold font for the mouth phenotype(s). Details on the nominal type(s) have been added in subscript: h, holotype; l, lectotype; s, syntypes. An 'x' has been used when the literature refers to the existence of one of the three major mouth phenotypes without, however, providing the necessary details to add more information. As a general rule, we have refrained from explicitly tabulating mouth phenotype(s) as found in junior synonym(s); however, when former *Varicorhinus* species have been synonymized with a valid *Labeebarbus* mouth phenotype species, this has explicitly been stipulated as follows: V. syn or V.-like syn, *Varicorhinus* or *Varicorhinus*-like mouth phenotype synonym(s), preceded by the number of such synonyms. A *Varicorhinus*-like mouth phenotype refers to the fact that it has a typical real cutting edge (ree), but nevertheless differs in other respects from the typical *Varicorhinus* mouth phenotype, which has been documented in the notes. Indeed, in the typical *Varicorhinus* mouth phenotype, the fleshy lips on the lateral sides of the lower jaw are poorly developed (see Boulenger, 1909: plate 33 for *V. beso*), i.e. covering approximately only half of the lateral sides of the lower jaw, but very often much less (one-third or even only one-quarter, as in *V. beso* itself; with important intraspecific variation in some species as currently delimited). Instead, in the *Varicorhinus*-like mouth phenotype, the fleshy lips on the lateral sides of the lower jaw are obviously more developed, i.e. covering approximately two-thirds or more of the lateral sides of the lower jaw (e.g. *L. rosae*; *Sanagia velifera*). Nevertheless, considering: (1) the very poor development of the lips in *V. beso* (see above); (2) the important inter- and sometimes even intraspecific variation, this character is certainly in need of further attention (see text). In addition, whenever relevant with regards to the tabulated overall intraspecific mouth phenotype variation, reference is also made to the mouth phenotype of the name-bearing/nominal type(s) of other junior synonyms (i.e. non *Varicorhinus* nominal species) in the notes. The junior synonyms examined have been listed in the notes, grouped according to their mouth phenotype, and listed from the *Labeebarbus* through the intermediate to the *Varicorhinus* mouth phenotype.

Abbreviations of the author names for the references cited are as follows: Ba, Banister; Ba&Ba, Banister & Bailey; Ba&Po, Banister & Poll; Bo, Boulenger; DeV&TvdA, De Vos & Thys van den Audenaerde; DeW, De Weirdt; DeW&Te, De Weirdt & Teugels; Fo, Fowler; Ec, Eccles; Ge, Getahun; Ho, Holly; Ke, Keilhack; Lé, Lévêque; Lé&Da, Lévêque & Daget; Lé&Gu, Lévêque & Guégan; Na&Si, Nagelkerke & Sibbing; Pa, Pappenheim; Pe, Pellegrin; Po, Poll; Sa, Sauvage; Sk, Skelton; Tw&Sk, Tweddle & Skelton; and Walu, Wamui Lunkwaylakio. **N1.** Intermediate mouth phenotype polymorphism [interrupted (i.e. no lobe) or continuous (i.e. attached lobe)] (see Nagelkerke & Sibbing, 1997: table 5.5, see also page 130)]. **N2.** No type (Lévêque & Daget, 1984: 220). Burchell (1822: 280) most probably had several specimens before him when describing the species, as he provided some variation for the number of pectoral fin rays. **N3.** *Labeebarbus* to *Varicorhinus* mouth phenotype specimens present (see Skelton, 2001: 169). Synonyms: holotype of *Labeebarbus gilchristi* (Boulenger, 1911) (BMNH 1909.12.8.1: 149 mm SL) with a typical *Labeebarbus* hypertrophied mouth phenotype (h) and holotype of *Labeebarbus mentalis* (Gilchrist & Thompson, 1913) (SAIAB 134770: 257 mm SL) with a typical *Labeebarbus* free mental lobe (f). **N4.** *Labeebarbus* + intermediate mouth phenotype polymorphism (see Worthington, 1929: 432, fig. 3; 1932: 126; fig. 1). Synonyms: one of both syntypes of *Labeebarbus lobogenys* (Boulenger, 1906) [BMNH 1906.5.30.117–221 (two instead of five syntypes): 218–223 mm SL] with a typical *Labeebarbus* free mental lobe (f); at least some of the syntypes of *Labeebarbus kiogae* (Worthington, 1929) [BMNH 1929.1.24.105–108 (seven instead of four syntypes): 185–417 mm SL] with an intermediate mouth phenotype (r); and holotype of *Labeebarbus eduardianus* (Boulenger, 1901) (BMNH 1906.9.7.42–43: 223–224 mm SL) with an intermediate mouth phenotype (a). **N5.** Although reported by Banister & Poll (1973: 84), the holotype (MRAC 1979.29: 286 mm SL) lacks an rce (see also illustration in Banister & Poll, 1973: 85, fig. 2); however, two paratypes have one (MRAC 1979.30.97 mm SL; MRAC 1979.35.338 mm SL). **N6.** Intermediate mouth phenotype polymorphism interrupted (i.e. no lobe) or continuous (i.e. attached lobe)] (see Thys van den Audenaerde, 1967: 35, fig. 12)]. **N7.** Replacement name for *Varicorhinus atirostris* Boulenger, 1910 (now *Labeebarbus*) (see text and annotated checklist 1). **N8.** MNHN 1935-0066 syntype (171 mm SL) with an rce; however, MRAC 42933 syntype (195 mm SL) actually without an rce, possibly lost over time. **N9.** Intermediate mouth phenotype [interrupted (i.e. no lobe) (see Nagelkerke & Sibbing, 1997: table 5.5., see also page 131)]. **N10.** Synonyms: holotype of *Labeebarbus seguenis* (Pellegrin, 1925) (MNHN 1925-0193, 495 mm SL) with a typical *Labeebarbus* free mental lobe (f); holotype of *Labeebarbus occidentalis* (Boulenger, 1911) (BMNH 1909.3.3.14, 74 mm SL) with an intermediate mouth phenotype (a); and holotype of *Labeebarbus meneliki* (Pellegrin, 1905) (MNHN 1905-0275, 191 mm SL) with an intermediate mouth phenotype (n). **N11.** Synonyms: holotype of *Labeebarbus euchilus* (Boulenger, 1920) (BMNH 1919.7.24.7, 66 mm SL) with a typical *Labeebarbus* free mental lobe (f); syntypes of *Labeebarbus miichilus* (Boulenger, 1920) (BMNH 1919.4.24.8–9, 70–71 mm SL; MRAC 6992, 61 mm SL) with an intermediate mouth phenotype (n); and syntypes of *Varicorhinus stappersii* Boulenger, 1917 (now *Labeebarbus*) [BMNH 1920.5.25.36–37, 186–244 SL; MRAC 14197, 250 mm SL; and 14222, 175–172 mm SL (two instead of one syntype)], with a typical *Varicorhinus* mouth phenotype rce. **N12.** Variable *Labeebarbus* mouth phenotype polymorphism present, with frequently thickened lips (rubber lips) (see Skelton, 2001: 173). Synonyms: holotype of *Labeebarbus allicorialis* (Boulenger, 1908) (BMNH 1908.11.6.26, 3212 mm SL) and syntypes of *Labeebarbus chilotes* (Boulenger, 1908) (BMNH 1908.11.6.24–25, 125–199 mm SL), with a typical *Labeebarbus* free mental lobe (f). **N13.** *Labeebarbus* mouth phenotype polymorphism. Synonyms: holotype of *Labeebarbus tabatomimus* (Pellegrin, 1914) (MNHN 1886-0395, 240 mm

SL), with a typical *Laboeobarbus* hypertrophied mouth phenotype (h). **N14**. Intermediate mouth phenotype polymorphism [interrupted (i.e. no lobe) or continuous (i.e. attached lobe)] (see Nagelkerke & Sibbing, 1997, table 5.5., see also page 132). **N15**. Intermediate + *Laboeobarbus* mouth phenotype polymorphism [interrupted (i.e. no lobe) or continuous (i.e. attached lobe), or small lobe (see Nagelkerke & Sibbing, 1997, table 5.5., see also page 133)]. **N16**. See also Tweedle & Skelton (1998: 372). **N17**. Boulenger (1910: 546, 1916a: 214) reports a cutting-edge for (some?) syntypes, but there is none. **N18**. Holotype (MCZR) not seen. Based on three BMNH, non-type, specimens (BMNH 1971.7.12.1–3, 240–258 mm SL; see Banister, 1973: 41). **N19**. Synonyms: syntypes of *Laboeobarbus rothschildi* (Günther, 1901) (BMNH 1901.4.26.6–7, 127–134 mm SL), *Laboeobarbus riggenbachi* (Günther, 1902) (BMNH 1902.7.28.19, 115 mm SL and 1902.7.28.20–21, 136–137 mm SL) and *Laboeobarbus payonitii* (Boulenger, 1911) (BMNH 1903.10.29.17–20, 50–116 mm SL (seven instead of four syntypes)), all with intermediate mouth phenotypes (n); syntypes of *Capoeta atlantica* Boulenger, 1902 (BMNH 1902.1.4.18–19, 99–112 mm SL) and one of both syntypes of *Capoeta waldoii* Boulenger, 1902 (BMNH 1902.1.4.16–17: 129–140 mm SL (probably lost over time in the largest of both syntypes)) have a *Varicorhinus* mouth phenotype with a typical rce; however, the rce is very fine, does not cover the entire anterior width of the lower jaw, and the fleshy lips of the sides of the lower jaw are better developed than in the typical *Varicorhinus* mouth phenotype. **N20**. Intermediate mouth phenotype polymorphism [interrupted (i.e. no lobe) or continuous (i.e. attached lobe)] (see Nagelkerke & Sibbing, 1997, table 5.5., see also page 134). **N21**. Intermediate mouth phenotype polymorphism [interrupted (i.e. no lobe) or continuous (i.e. attached lobe)] (see Nagelkerke & Sibbing, 1997, table 5.5., see also page 135). **N22**. Synonyms: most of the syntypes of *Laboeobarbus guadaricus* (Boulenger, 1906) [BMNH 1908.1.20.131–132, 140–218 mm SL (six instead of two specimens) except BMNH 1908.1.20.133, 234 mm SL, which has an intermediate mouth phenotype (a)], with a typical *Laboeobarbus* free mental lobe (f) and sometimes even a hypertrophied mouth phenotype (h); as reported by Nagelkerke & Sibbing (1997: 121), two syntypes of *Laboeobarbus leptosoma* (Boulenger, 1902) (BMNH 1902.12.13.300–302), two of the syntypes have a continuous lower lip (f; 138 and 205 mm SL), whereas it is indeed interrupted in the third one (t; 208 mm SL) as in *Barbus intermedius*; although both have originally been described as *Barbus* species, at least one of the syntypes of *Laboeobarbus macmillani* (Boulenger, 1906) [BMNH 1908.1.20.103–106, 141–192 mm SL (i.e. the largest syntype; cover seems lost over time in the other syntypes) and 1937.4.20.68, 176 mm SL] and most of the syntypes of *Laboeobarbus plagiostomus* (Boulenger, 1902) [BMNH 1902.12.13.271–272, 176–193 mm SL (i.e. the smallest of both syntypes) cover seems lost over time in the other syntype] and 1902.12.13.273, 176 mm SL], with a typical *Varicorhinus*-like rce, except for one of the syntypes of the latter species, where it seem lost through time; and holotype of *Capoeta bingeri* Pellegrin, 1905 (MNHN 1905-0252), also with a typical *Varicorhinus* mouth phenotype, i.e. an rce. **N23**. Holotype (NMW) apparently lost. **N24**. Intermediate and *Varicorhinus* mouth phenotype polymorphism present (see Banister & Clarke, 1980: 500–504). Synonyms: at least one of the syntypes of *Laboeobarbus globiceps* (Worthington, 1933) (BMNH 1932.11.15.275–282, 235 mm SL) with a typical *Laboeobarbus* free mental lobe (f); and one of the two syntypes of *Laboeobarbus njassae* (Keilhack, 1908) [ZMB 18163, 107 mm SL, and ZMB 18164, 74 mm SL (cover seems lost over time in the smallest of both syntypes)] and the syntypes of *Laboeobarbus nyasensis* (Worthington, 1933) (BMNH 1932.11.15.387–392, 207 mm SL, and BMNH 1932.11.15.393–395, 202–298 mm SL) – the latter a former *Varicorhinus* species – with a typical *Varicorhinus* rce. **N25**. See also Levin *et al.* (2013: 401, fig. 1b). **N26**. Holotype (Museo do Dundo: MD 1078) not seen. Statement based on a re-examination of paratypes (MRAC 161065 and 161066, 63 and 85 mm SL, respectively) only. **N27**. Previously identified as a junior synonym of *Laboeobarbus johnstonii* (Boulenger, 1907), but to be considered a valid species. Species revaluated in the present paper (see text and annotated checklist 1). **N28**. Intermediate mouth phenotype polymorphism [interrupted (i.e. no lobe) or ± continuous (i.e. rudimentary lobe)] (see Nagelkerke & Sibbing, 1997, table 5.5., see also page 135). **N29**. Whereas all syntypes of *Laboeobarbus macrolepidotus* lack an rce and therefore have an intermediate mouth phenotype (n), the specimens of the Inkisi Basin all have a typical *Varicorhinus* mouth phenotype, i.e. an rce. **N30**. Intermediate mouth phenotype polymorphism [interrupted (i.e. no lobe) or continuous (i.e. attached lobe)] (see Nagelkerke & Sibbing, 1997: table 5.5., see also page 136). **N31**. Synonyms: two syntypes of *Laboeobarbus zambezensis* Peters, 1852 (ZMB 3246, 80 and 93 mm SL), with a typical *Laboeobarbus* free mental lobe (f) and another (NMW 49730: 77 mm SL) with an intermediate mouth phenotype (n); holotype of *Laboeobarbus brucii* (Boulenger, 1907) (BMNH 1907.3.15.34, 131 mm SL) with a typical *Laboeobarbus* free mental lobe (f); at least one of the syntypes of *Laboeobarbus inermis* (Peters, 1852) (ZMB 4736, syntype of 58 mm SL) with an intermediate mouth phenotype (r); holotype of *Varicorhinus nasutus* Gilchrist & Thompson, 1911 (now *Laboeobarbus*) [SAIAB 134736, +367 mm SL, 149 mm SL] (with replacement name *Barbus oliphanti* Keilhack, 1910 (now *Laboeobarbus*)) and holotype of *Varicorhinus* (see text and annotated checklist 1). **N32**. Originally described SL), both with a typical *Varicorhinus* rce; and holotype of *Laboeobarbus sector* (Boulenger, 1907) also with a typical *Varicorhinus* rce (BMNH 1907.3.15.35, 116 mm SL). **N33**. Originally described as a *Varicorhinus* species by Holly (1926); however, without special reference to the rce in the original description. In two of the three syntypes the cornified cover is entirely absent (NMW 7221, 128 mm SL, and NMW 7222–223, 88 mm SL), and most probably lost over time. Only in the third syntype (NMW 7222–223, 107 mm SL) does a faint rce seem to remain; however, all syntypes have well-developed fleshy lips on the lateral sides of the lower jaw, not at all resembling the almost entire absence of lips as found in the typical *Varicorhinus* mouth phenotype. **N34**. Apparently no type (see Léveque & Daget, 1984: 271). **N35**. *Laboeobarbus* and *Varicorhinus* mouth phenotype polymorphism present (see Grass, 1964: 53, fig. 7; Skelton, 2001: 170). Synonyms: holotype of *Laboeobarbus lobochilus* (Boulenger, 1911) (BMNH 1908.12.28.96, 143 mm SL) with a hypertrophied typical *Laboeobarbus* free mental lobe (h); holotype of *Laboeobarbus mfangosi* (Gilchrist & Thompson, 1913) [SAIAB 135057, 200 mm SL] with a typical *Laboeobarbus* free mental lobe (f); syntypes of *Laboeobarbus boukeri* (Boulenger, 1902) (BMNH 1862.8.28.3–8, 179–222 mm SL; BMNH 1874.5.1–2, 124–128 mm SL; BMNH 1894.7.10.4, 101 mm SL) with an intermediate mouth phenotype (a, r, or n) or a typical, although small, *Laboeobarbus* free mental lobe (f); holotype of *Laboeobarbus robinsoni* (Gilchrist & Thompson, 1913) [SAIAB 135055, 164 mm SL] with an intermediate mouth phenotype (a, r, or n); and holotype of *Laboeobarbus zuluensis* (Gilchrist & Thompson, 1913) [SAIAB 134939, 325 mm SL] with an intermediate mouth phenotype (n). **N36**. *Laboeobarbus* mouth polymorphism [lobe: small or large (see Nagelkerke & Sibbing, 1997: table 5.5., see also page 138)]. **N37**. Greenewald (1958: 277) and others. **N38**. Intermediate and *Varicorhinus*-like mouth phenotype polymorphism present (see Tweedle & Skelton, 2008: 30). Indeed, one of the paratypes (SAIAB 51928, 94 mm SL) has an rce. **N39**. Intermediate + *Laboeobarbus* mouth phenotype polymorphism [interrupted (i.e. no lobe) or continuous (i.e. attached lobe), or small lobe (see Nagelkerke & Sibbing, 2000: table 3)]. **N40**. Synonyms: holotype of *Laboeobarbus labiatus* (Boulenger, 1902) (BMNH 1902.5.26.37, 236 mm SL) with a hypertrophied lobe mouth phenotype (h); at least some of the syntypes of *Laboeobarbus tanensis* (Günther, 1894) (BMNH 1893.12.2.24–29, 191–286 mm SL) with a typical, although small, *Laboeobarbus* free mental lobe (f); syntypes of *Laboeobarbus hindii* (Boulenger, 1902) (BMNH 1902.5.26.25–28, 84–202 mm SL) with an intermediate mouth phenotype (a, r, or n); and holotype of *Barbus (Capoeta) babaulti* Pellegrin, 1926 (MNHN 1926-0285, 290 mm SL) and both syntypes of *Barbus (Capoeta) perplexicans* Boulenger, 1902 (BMNH 1902.5.26.35–36, 115–144 mm SL), both with a *Varicorhinus*-like mouth phenotype, i.e. with well-developed fleshy lips on the lateral sides of the lower jaw (and even more so in the latter of both nominal species), not at all resembling the almost entire absence of lips as found in the typical *Varicorhinus* mouth phenotype. **N41**. We follow Ladiges *et al.* (1958) with regards to the lectotype designation for *Laboeobarbus pagenstecheri* (see annotated checklist 1): The mouth is sub-terminal with a sharp (*Varicorhinus* rce) edge to the lower jaw in the paralectotype [ZMH H342, 210 mm SL] but rubber lips are developed in the . . . lectotype [ZMH H341, 319 mm SL] (see Banister, 1973: 101; see also Seegers, 2008: 155); however, the paralectotype has well-developed fleshy lips on the lateral sides of the lower jaw, not at all resembling the almost entire absence of lips as found in the typical *Varicorhinus* mouth phenotype. **N42**. *Laboeobarbus* mouth polymorphism [see Léveque *et al.*, 1987: 348, fig. 1]. **N43**. Holotype of *Laboeobarbus altianalis lobogenysoides* (Pellegrin, 1935) (MNHN 1935-0154) with a hypertrophied lobe mouth phenotype (h). **N44**. Lower jaw not bearing a cornified cover anymore; the cover seems to have fallen off. As such, the presence of an rce cannot be fully confirmed for this species. No details provided by Pellegrin (1932) in the original description. **N45**. See also Daget (1962: 78, fig. 16). **N46**. Intermediate mouth phenotype polymorphism [interrupted (i.e. no lobe) or continuous (i.e. attached lobe)] (see Nagelkerke & Sibbing, 1997: table 5.5., see also page 139). **N47**. Gaigher (1975: 162) reports the presence of *Varicorhinus* mouth phenotype in *Laboeobarbus polylepis*. Skelton (2001: 170) reported that the lips are variable, but without any further details. **N48**. See also Jubb (1959: 308). **N49**. Substitute name for *Barbus mariae* Holly, 1929 (see text and annotated checklist 1). With the kind help of Helmut Wellendorf (2013), former curator of fishes at the NMW, the holotype of *Barbus mariae* (NMW 8000, 243 mm SL) and paralectotype [NMW 96652 (ex. 6562), 225 mm SL] and lectotype [NMW 96653 (ex. 6562), 206 mm SL], the latter two designated but not seen by Banister (1973: 93–94), have all been traced (see text and annotated checklist 1). **N50**. An rce present in the two largest syntypes (79 and 80 mm SL).

Nevertheless, absent in the smallest syntype (44 mm SL), but possibly lost over time. Despite the presence of a typical *Varicorhinus* roe in both the largest syntypes, they both also have well-developed fleshy lips on the lateral sides of the lower jaw, not at all resembling the almost entire absence of lips as found in the typical *Varicorhinus* mouth phenotype species. **N51.** All syntypes have an roe (MNHN 1909-0583-0585, 63–68 mm SL). According to Banister (1972: 121), present with increasing size, and absent in a specimen of 40 mm SL only (no further details provided). Note, however, that Banister (1972: 271) himself states that he studied specimens from 57 to 231 mm SL only. **N52.** *Laboeobarbus* and intermediate mouth phenotype polymorphism [see Lévêque & Guégan, 1990: 54, fig. 14 (syntypes) & 55, fig. 15 (specimen: from Daget, 1962: 76, fig. 15 as *Barbus gruevici*)]. **N53.** An roe is present in the lectotype but absent in two paralectotypes, i.e. the smallest of the BMNH 1912.4.1.334–336 paralectotypes (149 mm SL), as well as in the MRAC 1526 paralectotype (173 mm SL). **N54.** As demonstrated by E. Vreven, P.H. Skelton & E.R. Schwartz (unpubl. data), *Barbus capensis* is not a *Laboeobarbus* but instead a senior synonym of *Barbus andrewi*. Therefore, *Barbus seeberti*, previously a junior synonym of *Barbus capensis*, and indeed a yellowfish or *Laboeobarbus*, becomes the valid species name for the clannwilliam yellowfish (see also text and annotated checklist 1). **N55.** *Laboeobarbus* mouth phenotype polymorphism (see Skelton, 2001: 171). In addition, specimens with an roe have been found (SAIAB 54113, 134 mm SL; SAIAB 54688, 176 mm SL); however, both have well-developed fleshy lips on the lateral sides of the lower jaw, not at all resembling the almost entire absence of lips as found in the typical *Varicorhinus* mouth phenotype. In addition, specimens with a typical *Laboeobarbus* free mental lobe (f) (SAIAB 58362: 179 mm SL) and hypertrophied lips have also been found (h) (SAIAB 58418, 141 mm SL; SAIAB 65536, 101 mm SL). **N56.** One syntype with (MNHN 1924-0052, 56 mm SL) and one actually without (MNHN 1924-0052, 117 mm SL) an roe; however, the roe was most probably lost over time in the latter syntype. **N57.** Synonyms: holotype of *Laboeobarbus moerueusis* (Pellegri, 1922) (MRAC 14765, 578 mm SL) and holotype of *Laboeobarbus oxycephalus* (Boulenger, 1915) (MRAC 14233, 266 mm SL), both with a typical *Laboeobarbus* free mental lobe (f); holotype of *Laboeobarbus curtus* (Boulenger, 1915) (MRAC 17172, 233 mm SL) with an intermediate mouth phenotype (a). **N58.** Intermediate mouth phenotype polymorphism [interrupted (i.e. no lobe) or ± continuous (i.e. attached lobe)] (see Nagelkerke & Sibbing, 1997: table 5.5., see also page 132). **N59.** Synonyms: *Varicorhinus bredoi* Poll, 1948 (now *Laboeobarbus*) [holotype IRSNB 76(1), 130 mm SL; paratypes IRSNB 77(2), 60–67 mm SL], with an roe (see Poll, 1948: 9–10, fig. 1–2), although, as mentioned by Poll (1948) himself, clearly absent in the smallest of both paratypes, which has an intermediate mouth phenotype (n). **N60.** Synonyms: *Varicorhinus chapini* Nichols & La Monte, 1950 (now *Laboeobarbus*) [holotype: AMNH 18785] with . . . a narrower, less specialized mouth than is usual in the genus [*Varicorhinus*] . . . (Nichols & La Monte, 1950: 175). Indeed, holotype with . . . lower jaw with a sharp, firm but not cartilaginous, edge. . . (Nichols & La Monte, 1950: 175), i.e. without the typical *Varicorhinus* mouth cutting edge, but with an attached lobe (a), and therefore with an intermediate mouth phenotype instead. **N61.** Intermediate mouth phenotype [interrupted (i.e. no lobe) or continuous (i.e. attached lobe)] (see Nagelkerke & Sibbing, 1997: table 5.5., see also page 141). **N62.** Intermediate mouth phenotype polymorphism [interrupted (i.e. no lobe) or continuous (i.e. attached lobe)] (see Nagelkerke & Sibbing, 1997: table 5.5., see also page 142). **N63.** Based on pers. observ. (E. Vreven 2013, pers. observ.) of the syntypes (BMNH 1912.12.6.5, 38 mm SL; MRAC 1191, 36 mm SL; MRAC 1192, 41 mm SL), clearly described based on three juvenile *Laboeobarbus* syntype specimens: i.e. the one MRAC syntype with a typical *Laboeobarbus* free mental lobe (f) (MRAC 1192) and the BMNH and the other MRAC syntype with an intermediate mouth phenotype (a). **N64.** See also Holly (1930: plate 1, fig. 8a), as illustrated for one of the syntypes. **N65.** Syntype (NMW 13948, 59 mm SL) seemingly without an roe. Most probably lost over time as Holly (1929: 32), in his original description of the species, refers to an roe: 'Der unterkiefer trägt eine dünne Hornschneide; an roe have been found in collections (MNHN and MRAC) and, most probably, represent a species new to science (see text)'. **N66.** Banister & Poll (1973: 91) reported the presence of a cornified cover, but not the presence of an roe. Indeed, the holotype lacks the roe, which conforms to the illustration provided by Banister & Poll (1973: 93, fig. 10); however, one paratype clearly has one (MRAC 179742, 385 mm SL). **N67.** The holotype of *Laboeobarbus wurtzi* lacks an roe. Instead, a cornified cover, although damaged, and without an roe, is still present on the lower jaw; however, specimens with an roe have been found in collections (MNHN and MRAC) and, most probably, represent a species new to science (see text). **N68.** See Tweddle & Skelton (1998: 377). **N69.** According to Banister (1976a: 177), the anterior edge of the lower jaw is gently curved and a cornified cover is altogether lacking in fishes less than 60 mm SL. **N70.** Although an roe is present, it covers, approximately, only half of the anterior width of the lower jaw (see also Banister & Thys van den Audenaerde, 1973: 184, fig. 2) instead of almost the entire anterior width, resulting in a spoon-like rather than a spade-like cutting edge, as found in *Laboeobarbus* spp. with a *Varicorhinus*-like, mouth phenotype. In addition, both syntypes have well-developed fleshy lips on the lateral sides of the lower jaw, not at all resembling the almost entire absence of lips found in the typical *Varicorhinus* mouth phenotype.

Furthermore, *Varicorhinus capoetoides* Pellegrin, 1938 has not been retained in our list either. Two characters, and especially the first one, make the placement of this species in the genus *Varicorhinus*, now *Labeobarbus s.l.*, untenable: (1) the last dorsal fin ray is a long, bony, and serrated spine (see also Pellegrin, 1938) not known to occur in any other African *Varicorhinus*, now *Labeobarbus s.l.*, species; (2) the high number of lateral line scales, i.e. 87 (see Pellegrin, 1938), a number only comparable with that found in *Acapoeta tanganicæ*. Furthermore, as stipulated by Pellegrin (1938; see also Blache, 1964), the type locality is highly doubtful. In addition, the species is only known from its holotype and has not been found in the Chad Basin since then. As such, the holotype, which is in poor condition, is here identified as a mislabelled *Capoeta* species, possibly *Capoeta trutta* (Heckel, 1843) (J. Freyhof, pers. comm., 2014). Indeed, although Pellegrin (1938: 373–374) did not explicitly mention a typical real cutting edge, and the specimen currently lacks one, this might have been fallen off, i.e. lost over time.

2. Two Southern African species have not been listed as valid species, i.e. *Labeobarbus altidorsalis* (Boulenger, 1908) and *Labeobarbus elephantis* (Boulenger, 1907). Both are here considered implicit synonyms (P.H. Skelton, pers. comm., 2015), respectively, of *Labeobarbus codringtonii* (Boulenger, 1908) and *Labeobarbus polylepis*, following Skelton's (1993, 2001) work (see annotated checklist 1).
3. Listing of all African species to be included into *Labeobarbus* is mainly hampered by the fact that during this study, at least one *Barbus* species previously identified as a small barb, i.e. *Barbus urotaenia* Boulenger, 1913 (see Table 1), was revealed to be a *Labeobarbus* species. Although described from small specimens, based on the presence of a free mental lobe and nine branched dorsal fin rays it is readily identifiable as a *Labeobarbus* species.
4. In addition, three nominal species, i.e. *L. alluaudi*, *Labeobarbus microbarbis* (David & Poll, 1937), and *Labeobarbus microterolepis* (Boulenger, 1902), have been listed as hybrids or possible hybrids already. For *L. alluaudi*, the case has been convincingly documented by Banister (1972), and is followed here. For *L. microbarbis*, the case has been first suggested by Banister (1973) and further documented by De Vos & Thys van den Audenaerde (1990), who confirmed Banister's (1973) suggestion; however, for *L. microterolepis*, the case has only been suggested by Banister (1973) and subsequently confirmed by Golubtsov, Dgebuadze & Mina (2002), but without providing new supporting evidence. The status of *L. microterolepis* as a possible hybrid thus certainly needs further attention. As hybrid nominal species

are never formally synonymized, these nominal species already previously identified as hybrids or possible hybrids have been listed separately (see Table 1 and annotated checklist 2), as these names should not be used as valid names (see ICZN, 1999: article 23.8).

5. *Varicorhinus beso* was described from Lake Tana (Ethiopia) by Rüppell in 1835 based on a single specimen, the holotype; however, as reported by Eschmeyer (2015) the SMF holotype cannot be found, a statement further confirmed by Mr T. Alperman (pers. comm., 2013), curator at the SMF, Frankfurt, Germany. As a result the holotype is here considered lost. The present situation is highly unsatisfactory for several reasons. *Varicorhinus beso* is the type species of the genus *Varicorhinus* and, although the genus *Varicorhinus* has recently been synonymized with *Labeobarbus* (see Berrebi *et al.*, 2014), its status and delimitation as a valid genus has been (see Levin *et al.*, 2013) and most probably will be further debated. Therefore, a neotype is needed (see ICZN, 1999: article 75), and is designated here, following the qualifying conditions provided in ICZN (1999: article 75.3). The NHM, London, UK, houses an unpublished, and as such unavailable, neotype (BMNH 1968.7.24.18; 156.8 mm SL), collected by Sandhurst in 1964, originating from Bahardar (Baherdar  $\pm 11^{\circ}37'N$ ,  $37^{\circ}24'E$ ), also on Lake Tsana (i.e. Tana, Ethiopia), and most probably selected by the late K.E. Banister (NHM); however, we have refrained from identifying this specimen as the neotype of *V. beso*. Instead, BMNH 1902.12.13.365 (290.6 mm SL), also originating from Bahardar, Lake Tsana (i.e. Tana, Ethiopia), and collected by E. Degen (1 June 1902), is here designated as the neotype of *V. beso*. The latter specimen has been illustrated by Boulenger (1907c: plate 33) in his *Fishes of the Nile*, and the illustration has been further reproduced in his monumental *Catalogue of the Fresh-Water Fishes of Africa* (Boulenger, 1909: fig. 268). Boulenger (1907c: plate 33) illustrates a specimen of  $\pm 293$  mm SL ( $\pm 205$  mm SL on the drawing, scale 7/10), which indeed can be identified as BMNH 1902.12.13.365 based on its size (SL) and exact disposition of the tubercles on the right-hand side of the head that perfectly match between the illustration and those on the NHM specimen. A detailed description of *V. beso* and a key to the species of the genus *Varicorhinus* as recognized at the time can be found in Boulenger (1907c, 1909). As such, the neotype exemplifies and corresponds with what has since been identified as *V. beso*. In addition, considering (1) the subsequent importance of the presence of a cornified, clear cutting edge as a diagnostic character for *Varicorhinus*, and (2) the general importance of the mouth

phenotype and its polymorphism in these hexaploid Torini, the mouth of the neotype is in excellent condition and exemplifies a well-developed, cornified, clear cutting edge. This is especially important considering the fact that Rüppell (1835) himself did not mention the presence of a cornified, clear cutting edge (see Persistent generic problems: morphology, cytogenetic, and molecular approaches) as a diagnostic character for either the genus *Varicorhinus* or the species *V. beso*. Furthermore, the illustration of *V. beso* as provided by Rüppell (1835: plate 3; fig. 2) shows a fish without a clear cutting edge on the lower jaw, and in that respect looks more reminiscent of intermediate mouth phenotypes. Nevertheless, to stabilize the current nomenclature the neotype has been identified to match with what has been considered *V. beso* since Boulenger (1902f, 1906c; and more explicitly 1907c: plate 33).

6. As a result of the proposed (Tsigenopoulos *et al.*, 2010) and recently applied (Berrebi *et al.*, 2014) synonymy of *Varicorhinus* with *Labeobarbus*, and in concordance with other discoveries (see below), two valid species names become secondary junior homonyms, and are in need of a substitute name (see ICZN, 1999: article 60). A third case of secondary homonymy is also discussed, although a replacement name is not needed in this specific case. Finally, a fourth case of possible future secondary homonymy is also highlighted.

With regards to *L. brevicauda*, the right pharyngeal bone illustrated by Banister & Clarke (1980: fig. 5; 335 mm SL), and which according to the legend to the figure belongs to the holotype (ZMB 18175: 351 mm SL), does not in fact belong to this species. Indeed, the holotype has the left instead of the right pharyngeal bone dissected. This pharyngeal bone clearly has five teeth on row I and not four teeth, as in the illustrated pharyngeal bone. In addition, it has no molariform teeth at all. The drawing, however, perfectly matches the right pharyngeal bone, with four teeth on row I, of one of the syntypes of *Labeobarbus latirostris* Keilhack, 1908 (i.e. the whole specimen here designated as the lectotype, ZMB 18174, but not the head-only specimen, which here becomes the paralectotype, ZMB 34766; see below). The lectotype of *L. latirostris* also matches the size provided by Banister & Clarke (1980: 485; 335 mm SL) of the holotype of *L. brevicauda*. In addition, the barbels of the lectotype of *L. latirostris* are long, and therefore match the diagnosis given for *Labeobarbus eurystomus* by Banister & Clarke (1980: 489) rather than that for *L. johnstonii* [anterior barbels (Ab), mean 5.7% SL, and posterior barbels (Pb), mean 5.6% SL, in *L. eurystomus*, following Banister & Clarke (1980) = *L. brevicauda*, following Seegers, 1995 (see below), versus Ab

2.5% SL and Pb 3.5% SL in *L. johnstonii*]. Banister & Clarke (1980) also referred to some typical differences in colour pattern, but we have been unable to confirm this as, at least in these specimens, the colour pattern is entirely faded. These discoveries strongly suggest that Banister & Clarke (1980) unfortunately seem to have switched parts of their synonymizations, as *L. brevicauda* was identified as a junior synonym of *L. eurystomus* (= *L. brevicauda*, following Seegers, 1995), although it has five non-molariform pharyngeal teeth on the first row, as in *L. johnstonii*, whereas *L. latirostris* was identified as a junior synonym of *L. johnstonii*, although it has four molariform teeth on the first row, unlike in the latter species. As a result, the nomenclatural consequences of these findings are twofold: (1) *L. brevicauda* becomes a junior synonym of *L. johnstonii*; and (2) *L. latirostris* becomes the valid species name for what Banister & Clarke (1980) incorrectly referred to as *L. eurystomus*, and had been renamed by Seegers (1995) as *L. brevicauda*, following the invalid lectotype designation of Banister & Clarke (1980) for *L. eurystomus* (for more details, see annotated checklist 1 for *L. johnstonii* under the 'Notes' section), but unfortunately overseeing the additional errors of the latter authors (see above). The complete syntype of *L. latirostris* is here identified as the lectotype, as the second specimen (a head only), the paralectotype (now ZMB 34766), belongs to *L. johnstonii* (five teeth on row I and none of them molariform). As a result, a new replacement name (*nomen novum*; see ICZN, 1999: article 60.3) is needed for *Varicorhinus latirostris* Boulenger, 1910, which also becomes a *Labeobarbus* and has no synonyms. *Labeobarbus boulengeri* is here proposed in acknowledgement of George Boulenger's extensive work on Angolan large *Barbus* and *Varicorhinus*, both now *Labeobarbus*. For full details on the types see annotated checklist 1. The largest of the syntypes is here designated as the lectotype of the species (BMNH 1911.6.1.6: 136.6 mm SL), whereas the others become paralectotypes [ANSP 37905(1) (not seen), BMNH 1911.6.1.7–10(4), NMW 48865(1), and ZMB 18211(1)]. Indeed, following the recommendation of the ICZN (1999: recommendation 74B), the illustrated specimen should, by preference, be identified as the lectotype. The illustrated specimen in Boulenger (1916a: fig. 139) is about 95.0 mm SL. The scale provided is 2/5, which would give ~237.5 mm SL. As the largest of the syntypes does not even come close to this size, we suspect the scale is in error and should most probably read 2/3 instead, as this would give an SL of approximately 142.5 mm, which is much closer to the 136.6 mm SL of the largest of the BMNH syntypes.

*Varicorhinus mariae* Holly, 1926 has become *L. mariae*. As a result, *Barbus* (now *Labeobarbus*) *mariae* Holly, 1929 described from the Kitui River in Kenya needs a substitute name (see ICZN, 1999: article 60). Banister (1973: 283) stated that although the original description of both *L. matris* (Holly, 1928) and *L. mariae* (Holly, 1929) were very similar, he refrained from putting them in synonymy without having seen the types; however, several authors (Lévêque & Daget, 1984; Seegers, De Vos & Okeyo, 2003) have since considered *B. matris* a synonym of *B. mariae*, but with hesitation, without further justification, and without respecting the proper priority of names. The types of both species, previously considered lost, have been located in the NMW, and both nominal species are clearly distinguishable from each other, rejecting any claims regarding their possible synonymization. Amongst other character states, both nominal species differ from each other in the number of gill rakers [15 + 1 + 3 (=19) in *B. matris* versus 9 + 1 + 2 (=12) or 10 + 1 + 2 (= 13), in *B. mariae*], the number of scales below the lateral line (3.5 versus 4.5), and the length of the unsegmented dorsal spine (18.8 versus 26.3–29.0% SL; E. Vreven, pers. observ., 2013). Therefore, both are here retained as valid species. Furthermore, *Barbus* (now *Labeobarbus*) *rhinoceros* Copley, 1938 has been identified as a junior synonym of *B. mariae* by Banister (1973: 83). As a result, and according to ICZN (1999: article 60.2), it becomes the valid replacement name for the latter taxon. Contrary to Seegers *et al.* (2003), *L. rhinoceros* is not considered a *nomen nudum* (see ICZN, 1999: glossary) as, according to ICZN (1999: article 13): (1) the name is accompanied by a brief description making reference to a ‘pronounced horn’ [see Copley (1938: 191); for an illustration see Banister (1973: fig. 68 for *B. mariae*)], distinguishing it from all other East African *Barbus* (now *Labeobarbus*); (2) although Copley (1938) seems to have had a single specimen (holotype) presented by Playford before him, a name bearing type designation only became mandatory for species descriptions after 1999 (see ICZN, 1999: article 72.3). No type(s) is/are known (see Lévêque & Daget, 1984; Eschmeyer, 2015); however, in the past, one and four additional specimens, all originating from the Athi River and presented to the NHM by Copley (BMNH 1936.12.22.35 and 1936.12.36–39, all currently in the same jar) have been labelled as the holotype and paratypes of *B. rhinoceros*, respectively, but this has been subsequently amended. Therefore, and considering that (1) the specimens were deposited at the NHM in 1936, i.e. well before the actual description of the species in 1938, and (2) that Copley (1938) refers to a single specimen, the

type status of these specimens remains doubtful and in need of further research. Nevertheless, those are the specimens used by Banister (1973) for his detailed redescription of *B. mariae* now *B. rhinoceros*. For full details on the types of *B. matris* and *B. mariae*, also see annotated checklist 1. The suggested possible synonymy of both *B. matris* and *B. mariae* (now *L. rhinoceros*) with *L. oxyrhynchus* (see Seegers *et al.*, 2003: 32) is not followed, as no evidence was provided by the authors.

*Labeobarbus macrolepis* (Pfeffer, 1889), a new combination first proposed by Skelton & Bills (2008), and later confirmed (see Banyankimbona *et al.*, 2012a; present paper), is preoccupied by *Labeobarbus macrolepis* Heckel, 1838, currently a junior synonym of *Tor putitora* (Hamilton, 1822) (Kottelat, 2013). The junior secondary homonym *L. macrolepis* (Pfeffer, 1889) does not need a replacement name as: (1) ‘the junior species-group name has not been replaced’; and (2) ‘the relevant taxa are no longer considered congeneric’ (ICZN, 1999: article 59.2).

Following Banister (1973), *Varicorhinus stappersii* Boulenger, 1917 is to be considered a junior synonym of *L. caudovittatus* (see annotated checklist 1); however, the syntypes of *V. stappersii* Boulenger, 1917 all have a *Varicorhinus* mouth phenotype, whereas both syntypes of *L. caudovittatus* have an intermediate mouth phenotype (see Table 1). Therefore, its current status as a junior synonym needs further attention. If, contrary to Banister’s (1973) opinion, further research reveals *V. stappersii* to be a valid species instead, a replacement name will be needed for the former as it is preoccupied by *Barbus* (now *Labeobarbus*) *stappersii* Boulenger, 1915. Being currently a junior synonym, however, it is not (yet) to be replaced, as the replacement name would be unavailable (see ICZN, 1999: articles 11.5 and 15.1).

- The syntype series of *L. sandersi*, originally described as *Varicorhinus sandersi* by Boulenger (1912), is revealed to be polymorphic, including specimens with a real *Varicorhinus* cornified cutting edge, such as the one illustrated by Boulenger (1912: fig. 1, plate 19; see Table 1) in the original description (size of the drawn specimen: ±315 mm SL), and specimens with an intermediate mouth phenotype, i.e. having a horny cover but lacking the real *Varicorhinus* cutting edge or *Labeobarbus*-like mental lobe (see notes to Table 1). Following ICZN (1999: recommendation 74B), the illustrated specimen (BMNH 1912.4.1.333; i.e. the largest of the syntypes, 316 mm SL), is here identified as the lectotype of the species. In addition, for reasons of nomenclatural stability, we have preferred to identify a specimen with a *Varicorhinus* mouth phenotype as the name-bearing type of *L. sandersi* rather than an

intermediate one that might, in analogy to Banister's (1972, 1976a) documented cases of hybridization, subsequently reveal to represent a hybrid mouth phenotype rather than a valid species.

8. The past recognition of *Barbus* as a 'monstrous aggregation' (Myers, 1960: 213) has resulted in the synonymization of numerous genera. Following the recognition of *Labeobarbus* as a separate genus, several of these junior synonyms have to be reallocated to *Labeobarbus* instead of *Barbus*.

As such, in addition to the synonymization of *Varicorhinus* with *Labeobarbus* (see Berrebi *et al.*, 2014), and taking into account all African *Labeobarbus* species identified in the present paper, at least three African junior synonyms are also to be listed under *Labeobarbus*: (1) *Barbellion* Whitley, 1931; (2) *Barynotus* Günther, 1868 (*sensu* Jordan, 1919), both with *Barynotus lagensis* Günther, 1868 (Nigeria) as the type species; and (3) *Lanceobarbus* Fowler, 1936 (originally described as a subgenus of *Barbus*), with *Barbus tanensis* Günther 1894 (Kenya; a junior synonym of *L. oxyrhynchus*; see annotated checklist 1) as the type species. Further details on these junior synonyms are provided in the notes to Table 1 and in annotated checklist 1. As *B. capensis* is in fact not a *Labeobarbus* (see E. Vreven, E.R. Swartz & P.H. Skelton, unpubl. data) and the name *L. seeberi* should be used for this southern African species instead, *Cheilobarbus* Smith, 1841 (originally described as a subgenus of *Barbus*) is not to be included as a junior synonym of *Labeobarbus*.

Although *Pseudotor* Karaman, 1971, with *B. fritschii* (Morocco) as the type species, has been identified as a junior synonym of *Carasobarbus* by Borkenhagen *et al.* (2011) and Borkenhagen & Krupp (2013), and the monospecific genus *Pterocapoeta*, with *Pterocapoeta maroccana* Günther, 1902 (Morocco) as the type species, has recently been revalidated by Borkenhagen *et al.* (2011), both are here included in *Labeobarbus s.l.* pending further research. Furthermore, when considering *Labeobarbus s.l.* several non-African genera are to be included as well. First, both *Carasobarbus*, with *Systemus luteus* Heckel, 1843 (Syria) as the type species, and *Kosswigobarbus*, with *Cyclocheilichthys kosswigi* Ladiges, 1960 (Turkey) as the type species, are included here. Although both were referred to as subgenera in Tsigenopoulos *et al.* (2010), this subgeneric nomenclature was not adopted in their tree, despite both type species being included in their analyses. Furthermore, Berrebi *et al.* (2014) did not retain any subgeneric nomenclature either. Therefore, pending further research, both are included here in *Labeobarbus s.l.* As stipulated elsewhere, we have refrained from following the revalidation of

*Carasobarbus* by Bănărescu (1997), as recently confirmed by Borkenhagen *et al.* (2011) and Borkenhagen & Krupp (2013), as this would render *Labeobarbus s.l.* paraphyletic according to the results of Tsigenopoulos *et al.* (2010) and Berrebi *et al.* (2014). The same holds true for the monospecific genus *Mesopotamichthys*, with *Barbus sharpeyi* Günther, 1874 as the type species, originally revalidated by Bănărescu (1997), as recently confirmed by Borkenhagen (2014), and the recently described genus *Arabibarbus*, with *Arabibarbus hadhrami* Borkenhagen 2014 (Yemen) as the type species. Indeed, these three nominal genera are here all included in *Labeobarbus s.l.* pending further research. Finally, although Tsigenopoulos *et al.* (2010) also included the (sub)genus *Tor*, we have refrained from doing so as the type species itself, *Cyprinus tor* Hamilton, 1822, was not included in the analysis of Tsigenopoulos *et al.* (2010), nor in the compilation of Berrebi *et al.* (2014). Indeed, *Tor*, including the type species *T. tor*, has been inferred to be: (1) a valid genus, and to represent (2) the sister group to the *Labeobarbus* clade, i.e. here referred to as *Labeobarbus s.l.*, by Yang *et al.* (2015: fig. 2) based on their mitochondrial DNA data set.

#### *The present overview: what is to be learned?*

Based on the tabulated overview (see Table 1), some revealing details with regard to the observed mouth phenotype diversity and its distribution are discussed: (1) valid African *Labeobarbus* spp. with one or several *Varicorhinus* or *Capoeta* genus or subgenus synonyms; (2) the generic history of *L. wurtzi*; (3) other African species originally described based on one or several specimens with an intermediate mouth phenotype; (4) African *Labeobarbus* spp. with a prognathous mouth; (5) species originally described as *Varicorhinus* spp. but lacking the typical cornified cutting edge; (6) African *Labeobarbus* spp., originally described as *Varicorhinus* spp. but with papillated lips instead of the typical cornified cutting edge; (7) details on the continental distribution of both the *Labeobarbus* and *Varicorhinus* mouth phenotypes.

1. Eight of the listed African *Labeobarbus s.l.* species currently have a *Varicorhinus* junior synonym or originally a *Capoeta* genus or subgenus one. These are: *L. caudovittatus* (one *Varicorhinus* synonym), *L. fritschii* (two *Capoeta* synonyms = *Varicorhinus*; E. Vreven, pers. observ., 2013), *L. intermedius* (one *Capoeta* synonym = *Varicorhinus*; E. Vreven, pers. observ., 2013), *L. johnstonii* (one *Varicorhinus* synonym), *L. marequensis* (two *Varicorhinus* synonyms), *L. oxyrhynchus* [two *Capoeta* (subgenus) synonyms = *Varicorhinus*; E. Vreven, pers. observ., 2013],



*L. trachypterus* (one *Varicorhinus* synonym), and *L. tropidolepis* (one *Varicorhinus* synonym) (for more details, see notes to Table 1). Although *Varicorhinus chapini* Nichols & La Monte, 1950 (currently a junior synonym of *L. tropidolepis*, following Banister, 1973) was described as a *Varicorhinus* species, it lacks a cornified real cutting edge on the anterior edge of the lower jaw (for more details, see Table 1). This means that seven (i.e. 5.6%) valid African *Labeobarbus* species have, at least, one nominal junior synonym for which the lower jaw, somehow, bears a cornified real cutting edge as found in *V. beso* (see Boulenger, 1907c: plate 33; Levin, 2012: fig. 2), now *L. beso*. In addition, three additional *Labeobarbus* species, i.e. *L. aeneus*, *L. natalensis*, and *Labeobarbus nthuwa* Tweddle & Skelton, 2008 have been reported to include *Labeobarbus* as well as *Varicorhinus* mouth phenotype specimens (see Skelton, 2001 and Tweddle & Skelton, 2008), which according to Gaigher (1975) also holds true for *L. polylepis* (four species, i.e. about 3%); however, the cutting edge is not always as well developed as in *V. beso*, as it may clearly not cover the entire width of the anterior edge of the lower jaw and may also lack the ventral cover of the lower jaw (here referred to as the plastron). This is the case, for instance, in the two largest of the BMNH syntypes (BMNH 1911.6.1.39–41: 79.3 and 80.1 mm SL) of *Labeobarbus rosae* (Boulenger, 1910). In addition, in these specimens the lateral sides of the lower jaw bear well-developed fleshy lips, illustrating additional intermediate mouth phenotype variation in need of further attention.

2. *Labeobarbus wurtzi*, although originally described as a large *Barbus* species (see Pellegrin, 1908), was transferred to the genus *Varicorhinus* by Daget (1962: fig. 14), although not stated explicitly, based on the fact that, as stipulated in his description of the Guinean *V. wurtzi* specimens he studied, the lower jaw has a horny cover with a striated surface forming a cutting edge (i.e. ‘bord trenchant’ see Daget, 1962: 72). Lévêque & Guégan (1990), however, based on both morphological as well as parasitological criteria (i.e. monogenea Dactylogyridae fauna), transferred it back to the group of the large *Barbus*, i.e. now *Labeobarbus*. Indeed, although Lévêque & Guégan (1990) reported the wide mouth with the presence of a horny covering (‘étui corné’) on the lower lip, they did not mention the presence of the typical *Varicorhinus* cutting edge that Daget (1962), instead, had explicitly reported. Re-examination of the holotype of *L. wurtzi* (MNHN 1908–0097; 112.0 mm SL) shows that, although damaged, the holotype still partially bears a horny cover on the lower jaw, but nevertheless lacks the typical *Varicorhinus* clear cutting edge and, in that respect,

as well as by the presence of fleshy lips on the lateral sides of the lower jaw, has a typical intermediate mouth phenotype. The smallest of both the *L. wurtzi* specimens from Kaba (Guinea) examined by Daget (1962) (MNHN 1959–0153; two specimens of 127.5–132.5 mm SL) has a real cornified *Varicorhinus* cutting edge on the lower jaw, however (see Table 1). In addition, verification of the MRAC and MNHN specimen holdings for *L. wurtzi* showed that other specimens also have a typical *Varicorhinus* mouth phenotype [MRAC 1986-13-P-114 (124.2 mm SL), MNHN 1959–0153(2) (smallest of both: 127.5 mm SL), MNHN 1987–0689(3) (116.6–165.5 mm SL), MNHN 1988–1955(3) (both largest specimens: 172.5 and 175.6 mm SL), and MNHN 1991–0519(1) (180.3 mm SL)]. These specimens illustrate that specimens with the typical *Varicorhinus* mouth phenotype are – although far less abundant compared with the numerous *L. wurtzi* intermediate mouth morphotype specimens in the MNHN and MRAC collections – not absent from this part of Africa, and might well represent an undescribed *Labeobarbus* species with a *Varicorhinus* mouth phenotype.

3. The fact that, as for *L. wurtzi*, a *Labeobarbus* species has originally been described on a single specimen or several specimens with one or several intermediate mouth phenotypes (see Table 1) is certainly not unique for the latter species. Indeed, this is, for instance, also the case for both *L. micronema* syntypes (BMNH 1904.2.29.37–38) originating from the Kribi River Basin (Cameroon), which both also lack the presence of a mental lobe, typical for the *Labeobarbus*-like phenotype (see Boulenger, 1911a: fig. 57) (see Table 1). As for the *L. wurtzi* holotype, however, both syntypes have well-developed lips on the lateral sides of the lower jaw (see Boulenger, 1911a: fig. 57). Furthermore, although both these specimens lack the typical real cornified cutting edge, they have a broad mouth like the typical broad mouth found in the *Varicorhinus*-like mouth phenotype, and in that respect clearly differ from the narrow mouth of the typical *Labeobarbus*-like mouth phenotypes. This kind of mouth phenotype is also reminiscent of the mouth phenotype illustrated for the hybrid specimens identified by Banister (1972: fig. 15; 1976a: plate 2).
4. It is to be noted, however, that all species with a prognathous lower jaw also lack the presence of a mental lobe [see *Labeobarbus aspius* (Boulenger, 1912), *Labeobarbus macrocephalus* (Fowler, 1936), *L. mariae*, *L. matris*, and *Labeobarbus progenys* (Boulenger, 1903), as riverine species; see also de Graaf *et al.* (2010: fig. 1) for the prognathous, i.e. piscivorous, Lake Tana *Labeobarbus* spp.: *Labeobarbus acutirostris* (Bini, 1940), *Labeobarbus*

- longissimus* (Nagelkerke & Sibbing, 1997), *Labeobarbus macrophthalmus* (Bini, 1940), *Labeobarbus megastoma* (Nagelkerke & Sibbing, 1997), *Labeobarbus truttiformis* (Nagelkerke & Sibbing, 1997), and to a lesser extent *Labeobarbus gorguari* (see Nagelkerke & Sibbing, 1997, 2000)]. Two additional Lake Tana *Labeobarbus* species, i.e. *Labeobarbus dainellii* (Bini, 1940) and *Labeobarbus platydorsus* (Nagelkerke & Sibbing, 1997), without a prognathous lower jaw, are also known to be piscivorous (see Nagelkerke & Sibbing, 1997; de Graaf *et al.*, 2010) and at least some specimens of *L. dainellii* are known to have a small lobe. As such, the lack of a mental lobe does not seem to unequivocally point towards an intermediate, possibly hybrid, status of the nominal species concerned; however, a hybrid origin is not to be excluded, and is certainly worth further detailed investigation.
5. In six currently valid African *Labeobarbus* species (i.e. about 5%), all originally described within *Varicorhinus*, i.e. *Varicorhinus altipinnis* Banister & Poll, 1973 (Lufira River Basin, DRC), *V. ansorgii* (Quango River Basin, Angola), *Varicorhinus fimbriatus* Holly, 1926 (Sanaga River Basin, Cameroon), *Varicorhinus lufupensis* Banister & Bailey, 1979 (Lufupa River Basin, DRC), *V. macrolepidotus* (Kasai River system, DRC), and *Varicorhinus wittei* Banister & Poll, 1973 (Lufira River Basin, DRC), the name-bearing type(s) (i.e. the holotype or all examined syntypes) lack the typical cornified, real cutting edge on the lower jaw (see Table 1). In that respect, these name-bearing types also resemble some of the intermediates, i.e. hybrid phenotypes, as described and illustrated by Banister (1972: fig. 15; 1976a: plate 2). As a result, in analogy with the cases documented by Banister (1972, 1976a), these might well represent hybrid phenotypes instead of valid species.
  6. Results also show that four currently valid *Labeobarbus* species (i.e. about 3%), namely *Labeobarbus robertsi* (Banister, 1984) (Inkisi River Basin, DRC) (see Banister, 1984: fig. 9), *Labeobarbus clarkeae* (Banister, 1984) (Quanza River Basin, Angola), *Labeobarbus ensifer* (Boulenger, 1910) (Lucalla River Basin, Angola), and *Labeobarbus varicostoma* (Boulenger, 1910) (Lucalla River Basin, Angola), all have papillae towards the anterior outer edge of the upper as well as the lower jaw (see Table 1). As all were originally described within the genus *Varicorhinus*, the existence of this additional, very distinct, mouth phenotype has largely been overlooked. Furthermore, this mouth phenotype seems, based on the current evidence, highly localized, as it has only been reported from the Quanza and Lucalla rivers in Angola and the Inkisi River, Lower Congo, in the DRC.
  7. Based on the currently available data resulting from the compilation provided, *Labeobarbus* as well as *Varicorhinus* mouth phenotype(s) and/or species seem to be widespread in Africa, as they both apparently occur in each of the ten ichthyofaunal provinces (see Snoeks *et al.*, 2011) recognized today (see Fig. 6 and associated table). The spacial distribution of *Varicorhinus* mouth phenotype species seems to have been particularly obscured. Several reasons can be put forward for this: (1) numerous synonymizations of nominal *Varicorhinus* mouth phenotype(s) species with similar sympatric *Labeobarbus* species (see above under no. 1); (2) unnamed *Varicorhinus* mouth phenotypes, within the current context of the accepted high intraspecific mouth phenotype polymorphism within *Labeobarbus* (see above under no. 1); and (3) apparently entirely overlooked *Varicorhinus* mouth phenotypes in other cases (see above under no. 2, *L. wurtzi*).
- In addition, the overall continental distribution shows the *Labeobarbus* mouth phenotype(s) and/or species to be, apparently, more widespread compared with the *Varicorhinus* mouth phenotype and/or species. For instance, the *Varicorhinus* mouth phenotype is currently unknown from within the *L. bynni* region – i.e. large parts of the Nilo Sudanic ichthyofaunal province – including the Upper Senegal, Volta, and Niger, including the coastal rivers between both, as well as the Chad and the ‘Lower’ Nile Basin. The latter mouth phenotype is not entirely absent from the Nilo Sudanic ichthyofaunal province, however, and is expressed, among other taxa, in *L. jubae*, originally described as a *Varicorhinus* species, from the Juba River (see Banister, 1984; Levin *et al.*, 2013; Table 1). In addition, the current state of knowledge should be taken cautiously. Indeed, as illustrated, the so-called established absence of the *Varicorhinus* mouth phenotype in the Upper Guinea ichthyofaunal province (*sensu* Lévêque, 1997: fig. 2.1.) is here refuted (see above under no. 2 for *L. wurtzi*). Although rare, the re-examination of existing collections revealed it to be present in the area and confirms Daget’s (1962) statement in this respect (see above under no. 2, *L. wurtzi*).
- The present compilation has also enabled us to illustrate the taxonomic evolution of the African *Labeobarbus s.l.* species numbers since the original description of the genus in 1835 (see Fig. 7). Several major trends can be observed. First, the highest number of described species per decade is between c. 1891 and c. 1940, which corresponds well with the period of intensive activity of G.A. Boulenger (1858–1937; NHM) and, later on, J. Pellegrin (1873–1944; MNHN) (see also Paugy, 2010: fig. 4; Skelton & Swartz, 2011). This activity curve is perfectly in tune with the expansion of exploration accompanying the colonial ‘scramble for

Africa' (see also Skelton & Swartz, 2011). Furthermore, although the cumulative number of valid species largely follows the trend of the cumulative number of nominal taxa up to c. 1960s, thereafter a period of intensive synonymization up to c. 1990 brought a strong decrease in the number of valid species. The conceptual shift in the interpretation of mouth phenotype variation also accounts for the peculiar history of the African valid *Labeobarbus s.l.* species numbers, which contrasts with the overall numbers of African fish species descriptions, and exemplifies the huge impact of the conceptualization of species on the practice of their recognition and delimitation. African fish species descriptions have been steadily increasing since the c. 1880s (see Paugy, 2010: fig. 5; Skelton & Swartz, 2011: fig. 1), but very few *Labeobarbus s.l.* species descriptions occurred after the active period of G.A. Boulenger and J. Pellegrin, c. 1930s. Also, revalidations have been rare except for the 1990s when numerous Lake Tana (Ethiopia) endemic species were revalidated by Nagelkerke & Sibbing (1997) after the extensive over-synonymization with *B. intermedius*, now *Labeobarbus*, by Banister (1973).

## DISCUSSION

### GENERAL REPERCUSSIONS AND PERSPECTIVES ON AN AFRICAN SCALE

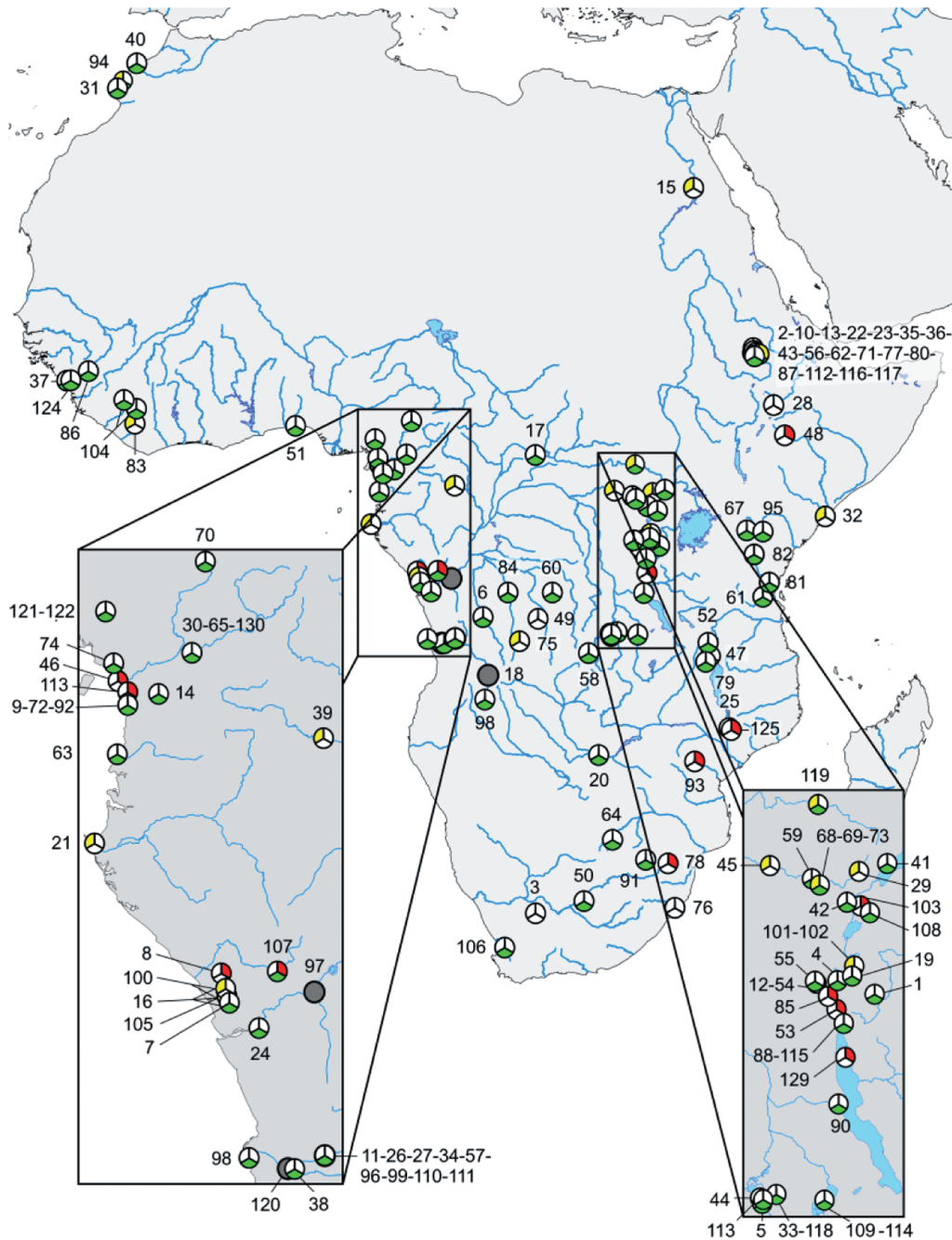
For a long time, the large, hexaploid barbs have been considered part of the genus *Barbus*, a 'monstrous aggregation' (Myers, 1960: 213). Recognition of the former as a separate lineage, now referred to as *Labeobarbus*, has at least enabled the delineation of a more easily surveyed entity; however, partially as a result of the recent synonymy of *Varicorhinus*, *Labeobarbus s.l.* currently still contains approximately 125(+2) valid African species, and as such still represents one of the largest genera of African freshwater fishes. With its numerous particularities, including the striking mouth phenotype polymorphism and the apparent, although still largely underestimated, propensity to hybridize, the alpha-taxonomy is still in a poor state of resolution and the tasks ahead, therefore, remain overwhelming.




The current taxonomic situation of the African Torini can be briefly summarized as follows. On the one hand, valid species with a *Labeobarbus*, *Varicorhinus*, or intermediate mouth phenotype are often considered monomorphic with regards to mouth phenotype, and these are often the more poorly investigated taxa. On the other hand, however, quite a few valid species are now regarded as being highly polymorphic, and they are often the seemingly better known species (see Table 1). These cases mostly include taxa with the extreme *Labeobarbus* and *Varicorhinus* mouth pheno-

types, as well as with intermediate mouth phenotypes, all assembled under the taxonomic umbrella of one valid species. These two rather opposing taxonomic manifestations of mouth phenotype diversity within *Labeobarbus s.l.* are historically rooted, and these roots still have their repercussions on the present-day taxonomic situation. Whereas Boulenger (1909, 1916a) and other early authors described most mouth phenotypes as discrete species, the gradual conceptual change in interpreting mouth phenotype polymorphism in some of the more extensively documented species, for example, the Southern African *L. marequensis*, led gradually to the present-day taxonomic solution that these species are taxa representing extreme cases of intraspecific polymorphism (see Skelton, 1993, 2001; Marshall, 2011). It is not unlikely that the systematics and taxonomy of *Labeobarbus s.l.* will remain in this schizophrenic and unsatisfactory state, because we seem as yet unable to fully grasp the nature of species in these African hexaploid Torini, and hence there is the need for integrated comprehensive and interdisciplinary studies to provide convincing and testable hypotheses. Although detailed morphological descriptions with a focus on documenting sympatric mouth polymorphism and ontogenetic development would provide the necessary detailed phenotypic data for many cases, mitochondrial and nuclear DNA-based phylogenetics as well as genomics including cross-breeding experiments would be indispensable to gain a better understanding of the evolutionary dynamics underlying the observed mouth phenotype megadiversity across Africa and the Middle East. The current review paper hopefully provides a first framework to taxonomically and phenotypically allocate results and implications of upcoming case studies, such as the one currently undertaken on the polymorphic species complexes in two Congo subdrainages, i.e. the Inkisi Basin (E. Vreven, S. Wamuini Lunkayilakio, T. Musschoot, E. Decru, J. Snoeks & U. Schliewen, unpubl. data) and the Epulu Basin (DRC; E. Decru, A. Walanga, J. Snoeks & E. Vreven, unpubl. data).

### SIMILARITIES BEYOND THE AFRICAN CONTINENT?

The occurrence of a highly specialized *Varicorhinus*-like mouth phenotype is not unique to the African species of the genus *Labeobarbus s.l.* Instead, a tentative compilation of its distribution illustrates that it is a recurrent phenomenon in several cyprinid genera with very different levels of ploidy, i.e. diploids, tetraploids, and again hexaploids. Indeed, altogether, one Leuciscinae genus (*sensu* Gaubert, Denys & Oberdorff, 2009) and eight Cyprininae genera (*sensu* Yang *et al.*, 2015) are composed entirely of species with the lower jaw bearing a horny cover with a sharp cutting edge on its anterior edge and often fleshy on the mouth



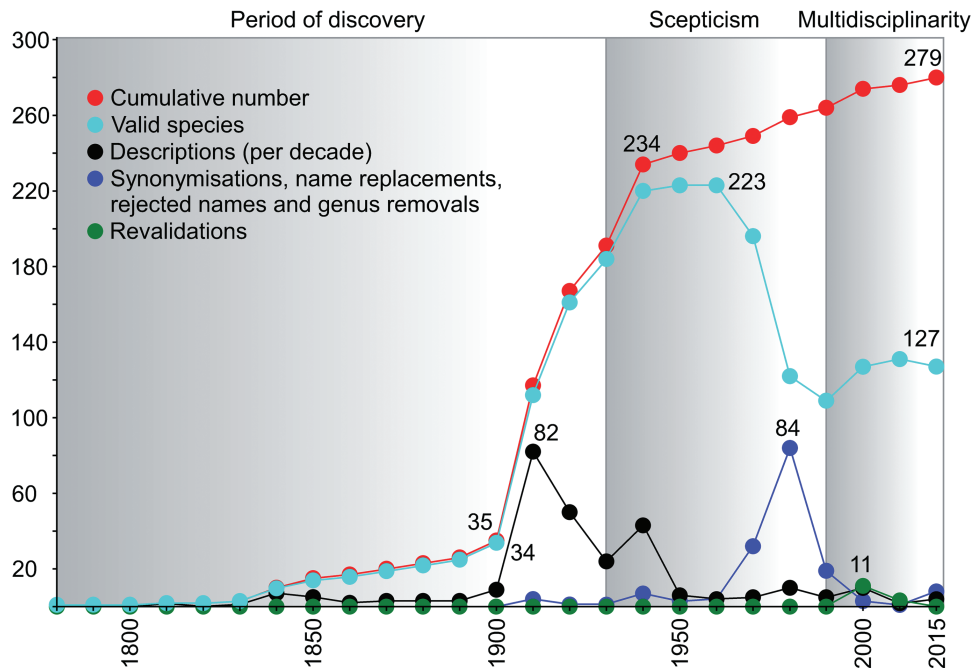
**Figure 6.** Map of Africa illustrating the overall distribution of the different mouth phenotypes over the continent. Mouth phenotype(s) and mouth phenotype polymorphism have been mapped according to: (1) the three major mouth phenotypes, i.e. *Labeobarbus*, intermediate, or *Varicorhinus* mouth phenotype, and the papillated mouth phenotype as retained in Table 1; (2) using the coordinates of the type localities of the valid species only. For the few cases where coordinates could not be attributed to the type locality, the type region has been used to map the data. Mouth phenotype polymorphism as illustrated on the map refers to that found in the nominal type specimen(s) (i.e. holotype, lectotype, neotype, or syntypes) of each valid species only. In addition, mouth phenotype polymorphism as documented for both – i.e. (1) the nominal type specimen(s) of each valid species only, and (2) all other type(s) and non-type specimens of each valid species – has been visualized on the right side of the map. For each of the valid species under consideration:  refers to the occurrence of the *Labeobarbus* mouth phenotype;  refers to the occurrence of the *Varicorhinus* mouth phenotype;  refers to the occurrence of the intermediate mouth phenotype; and a fully filled grey locality dot refers to the occurrence of the papillated mouth phenotype (never in combination with any of the other phenotypes).

1. <i>L. acuticeps</i>	☺ ☺	44. <i>L. ipthimostoma</i>	☹ ☹	87. <i>L. platydorsus</i>	☺ ☺
2. <i>L. acutirostris</i>	☺ ☺	45. <i>L. iturii</i>	☹? ☺	88. <i>L. platyrhinus</i>	☺ ☺
3. <i>L. aeneus</i>	☺ ☺	46. <i>L. jaegeri</i>	☹ ☺	89. <i>L. platystomus</i>	☺ ☺
4. <i>L. altianalis</i>	☺ ☺	47. <i>L. johnstonii</i>	☺ ☺	90. <i>L. pojeri</i>	☺ ☺
5. <i>L. altipinnis</i>	☺ ☺	48. <i>L. jubae</i>	☹ ☺	91. <i>L. polylepis</i>	☺ ☺?
6. <i>L. ansorgii</i>	☺ ☺	49. <i>L. jubbi</i>	☺ ☺	92. <i>L. progenys</i>	☺ ☺
7. <i>L. aspilus</i>	☺ ☺	50. <i>L. kimberleyensis</i>	☺ ☺	93. <i>L. pungweensis</i>	☺ ☺
8. <i>L. axelrodi</i>	☺ ☺	51. <i>L. lagensis</i>	☺ ☺	94. <i>L. reinii</i>	☺ ☺
9. <i>L. batesii</i>	☺ ☺	52. <i>L. latirostris</i>	☺ ☺	95. <i>L. rhinoceros</i>	☺ ☺
10. <i>L. beso</i>	☺ ☺	53. <i>L. leleupanus</i>	☺ ☺	96. <i>L. rhinophorus</i>	☺ ☺
11. <i>L. boulengeri</i>	☺ ☺	54. <i>L. longidorsalis</i>	☺ ☺	97. <i>L. robertsi</i>	☹ ☹
12. <i>L. brauni</i>	☺? ☺	55. <i>L. longifilis</i>	☺ ☺	98. <i>L. rocadasi</i>	☺ ☺
13. <i>L. brevicephalus</i>	☺ ☺	56. <i>L. longissimus</i>	☺ ☺	99. <i>L. rosae</i>	☺? ☺
14. <i>L. brevispinis</i>	☺ ☺	57. <i>L. lucius</i>	☺ ☺	100. <i>L. roylii</i>	☺ ☺
15. <i>L. bynni</i>	☺ ☺	58. <i>L. lufupensis</i>	☺ ☺	101. <i>L. ruandae</i>	☺ ☺
16. <i>L. cardozoi</i>	☺ ☺	59. <i>L. macroceps</i>	☺ ☺	102. <i>L. ruasae</i>	☺ ☺
17. <i>L. caudovittatus</i>	☺ ☺	60. <i>L. macrolepidotus</i>	☺ ☺	103. <i>L. ruwenzorii</i>	☺ ☺
18. <i>L. clarkeae</i>	☹ ☹	61. <i>L. macrolepis</i>	☺ ☺	104. <i>L. sacratus</i>	☺ ☺
19. <i>L. claudinae</i>	☺ ☺	62. <i>L. macropthalmus</i>	☺ ☺	105. <i>L. sandersi</i>	☺ ☺
20. <i>L. codringtonii</i>	☺ ☺	63. <i>L. malacanthus</i>	☺ ☺	106. <i>L. seeberi</i>	☺ ☺
21. <i>L. compiniei</i>	☺ ☺	64. <i>L. marequensis</i>	☺ ☺	107. <i>L. semireticulatus</i>	☺? ☺
22. <i>L. crassibarbis</i>	☺ ☺	65. <i>L. mariae</i>	☺? ☺	108. <i>L. somereni</i>	☺ ☺
23. <i>L. dainellii</i>	☺ ☺	66. <i>L. maroccanus</i>	☺ ☺	109. <i>L. stappersii</i>	☺ ☺
24. <i>L. dartevellei</i>	☺ ☺	67. <i>L. matris</i>	☺ ☺	110. <i>L. steindachneri</i>	☺ ☺
25. <i>L. dimidiatus</i>	☺ ☺	68. <i>L. mawambi</i>	☺ ☺	111. <i>L. stenostoma</i>	☺ ☺
26. <i>L. ensifer</i>	☹ ☹	69. <i>L. mawambiensis</i>	☺ ☺	112. <i>L. surkisi</i>	☺ ☺
27. <i>L. ensis</i>	☺ ☺	70. <i>L. mbami</i>	☺ ☺	113. <i>L. tornieri</i>	☺ ☺
28. <i>L. ethiopicus</i>	☺ ☺	71. <i>L. megastoma</i>	☺ ☺	114. <i>L. trachypterus</i>	☺ ☺
29. <i>L. fasolt</i>	☺ ☺	72. <i>L. micronema</i>	☺ ☺	115. <i>L. tropidolepis</i>	☺ ☺
30. <i>L. fimbriatus</i>	☺ ☺	73. <i>L. mirabilis</i>	☺ ☺	116. <i>L. truttiformis</i>	☺ ☺
31. <i>L. fritschii</i>	☺ ☺	74. <i>L. mungoensis</i>	☺ ☺	117. <i>L. tsanensis</i>	☺ ☺
32. <i>L. gananensis</i>	☺ ☺	75. <i>L. nanningsi</i>	☺ ☺	118. <i>L. upembensis</i>	☺ ☺
33. <i>L. gestetneri</i>	☺ ☺	76. <i>L. natalensis</i>	☺ ☺	119. <i>L. urotaenia</i>	☺ ☺
34. <i>L. girardi</i>	☺ ☺	77. <i>L. nedgia</i>	☺ ☺	120. <i>L. varicostoma</i>	☺ ☺
35. <i>L. gorgorensis</i>	☺ ☺	78. <i>L. nelspruitensis</i>	☺ ☺	121. <i>L. versluysii</i>	☺ ☺
36. <i>L. gorguari</i>	☺ ☺	79. <i>L. nthuwa</i>	☺ ☺	122. <i>L. weneri</i>	☺? ☺
37. <i>L. gruvelli</i>	☺ ☺	80. <i>L. osseensis</i>	☺ ☺	123. <i>L. wittei</i>	☺ ☺
38. <i>L. guilelmi</i>	☺ ☺	81. <i>L. oxyrhynchus</i>	☺ ☺	124. <i>L. wurtzi</i>	☺ ☺
39. <i>L. habereri</i>	☺ ☺	82. <i>L. pagenstecheri</i>	☺ ☺	125. <i>L. xyrocheilus</i>	☺ ☺
40. <i>L. harterti</i>	☺ ☺	83. <i>L. parawaldroni</i>	☺ ☺		
41. <i>L. huloti</i>	☺ ☺	84. <i>L. paucisquamatus</i>	☺ ☺	129. <i>A. tanganycae</i>	☺ ☺
42. <i>L. humphri</i>	☺ ☺	85. <i>L. pellegrini</i>	☺? ☺	130. <i>S. velifera</i>	☺ ☺
43. <i>L. intermedius</i>	☺ ☺	86. <i>L. petitjeani</i>	☺ ☺		

Figure 6. Continued

corners only (see Table 2). In addition, four more Cyprininae genera (*sensu* Yang *et al.*, 2015) are known to contain at least some species with a *Varicorhinus*-like mouth phenotype, and the same holds true for another Leuciscinae genus (*sensu* Gaubert *et al.*, 2009) (see Table 2). Furthermore, the occurrence of comparable *Labeobarbus/Varicorhinus*-like mouth phenotype polymorphism is not restricted to the African species of the genus *Labeobarbus s.l.* (see Table 2), because a similar *Labeobarbus/Varicorhinus* mouth phenotype polymorphism has been documented for *B. grypus* (see Roberts & Khaironizam, 2008: 47–48, 50), known from the Tigris–Euphrates Basin and rivers from southern Iran (Borkenhagen, 2014); now an *Arabibarbus*, following Borkenhagen (2014), and part of *Labeobarbus s.l.* (see Tsigenopoulos *et al.*, 2010; Berrebi *et al.*, 2014; Yang *et al.*, 2015). In addition, it has also

been documented outside *Labeobarbus s.l.* (see Table 2). First, Roberts & Khaironizam (2008) observed and documented a comparable mouth phenotype variation and polymorphism in *Neolissochilus*. Within *Neolissochilus soroides* (Duncker, 1904) from the Sungai Gombak, a small tributary of the Sungai Kelang River (Malaysia), they documented the occurrence of specimens with a generalized, normal, or *Neolissochilus*-like, i.e. an intermediate, mouth phenotype, besides specimens with a *Lissochilus*- or *Acrossocheilus*-like, i.e. *Varicorhinus*-like, mouth phenotype and specimens with a *Tor*-like, i.e. *Labeobarbus*-like, mouth phenotype. Recently, Khaironizam *et al.* (2015) confirmed the occurrence of three mouth phenotypes in *N. soroides* that are very similar to the *Labeobarbus*, intermediate, and *Varicorhinus* mouth phenotypes documented herein. Their meristic analyses identified no differences between



**Figure 7.** Diagram illustrating chronological changes in species numbers for *Labeobarbus*, *sensu* Tsigenopoulos *et al.* (2010) and Berrebi *et al.* (2014), in Africa. All numbers are provided per decade.

For this diagram, all species have been attributed to *Labeobarbus* although many of them have originally been described in other genera in use at the time of their original description. The two species of the monospecific genera *Acapoeta* and *Sanagia* have been included in these counts. *Nomina nuda* are not included in the counts, as they are unavailable for nomenclatural purposes. A preoccupied name is counted as +1 by its original description and replaced (−1) by its replacement name (+1) at the date of replacement. No distinction has been made between species or subspecies descriptions, and as such both have been counted as +1 at the time of their original description. Giving both equal weighting gives a better overview of overall taxonomic activity in the genus as currently recognized. As nowadays none of the valid species, except for the West African and Nilotic *Labeobarbus bynni* and the East African *Labeobarbus intermedius* (see annotated checklist 2), is considered to contain subspecies, all previously described subspecies have been considered as formally synonymized, which translates into −1 for each, at the date of the first publication formally rejecting or instead clearly neglecting them. As such, of course, a change from subspecies to species level is not visible, and neither is the reverse; however, what has been made visible is the synonymization of subspecies with other subspecies or with the valid species.

the mouth phenotypes, but morphometrics revealed selected mouth phenotype-related differences in lower jaw length and lower jaw width. Khaironizam *et al.* (2015) concur with Roberts & Khaironizam (2008) in interpreting the observed mouth phenotypes as trophic polymorphism, but they also stipulated the need to further examine the question with genomic techniques.

In addition, comparable mouth phenotype variation and intergradation has also been documented within the genus *Schizothorax*. Indeed, although according to Roberts & Khaironizam (2008: fig. 9) the genus *Schizothorax* (however, see Qi *et al.*, 2012) is composed of species having a *Labeobarbus*- or *Tor*-like mouth phenotype, the genus *Oreinus* McClelland, 1838 is composed of species with a *Varicorhinus*-, *Lissochilus*-, or *Arossocheilus*-like mouth phenotype and a variety of

intermediate mouth phenotypes bridging the mouth phenotypic gap between both these genera. Hora (1934 *vide* Roberts & Khaironizam, 2008: fig. 9) illustrated the mouth phenotype intergradation in between *Schizothorax labiatus* (McClelland, 1842) and *Oreinus sinuatus* var. *griffithi* McClelland, 1842 (both *Schizothorax sinuatus* Heckel, 1838 and *Oreinus griffithi* are now junior synonyms of *Schizothorax plagiostomus* Heckel, 1838 *vide* Coad, 1981) from the mountainous area of Chitral in north-eastern Afghanistan (see Roberts & Khaironizam, 2008). Interestingly, some of the illustrated intermediate mouth phenotypes are characterized by the presence of numerous papillae, on the lower jaw. This is remarkable, as some of the *Labeobarbus s.l.* species do not have a *Labeobarbus*, *Varicorhinus*, or a fully intermediate mouth phenotype, but instead bear numerous papillae on their lower

**Table 2.** Overview of the occurrence of comparable *Varicorhinus* mouth phenotype, and comparable *LabeobarbusVaricorhinus* mouth phenotype polymorphism, in other Cyprinid genera.

Genus	Author & date	Subfamily	No. of species	Occurrence	Ploidy level (2n)	References
<b>Occurrence of comparable <i>Varicorhinus</i> mouth phenotype</b>						
<i>Aerocheilus</i>	Agassiz, 1855	Leuciscinae	1	all spp.	50*	Robe, 1998: 132; Gau <i>et al.</i> , 2009: 669, fig. 13; Ar, 2011: 65
<i>Capoeta</i>	Valenciennes, 1842	Cyprininae (Ibrini)	22	all spp.	148 & 150*	Ar, 2011: 48–49; Le <i>et al.</i> , 2013: 400; Ya <i>et al.</i> , 2015: 99, table 3
<i>Cyprinion</i>	Heckel, 1843	Cyprininae (Barbini)	9	all spp.	50*	Ar, 2011: 49; Le <i>et al.</i> , 2013: 400; Ya <i>et al.</i> , 2015: 99, table 3
<i>Herzensteinia</i>	Chu, 1935	Cyprininae (Schizothoracini)	1	all spp.	unknown	Gau <i>et al.</i> , 2009: 664, fig. 8; Qi <i>et al.</i> , 2012: 3, fig. 1; Ya <i>et al.</i> , 2015: 99, table 3
<i>Onychostoma</i>	Günther, 1896	Cyprininae (Acrossocheilini)	21	all spp.	50	Ar, 2011: 50; Le <i>et al.</i> , 2013: 400; Ta, 1975: 143; Ya <i>et al.</i> , 2015: 99, table 3
<i>Platypharodon</i>	Herzenstein, 1891	Cyprininae (Schizothoracini)	1	all spp.	90*	Ar, 2011: 70; Qi <i>et al.</i> , 2012: 3, fig. 1; Ya <i>et al.</i> , 2015: 99, table 3
<i>Scaphiodonichthys</i>	Vinciguerra, 1890	Cyprininae (Barbini)	4	all spp.	50	Do, Ma&Ra, 2012: 439; Le <i>et al.</i> , 2013: 400; Ta, 1975: 143; Ya <i>et al.</i> , 2015: 99, table 3
<i>Scaphognathops</i>	Smith, 1945	Cyprininae (Poropuntini)	3	all spp.	unknown	Ta, 1975: 143; Ra, 1996: 100; Ya <i>et al.</i> , 2015: 99, table 3
<i>Semiplotus</i>	Bleeker, 1860	Cyprininae (Barbini)	3	all spp.	50	Sa, Na&Ba, 2009: 501; Le <i>et al.</i> , 2013: 400
<i>Chondrostoma s.l.</i>	Agassiz, 1832	Leuciscinae	20 s.s. / 37 s.l.	some spp.	50*	Ar, 2011: 62; Gan <i>et al.</i> , 2004; Gau <i>et al.</i> , 2009: 670, fig. 14; Ko&Fr, 2007: 150; Roba <i>et al.</i> , 2007
<i>Diptychus</i>	Steindachner, 1866	Cyprininae (Schizopygopsini)	2	some spp.	98 & 100*	Ar, 2011: 70; Qi <i>et al.</i> , 2012: 3, fig. 1; Ya <i>et al.</i> , 2015: 99, table 3
<i>Poropuntius</i>	Smith, 1931	Cyprininae (Poropuntini)	40	some spp.	50	Ar, 2011: 50; Le <i>et al.</i> , 2013: 400; Ya <i>et al.</i> , 2015: 99, table 3
<i>Schizocypris</i>	Regan, 1914	Cyprininae (Barbini)	3	some spp.	92	Ar, 2011: 70; Le <i>et al.</i> , 2013: 400; Ya <i>et al.</i> , 2015: 99, table 3
<i>Schizopygopsis</i>	Steindachner, 1866	Cyprininae (Schizopygopsini)	8	some spp.	90 & 92	Ar, 2011: 70; Qi <i>et al.</i> , 2012: 3, fig. 1; Ya <i>et al.</i> , 2015: 99, table 3
<b>Occurrence of comparable <i>LabeobarbusVaricorhinus</i> mouth phenotype polymorphism</b>						
<i>Neotissochilus</i>	Rainboth, 1985	Cyprininae (Ibrini)	23	at least one sp.	98 & 100	Ar, 2011: 49–50; Robe&Ka, 2008: 32–34; Ya <i>et al.</i> 2015: 99, table 3
<i>Schizothorax</i>	Heckel, 1838	Cyprininae (Schizothoracini)	62	at least one sp.	90–150	Ar, 2011: 71; Robe & Ka, 2008: 50–51, fig. 9; Ya <i>et al.</i> , 2015: 99, table 3

For more details, see the main text. Subfamily-level classification according to Gaubert *et al.* (2009) and Arai (2011), further updated following Yang *et al.* (2015) for the Cyprininae, with the addition of the Tribe (between brackets) for members of the latter subfamily. Species numbers as provided per genus follow FishBase (Froese & Pauly, 2015). Abbreviations of the author names for the references cited are as follows: Ar, Arai; Do, Ma&Ra, Donsakul, Magtoon & Rangsiruj; Gan, Gante; Gau, Gaubert; Ko&Fr, Kottelat & Freyhof; Le, Levin; Ra, Rainboth; Sa, Na&Ba, Sahoo, Nanda & Barat; Ta, Taki; Roba, Robalo; Robe&Ka, Roberts & Khaonizam; Ya, Yang.

\*Ploidy level (2n) as found in the type species of the genus.

as well as upper jaw. Within *Labeobarbus s.l.* this mouth phenotype is currently only reported from the Lower Congo, i.e. the Inkisi River Basin (DRC) and the Quanza River Basin (Angola) (see above), and seems to imply the recurrent occurrence of other, less widespread, mouth phenotypes as well.

The recurrent occurrence of *Varicorhinus*-like mouth phenotypes has already received particular attention in Schizothoracinae (*sensu* Qi *et al.*, 2012) as well as *Chondrostoma s.l.* (*sensu* Gante, Collares-Pereira & Coelho, 2004) (see below). Qi *et al.* (2012: fig. 3A) interpreted the paraphyletic occurrence of specimens with a *Varicorhinus*-like 'sharp outer horny sheath' on the lower jaw in their cytochrome *b* mtDNA phylogenetic tree of the Schizothoracinae, as evidence for convergent and parallel evolution. Although the recurrent occurrence of such highly similar and specialized mouth phenotypes, such as that with the *Varicorhinus*-like 'sharp outer horny sheath', might indeed result from convergent as well as parallel *de novo* evolution of character states, other possibly equally or more parsimonious explanations appear possible. Similar to *Labeobarbus s.l.* (Tsigenopoulos *et al.*, 2010: fig. 1), there is mtDNA-based phylogenetic signal for a paraphyly of the highly specialized cutting edge mouth phenotype in Schizothoracinae. Although the homology of these highly similar *Varicorhinus*-like mouth phenotypes has yet to be demonstrated, this recurrent and highly similar expression of a specific mouth phenotype allows us to hypothesize that the cutting edge phenotype might be encoded by ancient homologous Cyprinidae genes that are sometimes but not always expressed, e.g. possibly after hybridization events.

The same hypothesis might hold explanatory potential for the similar situation in *Chondrostoma s.l.* Here again, the paraphyletic occurrence of a ventral rasping mouth reinforced by a horny layer that forms a cutting edge on the lower lip, i.e. a cutting-edge phenotype, in their combined mitochondrial and nuclear DNA-based phylogeny, led Robalo *et al.* (2007) to hypothesize that this phenotype evolved several times through convergent evolution. Based on this, they proposed five morphologically poorly diagnosed (see Kottelat & Freyhof, 2007) new genera within the *Chondrostoma s.l.* lineage: two without a horny layer on the lower lip, *Achondrostoma* Robalo *et al.*, 2007 and *Iberochondrostoma* Robalo *et al.*, 2007, and three with a horny layer on the lower lip, i.e. *Parachondrostoma* Robalo *et al.*, 2007, *Pseudochondrostoma* Robalo *et al.*, 2007, and *Protochondrostoma* Robalo *et al.*, 2007. Although Robalo *et al.* (2007) mentioned the possibility of introgression/hybridization to explain the observed pattern, they argued against a causative role despite extensive evidence for hybridization within *Chondrostoma s.l.* (Gante *et al.*, 2004; I. Doadrio, unpubl. data, *vide* Robalo *et al.*, 2007). Furthermore, Perea *et al.*

(2010: fig. 4) revealed *Achondrostoma* as defined by Robalo *et al.* (2007) as paraphyletic in their mtDNA results, and they identified additional basal inconsistencies in the *Chondrostoma* phylogeny (see Perea *et al.*, 2010: figs 4, 6). This contradictory phylogenetic evidence might allow us to speculate that also within *Chondrostoma s.l.*, the mosaic pattern of occurrence of the specialized *Chondrostoma* mouth is at least partially based on complex patterns of past and current introgression/hybridization (see Gante *et al.*, 2004). Here, too, the genomic processes governing the expression of the specialized *Chondrostoma* mouth must be elucidated before a better understanding of its first apparition and re-apparition will be possible.

Finally, Roberts (1998) also reported the occurrence of a 'discrete trophic polymorphism' in two species of *Poropuntius* Smith, 1931, i.e. *Poropuntius bolovenensis* Roberts, 1998 from Laos and *Poropuntius genyognathus* Roberts, 1998 from Burma. The former case in particular was well documented by Roberts (1998), when he recognized 'four distinct forms or morphs' in this species with 'pronounced trophic polymorphism' (see Roberts, 1998: 124). He gave them subspecific rank: (1) *Poropuntius bolovenensis bolovenensis* Roberts, 1998, with the lips and horny jaw sheaths moderately developed and the margin of the lower horny jaw sheath rounded, with no trenchant cutting edge; (2) *Poropuntius bolovenensis acuticeps* Roberts, 1998, with hypertrophied lips but, however, with the lower lip not continuous and lacking the typical mental lobe of the *Labeobarbus* mouth phenotype; (3) *Poropuntius bolovenensis glaridostoma* Roberts, 1998, with the lower horny jaw sheath greatly thickened and broad, and with a sharp transverse cutting margin reminiscent of the *Varicorhinus* mouth phenotype; and finally (4) *Poropuntius bolovenensis laticeps* Roberts, 1998, with a mouth nearly as broad as that of *P. b. glaridostoma*, but without the extreme reduction of the lower lip or the development of a lower horny jaw sheath with a trenchant margin. In contrast to Roberts (1998), Kottelat (2000) interpreted this mouth phenotype variation very differently, i.e. he considered each of Roberts' (1998) subspecies as full species. As Roberts' infrasubspecific morph names are taxonomically unavailable (see Kottelat, 2000; see also Eschmeyer, 2015, although with different argumentation) he consequently provided new names for two of Roberts' morphs: *Poropuntius consternans* Kottelat, 2000, for *P. b. acuticeps*, and *Poropuntius lobocheiloides*, Kottelat, 2000, for *P. b. glaridostoma*, whereas *P. b. laticeps* was tentatively identified as conspecific with *P. lobocheiloides* (see Kottelat, 2013), and he even identified a fourth species for the Xe Nam Noi or Xe Nam Noy Basin, which he named *Poropuntius solitus* Kottelat, 2000. Kottelat (2000) based his interpretation on evidence from additional non-feeding-related, meristic



differences in these taxa, which had already been reported by Roberts (1998), and he complemented Roberts' (1998) data with his own additional observations on differences in meristics, habitus, and the relative position of the fins. Surprisingly, Kottelat (2000) did not consider interspecific hybridization as a hypothesis, which could at least explain part of the mouth phenotype variation in these taxa (see above for *Labeobarbus*). As for the *Labeobarbus/Varicorhinus* mouth phenotype polymorphism, here also the radically different interpretation of the mouth phenotype variation clearly points to the dissatisfactory state of our current understanding of this phenomenon across multiple cyprinid lineages.

Interestingly, Roberts (1998) already hypothesized that a genetic basis for such polymorphism could have already been present in proto-Cyprinidae Ostariophysi (our wording). He further pointed to the observation that these apparently ancient and genetically controlled phenotypic differences are repeatedly expressed as intraspecific mouth phenotype variation, mainly in species inhabiting lakes or streams isolated from neighbouring water bodies by barriers such as waterfalls, as is the case for *P. bolovenensis*, for example. Isolation from species-rich fish communities would enhance ecological opportunities for specialized mouth phenotypes, and thereby favour the rapid re-expression of ancient genomic potentialities, which only seemingly appear to be 'evolutionary novelties' (see Roberts, 1998: 132). Species not expressing alternative phenotypes would nevertheless silently carry all genomic information necessary to generate an array of discrete phenotypes, with their expression depending on ecological conditions (Roberts, 1998). Even if Kottelat (2000) classified the observed mouth phenotype polymorphism in *Poropuntius* drastically differently, the idea of ancient genomic processes governing – in combination with environmental factors – the expression of the highly specialized potentialities for alternative mouth phenotypes across multiple cyprinid lineages remains an appealing hypothesis to explain for its widespread occurrence.

#### IS THE COMBINATION OF HEXAPLOIDY AND RECURRENT HYBRIDIZATION PROMOTING PHENOTYPIC DIVERSITY?

All these numerous cases of a well-defined polymorphism within *Labeobarbus s.l.* and across genera raise numerous questions with regards to the origin of both the hexaploidy as well as the observed mouth phenotype characters, and their polymorphic variation. For example, both *Labeobarbus* and *Capoeta* are hexaploid, and mitochondrial DNA results (see Tsigenopoulos *et al.*, 2010; Yang *et al.*, 2015: fig. 2) support their reciprocal monophyly, i.e. an independent origin of both

haplotype lineages. Both these mitochondrial DNA phylogenies therefore support a primarily independent, possibly allopatric, origin of these lineages. Furthermore, Yang *et al.*'s (2015: fig. 4) analysis of a single nuclear gene (*RAG1*) suggests that these hexaploid lineages might have derived from two independent hybridization events between their respective tetraploid ancestors: i.e. tetraploid Torini and *Luciobarbus*, a member of the barbinae, respectively (maternal source), and *Cyprinion* (paternal source). Considering that the data presented are based on a single nuclear gene, and that many nodes are weakly supported, however, this hypothesis of hybridization cannot be tested against the one of incomplete lineage sorting without additional (genomic) data. Interestingly, the extreme *Labeobarbus/Varicorhinus* mouth polymorphism as found in *Labeobarbus s.l.* is altogether lacking, for example, in *Capoeta*, where all species are reported to have a clear cutting edge on the lower jaw (*vide* Bănărescu, 1999), as found in the *Varicorhinus* mouth phenotype of *Labeobarbus s.l.* Mouth phenotype variation is not entirely lacking in *Capoeta* (see Karaman, 1969), however, and instead has been reported for: (1) the overall shape of the mouth (horsehoe-shaped versus rectangular); (2) the development of a horny cover; and (3) the sharpness of the real cutting edge, which even seems to be entirely absent in some specimens (E. Vreven, pers. observ., 2015). In addition, Küçük *et al.* (2009) reported the presence of fleshy lips for *Capoeta pestai* (Pietschmann, 1933) and *Capoeta mauricii* Küçük *et al.*, 2009, as well as an overall superficial resemblance of both to the species of the genus *Luciobarbus* with regard to their pointed heads and general shape. Therefore, two major mouth phenotypes of *Labeobarbus s.l.* might well be, under a hybridization scenario, the product of introgression of *Capoeta*-type cutting edge genes into a fleshy lip proto-*Labeobarbus* genome, for example. A similar scenario may also be envisaged for the more distantly related cyprinine genus *Schizothorax*, which comprises tetraploid and hexaploid species alike (see Arai, 2011), and for which comparable mouth phenotype variation has also been reported (see above). Considering that for many cyprinine species and even genera the ploidy level remains unknown, additional cases of mixed tetraploidy and hexaploidy within the cyprinine genera, coupled with additional cases of a *Varicorhinus*-like mouth phenotype in sometimes polymorphic genera, cannot entirely be excluded. Indeed, Van de Peer, Maere & Meyer (2009) suggested that although descendants of whole-genome duplications (WGDs) often do not survive, they can be very successful if they do survive. Morphologically, however, most *Capoeta* species have the last unbranched dorsal fin ray denticulated (see Karaman, 1969; Bănărescu, 1999), at least in juveniles and subadults (but not in all, e.g. *Capoeta caelestis* Schöter,

Özuluğ & Freyhof, 2009), whereas such denticulations, although present in *Luciobarbus* (see Bănărescu & Bogutskaya, 2003), never occur in *Labeobarbus s.l.*

An alternative hypothesis for the recurrent origin of mouth phenotypes not only across genera but within *Labeobarbus s.l.* has been suggested by Levin *et al.* (2013) with regards to the *V. beso* and *Varicorhinus*-like mouth phenotypes. According to the mtDNA evidence of these authors, a cutting edge might have evolved multiple times de novo in Ethiopia, a hypothesis that these authors took as justification for the recognition of *Varicorhinus* as a monospecific genus; however, the occurrence of monomorphic phenotypes may camouflage a heterozygotic genome encoding a silent polymorphism (see Roberts, 1998), which under certain environmental circumstances and/or after hybridization events, for example, might become re-expressed and again produce polymorphic phenotypes, especially in polyploid taxa (Otto, 2007).

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#### ANNOTATED CHECKLIST 1: AFRICAN *LABEOBARBUS S.L.* SPECIES

*acuticeps*, *Barbus* Matthes, 1959. River Nyawarongo [Mbuye] ( $\pm 2^{\circ}26'S$ ,  $30^{\circ}21'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Rwanda. Holotype: MRAC 130313. Paratypes: MRAC 130310 (1), 130311–312 (2), 130314 (1). Current status: valid as *Labeobarbus acuticeps* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Nyabarongo, Akanyaru, upper Akagera (including some lakes in the Bugusera depression) and middle Akagera (below Rusumo Falls) basins (De Vos & Thys van den Audenaerde, 1990). Notes: (1) paratype MRAC 130310 is also a paratype of *Barbus* (now *Labeobarbus*) *claudinae* De Vos & Thys van den Audenaerde, 1990; (2) considered to be 'dubiously distinct from *B. altianalis*' by Banister (1973: 8), but De Vos & Thys van den Audenaerde (1990) mention clear differences in the number of gill rakers and lateral line scales, and the barbel length, to distinguish both species.

*acutirostris*, *Barbus brunelli* Bini, 1940. Debre Mariam (11°38'N, 37°24'E, Nagelkerke & Sibbing, 1997) (locality 1), Lake Tana, Ethiopia. Neotype: RMNH 32870 (designated by Nagelkerke & Sibbing, 1997). Current status: valid as *Labeobarbus acutirostris* (placed in *Labeobarbus* in Getahun, 2007a). Synonym of *Barbus intermedius* in Banister (1973); raised to species level and revalidated as *Barbus acutirostris* by Nagelkerke & Sibbing (1997). Synonyms: none. Distribution: Endemic to Lake Tana, Ethiopia (Nagelkerke & Sibbing, 1997). Notes: originally described as a subspecies of *Barbus* (now *Labeobarbus*) *brunellii*, a junior synonym of *L. intermedius*, following Banister (1973).

*aeneus*, *Cyprinus* Burchell, 1822. Zak River ( $\pm 29^{\circ}39'S$ ,  $21^{\circ}11'E$ , D.F.E. Thys van den Audenaerde, unpubl. data) [trib. of Orange River, South Africa]. No types known (Hocutt & Skelton, 1983). Current status: valid as *Labeobarbus aeneus* (placed in *Labeobarbus* in Skelton, 2001). Synonyms: *Barbus gilchristi* Boulenger, 1911 (synonymy in Jubb, 1963); *Barbus holubi* Steindachner, 1894 (synonymy in Barnard, 1943); *Barbus mentalis* Gilchrist & Thompson, 1913 (synonymy in Jubb, 1963). Distribution: natural range, Orange–Vaal system (Skelton, 2001). Various introductions in South Africa and Zimbabwe (Skelton, 2001; Marshall, 2011).

*alluaudi*, *Barbus* Pellegrin, 1909. A hybrid; see annotated checklist 2.

*altianalis*, *Barbus* Boulenger, 1900. Lake Kivu ( $\pm 2^{\circ}0'S$ ,  $29^{\circ}10'E$ , USBGN, 1964b), north-east of Lake Tanganyika. Lectotype: BMNH 1906.9.6.13 (designated by Banister, 1973). Paralectotypes: BMNH 1906.9.6.14 (1), 1906.9.6.15 (1). Current status: valid as *Labeobarbus altianalis* (placed in *Labeobarbus* in Skelton & Bills, 2008; Banyankimbona *et al.*, 2012a). Synonyms: *Barbus altianalis labiosa* Pellegrin, 1933 (synonymy in Banister, 1973); *Barbus bayoni* Boulenger, 1911; *Barbus eduardianus* Boulenger, 1901; *Barbus fergusonii* Boulenger, 1901 (synonymy in Worthington, 1932); *Barbus hollyi* Lohberger, 1929 (synonymy in Greenwood, 1966); *Barbus kiogae* Worthington, 1929; *Barbus kivuensis* Pappenheim, 1914 in Pappenheim & Boulenger, 1914 (synonymy in Banister, 1973); *Barbus lobogenys* Boulenger, 1906 (synonymy in Worthington, 1932); *Barbus longirostris* Worthington, 1929; *Barbus obesus* Worthington, 1929 (synonymy in Banister, 1973); *Barbus pietschmanni* Lohberger, 1929 (synonymy in Greenwood, 1966); *Barbus radcliffii* Boulenger, 1903 (synonymy in Norman, 1925); *Labeo rueppellii* Pfeffer, 1896 (suppressed name; see Reid, 1980). Distribution: Lake Kivu and its affluents, Ruzizi, middle Akagera (below Rusumo Falls), and lakes Edward, Albert, Victoria, and Kioga (De Vos & Thys van den Audenaerde, 1990). Also in the Victoria Nile and Lake George (Lévêque & Daget, 1984). Notes: based on colour differences, Banister (1973) distinguishes three subspecies (*B. a. altianalis*, *B. a. eduardianus* and

*B. a. radcliffii*), but these are not retained by De Vos & Thys van den Audenaerde (1990).

*altipinnis*, *Varicorhinus* Banister & Poll, 1973. Kilwezi ( $\pm 09^{\circ}06'S$ ,  $26^{\circ}46'E$ , collection database), right bank affluent of the Lufira, DRC. Holotype: MRAC 179729. Paratypes: BMNH 1972.10.2.1 (1), MRAC 179730 (1), 179731 (1), 179732-733 (2), 179734 (1), 179735 (1), IRSNB 643 (1). Current status: valid as *Labeobarbus altipinnis* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Lufira River system (Lévêque & Daget, 1984). Notes: NMBA 3983 (1), 3985 (1), and 3988-89 (2) given in Eschmeyer (2015) as paratypes, are verified as syntypes of *V.* (now *Labeobarbus*) *macrolepidotus*.

*anema*, *Barbus* Boulenger, 1903. Not a *Labeobarbus* species (see present paper).

*ansorgii*, *Varicorhinus* Boulenger, 1906. Fort Don Carlos [= Tembo Aluma] ( $\pm 7^{\circ}42'S$ ,  $17^{\circ}17'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), at junction of Cambo and Kwango rivers, Loanda, Angola. Holotype: BMNH 1904.5.2.161. Current status: valid as *Labeobarbus ansorgii* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Cuango River, Angola (Lévêque & Daget, 1984).

*arambourgi*, *Barbus* Pellegrin, 1935. Not a *Labeobarbus* species (see present paper).

*aspius*, *Barbus* Boulenger, 1912. Boma Vonde ( $\pm 5^{\circ}08'S$ ,  $12^{\circ}39'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Lebuzi River [Shiloango Basin, DRC]. Syntypes: BMNH 1912.4.1.354 (1), MRAC 1536 (1). Current status: valid as *Labeobarbus aspius* (placed in *Labeobarbus* in De Weirdt & Teugels, 2007). Synonyms: none. Distribution: Lower Guinea endemic, known from the Lebuzi River (Chiloango Basin) in Cabinda (Angola) and DRC (De Weirdt & Teugels, 2007). Notes: Lévêque & Daget (1984) only mention a holotype, whereas the original description clearly mentions and is based on two syntype specimens.

*axelrodi*, *Varicorhinus* Getahun, Stiassny & Teugels, 2004. Place called 'Porte du Mayombe' ( $4^{\circ}20'S$ ,  $12^{\circ}26'E$ ), Loukoula River, 9 km downstream of Mpounga, Republic of the Congo. Holotype: MRAC 91-68-P-1132. Paratypes: AMNH 232315 (1), 232907 (3), 233184 (1), CUMV 87041 (1), 88131 (1), MRAC 90-057-P-1297-1300 (4), 90-057-P-1314-1327 (14), 99-55-P-246-247 (2), 99-55-P-249 (1), 99-90-P-459-460 (2). Current status: valid as *Labeobarbus axelrodi* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Lower Guinea endemic, known from the Ogowe (Louetsi, Ngounie) River Basin and Nyanga River in southwestern Gabon, and the Kouilou system in Republic of the Congo (Getahun, 2007b). Notes: Getahun *et al.* (2004) and Eschmeyer (2015) incorrectly give MRAC 99-90-P-459-461, with three specimens, as part of the paratypes. The correct number for this record, with only two specimens, is MRAC 99-90-P-459-460.

*babaulti*, *Varicorhinus* Pellegrin, 1932. Preoccupied by *Barbus* (*Capoeta*) *babaulti* Pellegrin, 1926, junior synonym of *Labeobarbus oxyrhynchus* (Pfeffer, 1889); replaced by *Varicorhinus pellegrini* Bertin & Estève, 1948. Bertin & Estève (1948) transferred *Barbus babaulti* Pellegrin, 1926 to the genus *Varicorhinus*, creating the need for a replacement name for *Varicorhinus babaulti* Pellegrin, 1932.

*batesii*, *Barbus* Boulenger, 1903. Kribi [Kienke] River ( $\pm 2^{\circ}56'N$ ,  $9^{\circ}54'E$ , USBGN, 1962b), southern Cameroon. Holotype: BMNH 1902.11.12.128. Current status: valid as *Labeobarbus batesii* (placed in *Labeobarbus* in De Weirtdt & Teugels, 2007). Synonyms: *Barbus linnellii* Lönnberg, 1904 (synonymy in Trewavas, 1962). Distribution: widespread throughout Lower Guinea, from the Cross River in Cameroon to the Chiloango Basin; also reported from the Dja (middle Congo Basin) and from Tibesti (northern Chad) (Lévêque, 2003; De Weirtdt & Teugels, 2007). Notes: (1) although the species description is based on a single specimen, Lévêque & Daget (1984) give BMNH 1904.2.29.32–36 as paratypes. They are not listed as types in the BMNH collection (J. Maclaine, pers. comm., 2015). Eschmeyer (2015) also explicitly lists these BMNH specimens as nontypes. (2) Report of this species from Tibesti (De Weirtdt & Teugels, 2007) in northern Chad, far outside the common distribution area of the species, needs confirmation.

*beso*, *Varicorhinus* Rüppell, 1835. Bahardar ( $\pm 11^{\circ}37'N$ ,  $37^{\circ}24'E$ , USBGN, 1963), Lake Tana, Ethiopia. Neotype: BMNH 1902.12.13.365 (designated in present paper). Current status: valid as *Labeobarbus beso* (placed in *Labeobarbus* in Berrebi *et al.*, 2014). Synonyms: *Dillonia abyssinica* Heckel, 1847; *Chondrostoma dillonii* Valenciennes, 1844 in Cuvier & Valenciennes, 1844; *Labeo varicorhinus* Valenciennes, 1844 in Cuvier & Valenciennes, 1844 (synonymy in Boulenger, 1907c). Distribution: Lake Tana, Blue Nile, Awash (Lévêque & Daget, 1984; Levin *et al.*, 2013) and Atbara river systems (Levin *et al.*, 2013). Notes: (1) the NHM (London, UK) houses an unpublished, and as such unavailable, neotype (BMNH 1968.7.24.18: 156.8 mm SL), collected during the Sandhurst Ethiopian Expedition (1964), originating from Bahardar (Bahardar  $\pm 11^{\circ}37'N$ ,  $37^{\circ}24'E$ ), also on Lake Tsana (i.e. Tana, Ethiopia), and most probably selected by the late K.E. Banister (NHM); however, we have refrained from identifying this specimen as the neotype of *V. beso* (see present paper); (2) the junior synonym *Chondrostoma dillonii* Valenciennes, 1844 in Cuvier & Valenciennes (1844) is the type species of the genus *Dillonia* Heckel, 1847, and as such the latter genus becomes a junior synonym of *Varicorhinus* (see Lévêque & Daget, 1984), now *Labeobarbus*.

*boulengeri*, *Labeobarbus* (present paper). Lucala (near railway station) ( $\pm 9^{\circ}16'23''S$ ,  $15^{\circ}14'42''E$ , Google Earth), above the falls on the Lucala River, Angola. Lectotype: BMNH 1911.6.1.6 (designated in present paper).

Paralectotypes: ANSP 37905 (1), BMNH 1911.6.1.7–10 (4), NMW 48865 (1), ZMB 18211 (1). Current status: valid as *Labeobarbus boulengeri* (placed in *Labeobarbus* in present paper). Synonyms: replacement name for *Varicorhinus latirostris* Boulenger, 1910 (present paper), preoccupied by *Barbus* (currently *Labeobarbus*) *latirostris* Keilhack, 1908. Distribution: Luculla River system (Lévêque & Daget, 1984) and the lower Congo River (Lowenstein *et al.*, 2011). Notes: (1) the NMW paralectotype number was until now unknown from literature sources; (2) the total number of type specimens only adds up to eight, whereas the original publication mentions ten syntypes; (3) MRAC collection specimens from the Inkisi River, the major left-bank tributary of the lower Congo, were identified as *V. cf. latirostris* in Wamuini Lunkayilakio *et al.* (2010), and probably represent a species new to science.

*brauni*, *Varicorhinus* Pellegrin, 1935. Near Lukando ( $\pm 2^{\circ}05'S$ ,  $28^{\circ}30'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Kanséhété River, Luhoho River affluent, DRC. Syntypes: MNHN 1935-0066 (1), MRAC 42933 (1). Current status: valid as *Labeobarbus brauni* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Luhoho River system, Congo River Basin (Lévêque & Daget, 1984).

*brevicephalus*, *Barbus* Nagelkerke & Sibbing, 1997. Yigashu ( $11^{\circ}40'N$ ,  $37^{\circ}25'E$ , Nagelkerke & Sibbing, 1997) (locality 10), Lake Tana, Ethiopia. Holotype: RMNH 32880. Paratypes: RMNH 32881–32889 (9). Current status: valid as *Labeobarbus brevicephalus* (placed in *Labeobarbus* in Getahun, 2007a). Synonyms: none. Distribution: Lake Tana and tributaries, Ethiopia (Nagelkerke & Sibbing, 1997).

*brevispinis*, *Barbus ruspolii* Holly, 1927. Lolodorf ( $\pm 3^{\circ}14'N$ ,  $10^{\circ}44'E$ , USBGN, 1962b), Lokundje River and Nachtigal ( $\pm 4^{\circ}21'N$ ,  $11^{\circ}38'E$ , USBGN, 1962b) (rapids), Sanaga River, both in Cameroon. Syntypes: NMW 7315 (1), 7316 (1). Current status: valid as *Labeobarbus brevispinis* (raised to species level in Pellegrin, 1928b; placed in *Labeobarbus* in De Weirtdt & Teugels, 2007). Synonyms: *Barbus brevispinis monunensis* Pellegrin, 1928 (synonymy in Lévêque & Daget, 1984). Distribution: Lokundje and Sanaga river systems and Lake Monoun in Cameroon; also in the Faro-Bénué Basin in Cameroon/Nigeria (De Weirtdt & Teugels, 2007). Notes: originally described as a subspecies of *Barbus* (now *Labeobarbus*) *ruspolii*, which is currently a junior synonym of *L. bynni*, following Banister (1973).

*bynni*, *Barbus* Forsskål, 1775. Aswan ( $\pm 24^{\circ}05'N$ ,  $32^{\circ}53'E$ , Banister, 1973), Nile River, Egypt. Neotype: BMNH 1907.12.2.1230 (designated by Banister, 1973). Current status: valid as *Labeobarbus bynni* (placed in *Labeobarbus* in Getahun, 2007a). Synonyms: *Barbus bynni rudolfianus* Worthington, 1932 (synonymy in Lévêque & Daget, 1984); *Barbus foureaui* Pellegrin,



1919 (synonymy in Lévêque, 1990); *Barbus lancrenonensis* Blache & Miton, 1960 (synonymy in Trewavas, 1974); *Cyprinus lepidotus* Geoffroy St. Hilaire, 1809 (synonymy in Lévêque & Daget, 1984); *Barbus meneliki* Pellegrin, 1905 (synonymy in Banister, 1973); *Barbus occidentalis* Boulenger, 1911 (synonymy in Lévêque, 1990); *Barbus ruspolii* Vinciguerra, 1897 (synonymy in Banister, 1973); *Barbus seguensis* Pellegrin, 1925 (synonymy in Daget, 1954); *Barbus waldroni* Norman, 1935 (synonymy in Lévêque, 1990). Distribution: Nilo, Sudan. *Labeobarbus bynni bynni* (Forsskål, 1775): known from the Nile River and associated lakes. *Labeobarbus bynni occidentalis* (Boulenger, 1911): Senegal, Volta, Oueme, Ogun, Niger, and Chad basins. *Labeobarbus bynni waldroni* (Norman, 1935): Ivory Coast and Ghana, to the west of the Volta, including the Sassandra, Bandama, Niouniourou, Comoé, and Tano (Lévêque & Guégan, 1990; Lévêque, 2003). Notes: the subspecies *L. bynni occidentalis* was placed in '*Labeobarbus*' in Yang *et al.* (2015), whereas *L. bynni* specimens are classified in *Labeobarbus*; the classification of *L. b. occidentalis* may be based on a misidentified specimen.

*capensis*, *Barbus* Smith, 1841. Not a *Labeobarbus* species (E. Vreven, E.R. Swartz & P.H. Skelton, unpubl. data).

*capoetoides*, *Varicorhinus* Pellegrin, 1938. Not a *Labeobarbus* species (see present paper).

*cardozoi*, *Barbus* Boulenger, 1912. N'Kutu [= Ncutu, = Necuto] ( $\pm 4^{\circ}57'S$ ,  $12^{\circ}35'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Loango River [Shiloango Basin, Cabinda, Angola]; Buco Zau [= Bucozan] ( $\pm 4^{\circ}45'S$ ,  $12^{\circ}33'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Luali River [Shiloango Basin, Cabinda, Angola]; and Boma Vonde ( $\pm 5^{\circ}08'S$ ,  $12^{\circ}39'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Lebuzi River [Shiloango Basin, DRC]. Syntypes: ANSP 38550–52 (3), BMNH 1912.4.1.343–348 (6), 1912.4.1.349–352 (4), 1912.4.1.353 (1), MRAC 1528–29 (2), 1530–32 (3), NMW 9604–9607 (4), 54014 (1), 79712 (1), ZMB 18810 (6). Current status: valid as *Labeobarbus cardozoi* (placed in *Labeobarbus* in De Weirtdt & Teugels, 2007). Synonyms: none. Distribution: Chiloango Basin in Cabinda (Angola) and DRC, and the Dja River (middle Congo River Basin) (De Weirtdt & Teugels, 2007). Also reported from the Niari (Daget, 1961) and Loeme (map in De Weirtdt & Teugels, 2007) in Republic of the Congo, but this needs confirmation. Notes: (1) the total number of type specimens adds up to 31, whereas the original description mentions 28 syntypes; (2) BMNH 1912.4.1.343–348 contains six specimens (J. Maclaine, pers. comm., 2015), in contrast to Eschmeyer (2015) who only mentions five.

*caudovittatus*, *Barbus* Boulenger, 1902. Banzyville ( $\pm 4^{\circ}18'N$ ,  $21^{\circ}10'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Ubangi River, DRC. Syntypes:

BMNH 1901.12.26.26 (1), MRAC 1168 (1). Current status: valid as *Labeobarbus caudovittatus* (placed in *Labeobarbus* in De Weirtdt & Teugels, 2007). Synonyms: *Barbus chilotes sakaniae* Poll, 1938; *Barbus euchilus* Boulenger, 1920; *Barbus lestradei* David, 1936 (synonymy in Banister, 1973); *Barbus miochilus* Boulenger, 1920 (synonymy in Poll, 1946); *Varicorhinus stappersii* Boulenger, 1917 (synonymy in Banister, 1973). Distribution: Congo River system, including the lower Luapula system (Lévêque & Daget, 1984) and Lake Mweru (Van Steenberge *et al.*, 2014), tributaries of Lake Tanganyika, and the Rusisi (Lévêque & Daget, 1984); in Lower Guinea reported from the Ogooué, Nyanga, and Douigni basins in Gabon (De Weirtdt & Teugels, 2007). Notes: (1) as the original description is based on two specimens and a holotype designation is lacking, the holotype and paratype status of the type specimens as provided by Lévêque & Daget (1984), for the MRAC and BMNH specimen, respectively, is incorrect (see also ICZN, 1999: article 73.2). The holotype and paratype status in Lévêque & Daget (1984) are not to be considered valid lecto- and paralectotype designations (ICZN, 1999: article 74.6); (2) *Labeobarbus stappersii* (Boulenger, 1915) is currently a valid species. A replacement name for *Varicorhinus stappersii* Boulenger, 1917, currently a junior synonym of *L. caudovittatus*, is not needed following the rules of ICZN (1999: articles 11.5, 11.6, and 15.1; also see the text).

*clarkeae*, *Varicorhinus* Banister, 1984. Rio Cunje ( $\sim 12^{\circ}0'0''S$ ,  $17^{\circ}40'0''E$ ), Cuanza affluent, Ceilunga, Angola. Holotype: MRAC 164456. Paratype: MRAC 164457 (1). Current status: valid as *Labeobarbus clarkeae* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: only known from Cunaza, Ceilunga, Angola (Banister, 1984).

*claudinae*, *Barbus* De Vos & Thys van den Audenaerde, 1990. Satinsyi River, 7 km upstream of its confluence with the Nyabarongo ( $1^{\circ}51'0''S$ ,  $29^{\circ}38'0''E$ ), near Ngororero, Rwanda. Holotype: MRAC 86-01-P-501. Paratypes: MRAC 91755–56 (2), 92214 (1), 130310 (1), 85-44-P-141-144 (4), 85-44-P-269 (1), 85-44-P-281-289 (9), 86-01-P-502-508 (7), 86-09-P-444-451 (8), 87-11-P-1366-372 (7), 87-11-P-1373-384 (12). Current status: valid as *Labeobarbus claudinae* (placed in *Labeobarbus* in Banyankimbona *et al.*, 2012a). Synonyms: none. Distribution: Nyabarongo and upper Akagera basins (upstream of Rusumo Falls) (De Vos & Thys van den Audenaerde, 1990). Notes: (1) paratype MRAC 130310 is also a paratype of *Barbus* (now *Labeobarbus*) *acuticeps* Matthes, 1959; (2) the apparently single paratype in record MRAC 86-09-P-444, as given in the original species description, with a range of standard lengths, actually refers to MRAC 86-09-P-444-451, containing eight paratypes.

*codringtonii*, *Barbus* Boulenger, 1908. Zambesi River above Victoria Falls ( $\pm 17^{\circ}55'S$ ,  $25^{\circ}51'E$ , D.F.E. Thys van

den Audenaerde, unpubl. data) [Zambia]. Holotype: BMNH 1908.11.6.23. Current status: valid as *Labeobarbus codringtonii* (placed in *Labeobarbus* in Skelton, 2001). Synonyms: *Barbus altidorsalis* Boulenger, 1908 (implicit synonymy in Skelton, 1993, 2001; synonymy confirmed by P.H. Skelton, pers. comm., 2014; see also present paper); *Barbus chilotes* Boulenger, 1908 (synonymy in Jubb, 1963); *Barbus hypostomatus* Pellegrin, 1936 (synonymy in Jubb, 1963). Distribution: Okavango and upper Zambezi (Skelton, 2001). Also in the Cunene (Lévêque & Daget, 1984). Notes: including *Barbus altidorsalis* Boulenger, 1908 as a junior synonym. *Labeobarbus altidorsalis* is not reported in Skelton (2001), and as such must be considered an implicit junior synonym of *L. codringtonii*, the only *Labeobarbus* species known from the Kafue River, i.e. the Upper Zambezi. See also Jackson (1961) on the dubious status of this nominal species.

*compiniei*, *Barynotus* Sauvage, 1879. Ogowe ( $\pm 0^{\circ}49'S$ ,  $9^{\circ}0'E$ , USBGN, 1962a), French Congo [Gabon, Republic of the Congo]. Holotype: MNHN A-2845 (stuffed). Current status: valid as *Labeobarbus compiniei* (placed in *Labeobarbus* in De Weirdt & Teugels, 2007). Synonyms: *Barbus labiatomimus* Pellegrin, 1914 (synonymy in Mahnert & Géry, 1982). Distribution: Lower Guinea endemic, known from the Komo and Ogooué basins in Gabon, up to the Loeme in Republic of the Congo, including the Nyanga and Kouilou-Niari (De Weirdt & Teugels, 2007). Notes: specific epithet often misspelled as *compinei* (see Lévêque & Daget, 1984), a misspelling that can be traced back up to Sauvage (1880; as *Barynotus campiniei* on p. 22 and *B. compinei* on p. 49), who himself described the species only the year before.

*crassibarbis*, *Barbus* Nagelkerke & Sibbing, 1997. Angara ( $12^{\circ}13'N$ ,  $37^{\circ}18'E$ , Nagelkerke & Sibbing, 1997) (locality 14), Lake Tana, Ethiopia. Holotype: RMNH 32890. Paratypes: 32891–99 (9). Current status: valid as *Labeobarbus crassibarbis* (placed in *Labeobarbus* in Getahun, 2007a). Synonyms: none. Distribution: endemic to Lake Tana, Ethiopia (Nagelkerke & Sibbing, 1997).

*dainellii*, *Barbus* Bini, 1940. South-Dek ( $11^{\circ}52'N$ ,  $37^{\circ}14'E$ , Nagelkerke & Sibbing, 1997) (locality 27), Lake Tana, Ethiopia. Neotype: RMNH 32900 (designated by Nagelkerke & Sibbing, 1997). Current status: valid as *Labeobarbus dainellii* (placed in *Labeobarbus* in Getahun, 2007a). Synonym of *Barbus intermedius* in Banister (1973); revalidated by Nagelkerke & Sibbing (1997). Synonyms: *Barbus dainellii macrocephalus* Bini, 1940 (synonymy in Nagelkerke & Sibbing, 1997). Distribution: endemic to Lake Tana, Ethiopia (Nagelkerke & Sibbing, 1997).

*dartevellei*, *Barbus* Poll, 1945. Matadi ( $\pm 5^{\circ}49'S$ ,  $13^{\circ}27'E$ , USBGN, 1964b), Congo River, DRC. Holotype: MRAC 47781. Current status: valid as *Labeobarbus*

*dartevellei* (placed in *Labeobarbus* in Lowenstein *et al.*, 2011). Synonyms: none. Distribution: only known from the holotype (Lévêque & Daget, 1984).

*dimidiatus*, *Varicorhinus* Tweddle & Skelton, 1998. Likabula River ( $15^{\circ}56'S$ ,  $35^{\circ}30'E$ ), upper Ruo River, Malawi. Holotype: SAIAB 53080. Paratypes: SAIAB 53079 (15), SAIAB 53083 (21). Current status: valid as *Labeobarbus dimidiatus* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: River Ruo and several of its tributaries above Zoa Falls (Tweddle & Skelton, 1998).

*ensifer*, *Varicorhinus* Boulenger, 1910. Lucala (near railway station) ( $\pm 9^{\circ}16'23'S$ ,  $15^{\circ}14'42'E$ , Google Earth), above the falls on the Lucala River, Angola. Syntypes: ANSP 37994 (8), BMNH 1910.11.28.134–143 (10), 1910.11.28.144 (1), NMW 48864 (10), ZMB 18213 (8). Current status: valid as *Labeobarbus ensifer* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Lucalla River system (Lévêque & Daget, 1984). Notes: the original record BMNH 1910.11.28.134–44 at present contains only ten (not the expected 11) specimens, and was amended to BMNH 1910.11.28.134–43; there is a note saying a specimen was removed and mounted in the Fish Gallery in November 1931, which would be BMNH 1910.11.28.144, but the specimen has currently not yet been retrieved (J. Maclaine, pers. comm., 2015).

*ensis*, *Barbus* Boulenger, 1910. Lucala (near railway station) ( $\pm 9^{\circ}16'23'S$ ,  $15^{\circ}14'42'E$ , Google Earth), above the falls on the Lucala River, Angola. Syntypes: ANSP 37902 (2), BMNH 1911.6.1.11–18 (8), NMW 54083 (4), ZMB 18217 (4). USNM 28297, 28373, 29223, 29536 and 29611 are lost (see Eschmeyer, 2015). Current status: valid as *Labeobarbus ensis* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Luculla River, Rio Cunje system, Angola (Lévêque & Daget, 1984). Notes: (1) the total number of type specimens adds up to 17, excluding the USNM specimens that are lost (see Eschmeyer, 2015), whereas the original publication only mentions 15 syntypes; (2) Lévêque & Daget (1984) only give the BMNH and ANSP specimens as types (10); (3) the number of specimens in ZMB 18217 is verified as four, in contrast to the ZMB collection data, but in accordance with Eschmeyer (2015).

*ethiopicus*, *Barbus* Zolezzi, 1939. Lake Zwai ( $\pm 8^{\circ}00'N$ ,  $38^{\circ}48'E$ , USBGN, 1963), Ethiopia. Holotype: MCZR (number unknown). Current status: valid as *Labeobarbus ethiopicus* (placed in *Labeobarbus* in Getahun, 2007a). Synonyms: none. Distribution: Rift Lakes drainage basin (Getahun, 2007a), including Lake Tana (Tsigenopoulos *et al.*, 2002; Borkenhagen, 2014), Lake Zwai (type locality) (Lévêque & Daget, 1984), and its affluent Meki River (Golubtsov & Krysanov, 1993; Levin *et al.*, 2013). Notes: (1) BMNH 1971.7.12.1–3 (3), given syntype status in Lévêque & Daget (1984) and Eschmeyer (2015), do not have type status; (2) holotype,

previously housed at the Laboratorio centrale di Idrobiologia (Rome, Italy), and now at the Museo Civico di Zoologia di Roma (MCZR, Rome, Italy) (M. Capula, pers. comm., 2014), not seen; (3) the MCZR has recently (2014) been ravaged by a flood (S. Valdesalici, pers. comm., 2014). Unfortunately, no further details have been provided as to the whereabouts of the holotype after this misfortune.

*fasolt*, *Barbus* Pappenheim, 1914. Irumu ( $\pm 1^{\circ}29'N$ ,  $29^{\circ}51'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Ituri River, DRC. Holotype: ZMB 19061. Current status: valid as *Labeobarbus fasolt* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Rivers Aruwimi (Boulenger, 1920a), Ituri (Pappenheim & Boulenger, 1914; Boulenger, 1916a) and Uele (Nichols & Griscom, 1917), DRC. Possibly also at Kisangani (= Stanleyville) (Nichols & Griscom, 1917).

*fimbriatus*, *Varicorhinus sandersi* Holly, 1926. Nachtigal ( $\pm 4^{\circ}21'N$ ,  $11^{\circ}38'E$ , USBGN, 1962b) (rapids), Sanaga River, Cameroon. Syntypes: NMW 7224–7226 (3), 7227–7233 (7). Current status: valid as *Labeobarbus fimbriatus* (raised to species level in Holly, 1930; placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: a Lower Guinea endemic, found in the Sanaga River Basin, Cameroon (Lévêque & Daget, 1984; Getahun, 2007b). Notes: syntypes NMW 7224–7226 (3) not listed in Eschmeyer (2015), and incorrectly included in NMW 7224–7233 in Lévêque & Daget (1984).

*fritschii*, *Barbus* Günther, 1874. Oued Ksib [Oued el Ksib] ( $31^{\circ}28'59"N$ ,  $9^{\circ}46'3"W$ , Borkenhagen & Krupp, 2013), Morocco. Syntypes: BMNH 1874.1.30.27–31 (5). Current status: valid as *Labeobarbus fritschii* (placed in *Labeobarbus* in Doadrio, 1994). Synonyms: *Capoeta atlantica* Boulenger, 1902 (synonymy in Lévêque & Daget, 1984); *Barbus paytonii* Boulenger, 1911 (synonymy in Lévêque & Daget, 1984; revalidated by Azeroual *et al.*, 2000; again placed in synonymy in Borkenhagen & Krupp, 2013); *Barbus riggenbachi* Günther, 1902; *Barbus rothschildi* Günther, 1901; *Capoeta waldoi* Boulenger, 1902 (synonymy in Lévêque & Daget, 1984). Distribution: widespread and abundant in northern and central Morocco; occurs in the Oued al Maleh, Oued Bou Regreg, Oued Igrounzar, Oued Moulouya, Oued Oum er Rbia, Oued Sebou, and Oued Tensift drainage systems, and in numerous small coastal rivers; most records are from Morocco, but one specimen is from the Oued Kiss in Algeria (Borkenhagen & Krupp, 2013). Notes: (1) Eschmeyer (2015) mentions that SMF 636 (7) and 952 (8) are not syntypes, in contrast to the SMF online collection database. Borkenhagen & Krupp (2013), who consider this a *Carasobarbus* species, also do not include the SMF specimens in the type series. Unfortunately, the number of type specimens is not mentioned in the original description; (2) a *Carasobarbus* species in Borkenhagen

& Krupp (2013) and Yang *et al.* (2015); (3) type species of the genus *Pseudotor* Karaman, 1971. To be considered a junior synonym of the genus *Labeobarbus s.l.*; (4) *Labeobarbus paytonii* (Boulenger, 1911) considered to be a junior synonym of *Labeobarbus fritschii harterti* (Günther, 1901) by Lévêque & Daget (1984), valid by Doadrio (1994), but a junior synonym of *L. fritschii* by Borkenhagen & Krupp (2013).

*gananensis*, *Barbus* Vinciguerra, 1895. Ganana River ( $\pm 0^{\circ}15'S$ ,  $42^{\circ}38'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), between Lugh and Bardera [Somalia]. Holotype: MSNG 17525. Paratypes: MSNG 17331 (4). Current status: valid as *Labeobarbus gananensis* (placed in *Labeobarbus* in Getahun, 2007a). Synonyms: none. Distribution: Juba and Awata rivers in Somalia (Lévêque & Daget, 1984). Reported from the Wabi Shebele Basin (Getahun, 2007a), including the Genale River, on the Eastern Plateau in Ethiopia (Levin *et al.*, 2013). Notes: (1) Tortonese (1961), in his type catalogue, mentions 'Olotipo deteriorato' (= holotype deteriorated); (2) the species description is based on five type specimens, which means four paratypes exist next to the holotype, not five as mentioned in Eschmeyer (2015).

*gestetneri*, *Barbus* Banister & Bailey, 1979. Above the falls on the Kalumengonga River ( $8^{\circ}49'S$ ,  $27^{\circ}13'E$ ) (site 5), Upemba National Park, Shaba, DRC. Holotype: BMNH 1976.10.12.98. Paratypes: BMNH 1976.10.12.86–97 (12). Current status: valid as *Labeobarbus gestetneri* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: Only known from the type locality (Lévêque & Daget, 1984).

*girardi*, *Barbus* Boulenger, 1910. Lucala (near railway station) ( $\pm 9^{\circ}16'23"S$ ,  $15^{\circ}14'42"E$ , Google Earth), above the falls on the Lucala River, Angola. Syntypes: ANSP 37973 (1), BMNH 1911.6.1.31–36 (6), NMW 54137 (1), ZMB 18215 (1). Current status: valid as *Labeobarbus girardi* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: Lucalla River, Angola (Lévêque & Daget, 1984). Notes: the total number of type specimens only adds up to nine, whereas the original description mentions 11 syntypes.

*gorgorensis*, *Barbus intermedius* Bini, 1940. Debre Mariam ( $11^{\circ}38'N$ ,  $37^{\circ}24'E$ , Nagelkerke & Sibbing, 1997) (locality 1), Lake Tana, Ethiopia. Neotype: RMNH 32910 (designated by Nagelkerke & Sibbing, 1997). Current status: valid as *Labeobarbus gorgorensis* (placed in *Labeobarbus* in Getahun, 2007a). Synonym of *Barbus intermedius* in Banister (1973); raised to species level and revalidated as *Barbus gorgorensis* by Nagelkerke & Sibbing (1997). Synonyms: none. Distribution: Endemic to Lake Tana, Ethiopia (Nagelkerke & Sibbing, 1997).

*gorguari*, *Barbus* Rüppell, 1835. Lake Tana ( $\pm 12^{\circ}00'N$ ,  $37^{\circ}20'E$ , USBGN, 1963), possibly at Goraza [probably = Korata] ( $11^{\circ}45'N$ ,  $37^{\circ}27'E$ , Nagelkerke & Sibbing,

1997), Ethiopia. Holotype: SMF 2586 (stuffed). Current status: valid as *Labeobarbus gorguari* (placed in *Labeobarbus* in Getahun, 2007a). Synonym of *Barbus intermedius* in Banister (1973); revalidated by Nagelkerke & Sibbing (1997). Synonyms: none. Distribution: Endemic to Lake Tana, Ethiopia (Nagelkerke & Sibbing, 1997).

*gruveli*, *Barbus* Pellegrin, 1911. Dubreka ( $\pm 9^{\circ}48'N$ ,  $13^{\circ}31'W$ , D.F.E. Thys van den Audenaerde, unpubl. data; USBGN, 1965b), French Guinea [Guinea]. Holotype: MNHN 1911-0040. Current status: valid as *Labeobarbus gruveli* (placed in *Labeobarbus* in Skelton & Bills, 2008; Berrebi *et al.*, 2014). Synonyms: none. Distribution: only known from the holotype (Lévêque & Guégan, 1990; Lévêque, 2003).

*gulielmi*, *Barbus* Boulenger, 1910. Dondo ( $\pm 9^{\circ}38'S$ ,  $14^{\circ}25'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Quanza River, Angola. Syntypes: BMNH 1911.6.1.29–30 (2), NMW 54138 (1). Current status: valid as *Labeobarbus gulielmi* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: only known from the type locality (Lévêque & Daget, 1984).

*habereri*, *Barbus* Steindachner, 1912. Dscha [Dja] River ( $\pm 2^{\circ}2'N$ ,  $15^{\circ}12'E$ , USBGN, 1962b), southern Cameroon. Holotype: NMW 7274. Current status: valid as *Labeobarbus habereri* (placed in *Labeobarbus* in De Weirtdt & Teugels, 2007). Synonyms: none. Distribution: Sanaga Basin, Kelle River (Nyong River tributary) and Dja River (middle Congo River Basin) in Cameroon (De Weirtdt & Teugels, 2007). Notes: (1) placed in '*Labeobarbus*' in Yang *et al.* (2015); (2) according to Boulenger (1916: 231, 239), Steindachner (1914: plate 3, figs 1, 3) inverted the illustrations of *L. habereri* and *L. mawambiensis*. Indeed, Figure 1 on plate 3 illustrates a fish with a damaged caudal and anal fin, as stipulated in the original description of *L. habereri* by Steindachner (1914: 24) himself. As such, Figure 1 illustrates the holotype of *L. habereri*, whereas Figure 3 instead illustrates a specimen of *L. mawambiensis*. Note, however, that for the latter species the illustrated specimen has 5.5 scales between the lateral line and the dorsal midline, whereas all examined syntypes have 3.5 or 4.5 scales.

*harterti*, *Barbus* Günther, 1901. Oum Erbiah [Oum er Rbia River] ( $33^{\circ}19'40''N$ ,  $8^{\circ}20'2''W$ , Borkenhagen & Krupp, 2013), Morocco. Syntypes BMNH 1901.7.26.4–5 (2). Current status: valid as *Labeobarbus harterti* (placed in *Labeobarbus* in Doadrio, 1994). Subspecies of *Barbus fritschii* in Lévêque & Daget (1984); revalidated by Doadrio (1994). Synonyms: none. Distribution: rivers of the Oued Oum er Rbia and Tenssift drainage systems in Morocco (Borkenhagen & Krupp, 2013). Notes: (1) a *Carasobarbus* species according to Borkenhagen & Krupp (2013) and Yang *et al.* (2015); (2) misspelled

as '*harteti*' in Lévêque & Daget (1984) (as subspecies of *Barbus fritschii*) and Doadrio (1994).

*huloti*, *Barbus* Banister, 1976. Zega on the Vuda River ( $1^{\circ}44'N$ ,  $30^{\circ}45'E$ ), Lake Albert [= Lake Albert Nyanza, = Lake Mobuto Sese Seko] basin, DRC. Holotype: IRSNB 558. Paratypes: BMNH 1975.4.30.1 (1), IRSNB 563 (10). Current status: valid as *Labeobarbus huloti* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: only known from the type locality (Lévêque & Daget, 1984).

*humphri*, *Barbus* Banister, 1976. Tabie River, about 25 kilometers south of Beni ( $\pm 0^{\circ}30'N$ ,  $29^{\circ}28'E$ , USBGN, 1964b), North Kivu District, DRC. Holotype: IRSNB 559. Paratypes: BMNH 1975.4.30.2 (1), IRSNB 564 (10). Current status: valid as *Labeobarbus humphri* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: only known from the type locality (Lévêque & Daget, 1984).

*intermedius*, *Barbus* Rüppell, 1835. Lake Tana ( $\pm 12^{\circ}00'N$ ,  $37^{\circ}20'E$ , USBGN, 1963), possibly at Goraza [probably = Korata] ( $11^{\circ}45'N$ ,  $37^{\circ}27'E$ , Nagelkerke & Sibbing, 1997), Ethiopia. Holotype: SMF 6778 (stuffed). Current status: valid as *Labeobarbus intermedius* (placed in *Labeobarbus* in Getahun, 2007a). Synonyms: *Barbus affinis* Rüppell, 1835; *Barbus alticola* Boulenger, 1906; *Capoeta bingeri* Pellegrin, 1905; *Barbus bottegi* Boulenger, 1906; *Barbus brevibarbis* Boulenger, 1902; *Barbus brunellii* Bini, 1940; *Barbus duchesnii* Boulenger, 1902; *Barbus duchesnii ibridus* Bini, 1940; *Barbus duchesnii maximus* Bini, 1940; *Barbus elongatus* Rüppell, 1835; *Barbus erlangeri* Boulenger, 1904; *Barbus eumystus* Boulenger, 1906; *Barbus gregorii* Boulenger, 1902; *Barbus gudaricus* Boulenger, 1906; *Barbus harringtoni* Boulenger, 1902; *Barbus hursensis* Boulenger, 1902; *Barbus ilgi* Pellegrin, 1905; *Barbus intermedius microstoma* Bini, 1940; *Barbus jarsinus* Boulenger, 1902; *Barbus kassamensis* Boulenger, 1902 (synonymy in Banister, 1973); *Barbus leptosoma* Boulenger, 1902 (synonymy in Bini, 1940); *Barbus macmillani* Boulenger, 1906; *Barbus macronema* Boulenger, 1902; *Barbus macronema parenzani* Zolezzi, 1939; *Barbus margaritae* Boulenger, 1906; *Barbus mento* Boulenger, 1902; *Barbus newillei* Pellegrin, 1905; *Barbus oreas* Boulenger, 1902; *Barbus plagiostomus* Boulenger, 1902; *Barbus platystomus* Boulenger, 1902; *Barbus platystomus daga* Bini, 1940; *Barbus platystomus dekkensis* Bini 1940; *Barbus platystomus prognathus* Bini, 1940; *Barbus platystomus vatovae* Zolezzi, 1939; *Barbus procatopus* Boulenger, 1916; *Barbus rueppelli* Boulenger, 1902; *Barbus volpinii* Parenzan, 1940; *Barbus zaphiri* Boulenger, 1906; *Barbus zuaicus* Boulenger, 1906 (synonymy in Banister, 1973). Distribution: *Labeobarbus intermedius intermedius* Rüppell, 1835, widely distributed throughout southern Ethiopia and into northern Kenya, certainly as far as Lake Baringo, but excluding the lake itself; *Labeobarbus intermedius*

*australis* (Banister, 1973), only known from Lake Baringo (Lévêque & Daget, 1984). Notes: (1) Getahun (2007a) reports *Labeobarbus newvillei* (Pellegrin, 1905) [a misspelling for *L. newvillei* (Pellegrin, 1905)] as a valid species. As Getahun (2007a) did not provide any arguments for this revalidation *L. newvillei* is here still considered a junior synonym of *L. intermedius* following Banister (1973) and awaiting further research; (2) the same holds true for *L. zaphiri* (Boulenger, 1906), which has been used as a valid species name by Tsigenopoulos *et al.* (2010) and Yang *et al.* (2015), also without any argumentation for this revalidation since Banister's (1973) synonymization.

*iphthimostoma*, *Varicorhinus* Banister & Poll, 1973. Kateke ( $\pm 08^{\circ}56'S$ ,  $26^{\circ}42'E$ , collection database), affluent of the Muov'we, Lufira system, DRC, 960 m a.s.l. Holotype: MRAC 179736. Paratypes: BMNH 1972.10.2.2 (1), IRSNB 644 (1), MRAC 179737 (1). Current status: valid as *Labeobarbus iphthimostoma* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Muye and Kateke, Lufira system (Banister & Poll, 1973; Poll, 1976). Notes: following ICZN (1999: articles 31.2 and 34.2), the species name *iphthimostoma* [from the Greek adjective *iphthimos* (solid, robust) and the Greek noun *stoma* (mouth); meaning with a solid and robust mouth] does not need to agree in gender with the genus name *Labeobarbus* (masculine).

*iturii*, *Barbus* Holly, 1929. Ituri River ( $\pm 1^{\circ}40'N$ ,  $27^{\circ}01'E$ , USBGN, 1964b), DRC. Holotype: NMW (lost). Current status: valid as *Labeobarbus iturii* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: only known from the type locality (Lévêque & Daget, 1984). Notes: during a recent search in the NMW collection, the holotype could not be found (H. Wellendorf, pers. comm., 2014) and is thus considered lost.

*jaegeri*, *Varicorhinus* Holly, 1930. Sanaga ( $\pm 03^{\circ}35'N$ ,  $9^{\circ}38'E$ , USBGN, 1962b), Cameroon. Holotype: NMW 13957. Current status: valid as *Labeobarbus jaegeri* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Lower Guinea endemic, known from the Sanaga River Basin, Cameroon (Getahun, 2007b).

*johnstonii*, *Barbus* Boulenger, 1907. Between Kondowe [Livingstonia] ( $\pm 10^{\circ}36'S$ ,  $34^{\circ}07'E$ , D.F.E. Thys van den Audenaerde, unpubl. data) and Karonga ( $\pm 9^{\circ}56'S$ ,  $33^{\circ}56'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Lake Malawi [Malawi]. Holotype: BMNH 1897.6.9.280. Current status: valid as *Labeobarbus johnstonii* (placed in *Labeobarbus* in Skelton & Bills, 2008; Berrebi *et al.*, 2014). Synonyms: *Barbus intermedius brevicauda* Keilhack, 1908 (synonymy in Boulenger, 1911a; revalidated in Seegers, 1995; again placed in synonymy in the present paper); *Barbus intermedius eurystomus* Keilhack, 1908 (synonymy in Seegers, 1995); *Barbus globiceps* Worthington, 1933; *Barbus njassae*

Keilhack, 1908; *Varicorhinus nyasensis* Worthington, 1933 (synonymy in Banister & Clarke, 1980). Distribution: Lake Malawi Basin (Lévêque & Daget, 1984). Notes: *Labeobarbus eurystomus* is here considered a junior synonym of *L. johnstonii* (Boulenger, 1907), following Seegers (1995). According to Seegers (1995), the lectotype designation for *Barbus* (now *Labeobarbus*) *intermedius eurystomus* Keilhack, 1908, as undertaken by Banister & Clarke (1980) (ZMB 18175, 125 mm SL), is invalid as it is preceded by a lectotype designation by Keilhack (1910: 103, table 6, specimen no. 15 and plate. 2, fig. 6) himself, who even illustrated what he referred to as the 'typus', making this specimen (ZMB 18175, 255 mm SL from 'Njassa bei Langenbuarg, 77 m Tiefe, 31.8.99') indeed the lectotype of this, now, nominal species (see ICZN, 1999, especially articles 74.4 and 74.5), referred to as *L. eurystomus*. According to Seegers (1995) this specimen corresponds with one of the other three specimens originally belonging to ZMB 18175, and attributed by Banister & Clarke (1980) to *Barbus* (now *Labeobarbus*) *johnstonii* Boulenger, 1907. Given the standard lengths provided by Banister & Clarke (1980) (152, 183, and 245 mm SL, respectively) it seems to refer to the largest of these syntypes. As a result, *L. eurystomus* becomes a junior synonym of *L. johnstonii* and *Barbus* (now *Labeobarbus*) *intermedius brevicauda*, previously a junior synonym of *L. eurystomus sensu* Banister & Clarke (1980), became a valid species, *L. brevicauda*, following Seegers (1995); however, the correct name for *L. eurystomus sensu* Banister & Clarke (1980) and *L. brevicauda sensu* Seegers (1995) is *L. latirostris* (see text).

*jubae*, *Varicorhinus* Banister, 1984. Juba River, close to Sidam-Bale bridge ( $5^{\circ}45'N$ ,  $39^{\circ}37'E$ ), Ethiopia, 1200 m a.s.l. Holotype: BMNH 1976.7.1.13. Paratypes: BMNH 1976.7.1.14–15 (2). Current status: valid as *Labeobarbus jubae* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: known from the Welmel, Genale, and Awata rivers (Juba River system) in Ethiopia (Levin *et al.*, 2013).

*jubbi*, *Barbus* Poll, 1967. Muíta ( $\pm 7^{\circ}50'S$ ,  $21^{\circ}22'E$ , D.F.E. Thys van den Audenaerde, unpubl. data; USBGN, 1956), Luembe River, Angola. Holotype: MD 1078. Paratypes: MRAC 161065 (ex. MD 2299) (1), 161066 (ex. MD 6363) (1), MD 2299 (1), 6363 (1). Current status: valid as *Labeobarbus jubbi* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: various tributaries of the upper Kasai drainage, including the Luachimo and Luembe (middle Congo River Basin) (Poll, 1967; Lévêque & Daget, 1984).

*kerstenii*, *Barbus* Peters, 1868. Not a *Labeobarbus* species (see present paper).

*kimberleyensis*, *Barbus* Gilchrist & Thompson, 1913. Kimberley Reservoir ( $\pm 28^{\circ}45'S$ ,  $24^{\circ}46'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Cape Province, South Africa. Holotype: SAIAB 134771 (ex. SAM 9645).

Current status: valid as *Labeobarbus kimberleyensis* (placed in *Labeobarbus* in Skelton, 2001). Synonyms: *Barbus pienaarii* Fitzsimons, 1949 (synonymy in Jubb, 1963). Distribution: Orange-Vaal River system, South Africa (Skelton, 2001).

*lagensis*, *Barynotus* Günther, 1868. Lagos ( $\pm 6^{\circ}28'N$ ,  $3^{\circ}25'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), west Africa [Nigeria]. Holotype: BMNH 1866.3.8.12. Current status: valid as *Labeobarbus lagensis* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: only known from the holotype (Lévêque & Guégan, 1990; Lévêque, 2003). Notes: (1) type species of the genus *Barynotus* Günther, 1868. Objectively invalid as preoccupied by *Barynotus* Germar, 1817 (Coleoptera). Replaced by objective junior synonym *Barbellion* Whitley, 1931, which must be considered a junior synonym of the genus *Labeobarbus*; (2) species name misspelled as *lagoensis* by various authors (e.g. Boulenger, 1905b, 1911a; Pellegrin, 1923; Trewavas & Irvine, 1947; Lowe-McConnell, 1972; Lévêque & Daget, 1984; Skelton & Bills, 2008).

*latirostris*, *Barbus intermedius* Keilhack, 1908. Probably from Lake Malawi or the Kiwira River ( $\pm 9^{\circ}37'S$ ,  $33^{\circ}57'E$ , USBGN, 1965c), possibly the Kiwira River at Langenburg [= Neu Langenburg, = Tukuyu] ( $\pm 9^{\circ}15'S$ ,  $33^{\circ}39'E$ , USBGN, 1965c), Tanzania. Lectotype: ZMB 18174 (designated in present paper). Paralectotype: ZMB 34766 (1). Current status: valid as *Labeobarbus latirostris* [placed in *Labeobarbus* in Skelton & Bills (2008) (using the senior synonym name at that time *Labeobarbus johnstonii*; *L. latirostris* is at present a valid species, cf. infra); present paper]. Synonym of *Barbus johnstonii* in Banister & Clarke (1980); raised to species level and revalidated as *Labeobarbus latirostris* in present paper. Synonyms: none. Distribution: Lake Malawi Basin (Lévêque & Daget, 1984).

*latirostris*, *Varicorhinus* Boulenger, 1910. Preoccupied by *Barbus latirostris* Keilhack, 1908; replaced by *Labeobarbus boulengeri* (present paper).

*leleupanus*, *Varicorhinus* Matthes, 1959. Nyamagana River ( $\pm 02^{\circ}55'S$ ,  $29^{\circ}08'E$ , collection database), Burundi. Holotype: MRAC 92213. Paratypes: MRAC 92211 (1), 92212 (1), 130532–33 (2). Current status: valid as *Labeobarbus leleupanus* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Rusizi River (De Vos *et al.*, 2001) and Lake Tanganyika Basin (Matthes, 1962; Eccles, 1992). Notes: although the original species description by Matthes (1959b) does not mention the number of type specimens or any collection numbers, Matthes (1962) gives an additional paratype (71.2 mm SL, Luberizi River, collected by G. Marlier, date 13.4.55) without registration number, next to the ones listed above; a corresponding specimen could not be identified in the MRAC collection.

*litamba*, *Barbus* Keilhack, 1908. Not a *Labeobarbus* species (see present paper).

*longidorsalis*, *Varicorhinus* Pellegrin, 1935. Near Lukando ( $\pm 2^{\circ}05'S$ ,  $28^{\circ}30'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Kanséhété River, Luhoho River affluent, DRC. Holotype: MNHN 1935-0065. Current status: valid as *Labeobarbus longidorsalis* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: tributaries of the Congo River in the Kivu region (Lévêque & Daget, 1984).

*longifilis*, *Barbus altianalis* Pellegrin, 1935. Loama ( $\pm 2^{\circ}01'S$ ,  $28^{\circ}27'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), upper Luhoho Basin, DRC. Lectotype: MNHN 1935-0150 (designated by Banister, 1973). Paralectotypes: MNHN 1935-0145 (1), 1935-0146 (1), 1935-0147 (1), 1935-0148 (1), 1935-0149 (1), 1935-0151 (1), 1935-0152 (1). Current status: valid as *Labeobarbus longifilis* (raised to species level in Banister, 1973; placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: Nya-Barongo and Loama rivers, in Kivu region (Lévêque & Daget, 1984). Notes: Nyabarongo specimen in Pellegrin's type series (MNHN 1935-0075) put under *Barbus* (now *Labeobarbus*) *paucisquamatus* by Banister (1973).

*longissimus*, *Barbus* Nagelkerke & Sibbing, 1997. Kentefami ( $11^{\circ}40'N$ ,  $37^{\circ}23'E$ , Nagelkerke & Sibbing, 1997) (locality 11), Lake Tana, Ethiopia. Holotype: RMNH 32930. Paratypes: RMNH 32931–39 (9). Current status: valid as *Labeobarbus longissimus* (placed in *Labeobarbus* in Getahun, 2007a). Synonyms: none. Distribution: endemic to Lake Tana, Ethiopia (Nagelkerke & Sibbing, 1997).

*lucius*, *Barbus* Boulenger, 1910. Lucala (near railway station) ( $\pm 9^{\circ}16'23'S$ ,  $15^{\circ}14'42'E$ , Google Earth), above the falls on the Lucala River, Angola. Syntypes: BMNH 1911.6.1.42–43 (2), NMW 54246 (1). Current status: valid as *Labeobarbus lucius* (placed in *Labeobarbus* in De Weirdt & Teugels, 2007). Synonyms: none. Distribution: Lucalla River in Angola and Niari River in Republic of the Congo (De Weirdt & Teugels, 2007).

*lufupensis*, *Varicorhinus* Banister & Bailey, 1979. Nasondoye ( $10^{\circ}22'S$ ,  $25^{\circ}06'E$ ) (site 2), Lufupa River, Shaba, DRC. Holotype: BMNH 1975.9.5.1. Paratype: BMNH 1975.9.5.2 (1). Current status: valid as *Labeobarbus lufupensis* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Only known from the type locality (Banister, 1984).

*macroceps*, *Barbus* Fowler, 1936. Epulu River Ferry ( $\pm 1^{\circ}15'N$ ,  $28^{\circ}21'E$ , USBGN, 1964b), Ituri Basin, Kibali-Ituri District, DRC. Holotype: ANSP 65759. Current status: valid as *Labeobarbus macroceps* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: based on current evidence, a local endemic from above the falls on the Epulu River (A. Walanga, pers. comm., 2015).

*macrolepidotus*, *Varicorhinus* Pellegrin, 1928. Luluabourg [Kananga] ( $\pm 05^{\circ}53'S$ ,  $22^{\circ}25'E$ , collection database) area, Lulua River, Kasai affluent, DRC. Syntypes: MNHN 1928-0011 (1), MRAC 19945 (1), 138767 (1; ex. MNHN 1928-0012), NMB 3983 (1), 3985 (1), 3988 (1), 3989 (1). Current status: valid as *Labeobarbus macrolepidotus* (placed in *Labeobarbus* in present paper). Synonyms: *Barbus callewaerti* Nichols & La Monte, 1933 (synonymy in Poll, 1967). Distribution: Lower Congo River in DRC and the Kasai drainage (middle Congo River Basin) in Angola (Poll, 1967) and DRC (Pellegrin & Roux, 1928). Notes: the total number of type specimens adds up to seven, whereas the original description mentions only five syntypes.

*macrolepis*, *Barbus* Pfeffer, 1889. Mbusine [Mbusini] ( $\pm 6^{\circ}12'S$ ,  $38^{\circ}01'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Rukagura Stream, East Africa [Tanzania]. Lectotype: ZMH H330 (ex. 68 79) (designated by Ladiges, von Wahlert & Mohr, 1958). Paralectotypes: BMNH 1909.2.25.8 (ex. ZMH) (1), ZMB 31672 (ex. ZMH) (2), ZMH H331 (ex. 68 79) (2), H332 (ex. 380/7467) (4), H333 (ex. 69 19) (1), H474 (ex. 69 03) (1). Current status: valid as *Labeobarbus macrolepis* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: Katare, Malagarasi swamp, and Wami, Ruaha, and Rufiji rivers (Lévêque & Daget, 1984) [Tanzania]. Notes: (1) lectotype incorrectly referred to as ZMH H331 in Banister (1973: appendix 3), whereas the text itself correctly gives ZMH H330; (2) *Labeobarbus macrolepis* Heckel, 1838 is currently a junior synonym of *Tor putitora* (Hamilton, 1822) (*vide* Kottelat, 2013). A replacement name for *L. macrolepis* (Pfeffer, 1889) is not needed, following the rules of ICZN (1999: article 59.2; see also text).

*macrophthalmus*, *Barbus gorguarii* Bini, 1940. Bet Menzo ( $11^{\circ}45'N$ ,  $37^{\circ}25'E$ , Nagelkerke & Sibbing, 1997) (locality 4), Lake Tana, Ethiopia. Neotype: RMNH 32940 (designated by Nagelkerke & Sibbing, 1997). Current status: valid as *Labeobarbus macrophthalmus* (placed in *Labeobarbus* by Getahun, 2007a). Synonym of *Barbus intermedius* in Banister (1973); raised to species level and revalidated as *Barbus macrophthalmus* by Nagelkerke & Sibbing (1997). Synonyms: none. Distribution: endemic to Lake Tana, Ethiopia (Nagelkerke & Sibbing, 1997). Notes: although a junior homonym of *Barbus macrophthalmus* Bleeker, 1855 from Java and Indonesia [currently a synonym of *Barbonymus balleroides* (Valenciennes, 1842)], because of its transfer to *Labeobarbus* this species is no longer congeneric and thus does not need replacement (see ICZN, 1999: article 59.2).

*malacanthus*, *Barbus* Pappenheim, 1911. Uelleburg, Uelle River [= Benito River] ( $\pm 1^{\circ}36'N$ ,  $9^{\circ}37'E$ , USBGN, 1962), Equatorial Guinea. Holotype: ZMB 18392. Current status: valid as *Labeobarbus malacanthus* (placed in *Labeobarbus* in De Weirtdt & Teugels, 2007). Syno-

nymy: none. Distribution: equatorial Guinea and Gabon, including the Ogooué Basin and the rivers Nyanga and Douigni (De Weirtdt & Teugels, 2007).

*marequensis*, *Barbus (Cheilobarbus)* Smith, 1841. Marico River ( $\pm 24^{\circ}12'S$ ,  $26^{\circ}53'E$ , USBGN, 1954a), near the border of Bechuanaland and the Transvaal, South Africa (Greenwood & Crass, 1959). Holotype: BMNH 1845.7.3.95 (stuffed). Current status: valid as *Labeobarbus marequensis* (placed in *Labeobarbus* in Skelton, 2001). Synonyms: *Barbus brucii* Boulenger, 1907; *Varicorhinus brucii* Boulenger, 1907; *Barbus cookei* Gilchrist & Thompson, 1913; *Barbus dwaarsensis* Gilchrist & Thompson, 1913 (synonymy in Jubb, 1963); *Barbus fairbairnii* Boulenger, 1908; *Barbus gunningi* Gilchrist & Thompson, 1913 (synonymy in Jubb, 1963); *Barbus inermis* Peters, 1852 (synonymy in Lévêque & Daget, 1984); *Varicorhinus nasutus* Gilchrist & Thompson, 1911 (synonymy in Poll, 1976; revalidated in Skelton, 1993; again placed in synonymy in Tweddle & Skelton, 1998); *Barbus oliphanti* Keilhack, 1910; *Barbus rhodesianus* Boulenger, 1902; *Barbus sabiensis* Gilchrist & Thompson, 1913; *Barbus sector* Boulenger, 1907; *Barbus swierstrae* Gilchrist & Thompson, 1913; *Barbus victoriae* Boulenger, 1908; *Labeobarbus zambezensis* Peters, 1852 (synonymy in Jubb, 1963). Distribution: widely distributed from the middle and lower Zambezi south to the Pongolo system (Skelton, 2001). Notes: (1) the junior synonym *Barbus oliphanti* Keilhack, 1910 is a replacement name for *Varicorhinus brucii* Boulenger, 1907, preoccupied by *Barbus brucii* Boulenger, 1907, when Keilhack (1908) placed *Varicorhinus* in synonymy with *Barbus*; (2) the replacement name and junior synonym *Barbus oliphanti* Keilhack, 1910 (see also previous note) is not included in Lévêque & Daget (1984); (3) for more details on the status of BMNH 1845.7.3.95 as the holotype of the species, see Greenwood & Crass (1959).

*mariae*, *Barbus* Holly, 1929. Preoccupied by *Varicorhinus* (now *Labeobarbus*) *mariae* Holly, 1926; replaced by *Labeobarbus rhinoceros* (present paper).

*mariae*, *Varicorhinus* Holly, 1926. Nachtigal ( $\pm 4^{\circ}21'N$ ,  $11^{\circ}38'E$ , USBGN, 1962b) (rapids), Sanaga River, Cameroon. Syntypes: NMW-7221 (1), 7222–7223 (2). Current status: valid as *Labeobarbus mariae* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: endemic to Lower Guinea, where it is found in the Sanaga and Wouri river basins (Getahun, 2007b).

*maroccana*, *Pterocapoëta* Günther, 1902. Oum Erbiah [Oum er Rbia River] ( $\pm 33^{\circ}19'N$ ,  $8^{\circ}20'W$ , USBGN, 1970) and Talmist River, Morocco. Syntypes: BMNH 1902.7.28.37–38 (2), 1902.7.28.39 (1). Current status: valid as *Labeobarbus maroccanus* (placed in *Labeobarbus* in Berrebi *et al.*, 2014). Synonyms: none. Distribution: Morocco (Lévêque & Daget, 1984), including Oued Srou and Oued Oum er Rbia (Borkenhagen, 2014). Notes: (1) type species of the genus

*Pterocapoëta* Gunther, 1902, previously a junior synonym of *Varicorhinus* (see Boulenger, 1905b, 1909; Karaman, 1971; Lévêque & Daget, 1984) and now of *Labeobarbus s.l.*; (2) *Pterocapoëta* correctly spelled as *Pterocapoeta* (see ICZN, 1999: article 32.5.2), as all original names published with an apostrophe should be corrected; (3) to be in agreement with ICZN (1999: articles 31.2 and 34.2), the species name *maroccana* (adjective; meaning from Morocco) must become *maroccanus* to agree in gender with the genus name *Labeobarbus* (masculine); (4) valid as *Pterocapoeta maroccana* (monospecific genus) in Borkenhagen (2014), Geiger *et al.* (2014), and Yang *et al.* (2015).

*matris*, *Barbus* Holly, 1928. Near Nairobi ( $\pm 1^{\circ}17'S$ ,  $36^{\circ}49'E$ , USBGN, 1964a), Athi River, Kenya. Holotype: NMW 8000. Current status: valid as *Labeobarbus matris* (placed in *Labeobarbus* in present paper). Synonym of *Barbus mariae* in Lévêque & Daget (1984); revalidated in the present paper. Synonyms: none. Distribution: Only known from the type locality (Lévêque & Daget, 1984). Notes: Despite the very similar original descriptions of both *L. matris* (Holly, 1928) and *L. mariae* (Holly, 1929), Banister (1973) refrained to synonymize both without having seen the type specimens. Nevertheless, several authors (Lévêque & Daget, 1984; Seegers *et al.*, 2003) considered *L. matris* a senior synonym of *L. mariae* (now *L. rhinoceros*), indeed with hesitation, but without further justification for the synonymy, and not respecting the proper priority of names. Previously considered lost, types of both species were found back in the NMW and both species are clearly diagnosable from each other (see text), rejecting any claims regarding a possible synonymization of both.

*mawambi*, *Barbus* Pappenheim, 1914. Mawambi ( $\pm 1^{\circ}03'N$ ,  $28^{\circ}36'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Ituri [DRC]. Holotype: ZMB 19062. Current status: valid as *Labeobarbus mawambi* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: Ituri River, DRC (Lévêque & Daget, 1984). Notes: possibly the same species as *B. mirabilis* (Banister, 1973).

*mawambiensis*, *Barbus hindii* Steindachner, 1911. Mawambi ( $\pm 1^{\circ}03'N$ ,  $28^{\circ}36'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Ituri River [DRC]. Syntypes: NMW 54177 (2), 54286 (3), 54287 (2), 54288 (2). Current status: valid as *Labeobarbus mawambiensis* (raised to species level in Steindachner, 1912; placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: rivers Ituri and Dja (middle Congo River Basin) in DRC and Cameroon, respectively (Steindachner, 1914; Boulenger, 1916a; Poll, 1967), although some doubt is cast on the identity of the specimens from the Dja by Trewavas (1974). Notes: (1) originally described as a subspecies of *Barbus* (now *Labeobarbus*) *hindii*, currently a junior synonym of *L. oxyrhynchus* following Banister (1973); (2) the total

number of type specimens adds up to nine, whereas the original publication only mentions seven syntypes; (3) according to Boulenger (1916: 231, 239), Steindachner (1914: plate 3, figs 1, 3) inverted the illustrations of *L. habereri* and *L. mawambiensis*. Indeed, figure 1 on plate 3 illustrates a fish with a damaged caudal and anal fin, as stipulated in the original description of *L. habereri* by Steindachner (1914: 24) himself. As such, figure 1 illustrates the holotype of *L. habereri*, whereas figure 3 instead illustrates a specimen of *L. mawambiensis*. Note, however, that for the latter species the illustrated specimen has 5.5 scales between the lateral line and the dorsal midline, whereas all examined syntypes have 3.5 or 4.5 scales.

*mbami*, *Barbus perplexicans* Holly, 1927. Mbami [Mayo] River ( $\pm 6^{\circ}49'N$ ,  $12^{\circ}00'E$ , USBGN, 1962b), Cameroon. Holotype: NMW 7528. Current status: valid as *Labeobarbus mbami* (raised to species level in Holly, 1930; placed in *Labeobarbus* in De Weirdt & Teugels, 2007). Synonyms: none. Distribution: Lower Guinea endemic, only known from the Sanaga River Basin in Cameroon (De Weirdt & Teugels, 2007). Notes: originally described as a subspecies of *Barbus* (now *Labeobarbus*) *perplexicans*, a junior synonym of *L. oxyrhynchus* following Banister (1973).

*megastoma*, *Barbus* Nagelkerke & Sibbing, 1997. Rema ( $11^{\circ}51'N$ ,  $37^{\circ}28'E$ , Nagelkerke & Sibbing, 1997) (locality 25), Lake Tana, Ethiopia. Holotype: RMNH 32950. Paratypes: RMNH 32951–59 (9). Current status: valid as *Labeobarbus megastoma* (placed in *Labeobarbus* in Getahun, 2007a). Synonyms: none. Distribution: Lake Tana and its tributaries (Nagelkerke & Sibbing, 1997).

*microbarbis*, *Barbus* David & Poll, 1937. A hybrid; see annotated checklist 2.

*miconema*, *Barbus* Boulenger, 1904. Kribi [Kienke] River ( $\pm 2^{\circ}56'N$ ,  $9^{\circ}54'E$ , USBGN, 1962b), southern Cameroon. Syntypes: BMNH 1904.2.29.37–38 (2). Current status: valid as *Labeobarbus miconema* (placed in *Labeobarbus* in De Weirdt & Teugels, 2007). Synonyms: none. Distribution: Lower Guinea endemic, known from the Sanaga, Nyong, Kribi, and Ivindo rivers in Cameroon and Gabon (De Weirdt & Teugels, 2007).

*microterolepis*, *Barbus* Boulenger, 1902. A hybrid; see annotated checklist 2.

*mirabilis*, *Barbus* Pappenheim, 1914. Mawambi ( $\pm 1^{\circ}03'N$ ,  $28^{\circ}36'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Ituri [DRC]. Holotype: ZMB 19059. Current status: valid as *Labeobarbus mirabilis* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: only known from the type locality (Lévêque & Daget, 1984). Notes: possibly a synonym of *B. somereni* (Banister, 1973).

*mungoensis*, *Barbus* Trewavas, 1974. Wowe River, tributary of Mungo River ( $\pm 4^{\circ}04'N$ ,  $9^{\circ}31'E$ , USBGN, 1962b), Cameroon. Holotype: BMNH 1973.5.14.163.



Paratypes: BMNH 1973.5.14.164–182 (19). Current status: valid as *Labeobarbus mungoensis* (placed in *Labeobarbus* in De Weirdt & Teugels, 2007). Synonyms: none. Distribution: Blackwater, Menge, Mungo, and Sanaga river basins in Cameroon (De Weirdt & Teugels, 2007). Notes: Trewavas (1974) mentions 18 type specimens in the original description, but the total number of type specimens listed adds up to 20. Possibly two specimens in the paratypes series BMNH 1973.5.14.164–182 are not types (J. Maclaine, pers. comm., 2015).

*nanningsi*, *Labeobarbus* de Beaufort, 1933. Lunda Department ( $\pm 9^{\circ}30'S$ ,  $20^{\circ}00'E$ , USBGN, 1956), Angola. Holotype: ZMA 113010. Current status: valid as *Labeobarbus nanningsi* [described as a *Labeobarbus* species; placed in *Barbus* in Matthes (1964), in *Barbus* (subgenus *Labeobarbus*) in Poll (1967), and again in *Labeobarbus* in the present paper]. Synonyms: none. Distribution: Luachimo River (Kasai drainage, middle Congo River Basin) in Angola (Poll, 1967; Lévêque & Daget, 1984).

*natalensis*, *Barbus* de Castelnau, 1861. Umvoti Mission, Tugela River ( $\pm 29^{\circ}14'S$ ,  $31^{\circ}30'E$ , USBGN, 1954b) near the boundary between Zulu Land and Natal, South Africa. Syntypes: lost. Current status: valid as *Labeobarbus natalensis* (placed in *Labeobarbus* in Skelton, 2001). Synonyms: *Labeobarbus aureus* Cope, 1867 (synonymy in Crass, 1960); *Barbus bowkeri* Boulenger, 1902; *Barbus dendrotrachelus* Fowler, 1934; *Barbus grouti* Fowler, 1934; *Barbus loboehilus* Boulenger, 1911; *Barbus marleyi* Fowler, 1934; *Barbus mfongosi* Gilchrist & Thompson, 1913; *Barbus robinsoni* Gilchrist & Thompson, 1913; *Barbus stigmaticus* Fowler, 1934; *Barbus tugelensis* Fowler, 1934; *Barbus zuluensis* Gilchrist & Thompson, 1913 (synonymy in Jubb, 1963). Distribution: Kwazulu-Natal, widespread from the Mkuze southwards to the Umtamvuna on the Transkei border; translocated to the Save in Zimbabwe (Skelton, 2001). Notes: a recent search for the syntypes in the de Castelnau's fish collection at the University of Liège (see Loneux, 2005) did not produce any results (P. Skelton, pers. comm., 2014).

*nedgia*, *Labeobarbus* Rüppell, 1835. Goraza [probably = Korata] ( $11^{\circ}45'N$ ,  $37^{\circ}27'E$ , Nagelkerke & Sibbing, 1997) market, Lake Tana, Ethiopia. Holotype: SMF 2619 (stuffed). Current status: valid as *Labeobarbus nedgia* [described as a *Labeobarbus* species, placed in *Barbus* in Günther (1868), and again in *Labeobarbus* in Getahun (2007a)]. Synonym of *Barbus intermedius* in Banister (1973); revalidated in Nagelkerke & Sibbing (1997). Synonyms: *Barbus degeni* Boulenger, 1902; *Barbus degeni leptorhinus* Bini, 1940 (synonymy in Nagelkerke & Sibbing, 1997). Distribution: Lake Tana and tributaries (Nagelkerke & Sibbing, 1997), extending southwards to Lake Gandjule (Margherita) and the

Sagan River (which connects Lake Gandjule with Lake Stephanie), and including the rivers Didessa and Omo (Boulenger, 1907c). Notes: (1) type species of the genus *Labeobarbus*; (2) although the original description mentions several specimens, only a holotype exists.

*neglectus*, *Barbus* Boulenger, 1903. Not a *Labeobarbus* species (see present paper).

*nelspruitensis*, *Varicorhinus* Gilchrist & Thompson, 1911. Nelspruit ( $25^{\circ}57'S$ ,  $30^{\circ}59'E$ , collection database), Transvaal [Gauteng], South Africa. Syntypes: SAIAB 134824 (ex. SAM 10518) (1), 135756 (ex. SAM 21698) (1). Current status: valid as *Labeobarbus nelspruitensis* (placed in *Labeobarbus* in Berrebi *et al.*, 2014). Synonyms: none. Distribution: escarpment streams of the Incomati and Phongolo systems (Skelton, 2001).

*nthuwa*, *Labeobarbus* Tweddle & Skelton, 2008. Runyina ( $11^{\circ}01'S$ ,  $33^{\circ}47'E$ ), tributary of South Rukuru River, Lake Malawi affluent, Malawi. Holotype: SAIAB 39341. Paratypes: SAIAB 39293 (1), 40787 (6), 51928 (2), 79494 (2). Current status: valid as *Labeobarbus nthuwa* (no generic reallocations). Synonyms: none. Distribution: South Rukuru River, Malawi (Tweddle & Skelton, 2008).

*osseensis*, *Barbus* Nagelkerke & Sibbing, 2000. Debre Mariam ( $11^{\circ}38'N$ ,  $37^{\circ}24'E$ , Nagelkerke & Sibbing, 1997) (locality 1), Lake Tana, Ethiopia. Holotype: RMNH 33721. Paratypes: RMNH 33722–30 (9). Current status: valid as *Labeobarbus osseensis* (placed in *Labeobarbus* in Getahun, 2007a). Synonyms: none. Distribution: only known from the southern parts of Lake Tana (Nagelkerke & Sibbing, 2000).

*oxyrhynchus*, *Barbus* Pfeffer, 1889. Korogwe ( $\pm 5^{\circ}09'S$ ,  $38^{\circ}29'E$ , USBGN, 1965c), Rufu River, Tanzania. Lectotype: ZMH H339 (ex. 69 07) (designated by Ladiges *et al.*, 1958). Paralectotypes: ZMH H340 (ex. 69 07) (7). Current status: valid as *Labeobarbus oxyrhynchus* (placed in *Labeobarbus* in Skelton & Bills, 2008; Berrebi *et al.*, 2014). Synonyms: *Barbus ahlSELLi* Lönnberg, 1911; *Barbus athi* Hubbs, 1918; *Barbus (Capoeta) babaulti* Pellegrin, 1926; *Barbus donyensis* Holly, 1929; *Barbus hindii* Boulenger, 1902; *Barbus krapfi* Boulenger, 1911; *Barbus (Labeobarbus) labiatus* Boulenger, 1902 (synonymy in Banister, 1973); *Barbus mathoiae* Boulenger, 1911 (synonymy in Fowler, 1936); *Barbus nairobi* Holly, 1928; *Barbus (Capoeta) perplexicans* Boulenger, 1902; *Barbus tanensis* Günther, 1894 (synonymy in Banister, 1973). Distribution: Pangani, Athi-Tana, and Nero-Narok river systems, Lorian swamps in the northern Euasso Nyiro River system (Lévêque & Daget, 1984). Notes: senior synonym of *B. tanensis* Günther, 1894, the type species of the subgenus *Lanceobarbus* Fowler, 1936, to be considered a junior synonym of the genus *Labeobarbus*.

*pagenstecheri*, *Barbus* Fischer, 1884. Stream flowing from the Kilimandjaro ( $\pm 3^{\circ}04'S$ ,  $37^{\circ}22'E$ , USBGN, 1965c)

[Pangani Basin], Massai-Land, Tanzania. Lectotype: ZMH H341 (ex ZMH 3851) (designated by Ladiges *et al.*, 1958). Paralectotype: ZMH H342 (ex. ZMH 3850) (1). Current status: valid as *Labeobarbus pagenstecheri* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: (Upper?) Pangani drainage, Tanzania (Seegers, 2008). Notes: (1) the suggestion of Banister (1973: 103) that 'the 2 specimens referred to *B. pagenstecheri* [i.e. the two type specimens] may represent a local population of *B. oxyrhynchus*' is contested by Seegers (2008), arguing the sympatric and possibly even syntopic occurrence of both nominal species; (2) lectotype designation by Boulenger (1911a), as accepted by Banister (1973), is invalid following ICZN (1999: article 74.5). Boulenger (1911a) apparently did not consider the larger specimen as a (syn)type, and his subsequent use of the term 'type' for the other specimen does not constitute a valid lectotype designation. In contrast to Seegers (2008) we do accept the lectotype designation by Ladiges *et al.* (1958), which is not in contradiction to ICZN (1999: article 74.3, which is the same as ICZN, 1985: article 74(d), cited by Seegers, 2008). Lectotype designations by Ladiges *et al.* (1958) are made on a species-by-species basis (i.e. per nominal taxon), and not collectively by a general statement. As such, and in contrast to Boulenger (1911a) and Banister (1973), the largest of both syntypes is the lectotype.

*parawaldroni*, *Barbus* Lévêque, Thys van den Audenaerde & Traore, 1987. Toyebli ( $\pm 6^{\circ}37'N$ ,  $8^{\circ}29'W$ , USBGN, 1965a), Cess River, Ivory Coast. Holotype: MRAC 73-10-P-2296. Paratypes: MRAC 73-10-P-2297 (1), 73-10-P-2298-2299 (2), 73-5-P-1936 (1). Current status: valid as *Labeobarbus parawaldroni* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: Lofa, Saint Paul, Nipoué (= Cess) in eastern Liberia, and Cavally and Tabou in western Côte d'Ivoire (Lévêque & Daget, 1984; Lévêque, 2003).

*paucisquamata*, *Barbus altianalis* Pellegrin, 1935. Kitembo ( $\pm 5^{\circ}53'S$ ,  $19^{\circ}08'E$ , D.F.E. Thys van den Audenaerde, unpubl. data; USBGN, 1964b), Nya-Barongo River [DRC]. Lectotype: MNHN 1935-0076 (designated by Banister, 1973). Paralectotypes: MNHN 1935-0077 (1), 1935-0078 (1), MRAC 42932 (1). Current status: valid as *Labeobarbus paucisquamatus* (raised to species level in Banister, 1973; placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: *Barbus altianalis lobogenysoides* Pellegrin, 1935 (synonymy in Banister, 1973). Distribution: Luhoho River system, including the rivers Loama and Nyabarongo (Upper Congo River Basin), in DRC (Lévêque & Daget, 1984). Notes: (1) to be in agreement with ICZN (1999: articles 31.2 and 34.2), the species name *paucisquamata* [adjective; from the Latin adjective *paucus* (with a small number) and the Latin adjective *squamatus* (covered

with scales), meaning the one covered with few scales] must become *paucisquamatus* to agree in gender with the genus name *Labeobarbus* (masculine); (2) the junior synonym *Barbus altianalis lobogenysoides* Pellegrin, 1935 was described in Pellegrin 1935b, as given in Eschmeyer (2015).

*pellegrini*, *Varicorhinus* Bertin & Estève, 1948. River west of Bukavu ( $\pm 2^{\circ}30'S$ ,  $28^{\circ}52'E$ , USBGN, 1962c), at the extreme south-west of Lake Kivu, DRC. Holotype: MNHN 1932-0181. Current status: valid as *Labeobarbus pellegrini* (placed in *Labeobarbus* in present paper). Synonym of *Barbus oxyrhynchus* in Banister (1973); revalidated by Lévêque & Daget (1984). Synonyms: replacement name for *Varicorhinus babaulti* Pellegrin, 1932 (Bertin & Estève, 1948), preoccupied by *Barbus (Capoeta) babaulti* Pellegrin, 1926, currently a synonym of *Barbus oxyrhynchus* Pfeffer, 1889. Distribution: only known from the holotype (Lévêque & Daget, 1984), which probably originates from the Lowa River Basin, Kivu Region (Pellegrin, 1932; Marlier, 1954). Notes: the species name *Varicorhinus babaulti* Pellegrin, 1932 attributed to a species originally described from a 'Rivière près de Bukavu, région du Kivu' (MNHN 1932-0181) has been replaced by *V. pellegrini* Bertin & Estève, 1948 (see Bertin & Estève, 1948), as these authors considered *V. babaulti* to be preoccupied by *Barbus babaulti* Pellegrin, 1926, originally described from the 'Région de Nairobi, Kénia' (MNHN 1926-0285), and reallocated into the genus *Varicorhinus* by the same authors (see Bertin & Estève, 1948). In spite of their placement in *Varicorhinus*, Banister (1973) synonymized *V. babaulti* (Pellegrin, 1932), i.e. *V. pellegrini*, as well as *B. babaulti* Pellegrin, 1926, i.e. *V. babaulti*, with *Barbus*, now *Labeobarbus oxyrhynchus*; however, the latter synonymy has not been followed by Lévêque & Daget (1984), who considered *V. pellegrini* [= *V. babaulti* (Pellegrin, 1932)] to be a valid species (see also Eschmeyer, 2015). Their decision concurs with the fact that the type locality of *V. pellegrini* falls way out of the currently known East African distribution of *L. oxyrhynchus*, as given by Banister (1973) himself. Therefore, despite Banister's (1973) synonymization, the decision of Lévêque & Daget (1984) is followed here and *V. pellegrini* is retained as a valid species with the *Varicorhinus* mouth phenotype.

*petitjeani*, *Barbus* Daget, 1962. Ballay ( $\pm 10^{\circ}31'N$ ,  $11^{\circ}55'W$ , USBGN, 1965b), Bafing River, upper Senegal Basin, Guinea. Syntypes: MNHN 1959-0108 (3). Current status: valid as *Labeobarbus petitjeani* (placed in *Labeobarbus* in Skelton & Bills, 2008; Berrebi *et al.*, 2014). Synonyms: none. Distribution: Bafing River in the upper Senegal Basin and the upper Niger in Guinea (Lévêque & Guégan, 1990; Lévêque, 2003).

*platydorsus*, *Barbus* Nagelkerke & Sibbing, 1997. Rema ( $11^{\circ}51'N$ ,  $37^{\circ}28'E$ , Nagelkerke & Sibbing, 1997) (locality 25), Lake Tana, Ethiopia. Holotype:

RMNH 32970. Paratypes: RMNH 32971–79 (9). Current status: valid as *Labeobarbus platydorsus* (placed in *Labeobarbus* in Getahun, 2007a). Synonyms: none. Distribution: endemic to Lake Tana, Ethiopia (Nagelkerke & Sibbing, 1997).

*platyrhinus*, *Barbus* Boulenger, 1900. South of Usambura [= Usumbura, = Bujumbura] ( $\pm 3^{\circ}22'S$ ,  $29^{\circ}22'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Lake Tanganyika. Holotype: BMNH 1906.9.6.12. Current status: valid as *Labeobarbus platyrhinus* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: Lake Tanganyika and its affluent the Koki River; probably rare in the lake and more common in the tributaries (Lévêque & Daget, 1984). Notes: Banister (1973) leaves some doubt on the validity of this species, and identifies it as a possible junior synonym of *B. tropidolepis*.

*platystomus*, *Varicorhinus* Pappenheim, 1914. Wase River, Rwanda, 1800 m a.s.l. Syntypes: ZMB 19051 (1), 34769 (1). Current status: valid as *Labeobarbus platystomus* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Mukungwa River in Rwanda (De Vos *et al.*, 2001). Notes: (1) *Barbus platystomus* Boulenger, 1902 is currently a junior synonym of *Labeobarbus intermedius* (Rüppell, 1835). It is clear from the glossary of the ICZN (1999) that the word 'taxon' refers to a valid taxon, in our case a valid species, when used in article 57.3.1. of ICZN (1999) (M. Kottelat, pers. comm., 2015). As such, unless *Barbus platystomus* Boulenger, 1902 becomes a valid *Labeobarbus* species, a replacement name for *Labeobarbus platystomus* (Pappenheim, 1914) is not needed; (2) following ICZN (1999: articles 31.2 and 34.2), the species name *platystomus* [from the Greek adjective *platys* (wide and flat) and the Greek noun *stomus* (mouth); meaning with a wide and flat mouth] does not need to agree in gender with the genus name; (3) misspelled as *Varicorhinus platystoma* in Lévêque & Daget (1984).

*pojeri*, *Barbus* Poll, 1944. Albertville [Kalemie] ( $\pm 5^{\circ}56'S$ ,  $29^{\circ}12'E$ , USBGN, 1964b) region, Lukuga River, DRC. Holotype: IRSNB 71. Paratype: IRSNB 599 (1). Current status: valid as *Labeobarbus pojeri* (placed in *Labeobarbus* in Kullander & Roberts, 2012). Synonym of *Barbus euchilus* in Poll (1953), which was, together with *Barbus pojeri*, placed in synonymy with *Barbus caudovittatus* in Banister (1973); the latter was transferred to *Labeobarbus* by De Weirtdt & Teugels (2007); *Barbus pojeri* revalidated by Kullander & Roberts (2012) as *Labeobarbus pojeri*. Synonyms: none. Distribution: Lukuga River, from near Kalemie (Poll, 1944) up to the Kisimba–Kilia rapids (Kullander & Roberts, 2012) in DRC.

*polylepis*, *Barbus* Boulenger, 1907. Klein Olifant River ( $\pm 25^{\circ}41'S$ ,  $29^{\circ}20'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Transvaal [now Gauteng], South Africa.

Holotype: BMNH 1907.3.15.33. Current status: valid as *Labeobarbus polylepis* (placed in *Labeobarbus* in Skelton, 2001). Synonyms: *Barbus elephantis* Boulenger, 1907 (implicit synonymy in Skelton, 1993, 2001; synonymy confirmed by P.H. Skelton, pers. comm., 2015; see also present paper); *Barbus lineolatus* Gilchrist & Thompson, 1913 (synonymy in Jubb, 1963). Distribution: restricted to southern tributaries of the Limpopo, and the Incomati and Phongolo systems (Skelton, 2001). Notes: (1) including *Barbus elephantis* Boulenger, 1908 as a junior synonym. See also Jubb (1961, 1967) on the dubious status of this nominal species, as a possible synonym of *B. natalensis* (Jubb, 1961), a possible hybrid, or a synonym of *B. marequensis* (Jubb, 1967); (2) holotype in Eschmeyer (2015) incorrectly referred to as BMNH 1907.3.15.3 (probably a typographical error).

*progenys*, *Barbus* Boulenger, 1903. Kribi [Kienke] River ( $\pm 2^{\circ}56'N$ ,  $9^{\circ}54'E$ , USBGN, 1962), southern Cameroon. Holotype: BMNH 1902.11.12.127. Current status: valid as *Labeobarbus progenys* (placed in *Labeobarbus* in De Weirtdt & Teugels, 2007). Synonyms: none. Distribution: widespread in West–Central Africa, including the basins of the Sanaga, Ntem, Ogooué, Nyanga, and Niari (De Weirtdt & Teugels, 2007), and the Cross River in Cameroon (Vivien, 1991; Lévêque, 2003); also known from Dja River and Dundo (Angola) (De Weirtdt & Teugels, 2007). Notes: (1) holotype in Eschmeyer (2015) incorrectly referred to as BMNH 1902.11.13.127 (probably a typographical error); (2) Poll (1967) mentions *Barbus* sp. (aff. *progenys* Boulenger) from Dundo (Luachimo River, Angola); it is unclear if the report from Dundo in De Weirtdt & Teugels (2007) refers to the same specimen(s) or reference.

*pungweensis*, *Varicorhinus* Jubb, 1959. Pungwe River ( $18^{\circ}24'S$ ,  $32^{\circ}58'E$ ), Inyanga district, Zimbabwe. Holotype: SAIAB 120014 (ex. AMG 850). Paratypes: SAIAB 120015 (ex. AMG 851) (1), 120016 (ex. AMG 852) (1), 120017 (ex. AMG 853) (1), 120018 (ex. AMG 854) (1). Current status: valid as *Labeobarbus pungweensis* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Pungwe and Buzi rivers in Zimbabwe and Mozambique (Skelton, 2001). Notes: number of paratypes in Eschmeyer (2015) incorrectly given as seven instead of four.

*reinii*, *Barbus* Günther, 1874. Tensift River ( $\pm 32^{\circ}02'N$ ,  $9^{\circ}21'W$ , USBGN, 1970), Morocco. Syntypes: BMNH 1874.1.30.22–24 (3), SMF 579 (4). Current status: valid as *Labeobarbus reinii* (placed in *Labeobarbus* in Doadrio, 1994). Synonyms: none. Distribution: Rivers of Morocco (Lévêque & Daget, 1984), including Oued Tensift and Oued Ksob (Borkenhagen, 2014). Notes: (1) the original species description mentions only three type specimens, but the total number of type specimens given in Eschmeyer (2015) is seven, including

BMNH 1874.1.30.22–24 (3). The latter may be the true types (J. Maclaine, pers. comm., 2015); (2) placed in '*Labeobarbus*' in Yang *et al.* (2015).

*rhinoceros*, *Barbus* Copley, 1938. Athi River [Kenya?]. No types known (Eschmeyer, 2015). Holotype and paratype status of BMNH 1936.12.22.35–39 needs further research (see also text). Current status: valid as *Labeobarbus rhinoceros* (placed in *Labeobarbus* in Skelton & Bills, 2008; Berrebi *et al.*, 2014). Synonyms: replacement name for *Barbus mariae* Holly, 1929, preoccupied by *Varicorhinus* (now *Labeobarbus mariae* Holly, 1926 (present paper). Distribution: Athi and Tana river systems in Kenya (Lévêque & Daget, 1984). Notes: (1) see note for *Labeobarbus matris*; (2) Lévêque & Daget (1984) erroneously used 1958 instead of 1938 as the year of original description; (3) previously considered lost, the lectotype and paralectotype of *Barbus mariae* Holly, 1929, designated by Banister (1973), were found back at the NMW and are currently registered as NMW 96552 and 96553, respectively.

*rhinophorus*, *Barbus* Boulenger, 1910. Lucala (near railway station) ( $\pm 9^{\circ}16'23''S$ ,  $15^{\circ}14'42''E$ , Google Earth), above the falls on the Lucala River, Angola. Syntypes: BMNH 1911.6.1.37–38 (2). Current status: valid as *Labeobarbus rhinophorus* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: none. Distribution: only known from the type locality (Lévêque & Daget, 1984).

*robertsi*, *Varicorhinus* Banister, 1984. Sanga waterfalls ( $4^{\circ}50'S$ ,  $14^{\circ}57'E$ ) at the tailwaters of the hydroelectric dam at Sanga on the Inkisi River, Congo Basin, DRC. Holotype: BMNH 1983.3.30.20. Paratypes: BMNH 1983.3.30.21–38 (18). Current status: valid as *Labeobarbus robertsi* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Inkisi River, DRC (Wamuini Lunkayilakio *et al.*, 2010).

*rocadasi*, *Barbus* Boulenger, 1910. Rivers Quanza [= Cuanza] ( $\pm 13^{\circ}49'S$ ,  $17^{\circ}26'E$ , D.F.E. Thys van den Audenaerde, unpubl. data; USBGN, 1956) and Lucalla [= Lucala] ( $\pm 9^{\circ}20'S$ ,  $13^{\circ}11'E$ ), Angola. Syntypes: ANSP 37986–91 (6), BMNH 1911.6.1.19–20 (2), 1911.6.1.21–25 (6), 1911.6.1.26 (1, skeleton), 1911.6.1.27–28 (2), NMW 13347–13352 (6), ZMB 18214 (6). Current status: valid as *Labeobarbus rocadasi* (placed in *Labeobarbus* in De Weirdt & Teugels, 2007; Skelton & Bills, 2008). Synonyms: none. Distribution: Nyong River in Cameroon (De Weirdt & Teugels, 2007) and Quanza and Luculla rivers in Angola (Lévêque & Daget, 1984; De Weirdt & Teugels, 2007). Notes: (1) the presence of this species in the Nyong River in Cameroon (De Weirdt & Teugels, 2007) needs confirmation, but seems questionable given the species is otherwise only known from the Quanza Basin in Angola; (2) the number of syntypes in BMNH 1911.6.1.21–25 was verified as six, not the expected five.

*rosae*, *Barbus* Boulenger, 1910. Lucala (near railway station) ( $\pm 9^{\circ}16'23''S$ ,  $15^{\circ}14'42''E$ , Google Earth), above the falls on the Lucala River, Angola. Syntypes: BMNH 1911.6.1.39–41 (3), NMW 54500 (1), ZMB 18216 (1). Current status: valid as *Labeobarbus rosae* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: only known from the type locality (Lévêque & Daget, 1984). Notes: Lévêque & Daget (1984) incorrectly put the type locality in the Zambezi River system.

*roylii*, *Barbus* Boulenger, 1912. N'Kutu [Ncutu] ( $\pm 4^{\circ}57'S$ ,  $12^{\circ}35'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Loango River [Shiloango Basin, Cabinda, Angola] and Buco Zau [= Bucozan] ( $\pm 4^{\circ}45'S$ ,  $12^{\circ}33'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Luali River [Shiloango Basin, Cabinda, Angola]. Syntypes: ANSP 38548 (1), BMNH 1912.4.1.338–340 (3), 1912.4.1.341–342 (2), MRAC 1533 (1), 1534 (1), 1535 (1), NMW 54501 (1), ZMB 18809 (1). Current status: valid as *Labeobarbus roylii* (placed in *Labeobarbus* in De Weirdt & Teugels, 2007). Synonyms: none. Distribution: Lower Guinea endemic, known from the Kouilou and Chiloango basins in Republic of the Congo and DRC (De Weirdt & Teugels, 2007). Notes: The total number of type specimens adds up to 11, whereas the original description only mentions ten syntypes.

*ruandae*, *Varicorhinus* Pappenheim, 1914. Mkunga [Mukungwa] near Ruasa [Rwasa] ( $\pm 1^{\circ}32'S$ ,  $29^{\circ}42'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Rwanda. Holotype: ZMB 19050. Current status: valid as *Labeobarbus ruandae* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Rivers of Rwanda (Lévêque & Daget, 1984). Notes: the two paratypes of *Barbus* (now *Labeobarbus microbarbis*) have been reidentified as this species (Banister, 1973).

*ruasae*, *Barbus* Pappenheim, 1914. Mkunga [Mukungwa] near Ruasa [Rwasa] ( $\pm 1^{\circ}32'S$ ,  $29^{\circ}42'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Rwanda. Lectotype: ZMB 19053 (designated by Banister, 1973). Paralectotype: ZMB 22652 (1). Current status: valid as *Labeobarbus ruasae* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: only known from the Mukungwa River, an affluent of the Nyabarongo River in Rwanda (Lévêque & Daget, 1984).

*ruwenzorii*, *Capoëta* (*Pterocapoëta*) Pellegrin, 1909. Wimi River ( $\pm 0^{\circ}23'N$ ,  $29^{\circ}54'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Ruwenzori. Syntypes: MNHN 1909-0583 (1), 1909-0584 (1), 1909-0585 (1). Current status: valid as *Labeobarbus ruwenzorii* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Ruwenzori area, Mubuku and Sibwe systems (Lévêque & Daget, 1984).

*sacratu*, *Barbus* Daget, 1963. Zié ( $\pm 7^{\circ}44'N$ ,  $8^{\circ}22'W$ , USBGN, 1965b), Diougou Basin and Sérédou ( $\pm 8^{\circ}23'N$ ,  $9^{\circ}17'W$ , USBGN, 1965b), Diani River (upper Saint Paul Basin), Guinea. Syntypes: MNHN 1959-0119 (4), 1959-

0139 (1). Current status: valid as *Labeobarbus sacratus* (placed in *Labeobarbus* in Skelton & Bills, 2008; Berrebi *et al.*, 2014). Synonyms: none. Distribution: known from the coastal basins of the Guinean ridge, from the Tominé (= Corubal) River in Guinea to the Saint John River in east Liberia (Lévêque & Guégan, 1990; Lévêque, 2003). Notes: in his original description of *Barbus sacratus*, Daget (1963) designated four syntypes and a paratype, which are all to be considered syntypes following ICZN (1999: article 73.2).

*sandersi*, *Varicorhinus* Boulenger, 1912. N'Kutu [Ncutu] ( $\pm 4^{\circ}57'S$ ,  $12^{\circ}35'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Loango River [Shilongo Basin, Cabinda, Angola]. Lectotype: BMNH 1912.4.1.333 (designated in present paper). Paralectotypes: BMNH 1912.4.1.334–336 (two instead of three), 1912.4.1.337 (1), MRAC 1525 (1), 1526 (1), 1527 (1), ZMB 18808 (1). Current status: valid as *Labeobarbus sandersi* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Lower Guinea endemic, known from southern Cameroon to the Chiloango River in Cabinda (Angola) (Getahun, 2007b). Notes: the original BMNH syntype series, currently split into a lectotype and paralectotypes, consists of five consecutive numbers, although only four specimens are present; the whereabouts of a potential fifth specimen are unknown. Even if this specimen was to be located, the number of type specimens still only adds up to nine, whereas ten syntypes were reported in the original description.

*seeberi*, *Barbus* Gilchrist & Thompson, 1913. Olifants River ( $\pm 32^{\circ}11'S$ ,  $18^{\circ}54'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Cape Province, South Africa. Syntypes: BMNH 1936.8.4.6 (1), SAIAB 134867 (ex. SAM 10672) (2). Current status: valid as *Labeobarbus seeberi* [placed in *Labeobarbus* in Skelton & Bills (2008) (using the at that time senior synonym name *Labeobarbus capensis*; *L. seeberi* is at present the valid species name, cf. infra); present paper]. Synonym of *Barbus capensis* in Barnard (1937); revalidated in the present paper. See also E. Vreven, E.R. Swartz & P.H. Skelton, unpubl. data. Synonyms: none. Distribution: Clanwilliam Olifants system, Western Cape, South Africa (Skelton, 2001). Notes: as demonstrated by E. Vreven, E.R. Swartz & P.H. Skelton (unpubl. data), *Barbus capensis* is not a *Labeobarbus* but is instead a senior synonym of *B. andrewi*. *Barbus seeberi*, previously a junior synonym of *B. capensis* and indeed a yellowfish, or *Labeobarbus*, therefore becomes the valid species name for the clanwilliam yellowfish.

*semireticulatus*, *Varicorhinus* Pellegrin, 1924. Louvisi River ( $\pm 4^{\circ}17'S$ ,  $13^{\circ}57'E$ , USBGN, 1962c), Kouilou, Republic of the Congo. Syntypes: MNHN 1924-0052 (2). Current status: valid as *Labeobarbus semireticulatus* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: only known from the type locality (Getahun, 2007b).

*somereni*, *Barbus* Boulenger, 1911. Sebwe River ( $\pm 0^{\circ}10'N$ ,  $30^{\circ}12'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), snow-water stream on Mount Ruwenzori, Uganda, elevation 6000 feet. Holotype: BMNH 1911.7.26.1. Current status: valid as *Labeobarbus somereni* (placed in *Labeobarbus* in Skelton & Bills, 2008; Banyankimbona *et al.*, 2012a). Synonyms: *Barbus altianalis urundensis* David, 1937 (synonymy in Banister, 1973). Distribution: rivers Sibwe, Mubuku, Tokwe, and Kirimia in the Ruwenzori area; also found in the rivers Nyawarongo and Akianaru (Rwanda), Mutamphu, Chirangobwe (Lake Kivu Basin), Mwogo (Kagera system), upper Malagarasi (Burundi), Kitenge (Ruzizi), and the Nyamagana and Nyakagunda (Burundi) (Banister, 1973; Lévêque & Daget, 1984). Possibly also in the Kagera and Malagarasi in Tanzania (Eccles, 1992). Notes: possibly 'related' to *Varicorhinus* (now *Labeobarbus*) *ruwenzorii*, with which it may hybridize (Banister, 1973: 114).

*stappersii*, *Barbus* Boulenger, 1915. Lake Moero [= Mweru] ( $\pm 9^{\circ}00'S$ ,  $28^{\circ}45'E$ , USBGN, 1964b), in front of Lukonzolwa, DRC. Holotype: MRAC 14250. Current status: valid as *Labeobarbus stappersii* (placed in *Labeobarbus* in Skelton & Bills, 2008; Van Steenberge *et al.*, 2014). Synonyms: *Barbus curtus* Boulenger, 1915; *Barbus moeruensis* Pellegrin, 1922; *Barbus oxycephalus* Boulenger, 1915 (synonymy in Banister, 1973). Distribution: Lake Mweru (Lévêque & Daget, 1984; Van Steenberge *et al.*, 2014), Luapula River (Lévêque & Daget, 1984), and the Bangweulu-Chambesi (Van Steenberge *et al.*, 2014).

*steindachneri*, *Varicorhinus* Boulenger, 1910. Lucala (near railway station) ( $\pm 9^{\circ}16'23'S$ ,  $15^{\circ}14'42'E$ , Google Earth), above the falls on the Lucala River, Angola. Syntypes: ANSP 37992 (2), BMNH 1910.11.28.147–155 (9), 1910.11.28.156 (1), 1910.11.28.157 (1, glycerine), 1910.11.28.158 (1, skeleton), 1911.6.1.1–5 (5), NMW 48867 (3), USNM 86618 (1), ZMB 18212 (3). Current status: valid as *Labeobarbus steindachneri* (placed in *Labeobarbus* in Berrebi *et al.*, 2014). Synonyms: none. Distribution: Lower Guinea endemic found from Cameroon to Cabinda (Getahun, 2007b). Notes: (1) the type series of *V. steindachneri* revealed to be polyspecific with one specimen (BMNH 1911.6.1.5: 55.4 mm SL) identifiable as *V. ensifer*; nevertheless, it is clear from Boulenger's original description and the numerous diagnostic characters separating *V. steindachneri* and *V. ensifer* that the latter specimen was not intended to be considered part of the species, as conceived by Boulenger himself; (2) the original syntypes record BMNH 1910.11.28.147–158 contained only nine specimens, hence the collection number was amended to 1910.11.28.147–155. BMNH 1910.11.28.157 is in glycerine and BMNH 1910.11.28.158 is a skeleton. The latter specimen is probably found but there is at present not enough

data to say conclusively. The whereabouts of BMNH 1910.11.28.156 are currently unknown (J. Maclaine, pers. comm., 2015); (3) syntype BMNH 1910.11.28.158 is not mentioned in Lévêque & Daget (1984) or Eschmeyer (2015); (4) Lévêque & Daget (1984) gave BMNH 1910.11.20.147–157 as the syntype record numbers, which is probably a typographical error for BMNH 1910.11.28.147–157.

*stenostoma*, *Varicorhinus* Boulenger, 1910. Lucala (near railway station) ( $\pm 9^{\circ}16'23'S$ ,  $15^{\circ}14'42'E$ , Google Earth), above the falls on the Lucala River, Angola. Holotype: BMNH 1910.11.28.145. Current status: valid as *Labeobarbus stenostoma* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: only known from the holotype (Lévêque & Daget, 1984). Notes: identifications from the Inkisi (lower Congo River Basin, DRC) are incorrect (Wamuini Lunkayilakio *et al.*, 2010).

*stigmatopygus*, *Barbus* Boulenger, 1903. Not a *Labeobarbus* species (see present paper).

*surkis*, *Barbus* Rüppell, 1835. Entos ( $11^{\circ}39'N$ ,  $37^{\circ}22'E$ , Nagelkerke & Sibbing, 1997) (locality 17), Lake Tana, Ethiopia. Neotype: RMNH 32980 (designated by Nagelkerke & Sibbing, 1997). Current status: valid as *Labeobarbus surkis* (placed in *Labeobarbus* in Getahun, 2007a). Synonym of *Barbus intermedius* in Banister (1973); revalidated by Nagelkerke & Sibbing (2000). Synonyms: none. Distribution: Lake Tana; also described from the Didessa River (Nagelkerke & Sibbing, 1997).

*tornieri*, *Varicorhinus* Steindachner, 1906. Nyong district ( $\pm 3^{\circ}17'N$ ,  $9^{\circ}54'E$ , USBGN, 1962b), German Cameroon [Cameroon]. Holotype: NMW 46053. Current status: valid as *Labeobarbus tornieri* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Lower Guinea endemic, known from the Mungo, Sanaga, Nyong, and Ntem rivers (Cameroon), Rio Benito (Rio Muni), and Ogowe River (Gabon) (Getahun, 2007b). Notes: (1) date in Lévêque & Daget (1984) incorrect as 1907; (2) Eschmeyer (2015) reports the type series as 'syntypes: NMW', without collection number, but the original species description is based on a single specimen.

*trachypterus*, *Barbus* Boulenger, 1915. Lake Moero [= Mweru] ( $\pm 9^{\circ}00'S$ ,  $28^{\circ}45'E$ , USBGN, 1964b), in front of Lukonzolwa, DRC. Holotype: MRAC 11830. Current status: valid as *Labeobarbus trachypterus* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Synonyms: *Varicorhinus bredoi* Poll, 1948 (synonymy in Banister, 1973). Distribution: Upper Lualaba (David & Poll, 1937), Lake Mweru (Boulenger, 1915) and lower Luapula (below Mumbatuta Falls) (Banister, 1973; Balon & Stewart, 1983).

*tropidolepis*, *Barbus* Boulenger, 1900. Usambura (Usumbura) [= Bujumbura] ( $\pm 3^{\circ}22'S$ ,  $29^{\circ}22'E$ ,

D.F.E. Thys van den Audenaerde, unpubl. data), Lake Tanganyika [Burundi]. Lectotype: BMNH 1906.9.6.19 (designated by Banister, 1973). Paralectotypes: BMNH 1906.9.6.20–21 (2), MRAC 327 (1), 328 (1), 329 (1). Current status: valid as *Labeobarbus tropidolepis* (placed in *Labeobarbus* in Skelton & Bills, 2008; Banyankimbona *et al.*, 2012a). Synonyms: *Varicorhinus chapini* Nichols & La Monte, 1950 (synonymy proposed in Poll, 1953; established in Banister, 1973). Distribution: Lake Tanganyika Basin (Lévêque & Daget, 1984).

*truttiformis*, *Barbus* Nagelkerke & Sibbing, 1997. Wanzaie ( $11^{\circ}46'N$ ,  $37^{\circ}43'E$ , Nagelkerke & Sibbing, 1997) (locality 30), Gumara River ( $\pm 11^{\circ}53'N$ ,  $37^{\circ}32'E$ , USBGN, 1963), tributary of Lake Tana, Ethiopia. Holotype: RMNH 32990. Paratypes: RMNH 32991–99 (9). Current status: valid as *Labeobarbus truttiformis* (placed in *Labeobarbus* in Getahun, 2007a). Synonyms: none. Distribution: endemic to Lake Tana and its tributaries (Nagelkerke & Sibbing, 1997).

*tsanensis*, *Barbus* Nagelkerke & Sibbing, 1997. Blue Nile ( $11^{\circ}37'N$ ,  $37^{\circ}24'E$ , Nagelkerke & Sibbing, 1997) (locality 13), Lake Tana, Ethiopia. Holotype: RMNH 33000. Paratypes: RMNH 33001–09 (9). Current status: valid as *Labeobarbus tsanensis* (placed in *Labeobarbus* in Getahun, 2007a). Synonyms: none. Distribution: endemic to Lake Tana, Ethiopia (Nagelkerke & Sibbing, 1997).

*upembensis*, *Varicorhinus* Banister & Bailey, 1979. Above the falls on the Kalumengonga River ( $8^{\circ}49'S$ ,  $27^{\circ}13'E$ ) (site 5), Upemba National Park, Shaba, DRC. Holotype: BMNH 1975.9.5.5. Paratypes: BMNH 1975.9.5.6–12 (7), 1975.9.5.13–17 (5). Current status: valid as *Labeobarbus upembensis* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: only known from the type locality (Banister, 1984).

*urotaenia*, *Barbus* Boulenger, 1913. Dungu ( $\pm 3^{\circ}37'N$ ,  $28^{\circ}33'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), upper Uelé River, DRC. Syntypes: BMNH 1912.12.6.5 (1), MRAC 1791 (1), 1792 (1). Current status: valid as *Labeobarbus urotaenia* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: only known from the type locality (Lévêque & Daget, 1984).

*varicostoma*, *Varicorhinus* Boulenger, 1910. Lucala ( $\pm 9^{\circ}37'S$ ,  $14^{\circ}14'E$ , USBGN, 1956), above the falls on the Lucala River, Angola. Holotype: BMNH 1910.11.28.146. Current status: valid as *Labeobarbus varicostoma* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: only known from the holotype (Lévêque & Daget, 1984).

*versluysii*, *Barbus* Holly, 1929. Bakoko area ( $\pm 5^{\circ}28'N$ ,  $9^{\circ}18'E$ , USBGN, 1962b), Cameroon. Syntypes: NMW 13954–13956 (3). Current status: valid as *Labeobarbus versluysii* (placed in *Labeobarbus* in De Weirtdt & Teugels, 2007). Synonyms: none. Distribu-

tion: Lower Guinea endemic, present in the Wouri, Sanaga, and Nyong river basins in Cameroon (De Weirdt & Teugels, 2007).

*wernerii*, *Barbus* Boulenger, 1905. Not a *Labeobarbus* species (see present paper). Listed as a valid (*Labeobarbus*) species in Getahun (2007a), but considered a synonym of *Barbus stigmatopygus* in Lévêque (1989), Lévêque, Paugy & Teugels (1991), and Seegers *et al.* (2003).

*wernerii*, *Varicorhinus* Holly, 1929. Bakoko area ( $\pm 5^{\circ}28'N$ ,  $9^{\circ}18'E$ , USBGN, 1962b), Cameroon. Syntypes: NMW 13948 (1), 13949 (1). Current status: valid as *Labeobarbus wernerii* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Lower Guinea endemic, known from scattered localities throughout the region, including the Sanaga and Nyong in Cameroon, and the Rembo Nkomi and Nyanga in Gabon (Getahun, 2007b). Notes: only one specimen left according to the NMW collection; originally NMW 13948 and 13949 were in the same jar, but only the former is still present (with a label bearing the number 13948 attached to the specimen and on the jar); NMW 13949 thus seems to have been lost (H. Wellendorf, pers. comm., 2000).

*wittei*, *Varicorhinus* Banister & Poll, 1973. Muye ( $\pm 08^{\circ}59'S$ ,  $26^{\circ}48'E$ , collection database), right-bank affluent of the Lufira, 800–900 m a.s.l. Holotype: MRAC 179738. Paratypes: BMNH 1972.10.2.3 (1), MRAC 179739–741 (3), 179742 (1), IRSNB 645 (1). Current status: valid as *Labeobarbus wittei* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: Kilwezi and Muye, Lufira system (Banister & Poll, 1973).

*wurtzi*, *Barbus* Pellegrin, 1908. Near Tabili ( $\pm 9^{\circ}50'N$ ,  $13^{\circ}13'W$ , USBGN, 1965b), Grandes Chûtes (probably near the Grandes Chûtes Dam,  $\pm 9^{\circ}55'N$ ,  $13^{\circ}06'W$ , USBGN, 1965b) [Samu River, Konkouré Basin], French Guinea [Guinea]. Holotype: MNHN 1908-0097. Current status: valid as *Labeobarbus wurtzi* (placed in *Labeobarbus* in Skelton & Bills, 2008; Berrebi *et al.*, 2014). Synonyms: *Barbus barryi* Daget, 1962 (synonymy in Lévêque *et al.*, 1989); *Barbus holasi* Daget, 1965 (synonymy in Lévêque, 1983). Distribution: many coastal basins of West Africa, from the Konkouré River in Guinea to at least the Tano, west of the Volta in Ghana (Lévêque & Guégan, 1990; Lévêque, 2003).

*xyrocheilus*, *Varicorhinus* Tweddle & Skelton, 1998. Border Lujeri Tea Estate/Swazi Tea research station ( $16^{\circ}04'S$ ,  $35^{\circ}40'E$ ), upper Ruo River, lower Shire, Zambezi system, Malawi. Holotype: SAIAB 53082. Paratypes: SAIAB 34336 (11). Current status: valid as *Labeobarbus xyrocheilus* (placed in *Labeobarbus* in present paper). Synonyms: none. Distribution: River Ruo above Zoa Falls (Tweddle & Skelton, 1998). Notes: holotype in Eschmeyer (2015) incorrectly referred to as SAIAB 52082 (probably a typographical error).

## ANNOTATED CHECKLIST 2: AFRICAN NOMINAL *LABEOBARBUS S.L.* SPECIES IDENTIFIED AS HYBRID PHENOTYPES

*alluaudi*, *Barbus* Pellegrin, 1909. Wimi River ( $\pm 0^{\circ}23'N$ ,  $29^{\circ}54'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), Ruwenzori (lower zone). Syntypes: MNHN 1909-0586 (1), 1909-0587 (1). Current status: *Labeobarbus alluaudi* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Considered a hybrid in Banister (1972). Distribution: Ruimi (= Wimi), Mubuku and Sibwe rivers on the eastern flank of the Ruwenzori Mountain, Uganda (Lévêque & Daget, 1984). Notes: identified as a possible intergeneric hybrid between *B. somereni* and *V. ruwenzori* (now both *Labeobarbus* species) by Banister (1972).

*microbarbis*, *Barbus* David & Poll, 1937. Lake Luhondo ( $\pm 1^{\circ}30'S$ ,  $29^{\circ}45'E$ , USBGN, 1964c), Rwanda. Holotype: MRAC 41847. Paratypes: MRAC 41848–49 (2). Current status: *Labeobarbus microbarbis* (placed in *Labeobarbus* in Skelton & Bills, 2008; present paper). Considered a possible hybrid in Banister (1973); considered a hybrid in De Vos & Thys van den Audenaerde (1990). Distribution: only known from the holotype (Lévêque & Daget, 1984). Notes: (1) in Lévêque & Daget (1984: 268) as 'only known from the holotype', but two paratypes exist that are not mentioned in Lévêque & Daget (1984); (2) the two paratypes have been reidentified as *Varicorhinus ruandae* (Banister, 1973); (3) the holotype illustrated in figure 30 in David & Poll (1937; upper specimen) was incorrectly indicated as having an SL of 170 mm, instead of 270 mm; in addition, the second specimen illustrated is a paratype and thus not conspecific (see previous note); (4) identified as a possible intergeneric hybrid between *Barbus* and *Varicorhinus* (now both *Labeobarbus* species; see Banister, 1973), and between *B. ruasae* and *V. ruandae* (now both *Labeobarbus* species; see De Vos & Thys van den Audenaerde, 1990).

*microterolepis*, *Barbus* Boulenger, 1902. Buggali, Maki River ( $\pm 8^{\circ}05'N$ ,  $38^{\circ}50'E$ , D.F.E. Thys van den Audenaerde, unpubl. data), flowing towards Lake Swai from the eastern slope of the Adami Mountains, Addia country, Ethiopia, elevation about 4000 feet. Holotype: BMNH 1902.12.13.220. Current status: *Labeobarbus microterolepis* (placed in *Labeobarbus* in Getahun, 2007a). Considered a possible hybrid in Banister (1973); considered a hybrid in Golubtsov *et al.* (2002). Distribution: only known from the type locality (Lévêque & Daget, 1984). Notes: according to Banister (1973), an aberrant specimen of *Barbus* (now *Labeobarbus intermedius*, a valid species, or possibly a hybrid between *B. ethiopicus* and *B. intermedius* (now both *Labeobarbus* species), but more specimens are needed to confirm this (Banister, 1973). Golubtsov *et al.* (2002) confirmed the identification of *L. microterolepis* as a hybrid between

*L. ethiopicus* and *L. intermedius*, although no evidence whatsoever was provided to support this view.

### ANNOTATED CHECKLIST 3. ANNOTATED CHECKLIST FOR *ACAPOETA* AND *SANAGIA*

*tanganicae*, *Capoeta* Boulenger, 1900. North end of Lake Tanganyika. Lectotype: BMNH 1906.9.6.9 (designated by Banister, 1976a). Paralectotypes: BMNH 1906.9.6.10 (1), 1906.9.6.11 (1, skeleton). Current status: valid as *Acapoeta tanganicae* (placed in the new subgenus *Acapoeta* by Cockerell, 1910, raised to genus level by Fowler, 1976). Synonyms: none. Distribution: endemic to Lake Tanganyika (Lévêque & Daget, 1984), both in the lake and the affluent rivers (Poll, 1953; Banister, 1976a). Notes: (1) skeleton type given in the BMNH online collection needs verification. Although the original description by Boulenger (1900a) does not mention the number of specimens, Boulenger (1901b) mentions three specimens from ‘the northern end of Lake Tanganyika’, further specified in Boulenger (1909) as two types and one skeleton. It remains unclear from Boulenger (1909) if the latter specimen is a type, but a similar listing of the syntypes of *Barbus rocadasi* in Boulenger (1916a) also lacks ‘type’ for a syntype of this species denoted specifically as a skeleton; (2) type species of the monospecific genus *Acapoeta* Cockerell, 1910; (3) the placement of this species in the subgenus *Acapoeta* by Cockerell (1910) is not followed by subsequent authors (e.g. Boulenger, 1920c; Poll, 1953; Banister, 1976a), who treat it as a *Varicorhinus*, until it was raised to the genus level of *Acapoeta* by Fowler (1976); the few publications after Fowler (1976) that mention the species (e.g. Lévêque & Daget, 1984; Poll & Gosse, 1995) use *Acapoeta* as a valid genus.

*velifera*, *Sanagia* Holly, 1926. Nachtigal ( $\pm 4^{\circ}21'N$ ,  $11^{\circ}38'E$ , USBGN, 1962b) (rapids), Sanaga River, Cameroon. Syntypes: NMW 7261–7262 (2). Current status: valid as *Sanagia velifera* (no generic reallocations). Synonyms: none. Distribution: Sanaga and Nyong River basins in Cameroon (De Weirtdt, 2007). Notes: (1) the two syntypes that were reported as ‘apparently lost’ by Lévêque & Daget (1984) have been found back in the NMW (H. Wellendorf, pers. comm., 2014); (2) MNHN 1978-0721 and MRAC 174990–97 (8), mentioned as possible types in Eschmeyer (2015), are not types; (3) type species of the monospecific genus *Sanagia* Holly, 1926.

### APPENDIX

#### LIST OF (TYPE) SPECIMENS EXAMINED

#### AFRICAN *LABEOBARBUS S.L.* SPECIES: LIST OF EXAMINED (TYPE) SPECIMENS

*acuticeps*, *Barbus* Matthes, 1959. Holotype: MRAC 130313. Paratypes: MRAC 130310 (1), 130311–

312 (2), 130314 (1). – *acutirostris*, *Barbus brunelli* Bini, 1940. Neotype: RMNH 32870 (\*). – *aeneus*, *Cyprinus* Burchell, 1822. No types known. Synonyms: *Barbus gilchristi* Boulenger, 1911. Holotype: BMNH 1909.12.8.1; *Barbus mentalis* Gilchrist & Thompson, 1913. Holotype: SAIAB 134770 (ex SAM 9644). – *altianalis*, *Barbus* Boulenger, 1900. Lectotype: BMNH 1906.9.6.13. Paralectotypes: BMNH 1906.9.6.14 (1), 1906.9.6.15 (1). Synonyms: *Barbus eduardianus* Boulenger, 1901. Holotype: BMNH 1906.9.7.41; *Barbus fergusonii* Boulenger, 1901. Syntypes: BMNH 1906.9.7.42–43 (2); *Barbus kiogae* Worthington, 1929. Syntypes: BMNH 1929.1.24.105–108 (7 instead of 4); *Barbus lobogenys* Boulenger, 1906. Syntypes: 1906.5.30.117–121 (2 instead of 5). – *altipinnis*, *Varicorhinus* Banister & Poll, 1973. Holotype: MRAC 179729. Paratypes: BMNH 1972.10.2.1 (1), MRAC 179730 (1), 179731 (1), 179732–733 (2), 179734 (1), 179735 (1), IRSNB 643 (1). – *ansorgii*, *Varicorhinus* Boulenger, 1906. Holotype: BMNH 1904.5.2.161. – *aspius*, *Barbus* Boulenger, 1912. Syntypes: BMNH 1912.4.1.354 (1), MRAC 1536 (1). – *axelrodi*, *Varicorhinus* Getahun, Stiassny & Teugels, 2004. Holotype: MRAC 91-68-P-1132. Paratypes (partim): MRAC 90-057-P-1297-1300 (4), 90-057-P-1314-1327 (14), 99-55-P-246-247 (2), 99-55-P-249 (1), 99-90-P-459-461 (3). – *batesii*, *Barbus* Boulenger, 1903. Holotype: BMNH 1902.11.12.128. – *beso*, *Varicorhinus* Rüppell, 1835. Neotype: BMNH 1902.12.13.365. Specimens: BMNH 1968.7.24.18. – *boulengeri*, *Labeobarbus* (present paper). Lectotype: BMNH 1911.6.1.6. Paralectotypes (partim): BMNH 1911.6.1.7–10 (4), NMW 48865 (1), ZMB 18211 (1). – *brauni*, *Varicorhinus* Pellegrin, 1935. Syntypes: MNHN 1935-0066 (1), MRAC 42933 (1). – *brevicephalus*, *Barbus* Nagelkerke & Sibbing, 1997. Holotype: RMNH 32880 (\*). – *brevispinis*, *Barbus ruspolii* Holly, 1927. Syntypes: NMW 7315 (1), 7316 (1). – *bynni*, *Barbus* Forsskål, 1775. Neotype: BMNH 1907.12.2.1230. Synonyms: *Barbus meneliki* Pellegrin, 1905. Holotype: MNHN 1905-0275; *Barbus occidentalis* Boulenger, 1911. Holotype: BMNH 1909.3.3.14; *Barbus seguensis* Pellegrin, 1925. Holotype: MNHN 1925-0193. – *cardozoi*, *Barbus* Boulenger, 1912. Syntypes (partim): BMNH 1912.4.1.343–348 (6), 1912.4.1.349–352 (4), 1912.4.1.353 (1), MRAC 1528-29 (2), 1530-32 (3), ZMB 18810 (6). – *caudovittatus*, *Barbus* Boulenger, 1902. Syntypes: BMNH 1901.12.26.26 (1), MRAC 1168 (1). Synonyms: *Barbus euchilus* Boulenger, 1920. Holotype: BMNH 1919.7.24.7; *Barbus miochilus* Boulenger, 1920. Syntypes: BMNH 1919.7.24.8-9 (2), MRAC 6992 (1); *Varicorhinus stappersii* Boulenger, 1917. Syntypes: BMNH 1920.5.25.36-37 (2), MRAC 14197 (1), 14222 (2 instead of 1). – *clarkeae*, *Varicorhinus* Banister, 1984. Holotype: MRAC 164456. Paratype: MRAC 164457 (1). – *claudinae*, *Barbus* De Vos & Thys van den Audenaerde, 1990. Holotype: MRAC 86-01-P-501. Paratypes: MRAC 91755-756 (2), 92214 (1), 130310 (1),



- 85-44-P-141-144 (4), 85-44-P-269 (1), 85-44-P-281-289 (9), 86-01-P-502-508 (7), 86-09-P-444-451 (8), 87-11-P-1366-372 (7), 87-11-P-1373-384 (12). – *codringtonii*, *Barbus* Boulenger, 1908. Holotype: BMNH 1908.11.6.23. Synonyms: *Barbus altidorsalis* Boulenger, 1908. Holotype: BMNH 1908.11.6.26; *Barbus chilotes* Boulenger, 1908. Syntypes: BMNH 1908.11.6.24–25 (2). – *compiniei*, *Barynotus* Sauvage, 1879. Holotype: MNHN A-2845 (stuffed). Synonym: *Barbus labiatomimus* Pellegrin, 1914. Holotype: MNHN 1886-0395. – *crassibarbis*, *Barbus* Nagelkerke & Sibbing, 1997. Holotype: RMNH 32890 (\*). – *dainellii*, *Barbus* Bini, 1940. Neotype: RMNH 32900 (\*). – *dartevellei*, *Barbus* Poll, 1945. Holotype: MRAC 47781. – *dimidiatus*, *Varicorhinus* Tweddle & Skelton, 1998. Holotype: SAIAB 53080. Paratypes: SAIAB 53079 (15), SAIAB 53083 (21). – *ensifer*, *Varicorhinus* Boulenger, 1910. Syntypes: BMNH 1910.11.28.134–143 (10), NMW 48864 (10), ZMB 18213 (8). – *ensis*, *Barbus* Boulenger, 1910. Syntypes (partim): BMNH 1911.6.1.11–18 (8), NMW 54083 (4), ZMB 18217 (4). – *ethiopicus*, *Barbus* Zolezzi, 1939. Holotype: Not seen. Specimens: BMNH 1971.7.12.1–3 (3). – *fasolt*, *Barbus* Pappenheim, 1914. Holotype: ZMB 19061. – *fimbriatus*, *Varicorhinus sandersi* Holly, 1926. Syntypes (partim): NMW 7224–7226 (3). – *fritschii*, *Barbus* Günther, 1874. Syntypes: BMNH 1874.1.30.27–31 (5). Synonyms: *Capoeta atlantica* Boulenger, 1902. Syntypes: BMNH 1902.1.4.18–19 (2); *Barbus paytonii* Boulenger, 1911. Syntypes: BMNH 1903.10.29.17–20 (7 instead of 4); *Barbus riegenbachi* Günther, 1902. Syntypes: BMNH 1902.7.28.19 (1), 1902.7.28.20–21 (2); *Barbus rothschildi* Günther, 1901. Syntypes: BMNH 1901.4.26.6–7 (2); *Capoeta waldoii* Boulenger, 1902. Syntypes: BMNH 1902.1.4.16–17 (2). – *gananensis*, *Barbus* Vinciguerra, 1895. Holotype: MSNG 17525 (\*). Paratypes: MSNG 17331 (4) (\*). – *gestetneri*, *Barbus* Banister & Bailey, 1979. Holotype: BMNH 1976.10.12.98. Paratypes: BMNH 1976.10.12.86–97 (12). – *girardi*, *Barbus* Boulenger, 1910. Syntypes (partim): BMNH 1911.6.1.31–36 (6), NMW-54137 (1), ZMB 18215 (1). – *gorgorensis*, *Barbus intermedius* Bini, 1940. Neotype: RMNH 32910 (\*). – *gorguarii*, *Barbus* Rüppell, 1835. Holotype: SMF 2586 (stuffed) (\*). – *gruveli*, *Barbus* Pellegrin, 1911. Holotype: MNHN 1911-0040 (\*). – *gulielmi*, *Barbus* Boulenger, 1910. Syntypes (partim): BMNH 1911.6.1.29–30 (2). – *habereri*, *Barbus* Steindachner, 1912. Holotype: NMW 7274. – *harterti*, *Barbus* Günther, 1901. Syntypes BMNH 1901.7.26.4–5 (2). – *huloti*, *Barbus* Banister, 1976. Holotype: IRSNB 558. Paratypes: BMNH 1975.4.30.1 (1), IRSNB 563 (10). – *humphri*, *Barbus* Banister, 1976. Holotype: IRSNB 559. Paratypes: BMNH 1975.4.30.2 (1), IRSNB 564 (10). – *intermedius*, *Barbus* Rüppell, 1835. Holotype: SMF 6778 (stuffed) (\*). Synonyms: *Capoeta bingeri* Pellegrin, 1905. Holotype: MNHN 1905-0252; *Barbus gudaricus* Boulenger, 1906. Syntypes: BMNH 1908.1.20.131–132 (6 instead of 2), 1908.1.20.133 (1); *Barbus leptosoma* Boulenger, 1902. Syntypes: BMNH 1902.12.13.300–302 (3); *Barbus macmillani* Boulenger, 1906. Syntypes: BMNH 1908.1.20.103–106 (4), 1937.4.20.68 (1) [a subsequently catalogued syntype (J Maclaine, pers. comm., 2015)]; *Barbus plagiostomus* Boulenger, 1902. Syntypes: BMNH 1902.12.13.271–272 (2), BMNH 1902.12.13.273 (1). – *iphthimostoma*, *Varicorhinus* Banister & Poll, 1973. Holotype: MRAC 179736. Paratypes: BMNH 1972.10.2.2 (1), IRSNB 644 (1), MRAC 179737 (1). – *iturii*, *Barbus* Holly, 1929. Holotype: NMW (lost). – *jaegeri*, *Varicorhinus* Holly, 1930. Holotype: NMW 13957. – *johnstonii*, *Barbus* Boulenger, 1907. Holotype: BMNH 1897.6.9.280. Synonyms: *Barbus globiceps* Worthington, 1933. Syntypes: BMNH 1932.11.15.275–282 (8); *Barbus njassae* Keilhack, 1908. Syntypes: ZMB 18163 (1); 18164 (1); *Varicorhinus niasensis* Worthington, 1933. Syntypes: BMNH 1932.11.15.387–392 (6), 1932.11.15.393–395 (3). – *jubae*, *Varicorhinus* Banister, 1984. Holotype: BMNH 1976.7.1.13. Paratypes: BMNH 1976.7.1.14–15 (2). – *jubbi*, *Barbus* Poll, 1967. Holotype: Not seen. Paratypes (partim): MRAC 161065 (ex MD 2299) (1), 161066 (ex MD 6363) (1). – *kimberleyensis*, *Barbus* Gilchrist & Thompson, 1913. Holotype: SAIAB 134771 (ex SAM 9645). – *lagensis*, *Barynotus* Günther, 1868. Holotype: BMNH 1866.3.8.12. – *latirostris*, *Barbus intermedius* Keilhack, 1908. Lectotype: ZMB 18174. Paralectotype: ZMB 34766. *leleupanus*, *Varicorhinus* Matthes, 1959. Holotype: MRAC 92213. Paratypes: MRAC 92211 (1), 92212 (1), 130532–33 (2). – *longidorsalis*, *Varicorhinus* Pellegrin, 1935. Holotype: MNHN 1935-0065. – *longifilis*, *Barbus altianalis* Pellegrin, 1935. Lectotype: MNHN 1935-0150. Paralectotypes: 1935-0145 (1), 1935-0146 (1), 1935-0147 (1), 1935-0148 (1), 1935-0149 (1), 1935-0151 (1), 1935-0152 (1). – *longissimus*, *Barbus* Nagelkerke & Sibbing, 1997. Holotype: RMNH 32930 (\*). – *lucius*, *Barbus* Boulenger, 1910. Syntypes: BMNH 1911.6.1.42–43 (2), NMW 54246 (1). – *lufupensis*, *Varicorhinus* Banister & Bailey, 1979. Holotype: BMNH 1975.9.5.1. Paratype: BMNH 1975.9.5.2 (1). – *macroceps*, *Barbus* Fowler, 1936. Holotype: ANSP 65759 (\*). – *macrolepidotus*, *Varicorhinus* Pellegrin, 1928. Syntypes: MNHN 1928-0011 (1), MRAC 19945 (1), 138767 (1; ex MNHN 1928-0012), NMB 3983 (1), 3985 (1), 3988 (1), 3989 (1). – *macrolepis*, *Barbus* Pfeffer, 1889. Lectotype: ZMH H330 (ex 68 79). Paralectotypes: BMNH 1909.2.25.8 (ex ZMH)(1), ZMB 31672 (ex ZMH)(2), ZMH H331 (ex 68 79)(2), H332 (ex 380/7467)(4), H333 (ex 69 19)(1), H474 (ex 69 03)(1). – *macrophthalmus*, *Barbus gorguarii* Bini, 1940. Neotype: RMNH 32940 (\*). – *malacanthus*, *Barbus* Pappenheim, 1911. Holotype: ZMB 18392. – *marequensis*, *Barbus* (*Cheilobarbus*) Smith, 1841. Holotype: BMNH 1845.7.3.95 (stuffed). Synonyms: *Barbus brucii* Boulenger, 1907. Holotype: BMNH 1907.3.15.34; *Varicorhinus nasutus* Gilchrist & Thompson, 1911. Holotype: SAIAB 134736 (ex SAM

- 8801); *Barbus oliphanti* Keilhack, 1910. Holotype: BMNH 1907.3.15.37; *Barbus sector* Boulenger, 1907. Holotype: BMNH 1907.3.15.35; *Barbus zambezensis* Peters, 1852. Syntypes: NMW 49730 (1); ZMB 3246 (2), 4744 (7). – *mariae*, *Varicorhinus* Holly, 1926. Syntypes: NMW-7221 (1), 7222–7223 (2). – *maroccana*, *Pterocapoëta* Günther, 1902. Syntypes: BMNH 1902.7.28.37–38 (2), 1902.7.28.39 (1). – *matris*, *Barbus* Holly, 1928. Holotype: NMW 8000. – *mawambi*, *Barbus* Pappenheim, 1914. Holotype: ZMB 19062. – *mawambiensis*, *Barbus hindii* Steindachner, 1911. Syntypes: NMW 54177 (2), 54286 (3), 54287 (2), 54288 (2). – *mbami*, *Barbus perplexicans* Holly, 1927. Holotype: NMW 7528. – *megastoma*, *Barbus* Nagelkerke & Sibbing, 1997. Holotype: RMNH 32950 (\*). – *micronema*, *Barbus* Boulenger, 1904. Syntypes: BMNH 1904.2.29.37–38 (2). – *mirabilis*, *Barbus* Pappenheim, 1914. Holotype: ZMB 19059. – *mungoensis*, *Barbus* Trewavas, 1974. Holotype: BMNH 1973.5.14.163. Paratypes: BMNH 1973.5.14.164–182 (19). – *nanningsi*, *Labeobarbus* de Beaufort, 1933. Holotype: ZMA 113010. – *natalensis*, *Barbus* de Castelnau, 1861. Syntypes: lost. Synonyms: *Barbus bowkeri* Boulenger, 1902. Syntypes: BMNH 1862.8.28.3–7 (5), 1874.3.5.1–2 (2), 1894.7.10.4 (1) [Note: BMNH 1862.8.28.3–7 non-conspecific syntypes of *Enteromius gurneyi* (Günther, 1868)]; *Barbus loboehilus* Boulenger, 1911. Holotype: BMNH 1908.12.28.96; *Barbus mfongosi* Gilchrist & Thompson, 1913. Holotype: SAIAB 135057 (ex SAM 11392); *Barbus robinsoni* Gilchrist & Thompson, 1913. Holotype: SAIAB 135055 (ex SAM 11371); *Barbus zuluensis* Gilchrist & Thompson, 1913. Holotype: SAIAB 134939 (ex SAM 10745). – *nedgia*, *Labeobarbus* Rüppell, 1835. Holotype: SMF 2619 (stuffed) (\*). – *nelspruitensis*, *Varicorhinus* Gilchrist & Thompson, 1911. Syntypes: SAIAB 134824 (ex SAM MB-F010518)(1), 135756 (ex SAM MB-F021698)(1). – *nthuwa*, *Labeobarbus* Tweddle & Skelton, 2008. Holotype: SAIAB 39341. Paratypes: SAIAB 39293 (1), 40787 (6), 51928 (2), 79494 (2). – *osseensis*, *Barbus* Nagelkerke & Sibbing, 2000. Holotype: RMNH 33721 (\*). – *oxyrhynchus*, *Barbus* Pfeffer, 1889. Lectotype: ZMH H339 (ex 69 07). Paralectotypes: ZMH H340 (ex 69 07)(7). Synonyms: *Barbus babaulti* Pellegrin, 1926. Holotype: MNHN 1926-0285; *Barbus hindii* Boulenger, 1902. Syntypes (partim): BMNH 1902.5.26.25–28 (4); *Barbus (Labeobarbus) labiatus* Boulenger, 1902. Holotype: BMNH 1902.5.26.37; *Barbus perplexicans* Boulenger, 1902. Syntypes: 1902.5.26.35–35 (2); *Barbus tanensis* Günther, 1894. Syntypes (partim): BMNH 1893.12.2.24–29 (6), 1893.12.2.32–34 (3), BMNH 1893.12.2.37–39 (3). – *pagenstecheri*, *Barbus* Fischer, 1884. Lectotype: ZMH H341 (ex ZMH 3851). Paralectotypes: ZMH H342 (ex ZMH 3850)(1). – *parawaldroni*, *Barbus* Lévêque, Thys van den Audenaerde & Traore, 1987. Holotype: MRAC 73-10-P-2296. Paratypes: MRAC 73-10-P-2297 (1), 73-10-P-2298–2299 (2), 73-5-P-1936 (1). – *paucisquamata*, *Barbus altianalis* Pellegrin, 1935. Lectotype: MNHN 1935-0076. Paralectotypes: MNHN 1935-0077 (1), 1935-0078 (1), MRAC 42932 (1). Synonyms: *Barbus altianalis lobogenysoides* Pellegrin, 1935. Holotype: MNHN 1935-0154. – *pellegrini*, *Varicorhinus* Bertin & Estève, 1948. Holotype: MNHN 1932-0181. – *petitjeani*, *Barbus* Daget, 1962. Syntypes: MNHN 1959-0108 (3). – *platydorsus*, *Barbus* Nagelkerke & Sibbing, 1997. Holotype: RMNH 32970 (\*). – *platyrhinus*, *Barbus* Boulenger, 1900. Holotype: BMNH 1906.9.6.12. – *platystomus*, *Varicorhinus* Pappenheim, 1914. Syntypes: ZMB 19051 (1), ZMB 34769 (1). – *pojeri*, *Barbus* Poll, 1944. Holotype: IRSNB 71. Paratype: IRSNB 599 (1). – *polylepis*, *Barbus* Boulenger, 1907. Holotype: BMNH 1907.3.15.33. – *progenys*, *Barbus* Boulenger, 1903. Holotype: BMNH 1902.11.12.127. – *pungweensis*, *Varicorhinus* Jubb, 1959. Holotype: SAIAB 120014 (ex AMG 850). Paratypes: SAIAB 120015 (ex AMG 851)(1), 120016 (ex AMG 852)(1), 120017 (ex AMG 853)(1), 120018 (ex AMG 854)(1). – *reinii*, *Barbus* Günther, 1874. Syntypes (partim): BMNH 1874.1.30.22–24 (3). – *rhinoceros*, *Barbus* Copley, 1938. Types?: BMNH 1936.12.22.35–39. Synonyms: *Barbus mariae* Holly, 1929. Lectotype: NMW 96552 (ex 6562)(designated by Banister, 1973). Paralectotypes: NMW 96553 (ex 6562)(1). – *rhinophorus*, *Barbus* Boulenger, 1910. Syntypes: BMNH 1911.6.1.37–38 (2). – *robertsi*, *Varicorhinus* Banister, 1984. Holotype: BMNH 1983.3.30.20. Paratypes: BMNH 1983.3.30.21–38 (18). – *rocadasi*, *Barbus* Boulenger, 1910. Syntypes (partim): BMNH 1911.6.1.19–20 (2), 1911.6.1.21–25 (6 instead of 5), 1911.6.1.27–28 (2), NMW 13347–13352 (6), ZMB 18214 (6). – *rosae*, *Barbus* Boulenger, 1910. Syntypes: BMNH 1911.6.1.39–41 (3), NMW 54500 (1), ZMB 18216 (1). – *roylii*, *Barbus* Boulenger, 1912. Syntypes (partim): BMNH 1912.4.1.338–340 (3), 1912.4.1.341–342 (2), MRAC 1533 (1), 1534 (1), 1535 (1), NMW 54501 (1), ZMB 18809 (1). – *ruandae*, *Varicorhinus* Pappenheim, 1914. Holotype: ZMB 19050. – *ruasae*, *Barbus* Pappenheim, 1914. Lectotype: ZMB 19053. Paralectotype: ZMB 22652 (1). – *ruwenzorii*, *Capoëta (Pterocapoëta)* Pellegrin, 1909. Syntypes: MNHN 1909-0583 (1), 1909-0584 (1), 1909-0585 (1). – *sacratus*, *Barbus* Daget, 1963. Syntypes: MNHN 1959-0119 (4), 1959-0139 (1). – *sandersi*, *Varicorhinus* Boulenger, 1912. Lectotype: BMNH 1912.4.1.333. Paralectotypes: BMNH 1912.4.1.334–336 (2 instead of 3), 1912.4.1.337 (1), MRAC 1525 (1), 1526 (1), 1527 (1), ZMB 18808 (1). – *seeberi*, *Barbus* Gilchrist & Thompson, 1913. Syntypes: BMNH 1936.8.4.6 (1), SAIAB 134867 (ex SAM 10672)(2). Specimens: SAIAB 54133 (1), 54688 (1), 58362 (1), 58418 (1), 65536 (6). – *semireticulatus*, *Varicorhinus* Pellegrin, 1924. Syntypes: MNHN 1924-0052 (2). – *somereni*, *Barbus* Boulenger, 1911. Holotype: BMNH 1911.7.26.1. – *stappersii*, *Barbus* Boulenger, 1915. Holotype: MRAC 14250. Synonyms: *Barbus curtus* Boulenger, 1915.

Holotype: MRAC 14172; *Barbus moeruensis* Pellegrin, 1922. Holotype: MRAC 14765; *Barbus oxycephalus* Boulenger, 1915. Holotype: MRAC 14233 (Note: not MRAC 14113 as in Lévêque & Daget, 1984; Eschmeyer, 2015). – *steindachneri*, *Varicorhinus* Boulenger, 1910. Syntypes (partim): BMNH 1910.11.28.147–155 (9), 1911.6.1.1–5 (5), NMW 48867 (3), ZMB 18212 (3). – *stenostoma*, *Varicorhinus* Boulenger, 1910. Holotype: BMNH 1910.11.28.145. – *surkis*, *Barbus* Rüppell, 1835. Neotype: RMNH 32980 (\*). – *tornieri*, *Varicorhinus* Steindachner, 1906. Holotype: NMW 46053. – *trachypterus*, *Barbus* Boulenger, 1915. Holotype: MRAC 11830. Synonym: *Varicorhinus bredoi* Poll, 1948. Holotype: IRSNB 76. Paratypes: IRSNB 77 (2). – *tropidolepis*, *Barbus* Boulenger, 1900. Lectotype: BMNH 1906.9.6.19. Paralectotypes: BMNH 1906.9.6.20–21, MRAC 327 (1), 328 (1), 329 (1). Synonym: *Varicorhinus chapini* Nichols & La Monte, 1950. Holotype: AMNH 18785. – *truttiformis*, *Barbus* Nagelkerke & Sibbing, 1997. Holotype: RMNH 32990 (\*). – *tsanensis*, *Barbus* Nagelkerke & Sibbing, 1997. Holotype: RMNH 33000 (\*). – *upembensis*, *Varicorhinus* Banister & Bailey, 1979. Holotype: BMNH 1975.9.5.5. Paratypes: BMNH 1975.9.5.6–12 (7), 1975.9.5.13–17 (5). – *urotaenia*, *Barbus* Boulenger, 1913. Syntypes: BMNH 1912.12.6.5 (1), MRAC 1791 (1), 1792 (2). – *varicostoma*, *Varicorhinus* Boulenger, 1910. Holotype: BMNH 1910.11.28.146. – *versluysii*, *Barbus* Holly, 1929. Syntypes: NMW 13954–13956 (3). – *werneri*, *Varicorhinus* Holly, 1929. Syntypes: NMW 13948 (1). – *wittei*, *Varicorhinus* Banister & Poll, 1973. Holotype: MRAC 179738. Paratypes: BMNH 1972.10.2.3 (1), MRAC 179739–741 (3), 179742 (1), IRSNB 645 (1). – *wurtzi*, *Barbus* Pellegrin, 1908. Holotype: MNHN 1908-0097. Specimens cf. *wurtzi* [undescribed species (see text)]: MRAC 1986-13-P-114; MNHN 1959-0153 (2) (smallest of both: 127.5 mm

SL), MNHN 1987-0689 (3), 1988-1955(3) (both largest specimens: 172.5 and 175.6 mm SL), 1991-0519. – *xyrocheilus*, *Varicorhinus* Tweddle & Skelton, 1998. Holotype: SAIAB 53082. Paratypes: SAIAB 34336 (11).

AFRICAN NOMINAL *LABEOBARBUS* S.L. SPECIES  
IDENTIFIED AS HYBRID PHENOTYPES: LIST OF  
EXAMINED SPECIMENS

*alluaudi*, *Barbus* Pellegrin, 1909. Syntypes: MNHN 1909-0586 (1), 1909-0587 (1). – *microbarbis*, *Barbus* David & Poll, 1937. Holotype: MRAC 41847. Paratypes: MRAC 41848–49 (2). – *microterolepis*, *Barbus* Boulenger, 1902. Holotype: BMNH 1902.12.13.220.

ACAPOETA AND SANAGIA:  
LIST OF EXAMINED SPECIMENS

*tanganicae*, *Capoeta* Boulenger, 1900. Lectotype: BMNH 1906.9.6.9. Paralectotype: BMNH 1906.9.6.10 (1). – *velifera*, *Sanagia* Holly, 1926. Syntypes: NMW 7261–7262 (2).

NON-*LABEOBARBUS* S.L. SPECIES:  
LIST OF EXAMINED SPECIMENS

*capensis*, *Barbus* Smith, 1841. Not a *Labeobarbus* species (E. Vreven, E.R. Swartz & P.H. Skelton, unpubl. data). Holotype: BMNH 1845.7.3.99 (stuffed). – *capoetoides*, *Varicorhinus* Pellegrin, 1938. Not a *Labeobarbus* species (see present paper). Holotype: MNHN 1938-0030. – *litamba*, *Barbus* Keilhack, 1908. Not a *Labeobarbus* species (see present paper). Holotype (unique): ZMB 18162.