Disentangling the taxonomy of the Mahseers (*Tor* spp.) of Malaysia: An integrated approach using morphology, genetics and historical records.

S.E. Walton • H.M. Gan • R. Raghavan • A.C. Pinder • A. Ahmad

S.E. Walton (Corresponding author)
Kenyir Research Institute, Universiti Malaysia Terengganu, Kuala Terengganu, Malaysia
Email: sam.walton@umt.edu.my, Phone: +60(0)194771066

H.M. Gan
School of Science, Monash University Malaysia, Petaling Jaya, Selangor, Malaysia
&
Genomics Facility, Tropical Medicine and Biology Multidisciplinary Platform, Monash University Malaysia, Petaling Jaya, Selangor, Malaysia

R. Raghavan
Department of Fisheries Resource Management Kerala University of Fisheries and Ocean Studies (KUFOS) Kochi, India

A.C. Pinder
Faculty of Science and Technology, Bournemouth University, Fern Barrow, Poole, Dorset, UK

R. Raghavan • A.C. Pinder
Mahseer Trust, The Freshwater Biological Laboratory, East Stoke River Laboratory, Wareham, Dorset, UK

A. Ahmad
School of Marine and Environmental Sciences, Universiti Malaysia Terengganu, Kuala Terengganu, Malaysia

Abstract

The establishment of appropriate taxonomic designations is essential for the effective management of fishery resources. Despite over a century of exploration and research, the cyprinid genus *Tor* represents a group of large bodied freshwater fishes whose taxonomy and systematics remains poorly known. While five species of *Tor* are currently listed as 'Endangered' on the IUCN Red List, a further 5 out 19 species currently recognized are assessed as 'Data Deficient', with an additional species, yet to be afforded formal scientific description believed to be on the brink of extinction (i.e. the Humpback Mahseer of the Cauvery River in India). *Tor* mahseers represent a suitable model for the application of an integrated approach using morphology, genetics and historical records to resolve species identities, where one or more of these fundamental approaches may have been deficient in the past. We focus specifically on the taxonomy and nomenclature of the *Tor* species recorded from peninsular Malaysia with an aim to define the identity of two nominal species, *T. tambra*, and *T. tambroides.* Original descriptions of these two nominal species contain little or practically no characters to distinguish them, and partly explains why secondary literature, fails to conclusively determine species boundaries. A phylogenetic analysis of mahseer specimens from this region, based on publicly available and newly sequenced mitochondrial *COX1* genes does not support species designation based on previously established morphological features. More importantly, multiple tree-based species delimination approaches showed that previously sequenced *Tor tambroides* from peninsular Malaysia and the newly described *Tor* spp. from Vietnam could not be delimited from the topotypic *Tor tambra*. A wider investigation of Mahseer taxonomy covering all of South East Asia, using such an integrated approach is recommended to resolve the taxonomy of Mahseer in the region and is of profound importance for the conservation and management of exploited and farmed populations of these highly valued and iconic fish.

Introduction

Freshwater fishes commonly known as 'mahseer' (Cypriniformes: Cyprinidae) belong to five genera, *Folifer, Naziritor, Neolissochilus*, *Parator* and *Tor* (Kottelat, 2013; Froese and Pauly, 2015; Eschmeyer, 2015); though fishes of the genus *Tor* are widely recognized as being the 'true mahseer' (Nguyen et al., 2008). These fishes are widely distributed throughout Asia in the rivers of Afghanistan, Pakistan, India, Sri Lanka, Nepal, Bhutan, Myanmar, Thailand, China, Laos, Cambodia, Vietnam, Indonesia and Malaysia (Ng, 2004; Nguyen et al., 2008; see ESM 1). They are popular icons of economic and recreational interest in many of these countries and are generally of conservation concern due to anthropogenic threats including degradation, fragmentation and loss of habitats, and overfishing (Raghavan et al., 2011; Pinder and Raghavan, 2013; Pinder et al., 2015; Pinder et al., in press). Despite their socio-economic importance and conservation-concern, mahseer comprise a poorly known and documented group of riverine fish with severe knowledge gaps regarding aspects of their taxonomy, population and biology (see Pinder and Raghavan 2013; Pinder et al. 2015).

Diversity of mahseers is highest in the South-East Asian region, especially in the Indo-Burma and the Sundaland biodiversity hotspots. Ten valid species of *Tor* viz, *T. ater, T. dongnaiensis, T. hemispinus, T. laterivittatus, T. mekongensis, T. polylepis, T. sinensis, T. tambra, T. tambroides* and *T. yingjiangensis* are reported to occur in this region (Kottelat, 2013; Hoàng et al., 2015) of which five are assessed as "Data Deficient" on the IUCN Red List of Threatened Species™ (IUCN, 2015). The confusing and contrasting evidence on species boundaries presented by different authors, and exacerbated by the absence of voucher specimens for most records continues to constrain the validity and value of any biological and demographic studies carried out on these fishes (Online Resource 1). As a group, mahseer also exhibit considerable morphological variation related to speciation, phenotypic plasticity, trophic polymorphism and sexual dimorphism, but the degree to which each of these processes contributes to the observed diversity of morphologies is yet to be defined

2. Mahseer (*Tor* spp) of peninsular Malaysia (PM)

Tor species represent the region's most important group of freshwater fishes in terms of culture and livelihoods, but also the least understood from a scientific viewpoint. Five species names, viz., *douronensis, soro, soroides, tambra* and *tambroides* have been continuously referred to in the literature dealing with mahseers of PM (e.g. Mohsin and Ambak, 1983; Ambak et al., 2012; Ng, 2004; Bishop, 1973; Kottelat, 2013) of which '*soroides*' and '*soro*' have already been assigned to the genus *Neolissochilus* (see Khaironizam et al., 2015).

Current knowledge (sensu Kottelat, 2013) indicates the presence of only two species of *Tor* in PM, one with a short median lobe (fleshy projection on the lower jaw), rounded snout and thin lips, currently classified as *T. tambra* and one with a long median lobe, pointed snout and thick lips currently classified as *T. tambroides.* Another nominal species, *T. dourenensis* has been reported in East Malaysia (Malaysian Borneo) (Kottelat, 2013). The range of *T. tambra* and *T. tambroides* is reported to extend throughout Southeast Asia (Java, Sumatra, Malaysia, Thailand, Cambodia, Laos, Myanmar and Vietnam) and so the validity of the nomenclature of these species in PM is of wider spatial relevance throughout the region. As the designation of these fish as separate species is still up for debate, hereafter we refer to them as two "morphotypes"; long lobe and short lobe.

3. The identity of mahseers in Peninsular Malaysia (PM) and the uncertainty in literature

The original descriptions of *T. Tambra*, *T. tambroides* and *T. douronensis* were based on specimens collected from Indonesia (Cuvier and Valenciennes, 1842; Bleeker, 1854; refer to ESM 2) (See Fig. 1). The type locality of *T. tambroides* is Sumatra: Padang, Paja kombo, Solok, Lake Maninjau /Java; and that of *T. tambra* and *T. douronensis* is Java: Bogor (see Kottelat, 2013). The proliferation of nominal names of *Tor* from Indonesia is attributed (by Roberts, 1993) to the work of Valenciennes (in Cuvier and Valenciennes, 1842), who described *T. tambra* and *T. douronensis*, and Bleeker (1854; 1863), who recognized all of Valenciennes' *Tor* species and added one more, *T. tambroides.* These names were subsequently recognized (without any detailed studies) and uncritically used in the literature pertaining to freshwater fishes of mainland S.E Asia, thus propagating un-reliable information over long periods of time. Further, the original descriptions of the three *Tor* species from Indonesia are vague and ambiguous, increasing the likelihood of misidentification (see Online Resource 2 for translation of the original descriptions).

#Figure 1 here#

Assuming that the distribution of the three nominal species of Indonesian *Tor* extends across the Sunda shelf, and that those populations have not been influenced by geographical isolation (as is currently assumed by most authors), the morphological and genetic evidence for the taxonomic distinction between the three species of *Tor* currently valid in Java/Sumatra needs to be firmly established before attempting to validate the nomenclature of the specimens throughout mainland SE Asia.

The data-poor nature of descriptions makes it difficult to find standard characters from which to distinguish differences in Indonesian *Tor* species, and this may be exacerbated by the mix of languages used in their description, and the subjective nature of translations. The description of *T. tambra* and *T. douronensis* by Valenciennes (in Cuvier and Valenciennes, 1842) provides some subtle morphological characters to distinguish the two species including the presence of pointed anal fins (*T. douronensis*) vs. rounded (*T. tambra*), however fails to provide further consistent comparisons to reliably distinguish between species. For instance, while the pelvic fins of *T. tambra* are reported to be small, no comparative description was provided for *T. douronensis*. Interestingly, there is no mention of the median lobe for any species in the descriptions by Valencinnes (in Cuvier and Valenciennes, 1842). Bleeker (1854) only mentions lobe size in *T. tambroides*, stating “the lower (lip) extending into a wide fleshy projecting lobe” but does not offer this statement in a comparative context with other fish. In his accompanying notes, he adds “it is variable with age” but does not imply that *T. tambroides* has a larger lobe than *T. tambra* which is currently used as a diagnostic feature (e.g. Mohsin and Ambak, 1983; Kottlelat, 2001; Hoàng et al., 2015). It is only in his later descriptions (Bleeker, 1863, Online Resource 2) that the lobes are mentioned and used in the key to distinguish the three species. Using the lobe to differentiate the various species of *Tor* therefore seems to be the invention of Bleeker (1863) and subsequently followed by others.

Despite the availability of several recent records of *T. tambroides, T. tambra* and *T. douronensis* (see Froese & Pauly, 2015), these are largely based on material from the Mekong and are unlikely to be the same as those from Indonesia. Accordingly no attempt has been made to draw conclusions on taxonomic validity from comparisons of these descriptions. Throughout the growing literature focused on mahseer, evidence to determine whether the topotypic specimens from Indonesia are genotypically and phenotypically similar to *Tor* species currently recognized in PM, remains unresolved. Indeed, many authors have failed to acknowledge the Indonesian origin of descriptions, often referring to *T. tambroides* as the “Malaysian” or “Thai” Mahseer, and thus overlooked the importance of acquiring Indonesian voucher specimens (e.g. Norfatimah et al., 2014; Esa and Rahim, 2013; Kunlapapuk and Kulabtong, 2011; Hoàng et al., 2015).

Whilst there is a large body of secondary literature on the morphology of recently collected specimens, reference to original descriptions/museum specimens and supporting genetic analysis is typically lacking. One exception is Roberts (1993) who carried out considerable work to compare the morphology of Malaysian specimens with type materials, but unfortunately little data was reported. After re-examining Indonesian specimens, including the holotype of *T. tambra* and *T. douronensis,* Roberts (1993) concluded that Java may only have one *Tor* species, i.e. *T. tambra* and that this is probably the case on the peninsula as well, explaining that differences in the length of the median lobe on the lower jaw were attributed to the state of preservation or to individual variation. However, he cautions that this review was hindered by a lack of fresh specimens of adult and juvenile *Tor* from Java (the type locality), and thus any information on their colouration. In addition, type material of *T. tambroides* was not thoroughly investigated as the vertebrae and gill raker counts were not obtained from the Bleeker material.

Upon examination of topotypic Javan *Tor* kept at the Musuem Zoological Bogoriense' Research Center for Biology, Bogor, Indonesia, there does appear to be observable differences in the morphology of *Tor* specimens (see Haryono and Tjakrawidjaja, 2006 and Fig. 2); however Roberts (1993; 1999) argues that differences in the body shape of Javan specimens represents intra species variation and is not adequate to differentiate these fish into separate species. Kottelat (2013) was "not able to see real differences in the descriptions of *T. douronensis* and *T. tambra* by either Valenciennes (in Cuvier and Valenciennes, 1842), or Bleeker (1854) and so tentatively followed the synonymy of the species suggested by Roberts (1993; 1999). We partially agree with this statement in that Valenciennes (in Cuvier and Valenciennes, 1842) does not present enough evidence in isolation, to differentiate the species, but the information subsequently provided by Bleeker (1854) and Weber and de Beaufort (1916) does demonstrate more substantial evidence for the practical differentiation between Javan *Tor* species (Online Resource 2).

#Figure 2 here#

4. The efficacy of mouth structure as a diagnostic taxonomic feature in mahseer species

An observed dichotomy in mouth structures in *Tor*; namely a short median lobe associated with relatively thin lips and blunt head shape, and long median lobe associated with thicker lips and more pointed head shape, has been widely observed in *T. tambra* (Roberts and Khaironizam, 2008), in *T. putitora* (Macdonald, 1948; Laskar et al., 2013) and *T. khudree* (A. Pinder per obs.). Although widely used to differentiate Southeast Asian species (e.g. Mohsin and Ambak, 1983; Kottlelat, 2001; Hoàng et al., 2015) these features are hypothesized to represent polymorphism, wherein two or more clearly different phenotypes exist in the same population of a species (in other words, the occurrence of more than one 'form' or 'morph') but this is yet to be conclusively verified both in *Tor* and its allied genus *Neolissochilus*. Roberts and Khaironizam (2008) and Khaironizam et al. (2015) hypothesize the variation in mouth structures in *Tor* results from trophic polymorphism i.e. feeding adaptation. This is largely based on observations of a seemingly polymorphic population of a species of *Neolissochilus* (*N. soroides*) in sungai Gombak, Selangor (Roberts and Khaironizam, 2008; Khaironizam et al., 2015) and not from a species of *Tor*.

The exact mechanism or purpose of the mouth structures displayed in mahseer fishes is still unclear. The function of the lobe in feeding has not been observed, but comparative studies of the diets of *N. sorodies* morphotypes with '*Tor*' like mouths and '*Lissochilus*' type mouths have demonstrated differences in stomach content composition suggesting efficiency of feeding on certain food items is increased by alternative mouth structures (Roberts and Khaironizam, 2008). However, the stomach content compositions of morphotypes with '*Tor*' like mouths and '*Neolissochilus*' type mouths (no lobe, thin lips) were similar, suggesting how the food items are obtained may be more important than what is obtained in explaining the evolutionary advantage of these structures. It must be noted no statistical test was carried out to support the comparisons in Roberts and Khaironizam (2008).

Trophic polymorphism can be genetically predetermined (genetic polymorphism) or ecophenotypic i.e. environmentally induced plasticity (polyphenism). Ecophenotypic changes in colouration have been suggested and anecdotally reported in Southeast Asian *Tor* held in captivity (Kottelat et al., 1993). Further Siraj et al. (2007) was unable to find a genetic basis for the colour variants of *Tor* in Malaysia, thus suggesting environmental factors (e.g. diet, water quality) may induce colour variation. Whilst Siraj et al. (2007) provided some evidence for ecophenotypic variation in coloration in Southeast Asian *Tor* there is currently no formal evidence to suggest that polymorphism of the lips and median lobe (the mouth structures that currently differentiate *Tor* species within Malaysia) within mahseers result from direct environmental influences (Roberts and Khaironizam, 2008). Additionally, Roberts and Khaironizam (2008) reported that four groups of juvenile *Tor*-like *N. soroides* morphotypes with different mouth structures kept under different environmental conditions for a period of 66 days showed no change in the structure of their mouthparts. The documented evidence for polyphenism is therefore deficient. However the duration of the previously tested study period may not be sufficient for such changes to be observed as phenotypic changes in wild Malaysian *Tor* kept in holding tanks for a period of >2 years have been observed (S. Walton pers. comm.). Fish from the River Tembat, Terengganu, were observed to lose their red colour, turning silver and the lobe and lips noticeably reduced in size whilst in captivity but evidence of the observed polymorphism being trophic in nature (i.e. associated with feeding) remains deficient.

The assumption of a genetically homogeneous population across S.E. Asia, a vital condition for the validity of trophic polymorphism as an explanation of the observed diversity in the genus *Tor* has up till now not been tested and no previous attempts have been made to investigate intraspecific genetic polymorphism as a mechanism for generating observed morphological differences. Whilst Esa et al. (2008) and Nguyen et al. (2006) found their "tambroides" morphotype material had a low genetic diversity based on mitochondrial genes, their samples excluded other morphotypes e.g. short lobe material. Therefore the low genetic diversity observed could just be a reflection of selective sampling and cannot be used as evidence of a monophyletic polymorphic population.

As a proxy for genetic information, Roberts and Khaironizam (2008) use morphometric and meristic data to illustrate the general similarities between suspected *Neolissochilus* morphotypes to demonstrate that the population is monophyletic, however this data was not assessed statistically. An ordination technique such as PCA or discriminant analysis of such data may detect groupings within these morphotypes, indicating speciation as opposed to polymorphism. Recently, Khaironizam et al. (2015) addressed this deficiency, where a PCA carried out on morphometric data from the Gombak population demonstrated no separation of clusters between morphotypes, suggesting a monophyletic population exhibiting polymorphism. However the authors cautioned this should be confirmed with genetic techniques.

Although morphotypes were reportedly sympatric in Roberts and Khaironizam (2008), in a study based purely on collected specimens (no controlled experimental observations of phenotypic changes under variable treatments) polymorphism can only be proven if the population is found to be panmictic (individuals exhibit random mating) however this has yet to been demonstrated in *Tor* and genetic isolation through sexual or habitat selection may occur in natural populations. Polymorphism in closely related progeny from conspecific parents has recently been observed in a captive population (Fig 3 a, b) suggesting random mating between morphologically similar individuals can result in morphologically heterogeneous offspring.

#Figure 3 here#

Following examination of *Tor* specimens exhibiting variable lobe sizes from across mainland S.E. Asia, Roberts (1999) concluded "No characters were found which would distinguish a species with thickened lips and a long mental lobe from one with more normal lips and a short lobe", and that these differences arise from individual variation or polymorphism. There is doubt as to whether observed morphs fall into two distinct groups (short lobe vs. long lobe) or whether morphological variation in the mouth structure displays continuous variation across a spectrum of morphologies. Indeed, specimens with intermediate lobe/ lip sizes have been observed in *T. tambra* (S.Walton pers. comm.) and in *T. khudree* (A. Pinder, unpublished data). There is also doubt surrounding the conditions that may induce morphological variation in the mouthparts of *Tor*. However, regardless of the function of the lobe it is apparent that lobe size and shape is not a reliable diagnostic feature with which to identify S.E Asian *Tor* to species level.

5. What the mitochondrial *COX1* gene tells us?

If the geographical isolation between mainland S.E. Asian and Indonesian *Tor* populations has resulted in the accumulation of significant genetic and/or morphological differences, the taxonomy of *Tor* species in both Indonesia and S.E. Asia should be revised. Therefore, to explore the differences (or similarities) between mainland S.E. Asian and Indonesian *Tor* specimens, genetic data (mitochondrial *COX1* gene sequences) available from previous studies were collated and analyzed along with additional sequences generated from *Tor* material collected by the first author.

The majority of genetic information of Indonesian *Tor* involves only the 5' end of the mitochondrial *COX1* gene (standard, highest representation in BOLD database ~ 650 bp) (Wibowo et al., 2013), but unfortunately, Esa et al. (2008) sequenced the 3' end of the *COX1* gene (non-standard ~ 400 bp or less) for Malaysian specimens thus impeding direct genetic comparison between mainland and topotypic material. Nguyen et al. (2007; 2008) in their work on the phylogeographic patterns of mahseers in continental Asia did not use *COX1* at all, opting for multi-locus analysis consisting of 16S rRNA, *COB*, *ATP6* and *ATP8* genes instead. Therefore overlapping sequences are currently only available for fish with a complete mitogenome sequence. Recently, Norfatimah et al. (2014) reported the complete mitogenome of a specimen referred to as "*T. tambroides*" from Malaysia.

A phylogenetic tree based on the alignable region of the *COX1* gene (5' end) was constructed using the sequence by Norfatimah et al. (2014), alongside a sequence reported as "*Tor tambroides"* by Yang et al. (2010), several South East Asian *Tor spp.* (including the recently described *Tor mekongensis* and *Tor dongnaiensis* from Vietnam) sequences deposited in Genbank, and 21 additional new sequences that we generated consisting of one short-lobe *Tor* morphotype, eight long-lobe *Tor* morphotype, three *Neolissochilus* specimens from peninsular Malaysia, and nine *Tor* specimens from Java.

Since, no morphological information was reported by the author of the Sumatran sequences (Genbank No.: KC905001-KC905024) (Wibowo et al., 2013), these materials were re-examined to ensure the specimens were correctly identified. Although reported as "*Tor tambroides*" the preserved material, stored at the museum of the Institute of Inland Fisheries' in Palembang, Indonesia was found to contain a mix of long-lobe and short-lobe morphotypes (Online Resource 3).

The constructed Bayesian inference-based posterior consensus tree (maximum discrepancy of 0.09 observed across all bipartitions, <0.1 indicates a good run) demonstrated a clear separation between specimens originating from different localities albeit with low posterior probability in some nodes (Fig. 4). Notably, the newly sequenced *Tor* samples collected from both Java and Malaysia formed a monophyletic group with the recently described *Tor mekongensis*, *Tor dongnaiensis* and East Malaysian *Tor tambroides* (Norfatimah et al., 2014) with maximum node support.

#Figure 4 here#

Considerable genetic separation exists between *Tor tambroides* from West Sumatera and the potentially erroneously identified *Tor tambroides* in Malaysia thus rendering the value of conclusions drawn from many previous works questionable. The whole mitogenome of the fish reported as "*Tor tambroides*" by Norfatimah et al. (2014) is clearly genetically different to the fish collected from the type locality and should be taxonomically reassigned as *Tor tambra* (Fig. 4). In addition, Yang et al. (2010) report a voucher specimen of *T. tambroides* but unfortunately provide no information on its collection location. Interestingly, this specimen is a sister taxon to the newly sequenced *Tor* specimens, casting doubt on its taxonomic assignment as *T. tambroides*. Hoàng et al (2015) compared the genetic similarity of the *COX1* sequence from a *Tor* specimen collected from Vietnam with that of a specimen presumed to be *T. tambra* from Malaysian Borneo (*Tor douronensis* voucher DOFS_MB7 in Fig. 4). The authors concluded that their specimen represented a cryptic species of *T. tambra* based on genetic differences. However specimens collected from Malaysian Borneo are not representative of *T. tambra* (Fig. 4) and on the contrary, may represent a new *Tor* species based on our updated phylogenetic investigation. Given the monophyletic clustering of *T. mekongensis* and *T. dongnaiensis* with various *T. tambra* in addition to their classification as the same species as *T. tambra* by both Poisson Tree Processess (PTP) and Generalized Mixed Yule Coalescent (GMYC) approaches, the validity of *T. mekongensis* and *T. dongnaiensis* (Hoàng et al., 2015) is questionable and requires confirmation. Importantly, this exemplifies the importance of sampling from the type locality when reporting such species-specific information, and the improper designation of *Tor* "voucher" specimens in past studies has likely added to the confusion of *Tor* phylogeny in S.E. Asia.

Whilst West Sumatra (Padang) is recognized as the type locality for *T. tambroides*, studies would benefit from the inclusion of more varied material from Java (the Bogor area in particular) as this area is also stated as a type locality for *T. tambroides*; as well as the species described by Valenciennes (in Cuvier and Valenciennes, 1842), i.e. *T. tambra* and *T. douronensis*. The species delineation of *T. tambroides* from Tarusan River, West Sumatera, into two distinct groups suggests that one of the clades may in fact represent the previously described *T. tambra, T. douronensis* or a new species, warranting future taxonomic investigation. Inclusion of type material of all species/morphotypes from this area would eliminate the possibility of misidentification of cryptic species as a potential cause of the clustering observed here. Misidentification of specimens was apparent in the Sumatran sequences as some specimens identified as *T. tambroides* were found to have short lobes and a mix of characteristics described in other *Tor* species (see ESM 3). However, for the purposes of demonstrating biogeographic differences, this mixed material strengthens the case for real differences between Malaysian and Sumatran fish as we can confirm that all described morphotypes in both locations were represented in the phylogenetic analyses (see Fig. 4) and variation was found to be geographically dependent.

In addition to the biogeographical significance of the findings displayed in Fig. 4, the clustering of samples "*Tor tambra* TRG3 LL" (long lobe) and "*Tor tambra* TRG4 SL" (short lobe) reveals that these two individuals displaying different morphological traits (lobe lengths and head shapes) are likely to belong to the same species, adding weight to the redundancy of lobe size as a diagnostic feature for species classification within this group of fishes (Fig. 5). That being said, future study involving the *COX1* gene sequencing of a larger sample of long lobe and short lobe *T. tambra* specimens will be required to strengthen this assertion.

#Figure 5 here#

The potential confounding effect of fish translocation on taxonomic designations in S.E. Asian *Tor* species was first recognized by Bleeker (1863). While discussing the similarity of *Neolissochilus soro* to the Indian species *Tor putitora* (Hamilton 1822) Bleeker (1863) states: "*The distinction with which this species (Labeobarbus soro = currently Neolissochilus soro) was treated and still is treated by the Javanese and especially by the distinguished Javanese, does not make it entirely improbable that in the Hindu age of Java this species was brought here from Hindustan, whereas is also must be mentioned that this species also is found in the east of China*". Although great care was taken to ensure newly added samples were adequately typical of their type localities, including substantial investigation to determine they were not directly translocated, we cannot be certain that historical translocation does not influence our results and the results of previous workers. Fish may have been released into rivers outside their natural range a considerable time ago.

6. A critical assessment of taxonomic papers relating to *Tor* from Malaysia

Esa et al's. (2008) work enables the distinction between a "*T. tambroides"* morphotype and a fish referred to as *T. dourenensis* (this fish needs to be reclassified as it is now only recognized in Indonesia (Kottelat, 2013)), leading the author to conclude that these are separate species. However, the taxonomic description of *T. tambroides* was not included in Esa et al's. (2008) study and the authors assumption that *T. tambroides* is the most common species/ morphotype in Peninsular Malaysia is in direct contrast to observations of long lobe type/short lobe type abundance ratios made by other researchers i.e. ~1/20 (A. Ahmad pers. comm.). Based on variations in both mitochondrial *COX1* and 16S rRNA genes, the authors concluded populations of what was described as *T.*

tambroides possess a low genetic diversity (Esa et al., 2008). However their findings are in doubt as the lack of consideration of lobe lengths and taxonomic description suggests that the authors may have excluded one or more possible morphotypes from their samples.

In addition, whilst Nguyen et al. (2008) performed a relatively thorough investigation into the phylogeny and biogeography of Asian mahseer species, the samples of Malaysian *Tor* species used in this study were reported as *T. tambroides*, having a long median lobe. The short lobe morphotype which is also found in Malaysian rivers, often referred to as *T. tambra* was not considered in this study. The authors state "*Sequences reported herein are from specimens that have a long median lobe, and include samples from Pahang river system (TTA06 and TTA09), indicating that T. tambroides is a valid species although Roberts (1999) suggested it might be a junior synonym of T. tambra (Valenciennes, 1842)*". It is not clear how this conclusion validates the species.

Although Roberts (1999) does indeed suggest *T. tambroides* may be the same species as *T. tambra*, the morphological evidence from the Pahang *Tor* populations that he presented suggests otherwise (Fig. 6). The author made no mention of the apparent morphological differences of the two species in the Pahang populations, but instead drew conclusions based on his findings from the Mekong River system: "*The problem, however, is that often the only difference between smaller specimens [of tambra and tambroides] from a given Malaysian or Indonesian locality seems to be in the length of the mental lobe, which often varies continuously.* ***Differences that distinguish the two large-scaled Mekong species- coloration of juveniles and adults and vertebral counts*** *- either do not distinguish them or have not been discovered. All Malaysian and Indonesian specimens of which I have seen radiographs have total vertebrae of 39–41*". Gill raker counts were apparently not considered to be a difference that distinguishes the two species in this case, without explanation. This leads to a possibly flawed conclusion that only confuses the classification of Malaysian *Tor*.

#Figure 6 here#

The evidence of differences in gill-raker counts is enough to designate '*tambroides*' and '*tambra*' morphotypes as separate species, at least in Pahang; however the distinction of these two species should be confirmed by genetic analysis. This has not yet been performed as authors have excluded short lobe morphotypes from their samples in phylogenetic studies or failed to adequately describe voucher material on which identifications could be confirmed. In light of our current understanding, the fish described in Roberts (1999) as *T. tambra* could be a fish known locally as "Kelah Kejor" or what Roberts and Khaironizam (2008) later describe as a *Tor* like morph of *Neolissochilus*, explaining the apparent interspecific variation. Upon examination of fresh Mahseer material in Pahang, there appears to be two distinct species or morphotypes (Fig. 8). This dimorphism, clearly evidenced by differences in colouration, may not have been observable in preserved specimens. The fish referred to as "Kelah Kejor" in the Pahang river (Fig 7) was found to have a lower average gill-raker count than sympatric long-lobed *Tor* caught from the same area (16.5 vs. 18.5), however none of the long-lobed *Tor* caught in this sample demonstrated the high gill-raker count reported by Roberts (1999). Kelah Kejor which was recorded as distinct from "Tengas" (i.e. *N. soroides*) by local fisherman has been referred to as *Neolissochilus hexagonolepsis* (McClelland 1839) in the literature (e.g. Ambak and Jalal, 2006; Esa et al., 2007), but this was dismissed as a misidentification by Zakaria-Ismail (1989) and recently by Khaironizam et al. (2015). *COX1* gene sequence comparisons of this fish with a specimen of *N. soroides* collected from Terengganu (*Neolissochilus cf. soroides* TRG2) demonstrated they were very closely related (Fig. 4). Both *N. soroides* samples clustered separately from all *N. hexagonolepsis* in the generated phylogenetic tree (Fig. 4) confirming the latter as a misidentification in Peninsular Malaysia. The local names "kelah kejor" and "tengas" are therefore synonymous, both referring to *N. soroides.*

#Figure 7 here#

Apart from the apparent dimorphism in specimens from Pahang, overlooked by Roberts (1999), there is currently little formal evidence of multiple species of *Tor* in peninsular Malaysia, and *T. tambra* is suspected to be the only species present. However Esa and Rahim (2013) demonstrate the existence of a unique haplotype, in the Endau Rompin area, that could represent a cryptic lineage. This fish needs to be compared with material from the type localities of known species in Indonesia in order to confirm its correct identity.

7. Conclusions

Disentangling the taxonomic and systematic status of mahseers is essential for the conservation of these charismatic fishes, which are subjected to increasing anthropogenic pressures. Accurate and comparable genetic information is vital to determine evolutionary significant units (ESUs) and subsequently enable the designation of appropriate nomenclature allowing workers to better estimate the status of populations or management units (MUs) and assign proper conservation and management measures to protect species that may be at risk.

In this review, we discussed the evidence for speciation and polymorphism within the *Tor* species of peninsular Malaysia specifically focusing on two names, i.e. *T. tambra* and *T. tambroides*. We summarize the evidence underlying the theory that *T. tambra* and *T. tambroides* collected from Peninsular Malaysia could belong to one genetically homogeneous yet morphologically diverse species that is closely related to type material, and exhibiting intraspecific trophic polymorphism.

The evidence presented in this review demonstrates long-lobe and short-lobe morphotypes from the same population in Malaysia are likely to represent individuals from the same species. Clustering in the phylogenetic tree, alongside observations of phenotypic differences observed in closely related individuals in both Malaysia and Indonesia point to polymorphism as a key explanation of the described morphological differences within Southeast Asian *Tor* populations. It must be noted that whilst our findings suggest polymorphism is a valid explanation of the observed intrapopulation phenotypic diversity in Malaysia, it is likely that speciation also plays a part in interpopulation phenotypic diversity observed on a larger scale throughout mainland Southeast Asia.

Tor tambra from Java displayed remarkable similarity (in terms of genotype and phenotype) to Malaysian specimens previously described as *T. tambroides*. Given this evidence, and considering the opinions of previous workers (e.g. Roberts, 1993; Kottelat, 2013) we therefore conclude that the species present in Malaysia, previously classified as *T. tambroides* is in fact *T. tambra* and *T. tambra* alone (unless/until distinct lineages can be formally identified). We cannot conclude however that *T. tambra* and *T. tambroides* are synonymous as despite morphological similarities, topotypic *T. tambroides* specimens from Sumatra appear to form a monophyletic group, distinct from *T. tambra* and material from Borneo.

As the commercial culture of mahseer species expands in S.E. Asia, the risk of genetic contamination, gene pool dilution and disruption of locally adapted populations will also become elevated if taxonomic issues are not resolved and genetic identification of stocks not properly considered. This may eventually lead to the extinction of native stocks. Only through an integrated taxonomic approach using a combination of representative sampling, morphological, osteological and molecular analysis can we conclusively establish whether the species currently considered valid in the region, are representative of type material, genetically distinct enough from each other to be classified as multiple species, or should be reclassified as one (or more) morphologically diverse species. To fully understand the phylogeny and biogeography of Southeast Asian *Tor* species, a comprehensive investigation is necessary with the following revisions and extensions to previous investigations.

1) Samples must include Indonesian material, specifically the *T. tambra* type material from Java: Buitenzorg (Bogor) and *T. tambroides* type material from Sumatra: Padang, Pajakombo, Solok, Lake Maninjau/ Java: Tjampea, Buitenzorg (Bogor), Tjipanas.

2) Polymorphism within the mahseers of Peninsular Malaysia should be tested by including a range of suspected morphotypes of *N. soroides* and *Tor*. An extension to the work initiated by Roberts and

Khaironizam (2008) with the inclusion of a population genetics study of *N. soroides* in sungai Gombok would confirm the extent of polymorphism-generated diversity in this species.

3) Sampling from sites in peninsular Malaysia is to include a range of specimens of both *T. tambroides* (thick lips and long median lobes and sharp or pointed heads) and *T. tambra* (thin lips and short lobes with blunt or rounded heads) morphotypes distinguished by classical taxonomic methods so as to be sure that no morphotype is excluded as in previous studies.

4) A comprehensive selection of specimens to be collected from the geographical extent of the reported range of *T. tambra* and *T. tambroides* and sympatric species.

5) Morphological description of all specimens is to be included in the results, including those of the genetic analysis.

6) Although mitochondrial *COX1* gene sequences have been used to differentiate Northeastern Indian *Tor* species (Laskar et al., 2013) and Southeast Asian *Tor* species (Hoàng et al., 2015) previously, a range of mitochondrial and nuclear genes e.g. *COX1*, *COB*, rag1 may be required to establish accurate grouping when dealing with large phylogenies from the genus *Tor,* as they are known to hybridize (R. Raghavan pers. Comm). Therefore, additional gene sequences may be added to supplement the study.

This study provides the first robust evidence for the correct classification of mahseer species in Malaysia, which has significance to the identification of mahseer across SE Asia. The indication that peninsular Malaysia, Sumatra and Borneo have genetically distinct stocks of morphologically similar species requires appropriate restrictions on fish movements be introduced, and exploitation be regulated so as to protect the observed diversity within the *Tor* species of this region. Using our review as a point of reference, further studies are recommended employing a combination of a larger sample size, increased number of populations from the entire reported range of the species under investigation and robust markers such as mitochondrial markers or microsatellites (nuclear markers) in order to provide better resolution to unravel the morphological and genetic ambiguity of all Southeast Asian *Tor* species.

Acknowledgements

The authors are extremely grateful to the relevant authorities for granting permission to carry out this study; namely The Department of Wildlife and National Parks (PERHILITAN) and the power generation company; Tenaga Nasional Berhad (TNB) in Malaysia. Arif Wibowo and Siswanta Kaban from the Research Institute for Inland Fisheries, Palembang, Sumatra; Haryono and Reny Hadiaty from LIPI, Bogor, Java; Bing Urip Hartyo and Sidi Asih from Cipendok, Java are all warmly thanked for granting me access to specimens and providing me with information on the fish they hold. Thanks are also due to Steve Lockett (Mahseer Trust), Li Lian Wong, Reuben Clements, Mohd Shukri Adam and Mastura Malek for assistance with the organization and execution of field surveys. This work was funded by a Research Acculturation Collaborative (RACE) grant (Vot. No. 56033) provided by Ministry of Science Technology and Innovation (MOSTI), Malaysia.

References

Ambak, M.A. and K.A.C. Jalal. Sustainability issues of reservoir fisheries in Malaysia. *Aquat Ecosyst Health Manag* 9:165–173 (2006)

Ambak, M.A., M.M. Isa., M.Z. Zakaria, and M.A. Ghaffar. Fishes of Malaysia. 2nd Edn. Penerbit UMT, Terengganu, MY (2012).

Bishop, J.E. Limnology of a small Malayan River-Sungai Gombak. Dr. Junk Publisher, The Hague, 485p (1973).

Bleeker, P. Overzigt der ichthyologische fauna van Sumatra, met beschrijving van eenige nieuwe soorten. Natuurkd. Tijdschr. Neder.-Indië 7:49–108 (1854).

Bleeker, P. Atlas ichthyologique des Indes Orientales Neerlandaises. Tome Ill. Cyprins. Frederic Muller, Amsterdam. 150p. tabs. CII-CXLIV (1863).

Cuvier, G. and A. Valenciennes. Histoire naturelle des Poissons. Vol. 16. Paris. xx+472 pp., pIs. 456–487 (1842).

Esa, Y.B., K.R. Kammaruddin, A.A.R. Khairul, S.S. Siraj, and S.G. Tan. Phylogenetic relationship among three freshwater fishes of subtribe Tores (Cyprinidae) in Malaysia. In: Siraj SS, Christianus A, Kiat NC, De Silva SS (eds), Mahseer: The biology, culture and conservation. Proceedings of the International Symposium on the Mahseer, Kuala Lumpur, Malaysia. Malaysian Fisheries Society Occasional Publication No 14. 236p (2007).

Esa, Y.B., S.S. Siraj, S.K. Daud, K.A.A. Rahim, J.R.R. Japning, and S.G. Tan. Mitochondrial DNA diversity of *Tor tambroides* Valenciennes (Cyprinidae) from five natural populations in Malaysia. *Zool Stud* 47 (3): 360–367 (2008).

Esa, Y.B. and K.A.A. Rahim. Genetic structure and preliminary findings of cryptic diversity of the Malaysian Mahseer (*Tor tambroides* Valenciennes: Cyprinidae) inferred from mitochondrial DNA and microsatellite analyses. *BioMed Res Int* 2013:1–14 (2013).

Eschmeyer, W.N. (ed). Catalog of Fishes: Genera, Species, References.(http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp). Electronic version accessed 16 June 2015 (2015).

Froese, R., and D. Pauly (eds). FishBase. World Wide Web electronic publication version (11/2014). http://www.fishbase.org. Accessed 17 June 2015 (2015).

Hamilton, F. An account of the fishes found in the River Ganges and its branches. A. Constable and company, Edinburgh. 405p (1822).

Haryono, H. and A.H. Tjakrawidjaja. Morphological study for identification improvement of Tambra fish (*Tor* spp. Cyprinidae) from Indonesia. *Biodiversitas* 7(1) 59–62 (2006).

Hoàng, H.D., H.M. Pham, J-D. Durand, N.G. Tran, and P.D. Phan. Mahseers genera *Tor* and *Neolissochilus* (Teleostei: Cyprinidae) from southern Vietnam. *Zootaxa* 4006 (3): 551–568 (2015).

IUCN. The IUCN Red List of Threatened Species. Version 2015-3. http://www.iucnredlist.org. Accessed 9 September 2015 (2015).

Khaironizam, M.Z., M. Zakaria-Ismail, and J.W. Armbruster. Cyprinid fishes of the genus *Neolissochilus* in Peninsular Malaysia. *Zootaxa* 3962 (1): 139–157 (2015).

Kottelat, M., A.J. Whitten, S.N. Kartikasari, and S. Wirjoatmodjo Freshwater fishes of Western Indonesia and Sulawesi. Periplus Editions, Hong Kong, 221p.(1993).

Kottelat, M. Fishes of Laos. WHT Publications Ltd., Colombo 5, Sri Lanka. 198p (2001).

Kottelat, M. The fishes of the inland waters of Southeast Asia: a catalogue and core bibliography of the fishes known to occur in freshwaters, mangroves and estuaries. *Raffles Bull Zool* (Suppl. 27):1–663 (2013).

Kunlapapuk, S., and S. Kulabtong. Breeding, nursing and biology of Thai Mahseer (*Tor tambroides*) in Malaysia: an overview. *J Ag Sci Tech A* 1:1214–1216 (2011).

Laskar, B.A., M.J. Bhattacharjee, B. Dhar, P. Mahadani, S. Kundu, and S.K. Ghosh. The species dilemma of Northeast Indian mahseer (Actinopterygii: Cyprinidae): DNA barcoding in clarifying the riddle. *PLoS ONE*, e53704 (2013).

MacDonald, A.S.J. Circumventing the Mahseer. Natraj Publishers: Dehra Dun. (1948).

McClelland, J. Indian Cyprinidae. Asiatic Researches, 9 (2): 217–471, pls. 37–58 (1839).

Mohsin, A.M., and M.A. Ambak. Freshwater fishes of peninsular Malaysia. Penerbit Universiti Pertanian Malaysia (1983).

Ng, C.K. Kings of the River - Mahseer in Malaysia and the region. Inter Sea Fishery (M), Kuala Lumpur, Malaysia (2004).

Nguyen, T.T.T., B. Ingram, S. Sungan, G. Gooley, S.Y. Sim, D. Tinggi, and S.S. De Siliva. Mitochondrial DNA Diversity of broodstock of two indigenous mahseer species, *Tor tambriodes* and *T. douronensis* (Cyprinidae) cultured in Sarawak, Malaysia. *Aquaculture* 253 (1): 259–269 (2006).

Nguyen, T.T.T., M. Baranski, M. Rourke, and H. McPartlan. Characterization of microsatellite DNA markers for a mahseer species, *Tor tambroides* (Cyprinidae) and cross amplification in four congeners. *Mol Ecol Notes* 7 (1): 109–112 (2007).

Nguyen, T.T.T., U. Na-Nakorn, S. Sukmanomon, and C. ZiMing. A study on phylogeny and biogeography of mahseer species (Pisces: Cyprinidae) using sequences of three mitochondrial DNA gene regions. *Mol Phylogenet Evol* 48: 1223–1231 (2008).

Norfatimah, M.Y., L.K. Teh, M.Z. Salleh, M.N. Mat Isa, and M.N. SitiAzizah. Complete mitochondrial genome of Malaysian Mahseer (*Tor tambroides*). Gene 548: 263–269 (2014).

Pinder, A.C. and R. Raghavan. Conserving the endangered mahseers (*Tor* spp.) of India: the positive role of recreational fisheries. Curr Sci 104:1472–1475 (2013).

Pinder, A.C., R. Raghavan, and J.R. Britton. Efficacy of angler catch data as a population and conservation monitoring tool for the flagship Mahseer fishes (*Tor* spp.) of Southern India. *Aquat Conserv: Mar & FW Ecosyst* (in press).

Pinder, A.C., R. Raghavan, and J.R. Britton. The legendary hump-back mahseer *Tor* spp. of India's river cauvery: an endemic fish swimming towards extinction? *Endanger Species Res* 28: 11–17 (2015).

Pons, J., T.G. Barraclough, J. Gomez-Zurita, A. Cardoso, D.P. Duran, S. Hazell, S. Kamoun, W.D. Sumlin, and A.P. Vogler: Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Syst Biol*. 55 (4): 595-609. 10.1080/10635150600852011 (2006).

Puillandre, N., A. Lambert, S. Brouillet, and G. Achaz. ABGD, Automatic Barcode Gap Discovery for primary species delimitation, *Mol Ecol* 21(8):1864-1877 (2011).

Raghavan, R., A. Ali, N. Dahanukar, and A. Rosser. Is the Deccan Mahseer, *Tor khudree* (Sykes, 1839) (Pisces: Cyprinidae) fishery in the Western Ghats Hotspot sustainable? A participatory approach to stock assessment. *Fish Res* 110: 29–38 (2011).

Reid, N.M. and B.C. Carstens. Phylogenetic estimation error can decrease the accuracy of species delimitation: a Baysian implementation of the general mixed Yule-coalescent model. *BMC Evolutionary Biology* (12):196 (2012).

Roberts, T.R. Fishes of the cyprinid genus *Tor* in the Nam Theun watershed (Mekong basin) of Laos, with description of a new species. *Raffles B Zool* 47 (1): 225–236 (1999).

Roberts, T.R. The freshwater fishes of Java, as observed by Kuhl and van Hasselt in 1820–23. *Zoologische Verhandelingen* 285: 1–94 (1993).

Roberts, T.R. and M.Z. Khaironizam. Trophic polymorphism in the Malaysian fish *Neolissochilus soroides* and other old world barbs (Teleostei, Cyprinidae). *Nat Hist Bull Siam Soc* 56: 25–53 (2008).

Sathiamurthy, E.V.H.K. and H.K. Voris. Maps of holocene sea level transgression and submerged lakes on the Sunda Shelf. *Nat Hist J Chulalongkorn Univ*, Supplement 2:1–43 (2006).

Siraj, S.S., Y.B. Esa, B.P. Keong, and S.K. Daud. Genetic characterization of the two colour-type of kelah (*Tor tambroides*) using random amplified polymorphic DNA (RAPD). *Malays Appl Biol* 36(1): 23–29 (2007).

Weber, M. and L.F. de Beaufort. The fishes of the Indo-Australian Archipelago. Ill. Ostariophysi: II Cyprinoidea, Apodes, Synbranchi. E. J. Brill, Leiden. xv+455 pp (1916).

Wibowo, A., A. Farajalah, Husnah. DNA barcoding of freshwater fish species of Manna River (Bengkulu) and Semanka river (lampung). *Ind Fish Res J* 19 (1): 9–17 (2013) .

Yang, L., R.L. Mayden, T. Sado, S. He, K. Saitoh, and M. Miya. Molecular phylogeny of the fishes traditionally referred to Cyprinini sensu stricto (Teleostei: Cypriniformes). *Zool Scripta* 39 (6), 527–550 (2010).

Zakaria-Ismail, M. Systematics, zoogeography and conservation of the freshwater fishes of peninsular Malaysia. Ph.D. thesis, Colorado State University, Fort Collins, Colorado, xvii+473p (1989).

Zhang, J., P. Kapli, P. Pavilidis, and A. Stamatakis. A general species delimitation method with applications to phylogenetic placements. Bioinformatics. 29(22):2869-76. doi: 10.1093/bioinformatics/btt499 (2013).

List of Figures Captions

Fig. 1 Map of Southeast Asia highlighting the type locations of significant mahseer species in Sumatra (Su) and Java (Ja) and their proximity to peninsular Malaysia (PM), Malaysian Borneo (MB), Thailand (Th), Myanmar (My), Cambodia (Ca) and Vietnam (Vi). The numbers in parenthesis refer to the species first described from these locations 1 = *Tor tambra*, 2 = *Tor douronensis*, 3 = *Neolissochilus soro* and 4 = *Tor tambroides*. The shaded area between landmasses represents the Sunda shelf c. 21ka BP adapted from Sathiamurthy and Voris (2006).

Fig. 2 Specimens contained at LIPI, Museum Zoological Bogor, Java and collected from the Bogor area (approximate type location). 9090 was classified as *Tor douronensis* and 7999 was classified as *Tor soro* according to the key of Kottlelat (2001)

Fig. 3 A. Adult *Tor tambra* from Cipendok, Java. B. Progeny of *T. tambra* broodstock displaying a typical "tambra like" morphology; short lobe, and blunt snout SL=152mm (Fig. 4:*Tor tambra* JavaS5) C. Progeny of *T. tambra* broodstock displaying a "tambroides like" morphology; long lobe and pointed snout SL=156mm (Fig. 4:*Tor tambra* JavaS7)

Fig. 4 Phylogeny of *Tor* and *Neolissochilus* spp. based on Phylobayes Bayesian inference. The tree was rooted using *Neolissochilus* spp. sequences as outgroup. Four independent MCMC chains were run on the trimmed *COX1* alignment with the CAT-GTR model for a total of 10,000 generations for each chain. 10% of the initial trees were discarded as burn-in and the remaining trees were used to construct a majority-rule consensus tree. Values at nodes represent posterior probability (PP) values. PHG and TRG refer to the sampling locations Pahang and Terengganu, peninsular Malaysia, respectively. LL indicates a long lobe and SL indicates a short lobe. Stacked bars next to the *Tor* spp. branch tips are result of species delimitation analyses using Maximum Likelihood (ML) /Bayesian (b) Poisson Tree Processess (PTP; Zhang et al., 2013) and General Mixed Yule Coalescent (GMYC; Pons et al., 2006, Reid and Carstens, 2012) whereby each bar indicate a primary species hypothesis partition.

Fig. 5 *Tor tambra* specimens from the F, Malaysia; A. *Tor tambra* TRG3 LL displaying a long lobe, pointed snout and distinctive red colour SL=309mm. B. *Tor tambra* TRG4 SL displaying a short lobe, more blunt snout and silver colouration SL=143mm. N.B. dimorphism was observed at all sizes and not related to developmental stage or size.

Fig. 6 Counts of gill rakers and vertebrae in Southeast Asian *Tor* from Roberts (1999). Statistical comparison of the two groups of gill raker counts confirmed a highly significant difference (Independent samples Mann-Whitney U Test: U (24) = 135, Z =4.083 p=<0.001).

Fig. 7 Mahseer specimens from Sungai Keniam, Pahang, Malaysia; A. Kelah kejor *Neolissochilus soroides* (*Neolissochilus* cf. *soroides* PHG9) SL=377mm B. Kelah merah *Tor tambra* SL=390mm C. Tengas *Neolissochilus soroides* (Neolissochilus cf. soroides TRG2) SL=186mm

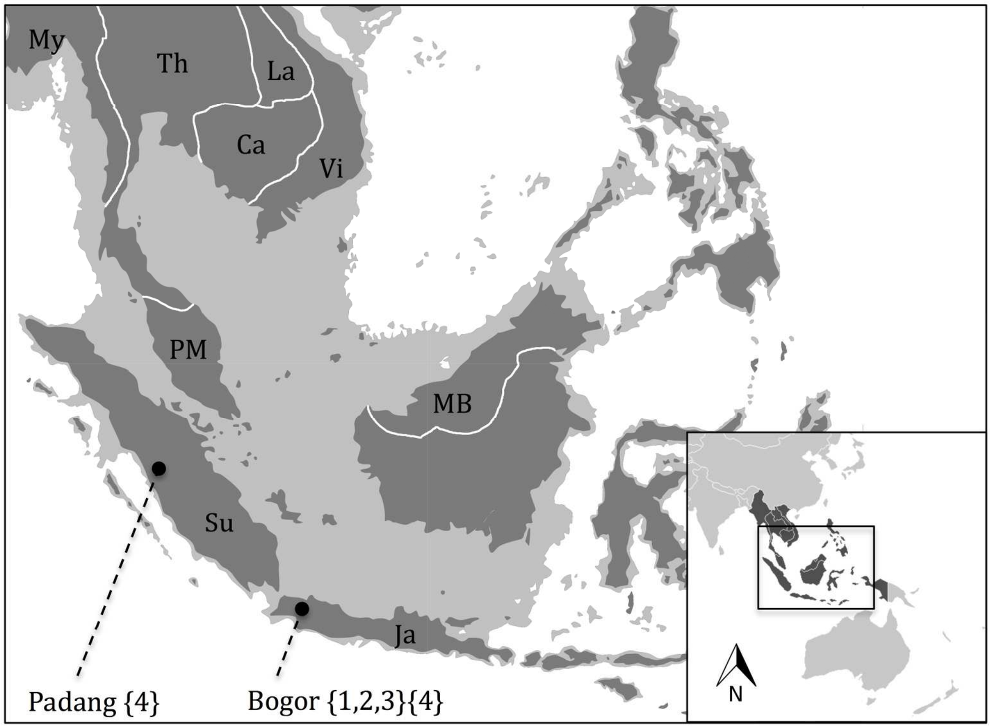

Fig. 1 Map of Southeast Asia highlighting the type locations of significant mahseer species in Sumatra (Su) and Java (Ja) and their proximity to peninsular Malaysia (PM), Malaysian Borneo (MB), Thailand (Th), Myanmar (My), Cambodia (Ca) and Vietnam (Vi). The numbers in parenthesis refer to the species first described from these locations 1 = *Tor tambra*, 2 = *Tor douronensis*, 3 = *Neolissochilus soro* and 4 = *Tor tambroides*. The shaded area between landmasses represents the Sunda shelf c. 21ka BP adapted from Sathiamurthy and Voris (2006).
109x80mm (600 x 600 DPI)


#9090.
#7999
7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30


A.
B.
C.

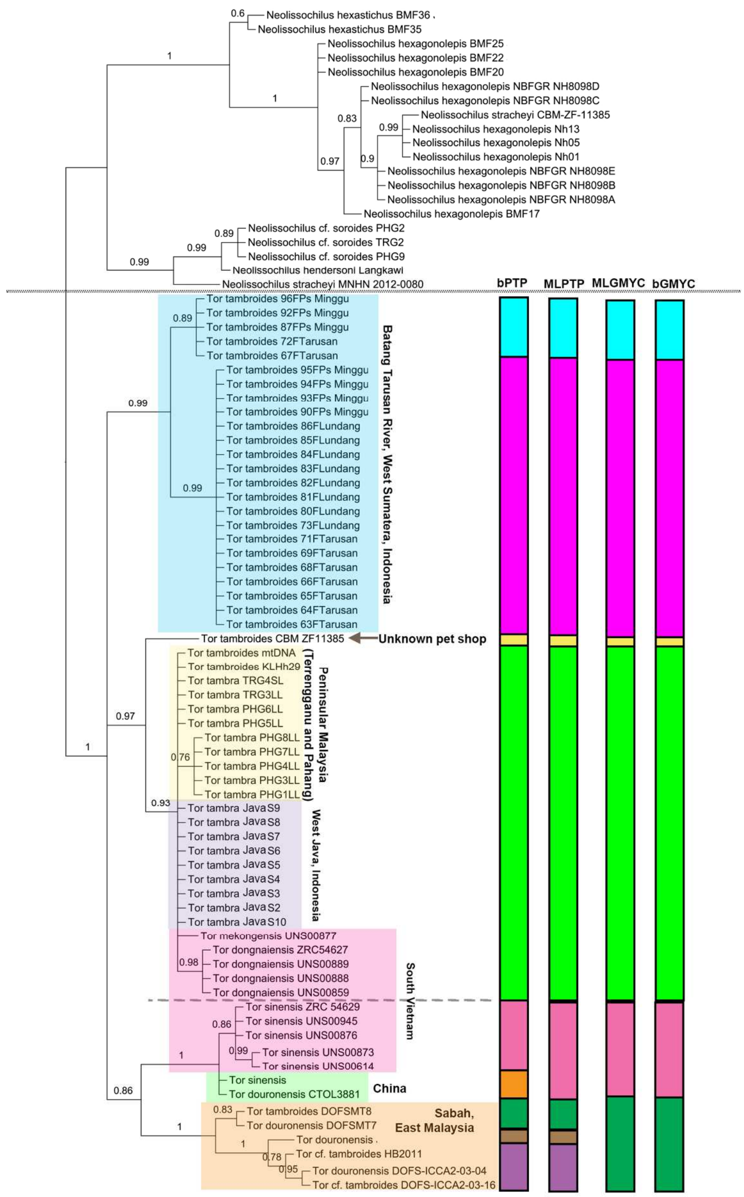

Fig. 4 Phylogeny of *Tor* and *Neolissochilus* spp. based on Phylobayes Bayesian inference. The tree was rooted using *Neolissochilus* spp. sequences as outgroup. Four independent MCMC chains were run on the trimmed *COX1* alignment with the CAT-GTR model for a total of 10,000 generations for each chain. 10% of the initial trees were discarded as burn-in and the remaining trees were used to construct a majority-rule consensus tree. Values at nodes represent posterior probability (PP) values. PHG and TRG refer to the sampling locations Pahang and Terengganu, peninsular Malaysia, respectively. LL indicates a long lobe and SL indicates a short lobe. Stacked bars next to the *Tor* spp. branch tips are result of species delimitation analyses using Maximum Likelihood (ML) /Bayesian (b) Poisson Tree Processess (PTP; Zhang et al., 2013) and General Mixed Yule Coalescent (GMYC; Pons et al., 2006, Reid and Carstens, 2012) whereby each bar indicate a primary species hypothesis partition.
128x209mm (300 x 300 DPI)


A
B

Table 1. Counts of gill rakers and vertebrae in Southeast Asian *Tor*.

	gill rakers										vertebrae				
	15	16	17	18	19	20	21	22	23	24	39	40	41	42	43
Tor ater															
Nam Theun	1		1	1											3
Tor sinensis															
Nam Theun						2	4	2	1	1			2	6	2
Houai Mor										1				1	
Tor tambra															
Nam Theun			2		1						1	1			1
Java*					1	1						1	1		
Pahang		1	2	6	5	1					1	11	3		
Danum			2	2	1	1					6	9	1		
Brunei		1											1		
Sarawak								1	1			2			
Tor tambroides															
Pahang							3	2	3	1	3	6			
Endau								1	1				2		
Danum					1										
Brunei			1								1				
Long Padas			2	1		1					2	2			

* data from Roberts, 1993.


A
B
A
B
C
C

SUPPLEMENT 1

Notes on the occurrence and validity of *Tor* and *Neolissochilus* species in the countries of mainland Southeast Asia. Museum acronyms: ZRC: Raffles Museum of Biodiversity Research, National University of Singapore, Singapore. KIZ: Kunming Institute of Zoology, Kunming, China. IHB: Institute of Hydrobiology, Wuhan, China. MNHN: Muséum National d'Histoire Naturelle, Paris, France.
NMW: Naturhistorisches Museum, Wien, Austria. ZSI: Zoological Survey of India, Calcutta, India. BMNH: Natural History Museum [formerly British Museum, Natural History], London, UK. AMS: Australian Museum, Sydney, Australia. USNM: National Museum of Natural History, Washington, USA. NT: indicates that there is no (or apparently no) preserved type material.

Country (in mainland SE asia)	Tor and Neolissochilus species reported	Described by	Notes
Cambodia	*T. douronensis*		(See Peninsular Malaysia)
	T. tambra		(See Peninsular Malaysia)
	T. tambroides		(See Peninsular Malaysia)
	N. soroides		(See Peninsular Malaysia)
Laos	*T. ater*	Roberts, 1999	This species is known only from the three type specimens collected at Ban Talang, Laos and is thought to be rare (Roberts 1999). Type locality: Laos: Nam Theun at Ban Talang; holotype: ZRC 40356
	T. douronensis		(See Peninsular Malaysia)
	T. laterivittas	Zhou & Cui, 1996	Considered by Roberts (1999) to be a junior synonym of *Tor sinensis* Wu, 1977 but remains a valid species (Kottelat 2013). Type locality: China: Yunnan: Mengla County: Nanla River, a tributary of Lancangjiang [Mekong], near Mengla city, 21°29'N 101°34'E; holotype: KIZ 8840041
	T. sinensis	Wu, 1977	Type locality: China: Yunnan: Luosuo Jiang [Bu-Yuan Jiang], Jing- hong and Menghan; syntypes: IHB 00433, 7090, 584139, 584218, 584252, 584268, 634047, 634101, 638199, 638241–243, 638245 [13]
	T. tambra		(See Peninsular Malaysia)
	T. tambroides		(See Peninsular Malaysia)
	N. blanci	Pellegrin & Fang, 1940	Type locality: Laos: Ban Nam Khueng, 30 km northwest of Ban Houei Sai, about 6 km from Mekong; syntypes: MNHN 1939-0203–0205 [3])
	N. stracheyi	Day, 1871	(see Myanmar below)

Myanmar (Burma)	*T. putitora*	Hamilton, 1822	Identity of specimens from Myanmar requires confirmation (Kottelat 2013). Material earlier recorded as T. putitora from the Irrawaddy in Yunnan has been described as *T. yingjiangensis* by Chen & Yang (2004) so it follows that putitora in this region, which is known in the Ganges and Indus River basins (Hamilton 1822, Hora 1939, Chen & Chu 1985, Chu & Chen 1989, Shan et al. 2000) may be a misidentification of *T. yingjiangensis*. Cyprinus putitora Hamilton, 1822: 303, 388 (type locality: India: eastern parts of Bengal; types: NT) Labeobarbus macrolepis Heckel, 1838: 60, pl. 10 fig. 2 (type locality: India: Kashmir: Tschilum River [Jhelum] and connected lakes; holotype: NMW 54284, (Eschmeyer, 2015))□ Barbus macrocephalus M'Clelland, 1839: 270, 335, pl. 55 fig. 2 (type locality: India: rapids in Upper Assam; holotype: Location Unknown)
	T. soro		(See Peninsular Malaysia)
	T. tambroides		(See Peninsular Malaysia)
	T. tor	Hamilton 1822	Type locality: India: Mahananda River; types: NT; Hamilton's unpublished figure reproduced in Gray, 1834: vol. 2, pl. 96 fig. 1)
	N. blythii	Day, 1870	Type locality: Burma: Tenasserim provinces; holotype: ZSI A.787
	N. compressus	Day, 1870	The type locality of this species is unknown. The label on the jar of the holoptype states "with an Oreinus from Cashmere". Kottelat (2013) notes this as erroneous, and the type locality is probably Burma; Mukerji, 1934: 62]; holotype: ZSI 5513/1, Mukerji, 1934: 59, fig. 8, Rainboth, 1985: 29, or ZSI A.786, Whitehead & Talwar, 1976: 155
	N. dukai	Day, 1878	Type locality: India: Darjeeling: Teesta River; syntypes: among ZSI 2388 [1], RMNH 2681 [1], ? 8659 [1], BMNH 1889.2.1.518–519 [2], AMS B.7983, NMW 54061
	N. hexagonolepsis	McClelland, 1839	Considered native in Myanmar. Reports of the species from Myanmar and Thailand may be due to the misidentification of *Neolissochilus stracheyi,* which Day (1871) described from the Irrawaddy basin in Myanmar (Arunachalam, 2010)
	N. hexastichus		
	N. nigrovittatus		
	N. pancisquamatus		See Thailand
	N. stevensoni		

	N. stracheyi		Questionably synonymous with *Barbus mortonius* Mason, 1850: 312 (type locality: Burma: Tenasserim: "Sacred Lakes in the vicinity of Tavoy", two basins in Pagaya River, "at the foot of pagoda- crowned precipices from one to two hundred feet high"; syntypes: NT) Barbus stracheyi Day, 1871: 307 (type locality: Burma: Moulmein; lectotype: ZSI F 2175, designated by Rainboth, 1985: 29) (Kottelat 2013)
Thailand	*T. tambroides*		(See Peninsular Malaysia)
	T. douronensis		(See Peninsular Malaysia)
	T. sinensis		(See Laos)
	T. soro		(See Peninsular Malaysia)
	T. tambra		(See Peninsular Malaysia)
	N. dukai		(See Myanmar)
	N. hexagonolepsis		Records require confirmation as this species is only known with certainty from India (Assam), Bangladesh and Myanmar. Could be confused with other neolisscohilus species.
	N. nigrovittatus	Boulenger, 1893	Type locality: Burma: Southern Shan States: Fort Stedman; syntypes: BMNH 1893.6.30.41–42 [2]
	N. pancisquamatus	Smith, 1945	Previously described as *Puntius paucisquamatus*; Type locality: Thailand: Nakhon Sritamarat Prov: brook near base of Kao Luang; holotype: USNM 119713
	N. soroides		(See Peninsular Malaysia)
	N. stratcheyi		(See Myanmar)
	N. subterraneus	Vidthayanon & Kottelat, 2003	A cave inhabitant thought to be endemic to caves in northern Thailand. Type locality: Thailand: Phitsanulok Province: Thung Salaeng Luang National Park: subterranean stream in Tham Phra Wang Daeng cave, about 200 m from entrance upstream section; 16°40'41"N 100°41'24"E; holotype: NIFI 3148 (Kottelat, 2013)
	N. sumatranus	Weber & de Beaufort, 1916	Described from Bandar Baru, Sumatra and considered endemic to Sumatra. Roberts and Khaironizam (2008) suggested *N. sumatranus* is a junior synonym of *N. soroides.*
	N. Vittatus	(Smith, 1945)	Known from the Salween basin in eastern Myanmar and associated tributaries in Mae Hong Son Province, western Thailand (Kottelat 1989).

Peninsular Malaysia	*T. douronensis*	(Valenciennes, 1842)	Evidence from Ngyuen et al. (2008) suggests three different lineages are identified as *T. douronensis* in SE Asia. The species present in Malaysian Borneo and throughout mainland SE Asia cannot be confirmed to be *T. dourenensis* as it has not been compared with topotypic material. Kottelat 2013 tentatively treats *T. douronensis* as a synonym of *T.tambra*. This species needs to be reclassified throughout its range pending comparison with topotypic material. Type locality: Indonesia: Java; holotype ?: MNHN 3826, Bertin & Estève, 1948: 49, Roberts, 1993: 22
	T. soro	(Valenciennes, 1842)	Described by Weber and de Beaufort (1916) as “without lobe” so could be reclassified as *Neolissochilus*. Roberts (1999) states: “Although tentatively regarded previously as a junior synonym of *Tor tambra* (Roberts 1993), *Labeobarbus* soro (*T. soro*), which does not have a mental lobe, may belong instead in the genus *Neolissochilus* (Rainboth 1985)” Kottelat (2013) tentatively describes *T. soro* as a synonym of *T. tambra* based on Roberts (1993), perhaps overlooking Weber and de Beaufort (1916) and Roberts (1999) but also offers *Neolissochilus soro* as a separate valid species. Fish formerly described as *T. soro* in Peninsular Malaysia are generally considered to be *N. soroides* (Khaironizam et al. 2015). Most fish currently described as *T. soro* in Indonesia appear to have a lobe, albeit very short, so could be considered *T. tambra.* Type locality: Indonesia: Java: Bantam , Sadingwetan River; syntypes: RMNH presumed lost.
	T. tambra	(Valenciennes, 1842)	This fish is widely reported throughout SE Asia. The identification of this fish throughout its range is problematic, as past workers have not had access to Javan type material or even data from this material. Roberts (1993,1999) maintains this fish is the senior synonym of several species *T. soro, T. douronensis, T.tambroides* but provides little quantitative evidence. Kottelat (2013) considers the species valid and agrees with the synonmy of *T. douronensis* and *T. tambra* based on the similarity of original descriptions of both species. Type locality: Indonesia: Java: Buitenzorg [Bogor]; syntypes: apparently RMNH.PISC.D.2280 [1, Roberts, 1993: 22, figs. 23–24] and specimen on which is based Kuhl and van Hasselt's drawing [Roberts, 1993: fig. 22] (Kottelat 2013).

	T. tambroides	(Bleeker, 1854)	Considered to be junior synonym of *T.tambra* by Roberts (1993,1999). Kottelat (2013) lists it as a valid species (at least in its type location) but states "If *Tor tambroides* is treated as synonym of *T. tambra*, then *T. tambra* is the valid name" Type locality: Indonesia: Sumatra: Padang, Pajakombo, Solok, Lake Maninjau / Java: Tjampea, Buitenzorg [Bogor], Tjipanas; syntypes [12, 88–430 mm TL]: part of RMNH.PISC.2089 [9], 7026 [1], BMNH 1866.5.2.64 [1], AMS B.7654 [1], NMV 46320 [1], (Eschmeyer, 2015)
	N. hendersoni	Herre, 1940	Previously considered endemic to Penang island (West Malaysia) but has also been reported on Langkawi Island (Ahmad & Lim 2006) and recently on the mainland; Merbok and Muda drainage in Kedah and Golok drainage in Kelantan (Khaironizam et al. 2015). Type locality: Malaysia: creek on Penang Island; holotype: CAS- SU 32632. Synonomy with *N. hutchinsoni* (Fowler 1938), described in southern Thailand is possible and requires investigation.
	N. hexagonolepsis	McClelland, 1839	Does not occur in Malaysia. Misidentified Indian species (Zakaria-Ismail, 1989 ; Khaironizam et al. 2015)
	N. soroides	(Duncker, 1904)	Topotype is mainland SE Asia (Pahang river system, peninsular Malaysia) so is more likely to be correctly classified throughout its range than species with Indonesian type localities. Can be adequately distinguished from *Tor* by absence of median lobe (Nguyen et al. 2008, this study). However, some populations may display trophic polymorphism with some individuals possessing a lobe (Roberts and Khaironizam 2008; Khaironizam et al. 2015). Synonomy with *N. sumatranus* requires confirmation. Type locality: Malaysia: eastern slope of Sangka-Dua pass, head-waters of Pahang River; lectotype: ZMH 368 [formerly 8441], designated by Ladiges et al., 1958: 158)
	N. tweediei	Herre and Myers 1937	Concluded to be indistinguishable from *N. soroides* by Zakaria-Ismail (1989) but still considered valid by Kottlelat (2013). Type locality: Malaysia: Perak: Yum River, tributary to Plus River; holotype: CAS-SU 30969
Vietnam	*T. douronensis*		(See Peninsular Malaysia)
	T. tambra		(See Peninsular Malaysia)
	T. tambroides		(See Peninsular Malaysia)
	N. benasi	Pellegrin & Chevey, 1936	Type locality: Vietnam: Laokay Province: Muong Hum [22°31'45"N 103°42'42"E], Ngoi Pho Tao River, Red River drainage; lectotype: MNHN 1935.338, by present designation [listed as holotype by Bertin & Estève, 1948:54])
	N. hexagonolepsis		Probable misidentification in Vietnam (see Mynamar for additional species notes)

N. namlenensis	Nguyen & Doan, 1969	*Crossochilus namlenensis* (as *N. namlenensis* was first described) is currently considered to be an objective junior synonym of *N. benasi* (Kottelat 2013). However the type localities of both species are not well surveyed (or reported) and far enough apart to warrant further investigation into the occurrence of distinct species. *Neolissochilus benasi* was described from the Red River drainage and *C. namlenensis* from the Song Ma, which enters the Gulf of Tonkin South of the estuary of the Red River.Type locality: Vietnam: Lai Chau Province [now Dien Bien Province]: Tuan Giao District [21°35'15"N 103°25'10"E]. Syntypes: NCNTTSI H.01.59.59.01 – H.01.59.01.03, lost.
N. stracheyi		(See Myanmar)
T. mekongensis	Hoàng et al., 2015	Described in 2015 by Hoàng et al (2015) this species, which resembles *T.tambra* is claimed to be a cryptic lineage of *T.tambra*. However, the genetic comparison performed to make this conclusion included only a reference specimen, supposedly representing *T.tambra* from Sabah, Malaysian Borneo. *T. tambra* is not a valid species in this location thus the validity of *T. mekongensis* remains to be confirmed with comparison to topptypic (Javan) material. Type locality: Vietnam; upper Ea Krong No drainage: upper Mekong basin in montane evergreen forest in Bidoup-Núi Bà National Park, Lâm Đồng Province (12°16’23.68” N 108°26’30.17”E). Holotype: UNS00877. Paratypes: UNS00878, UNS00879
T. dongnaiensis	Hoàng et al., 2015	Recently described by Hoàng et al (2015) alongside *T. mekongensis*. Although morphological differences form other Tor species are reported, it’s designation as a new species was largely based on an unreliable genetic comparison with an inappropriate voucher specimen of *T.tambra.* The validity of this species therefore requires confirmation as in *T. mekongensis* Type locality: Vietna; middle Đồng Nai drainage: Cát Tiên National Park, Lâm Đồng Province (11°26’33.32” N 107°26’4.01” E, 162 m). Holotype: UNS00859. Paratypes: ZRC 54628, UNS00861, UNS00862, ZRC 54627, UNS00880, UNS00888, UNS00889

References

Ahmad, A. and K.K.P. Lim. Inland fishes recorded from the Langkawi Island, Peninsular Malaysia. *Malayan Nat J* 59:103-120 (2006).

Arunachalam, M. *Neolissochilus hexagonolepis*. The IUCN Red List of Threatened Species. Version 2015.2. http://www.iucnredlist.org/details/166479/0. Accessed 15 July 2015 (2010) .

Bertin, L. and R. Estève. Catalogue des types de poissons du Muséum national d'Histoire naturelle. 4e partie. Ostariophysaires (Cypriniformes). Muséum National d'Histoire Naturelle, Paris, 117 pp (1948).

Bleeker, P. Overzigt der ichthyologische fauna van Sumatra, met beschrijving van eenige nieuwe soorten. Natuurkd. Tijdschr. Neder.-Indië 7:49-108 (1854).

Boulenger, G.A. List of the fishes collected by Mr. E. W. Oates in the Southern Shan States, and presented by him to the British Museum. Annals and Magazine of Natural History, Ser. 6, 12 (69): 198–203 (1893).

Chen, Y.R. and X.L. Chu. Systematic study of the genus *Tor* (Pisces: Cyprinidae) with description of a new species. *Zool Res* 6: 79–86 (1985).

Chen, ZM, Yang JX (2004) A new species of the genus Tor from Yunnan, China (Teleostei: Cyprinidae). *Environ Biol Fishes* 70: 185–191

Chu, X.L. and Y.R. Chen (ed.) The Fishes of Yunnan, China. Part I. Cyprinidae. Science Press, Beijing. 377 pp (1989).

Day, F. Remarks on some of the fishes in the Calcutta Museum. – Part II. Proceedings of the Scientific Meetings of the Zoological Society of London, 1869 (3): 548– 560 (1870).

Day, F. Monograph of Indian Cyprinidae. *J Roy Asiatic Soc Bengal* 40, 277-336 (1871).

Day, F. The fishes of India; being a natural history of the fishes known to inhabit the seas and fresh waters of India, Burma, and Ceylon. Quaritsch, London, i–xx, 553–778, pls. 139–195 (1878).

Duncker, G. Die Fische der malayischen Halbinsel. Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten, 2. Beiheft, Mitteilungen aus dem Naturhistorischen Museum in Hamburg, 21: 133–207, 2 pls (1904).

Hamilton, F. An Account of the Fishes Found in the River Ganges and its Branches. A. Constable and company, Edinburgh. 405 pp (1822).

Herre, A.W.C.T. New species of fishes from the Malay Peninsula and Borneo. *Bulletin of the Raffles Museum* 16: 5–26, 20 pls (1940).

Herre, A.W.C.T. and G.S. Myers. A contribution to the ichthyology of the Malay Peninsula. *Bulletin of the Raffles Museum* 13: 5–75, pls. 1–7 (1937).

Hoàng, H.D., H.M. Pham, J-D. Durand, N.G. Tran, and P.D. Phan. Mahseers genera *Tor* and *Neolissochilus* (Teleostei: Cyprinidae) from southern Vietnam. *Zootaxa* 4006 (3): 551–568 (2015).

Hora, S.L. The game fishes of India. VIII. The mahseers or the large-scaled barbels of India. *J Bombay Nat Hist Soc* 41: 272–285 (1939).

Khaironizam, M.Z., M. Zakaria-Ismail, J.W. Armbruster. Cyprinid fishes of the genus *Neolissochilus* in Peninsular Malaysia. *Zootaxa* **3962** (1) 139-157 (2015)

Kottelat, M. Zoogeography of the fishes from Indochinese inland waters with an annotated check-list. *Bull Zool Mus Univ Amsterdam* 12(1): 1-55 (1989).

Kottelat, M. The fishes of the inland waters of Southeast Asia: a catalogue and core bibliography of the fishes known to occur in freshwaters, mangroves and estuaries. *Raffles B Zool* (Suppl. 27):1-663 (2013).

M'Clelland, J. Indian Cyprinidae. Asiatic Researches, 9 (2): 217–471, pls. 37–58 (1839).

Nguyen, T.T.T., U. Na-Nakorn, S. Sukmanomon, C. ZiMing. A study on phylogeny and biogeography of mahseer species (Pisces: Cyprinidae) using sequences of three mitochondrial DNA gene regions. *Mol Phylogenet Evol* 48: 1223-1231 (2008).

Nguyen, V.H. and L.H. Doan [Some data on composition, origin and distribution of cyprinid species in the north of Vietnam]. [Scientific Seminar of Fisheries Division], 1: 1–19. [In Vietnamese]. Text refers to figures, which do not exist in the examined copy. See translation in: Nguyen & Doan, 2007 (1969).

Nguyen, V.H. and L.H. Doan Some data on composition, origin, and distribution of cyprinid fish species in northern Vietnam with description of new taxa]. Natural History Bulletin of the Siam Society, 55 (1): 59–76. [Translation of Nguyen & Doan, 1969]. (2007)

Pellegrin, J. and P. Chevey. Poissons nouveaux ou rares du Tonkin et de l'Annam. *B Soc Zool Fr* 61: 219–232 (1936).

Pellegrin, J. and P.W Fang. Poissons du Laos recueillis par MM. Delacour, Greenway, Ed. Blanc. Descrip- tion d'un genre, de cinq espèces et d'une variété. *B Soc Zool Fr* 65: 111–123. (1940).

Rainboth, W.J. Neolissochilus, a new genus of South Asian cyprinid fishes. *Beaufortia* 35 (3): 25–35 (1985).

Roberts, T.R. The freshwater fishes of Java, as observed by Kuhl and van Hasselt in 1820–23. Zoologische Verhandelingen 285: 1–94 (1993).

Roberts, T.R. Fishes of the cyprinid genus Tor in the Nam Theun watershed (Mekong basin) of Laos, with description of a new species. *Raffles B Zool* 47 (1): 225–236 (1999).

Roberts, T.R. and M.Z Khaironizam. Trophic polymorphism in the Malaysian fish Neolissochilus soroides and other old world barbs (Teleostei, Cyprinidae). *Nat Hist Bull Siam Soc* 56: 25-53 (2008).

Shan, X.H., R.D. Lin, P.Q. Yue, and X.L. Chu. Barbinae. pp. 3–170. *In*: P.Q. Yue (ed.) Fauna Sinica, Osteichthyes, Cypriniformes III, Science Press, Beijing (2000).

Smith, H.M. The fresh-water fishes of Siam, or Thailand. Bulletin of the United States National Museum, 188: i–xi + 1–622, 9 pls. [Reprinted 1965, Smithsonian Institution, Washington] (1945).

Valenciennes, A. Ichthyologie des îles Canaries, ou histoire naturelle des poissons rapportés par MM. P.-B. Webb et S. Berthelot. In: P. Barker-Webb & S. Berthelot, Histoire naturelle des îles Canaries. Béthune, Paris, 2 (2): 1–8, 19 pls (1842).

Vidthayanon, C. and M. Kottelat. Three new species of fishes from Tham Phra Wang Daeng and Tham Phra Sai Ngam caves in northern Thailand (Teleostei: Cyprinidae and Balitoridae). Ichthyol Explor Fres 14 (2): 159–174 (2003).

Weber, M. and L.F. de Beaufort. The fishes of the Indo-Australian Archipelago. Ill. Ostariophysi: II Cyprinoidea, Apodes, Synbranchi. E. J. Brill, Leiden. xv+455 pp (1916).

Wu, X.W. (Ed.). *Cyprinid fishes of China, Vol.* 2. Science and Technology Publishing House, Shanghai. p. 209-598, 109 pIs. (In Chinese) (1977).

Zakaria-Ismail, M. Systematics, zoogeography and conservation of the freshwater fishes of peninsular Malaysia. Ph.D. thesis, Colorado State University, Fort Collins, Colorado, xvii+473 pp. (1989).

Zhou, W. and G.H. Cui. A review of *Tor* species from the Lancangjiang River (Upper Mekong River), China (Teleostei: Cyprinidae). *Ichthyol Explor Fres* 7(2):131-142 (1996).

Supplement 2

COMPARISON OF TAXONOMIC DESCRIPTIONS BASED ON MORPHOLOGY OF JAVAN TOR SPECIES

The data poor nature of descriptions from earlier workers makes it difficult to find standard characters from which to distinguish differences in Indonesian Tor species. The difficulty in finding common terms to identify real differences is exacerbated by the mix of languages used by different authors and the subjective nature of translation. As such, it was not possible to present all comparisons in tabular form (but see Table S2.1) in this review so the full translated description is provided with key points highlighted in bold to reveal any key distinguishing features between descriptions by the same author or underlined to demonstrate disagreements or contradictions between authors. These points are briefly discussed at the conclusion of this supplement.

Valenciennes (in Cuvier & Valenciennes, 1842)

The descriptions of Valenciennes (in Cuvier & Valenciennes, 1842) are translated below. The description of *B. tambra* is accompanied by a picture of Kuhl & Van Haselt's specimen upon which the author is thought to have based his original description (Roberts 1993). *B. douronensis* is accompanied with a photograph of the holotype of *Tor douronensis* kept at the Natural History Museum, Paris (MNHN) (MNHN 0000-3826). The holotype of *B. soro* is lost but the illustration of Kuhl and van Hasselt ((XVIB 30). Photo. Bibl. MNHN in Roberts 1993)) is provided.

The Soro Barbel

(Barbus soro)

Another species, also based on the description of a dried conserved specimen in the same museum, displayed a long body **with a slightly more bent back profile**; **the length is 4 2/3 times the height**; the head is meagre[1]; the mouth is slightly split with four barbels: two thin ones at the corner of the mouth, and two at the top of the jawbone; dorsal fin with smooth spiny rays; **its edge is a little indented[2]**; the shoulder bone[3] has a rounded edge, and the pectoral is meagre[1]; **the ventral fins are large**; **the anal fin is pointed**; the indented[2] caudal fin is composed of two equal lobes. **The lateral line, curved at first, rises above the anal fin to run straight to the tail.** The scales, large smooth and narrow[4], number **25 in length** and 6 rows in height. **The colour on the back is dark green: it lightens on the flanks, acquiring a golden shade**; the stomach is whitish; the dorsal and caudal fins are the same colour as the back; the pectoral fin is lighter; the anal and ventral fins are grey. The length is about 10 inches. This fish, found in the fresh water of Bantam in the river called *Sading-Vetang* in Malay, is named *Soro*: due to the research of the same naturalists.

Notes:

1. Probably means 'small' but he uses the French word 'mediocre' and 'meagre' is the closest translation.
2. French word is 'echancre' which could also translate as 'jagged'
3. This is a literal translation, but probably refers to the nape, or hump, between the head and the dorsal fin

4. Could also be translated as 'thin'

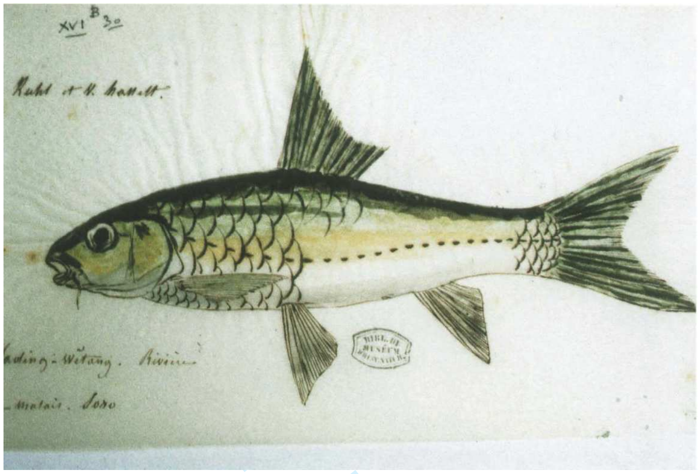

Figure S2.1 Illustration of "*Barbus soro*" juvenile by Kuhl and van Hasselt ((XVIB 30). Photo. Bibl. MNHN in Roberts 1993))

The Tambra Barbel

(Barbus tambra)

In 1824, in Leyde (Leiden, Netherlands), I drew a large dried *Cyprinus* which had a long body covered in large scales with a slightly raised profile rising to the dorsal fin. **The height is a quarter of the total length**; the four barbels are long: they reach to the eye[1]; the spiny ray of the dorsal fin, strong and smooth, **has no indentations/serrations[2]**; the dorsal fin, pointed forwards, has an indented edge; the rounded shoulder bone supports a pointed pectoral fin. **The ventral fin is meagre**; **the anal fin rounded**; the caudal fin is forked and its two lobes are normally pointed. However, on the large specimen in Leyde, the lower caudal lobe is truncated and rounded, and this does not seem to be the result of an accidental break.

The lateral line, almost straight, runs along the middle of the body. The scales, very large and narrow, have membranous edges and the disc is covered by fine, wavy and '*anastomosees*' striations/grooves[2]. I counted **22 of them along the length** and 7 in height. **The colour is a bright and shiny purple on the sides, becoming almost black on the top of the head**. These colours are laid out in large patches at the base of the scale and edged with a first yellow arc, which is followed by a second quite marginal pale blue one. The cheeks have yellow and purple spots; the thorax is purplish; the stomach is bluish. The dorsal fin is greyish yellow with some purple on the edge. The caudal fin has the same colours but lighter; the anal and ventral fins are brown[3].

The fish I have described is 2 feet long. It comes from fresh water near Buitenzorg; Kuhl and Van Hasselt give it the common name of *tambra*.

Notes:

1. ' Ils vont toucher a l'oeil': Could mean they are capable of reaching the eye.
2. '*anastamosees*': In medical English an anastomosis is a connection or join between two tubes, or tubular structures, so it might indicate that the striations fuse in some way.
3. Probably brown but could be 'dark'.

Figure S2.2. RMNH.PISC.D.2280 Barbus tambra: Reported as RMNH 2289 Roberts (1993) and RMNH D 2089 by Kottelat (2013) but this is incorrect because of a misreading of the number on the specimen. The last number looks like a "9" but in fact this should be a "0". RMNH.PISC.D.2289 is another species entirely.

The Douro Barbel
(*Barbus douronensis*)
I have received from the royal museum of Leyde (Leiden, Netherlands) a barbel with non-indented rays; 4 barbels; a long body; **the length is 4 1/2 times the height**; the head is short and is 1/5 of the body length; a narrow jaw/snout[1]; quite a large eye; the caudal fin is forked; **the anal fin is pointed**.
It has a silvery colour, with green tinges on the back; **21 large smooth scales** lengthways; **the lateral line is marked with a series of large dots**.
This fish, 4 1/2 inches in length, formed part of the collection made in Java by Kuhl and Van Hasselt; they named it Dourr.

Notes:
1. French word museau I have translated as ‘jaw’ but ‘snout’ is also possible.

Figure S2.3. MNHN 0000-3826. Holotype of *Tor douronensis* kept at the Natural History Museum, Paris (MNHN)

<u>Bleeker (1854, 1863)</u>

The following descriptions (with the exception of *Labeobarbus tambra*) are first given in Bleekers Natuurkundig tijdschrift voor Nederlandsch Indie/ uitgegeven door de Natuurkundige Vereeniging in Nederlandsch Indie, Volume 7, 1854 pp. 90-93. As the description of tambra was not available in in this document, the following translations of Oijen and Loots (2012), from Bleeker's Atlas Ichthyologique des Indes Orientales Néêrlandaises. Tome III, written in 1863 are provided here. The descriptions of *tambroides, douronensis* and *soro* are similar in both 1854 and 1863 documents and the translations of the latter document were deemed the most useful for comparative purposes. All species are accompanied with original illustrations and the description of *Labeobarbus tambroides* is accompanied by a photo of one of Bleeker's 9 paratypes (RMNH.PISC.2089_b1) deposited at the Leiden museum. The original key to species provided in Bleeker (1863) also follows the descriptions.

Labeobarbus tambroides Blkr,
Overz. Ichth. Faun. Sumatra, Nat T. Ned. Ind. VII p. 92. –
Tambra-achtige Lipbarbeel [Tambra-like Lip Barbel].
Atl. Cypr. Tab. XXIII.

A Labeobarbus with an oblong, compressed body, depth of body contained 4 to 4⅓ times in its length, width contained about 2 times in its depth. Head acute, not or hardly convex, contained 4¾ to 5¼ times in length of body with caudal fin, 3⅕ to slightly over 4 times in length of body without caudal fin; depth of head contained 1⅓ to 1¼ times, width contained 1¾ to 1⅗ times in its length; eye diameter contained slightly over 3 to 4 times in the length of the head, eye diameter contained 1¼ to 1⅗ times in the postocular part of the head; distance between the eyes once to 1⅘ times their diameter; palpebral membrane covering the external margin of the iris only, broader anteriorly than posteriorly, opening nearly circular; snout acute, in younger animals shorter than the eye, in adults longer than the eye, not sticking out in front of the mouth, nearly straight or slightly convex; nostrils much closer to the orbit than to the tip of the snout; rostro-dorsal profile nearly straight or slightly convex on the head, convex on the nape; anterior suborbital bone obliquely pentagonal, length not or hardly greater than depth, lower margin oblique, convex, anterior and posterior lower margins generally concave, anterior margin oblique, posterior margin nearly vertical, upper margins concave (posterior margin much shorter than anterior margin) united into an acute, forward pointing angle close to the nostrils, traversed around the middle by a longitudinal crest ascending posteriorly; 2nd suborbital bone obliquely quadrangular, much higher anteriorly than posteriorly, length about twice as great as height, about twice as low as 1st suborbital bone; upper jaw longer than lower jaw, strongly vertically downward protrusable, ending below the anterior margin of the eye, contained nearly 3 to slightly over 3 times in the length of the head; gape slightly oblique; barbels thin, upper jaw barbels slightly longer than nasal barbels, slightly longer to considerably longer than the eye; lips very broad, fleshy, transversely striped on the oral surface, upper lip protracted into a lobe which generally is obtusely rounded, lower lip into a lobe, generally longer than that of the upper lip, obtusely or acutely rounded; lower jaw at the symphysis with a conical, obtuse well visible tubercle, underside without visible pores; gill cover ray-like rugose, width contained 1⅔ to 1¾ times in its depth, lower margin nearly straight or slightly convex; gill opening ending below the posterior margin of the preoperculum. Pharyngeal teeth hooked to slightly spoon-shaped to grinding, 2.3.5/5.3.2, on the chewing surface partly rugose-tuberculate; scapula obtusely or slightly acutely rounded, obliquely truncate posteriorly; belly flat anterior to ventral fins, angular at the flanks, behind ventral fins obtusely ridged; back elevated, angular, much higher than the belly; scales on the free half and basal half with slightly ray-like longitudinal stripes; 24 to 26 scales in the lateral line, 9 in a transverse row (without the lowest ventral scales) of which 4 (3½) above the lateral line, 8 or 9 in a longitudinal row between occiput and dorsal fin, lowest ventral scales in three longitudinal rows, middle and posterior scales in medial row nearly equal, larger than anterior scales, but not larger than those in flanking rows; lateral line slightly curved, sloping downward anteriorly, nearly straight posteriorly, not or hardly reaching the rostro-caudal line, each scale marked by a simple tube reaching or not reaching the centre of the scale; dorsal fin starting above the base of the ventral fins, acute, emarginate, hardly lower to considerably lower than the body, twice to much less than twice as high as base length, spine medium-sized, posteriorly totally glabrous, without teeth, with the flexible part slightly longer to considerably longer than the head; pectoral and ventral fins acute, pectoral fins slightly longer than ventral fins, contained 5½ to 6 times in the length of the body, pectoral fins not or hardly reaching the ventral fins, ventral fins not or hardly reaching the anal fin; anal fin acute, in younger animals hardly emarginate, in adults not emarginate, considerably lower to not lower than dorsal fin, more than twice as high as base length, the simple third ray thin, nearly totally cartilaginous; caudal fin scaled only at the base, with a deep incision, lobes acute, nearly equal, contained 3¾ to 4⅓ times in the length of the body. Colour: upper part of the body olive, lower part silver; total body sometimes orange-green; iris yellow, upper part dark; all scales on the body towards the base with a membrane with a metallic copper or violetish splendid conspicuous sheen; fins yellowish or pink or, but more rarely, slightly olive, frequently more or less speckled with dark. B. 3. D. 4/9 or 4/10. P. 1/15 or 1/16. V. 2/8. A. 3/5 or 3/6. C. 6/17/6 or 7/17/7, short flanking ones included.

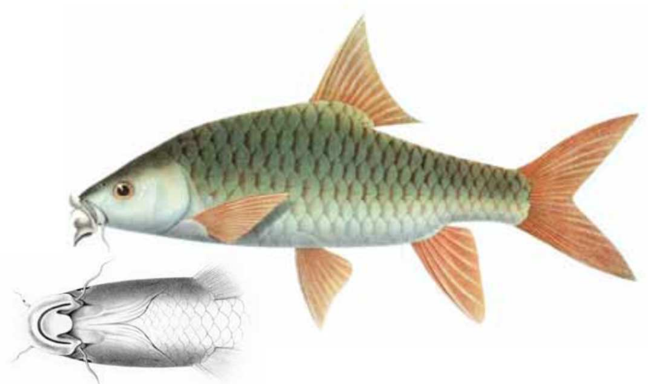

Figure S2.4. *Labeobarbus tambroides* Blkr. Atl. Ichth. Cypr. Tab. XXIII, TL figure 320 mm.

Figure S2.5. Image of paratype RMNH.PISC.2089_b1 deposited at the Leiden museum.

Labeobarbus tambra **Blkr,**

Descr. specier. Pisc. Jav. Nov. Nat. T. Ned. Ind. XIII p. 355. –
Vorstelijke Lipbarbeel **[*Royal Lip-barbel*].**
Atl. Cypr. Tab. XXII.

A *Labeobarbus* with an oblong, compressed body, depth of body contained slightly over 4 to slightly over 5 times in its length, width contained 2 to 11⁄2 times in its depth. Head slightly acute, convex, contained nearly 5 to 51⁄2 times in length of body with caudal fin, nearly 4 to 41⁄3 times in length of body without caudal fin; depth of head contained 11⁄3 to 12⁄5 times, width contained 13⁄4 to 13⁄5 times in its length; eye diameter contained 31⁄2 to 51⁄2 times in the length of the head, eye diameter contained 12⁄5 to 21⁄4 times in the postocular part of the head; distance between the eyes 11⁄4 to 21⁄3 times their diameter; palpebral membrane covering the external margin of the iris only, broader anteriorly than posteriorly, opening nearly circular; snout slightly acute, not to nearly twice as long as the eye, not sticking out in front of the mouth; nostrils much closer to the orbit than to the tip of the snout; rostro-dorsal profile on snout and nape convex, on forehead and crown nearly straight or slightly convex; anterior suborbital bone obliquely pentagonal, length not or hardly greater than depth, lower margin obliquely convex; anterior and posterior lower margins generally concave, anterior margin oblique, posterior margin nearly vertical, upper margins concave or slightly concave (posterior margin generally much shorter than anterior margin) united into an acute, upward pointing angle close to the nostrils, traversed around the middle by a longitudinal crest strongly ascending posteriorly; 2nd suborbital bone quadrangular, much higher anteriorly than posteriorly, length twice to less than twice as great as depth, about twice as low as 1st suborbital bone; upper jaw longer than lower jaw, strongly vertically downward protrusable, ending below the anterior margin of the eye or hardly anterior to the eye, contained 3 to 31⁄4 times in the length of the head; gape slightly oblique; barbels thin, upper jaw barbels generally slightly longer than nasal barbels, slightly to much longer than the eye; lips very broad, fleshy, transversely striped on the oral surface, upper lip not lobed, lower lip protracted into a medium-sized, broad, obtuse lobe; lower jaw at the symphysis with a conical, obtuse, short tubercle, underside on both branches with several conspicuous pores, placed in a longitu- dinal row, not always visible; gill cover ray-like rugose, width contained 12⁄3 to nearly 2 times in its depth, lower margin slightly concave to slightly convex; gill opening ending below the posterior margin of the preoperculum. Pharyngeal teeth hooked to slightly spoon-shaped to grinding, 2.3.5/5.3.2, on the chewing surface tumid or rugose-tuberculate; scapula triangular, obtusely rounded; belly flat anterior to ventral fins, slightly angular at the flanks, behind ventral fins rounded, not ridged; back elevated, angular, much higher than the belly; scales on the free half and basal half with slightly ray-like longitudinal stripes; 22 or 23 scales in the lateral line, 8 in a transverse row (without the lowest ventral scales) of which 4 (31⁄2) above the lateral line, 8 or 9 in a longitudinal row between occiput and dorsal fin, lowest ventral scales in three longitudinal rows, middle and posterior scales in medial row nearly equal, larger than anterior scales, but not larger than those in flanking rows; lateral line slightly curved, lightly concave anteriorly, nearly straight posteriorly, not reaching or hardly reaching the rostro-caudal line, each scale marked by a simple tube generally not reaching the centre of the scale; dorsal fin starting above the base of the ven-tral fins, acute, emarginate, slightly lower to considerably lower than the body, much higher than base length but much less than twice as high, spine thin, posteriorly totally glabrous, without teeth, with the flexible part not shorter to much shorter than the head; pectoral and ventral fins acute, pectoral fins slightly longer than ventral fins, contained 51⁄2 to slightly over 6 times in the length of the body, not reaching the ventral fins, ventral fins not reaching the anal fin; anal fin acute, generally convex, in older animals rounded at the tip, slightly lower to slightly higher than dorsal fin, more than twice as high as base length, the simple third ray thin, nearly completely cartilaginous; caudal fin scaled only at the base, with a deep incision, lobes acute, nearly equal, contained 41⁄4 to about 41⁄2 times in the length of the body. Colour: upper part of the body olive, or dark- or slightly-olive to olive; flanks and lower part silver or golden-green; iris yellow, upper part dark; all scales on the body towards the base on the membrane with a metallic copper or violetish splendid conspicuous sheen; fins yellowish or faintly pink or, in old animals slightly olive or slightly violet.

B. 3. D. 4/9 or 4/10, sometimes also 4/8 or 4/9. P. 1/14 to 1/16. V. 2/8, seldom also 2/7. A. 3/5 or 3/6. C. 5/17/5 or 7/17/7, short flanking ones included.

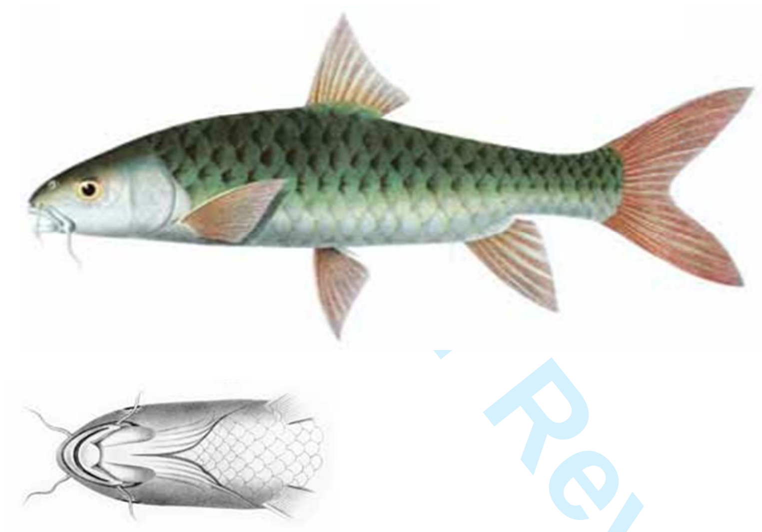

Figure S2.6. *Labeobarbus tambra* Blkr. Atl. Ichth. Cypr. Tab. XXII, Fig. 2. TL figure 330 mm.

***Labeobarbus soro* Blkr.**
***Soro-Lipbarbeel* [*Soro-Lip-barbel*].**
Atl. Cypr. Tab. XX

A *Labeobarbus* with an oblong or slightly elongate, compressed body, depth of body contained 4 1⁄4 to 5 times in its length, width contained about twice in its depth. Head slightly acute, convex, contained 5 to 6 times in length of body with caudal fin, 33⁄4 to 41⁄2 times in length of body without caudal fin; depth of head contained 11⁄3 to 11⁄4 times in its length, width 2 to 12⁄3 times; eye diameter contained 31⁄2 to nearly 4 times in the length of the head, eye diameter contained 11⁄2 to 13⁄4 times in the postocular part of the head; distance between the eyes 11⁄4 to 12⁄3 times their diameter; palpebral membrane covering the external margin of the iris only, opening nearly circular; snout slightly acutely convex, in younger animals shorter than the eye, in old animals longer than the eye, not sticking out in front of the mouth; nostrils closer to the orbit than to the tip of the snout; rostro-dorsal profile convex on crown and nape, nearly straight or slightly concave only on the forehead; interorbital line nearly straight or slightly concave; anterior suborbital bone obliquely pentagonal, length not or hardly greater than depth, lower margin obliquely convex; anterior and posterior lower margins concave, anterior margin oblique, posterior margin nearly vertical, upper margins concave (posterior margin much shorter than anterior margin) united into an acute, upward pointing angle close to the nostrils, traversed around the middle by a longitudinal crest which ascends posteriorly; 2nd suborbital bone obliquely quadrangular, much higher anteriorly than posteriorly, length less than twice as great as depth, twice or less than twice as low as 1st suborbital bone; upper jaw longer than lower jaw, strongly vertically downward protrusable, ending below the anterior rim of the eye, contained nearly 3 to slightly over 3 times in the length of the head; gape slightly oblique; barbels thin, nasal barbels not or slightly longer than the eye, upper jaw barbels much longer than the eye; lower jaw at the symphysis with a conical, obtuse very conspicuous tubercle, underside without conspicuous pores; lips fleshy, transversely rugose on the oral surface, upper lip terete, not protracted, lower lip broad, simply back- sheathed for the total width, broad between lateral sheaths, behind the symphysis fused with lower jaw; gill cover rugose ray-like, width contained $1\frac{1}{2}$ to $1\frac{3}{4}$ times in its depth, lower margin nearly straight or slightly concave; gill opening ending below the posterior rim of the preoperculum. Pharyngeal teeth hooked to slightly spoon-shaped to grinding 2.3.5/5.3.2, on the chewing surface rugose- tuberculate; scapula triangular, obtusely rounded; belly flat anterior to ventral fins, angular at the flanks, behind ventral fins rounded, not ridged; back rather elevated, angular, higher than the belly; scales on the basal half and free half with longitudinal stripes or slightly ray-like stripes, 26 to 28 scales in the lateral line, 8 in a transverse row (without the lowest ventral scales) of which 4 ($3\frac{1}{2}$) above the lateral line, 9 in a longitudinal row between occiput and dorsal fin, lowest ventral scales in three longitudinal rows, scales in medial row gradually increasing in size posteriorly, posterior scales not larger than those in flanking rows; lateral line lightly curved, nearly reaching the rostro-caudal line, each scale marked by a simple tube not reaching the centre of the scale; dorsal fin starting above or hardly anterior to the base of the ventral fins, acute, emarginate, only slightly lower than the body, much higher than base length but much less than twice as high, spine tapering, totally glabrous, with the flexible part not or only slightly longer than the head; pectoral and ventral fins acute, pectoral fins slightly longer than ventral fins, contained $5\frac{2}{3}$ to $5\frac{3}{4}$ times in the length of the body, pectoral fins not reaching the ventral fins, ventral fins not reaching the anal fin; anal fin acute, not or hardly emarginate, in older animals convex, not much lower than dorsal fin, much more than twice as high as base length, the simple third ray thin, bony only at the base; caudal fin scaled only at the base, with a deep incision, lobes acute, upper lobe hardly longer than lower lobe, contained nearly 4 to $4\frac{1}{4}$ times in the length of the body. Colour: upper part of the body olive, lower part slightly olive to golden or silver; iris yellow; scales on back, flanks and tail each with a transverse, crescent-shaped, violet band at the base; fins yellowish or pink-greenish.

B. 3. D. 4/8 or 4/9 or 4/10. P. 1/14 or 1/15. V. 2/8. A. 3/5 or 3/6. C. 6/17/6 or 7/17/7, short flanking ones included.

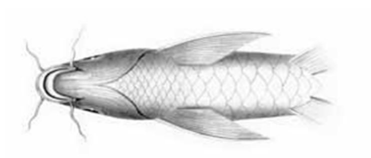

Figure S2.7. *Labeobarbus soro* Blkr. Atl. Ichth. Cypr. Tab. XX, Fig. 2. TL figure 284 mm.

Labeobarbus douronensis Blkr.

Semah-Lipbarbeel [*Semah-Lip-barbel*].
Atl. Cypr. Tab. XXI.

A Labeobarbus with an oblong, compressed body, depth of body contained 41⁄4 to 42⁄3 times in its length, width contained about twice in its depth. Head slightly acutely convex, contained 51⁄5 to nearly 6 times in length of body with caudal fin, nearly 4 to 41⁄2 times in length of body without caudal fin; depth of head contained 11⁄5 to 11⁄3 times, width contained 13⁄5 to 14⁄5 times in its length; eye diameter contained 3 to 41⁄4 times in the length of the head, eye diameter contained 1 2⁄5 to 2 times in the postocular part of the head; distance between the eyes slightly more than once to 1 3⁄4 times their diameter; palpebral membrane covering the external margin of the iris only, broader anteriorly than posteriorly, the opening nearly circular; snout slightly acutely convex, not protruding anterior to the mouth, in younger animals shorter than the eye, in old animals longer than the eye; nostrils much closer to the orbit than to the tip of the snout; rostro-dorsal profile on head and nape convex; interorbital line convex or nearly straight; anterior suborbital bone obliquely pentagonal, length not or hardly larger than height, lower margin obliquely convex; anterior and posterior lower margins concave, anterior margin oblique, posterior margin nearly vertical, upper margins concave (posterior margin much shorter than anterior margin) united into an acute, upward pointing angle close to the nostrils, traversed around the middle by a longitudinal crest ascending posteriorly; 2nd suborbital bone obliquely quadrangular, much higher anteriorly than posteriorly, length twice to much less than twice as great as depth, twice as low to much less than twice as low as 1st suborbital bone; upper jaw longer than lower jaw, strongly vertically downward protrusable, ending below the anterior margin of the eye or hardly anterior to the eye, contained 3 times to 31⁄4 times in the length of the head; gape slightly oblique; barbels thin, nasal barbels not to slightly longer than the eye, upper jaw barbels slightly to much longer than the eye; lower jaw at the symphysis with a conical, obtuse very conspicuous tubercle, underside without conspicuous pores; lips fleshy, transversely rugose on the oral surface, upper lip terete, not prolonged, lower lip broad, not lobed or lobed only over a very short distance, between the lateral folds behind the symphysis rather broadly fused with the lower jaw; gill cover ray-like rugose, width contained 12⁄3 to 14⁄5 times in its depth, lower margin nearly straight or slightly concave; gill opening ending below the posterior rim of the preoperculum. Pharyngeal teeth hooked to slightly spoon-shaped to grinding, 2.3.5/5.3.2, on the chewing surface rugose-tuberculate; scapula triangular, obtusely rounded; belly flat anterior to ventral fins, angular at the flanks, behind ventral fins rounded, not ridged; back rather elevated, angular, higher than the belly; scales on the basal half and free half with longitudinal stripes or slightly ray-like stripes, 21 to 23 scales in the lateral line, 8 in a transverse row (without the lowest ventral scales) of which 4 (31⁄2) above the lateral line, 7 or 8 in a longitudinal row between occiput and dorsal fin, lowest ventral scales in three longitudinal rows, scales in medial row gradually increasing in size posteriorly, scales in this row not larger than those in flanking rows; lateral line curved, slightly to not descending between the rostro-caudal line, each scale marked by a simple tube reaching or not reaching the centre of the scale; dorsal fin starting above or hardly ante- rior to the ventral fins, acute, emarginate, not much lower than the body, much less than twice as deep to nearly twice as high as base length, spine tapering, totally glabrous, with the flexible part slightly longer to not longer than the head; pectoral and ventral fins acute, pectoral fins slightly longer than ventral fins, contained 51⁄3 to 53⁄4 times in the length of the body, not or nearly reaching the ventral fins, ventral fins not reaching the anal fin; anal fin acute, not or hardly emarginate, in old animals slightly convex, not much lower than dorsal fin, much more than twice as high as base length, the simple third ray thin, bony only at the base; caudal fin scaled only at the base, with a deep incision, lobes acute, upper lobe slightly to not longer than lower lobe, contained nearly 4 to 42⁄5 times in the length of the body. Colour: upper part of the body olive, lower part olive -golden or silver; iris yellow or red; scales on back, flanks and tail each with a oblong, diffuse, transverse violetish spot on the base; fins yellow- ish- pink or red.

B. 3. D. 4/8 or 4/9 or 4/10. P. 1/14 to 1/16. V. 2/8. A. 3/5 or 3/6. C. 7/17/7 or 8/17/8, short flanking ones included.

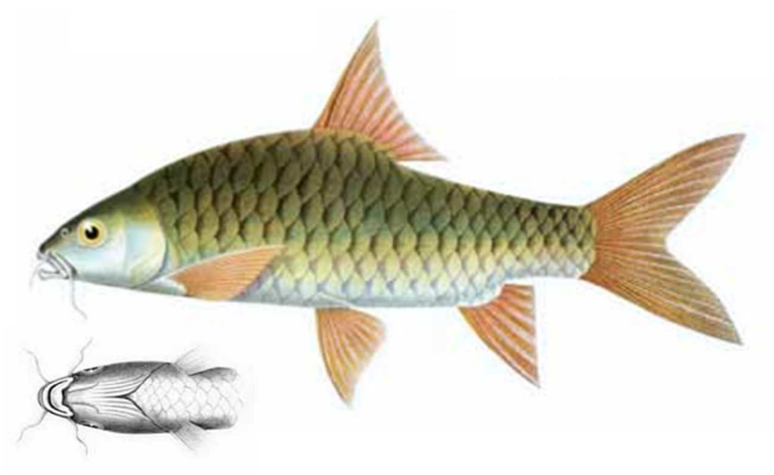

Figure S2.8. *Labeobarbus douronensis* Blkr. Atl. Ichth. Cypr. Tab. XXI, Fig. 2. TL figure 276 mm.

<u>Key to species</u>

I. Dorsal fin scaled at the base, spine robust, without teeth. Gill cover ray-like rugose. Snout acute or slightly acute. A. 21 to 28 scales in the lateral line, 4 above the lateral line.

a. Lower lip with a well developed, very conspicuous lobe.▪ † Upper lip prolonged into a lobe. 24 to 26 scales in the lateral line. D. 4/9 or 4/10. P. 1/15 or 1/16. Depth of the body contained 4 to 41⁄3 times in its length. Head acute, contained 4 3⁄4 to 5 1⁄4 times in the length of the body, depth contained 11⁄3 to 11⁄4 times in its length.

Labeobarbus tambroides Blkr.

†' Upper lip round, not prolonged. 22 or 23 scales in the lateral line. D 4/8 or 4/9 or 4/10. P. 1/14 to 1/16. Depth of body contained slightly over 4 times to slightly over 5 times in its length. Head

contained nearly 5 to 51⁄2 times in the length of the body, depth contained 11⁄3 to 12⁄5 times in its length.

Labeobarbus tambra Blkr.

b. Lower lip with a hardly visible lobe or simply back-sheathed over its total width. Upper lip round, not prolonged. D 4/8 or 4/9 or 4/10. P. 1/14 to 1/16.▪ † Lower lip over the total length simply back-sheathed. 26 to 28 scales in the lateral line. Depth of body contained 41⁄4 to 5 times in its length. Head contained 5 to 6 times in the length of the body, depth contained 11⁄3 to 11⁄4 times in its length.

Labeobarbus soro Blkr.

†' Lower lip with a hardly distinguishable lobe. 21 to 23 scales in the lateral line. Depth of body contained 41⁄4 to 42⁄3 times in its length. Head contained 51⁄2 to nearly 6 times in the length of the body, depth contained 11⁄5 to 11⁄3 times in its length.

Labeobarbus douronensis Blkr.

Weber and de Beaufort (1916)

The following descriptions are from weber and de Beaufort (1916).

Tor soro

Dorsal fin with 3 spines and 8-9 rays; anal fin with 3 spines and 5 rays; Pectoral fin with 1 spine and 14-16 rays; ventral fin with 2 spines and 8 rays; linea leteralis with 24- 28 scales. Height 3.4-3.8 in SL, 4.3-4.6 in length with caudal. Head about 4.3 in SL, 5.4 in length with caudal. Eye about 4 in head length, about 1 1/3 in somewhat prominent snout and nearly twice in interorbital space. Mouth inferior. Lips moderately thick, **median part of lower lip without lobe, but fixed to the skin**. Rostral barbels about as long as eye or longer, shorter than maxillary ones. **Length of operculum 11/2-13/4 in its height**. Origin of dorsal nearer to snout than to base of caudal, opposite 7th or 8th scale lateral line, somewhat before origin of ventrals, separated by 8 or 9 scales from occiput. **Dorsal concave, its third spine ossified, strong, somewhat shorter than head, without its flexible part shorter than head without snout.** Anal oblique, not reaching caudal when depressed, its longest ray somewhat less than dorsal spine. Ventrals conspicuously shorter than, pectorals and much shorter than height of dorsal, far distant from anus, separated by 2 scales from lateral line. Pectorals somewhat shorter than height of dorsal, far distant from ventrals. **Caudal deeply incised, the lobes pointed, much longer than head**. **Least height of caudal peduncle 1 1⁄2 in its length, surrounded by 12 scales.** Silvery, back olivaceous. Scales on upper surface with a darkish base, fins hyaline.

Tor tambroides

Dorsal fin with 3 spines and 9-10 rays; anal fin with 3 spines and 5 rays; pectoral fin with 1 spine and 15-16 rays; ventral fin with 2 spines and 8 rays; linea leteralis with 23-24 scales Height 3 to more than 3.4 or somewhat more in length with caudal. Head about 3.6- 3.8, 4.6 – 5 in length with caudal. Eye 4 – 5, 1 1⁄2 to 2 in interorbital space. Lips broad, swollen, thick, continuous, the upper one generally with an anterior lobe, the **lower one with a long free median lobe, which reaches to a line connecting the corners of the mouth**. Maxillary barbels somewhat longer than the rostral ones, slightly or much longer than eye. Origin of dorsal about in the middle between end of snout and root of caudal, separated by 8 or 9 scales from occiput, opposite to 7th scale of lateral line and slightly before origin of ventrals. Dorsal concave, third spine strong, **osseous about 1 1/3 in head, its stiff portion as long as the head without snout**. Anal truncate, depressed not reaching caudal, its height somewhat less than that of the dorsal. Ventral as long as height of anal, not reaching anus, separated by 2 scales from lateral line. Pectoral slightly shorter than height of dorsal. **Caudal deeply forked, its lobe pointed, the lower one the longer, equal to or longer than head. Least height of caudal peduncle about 1 1⁄2 times in its length, surrounded by 12 scales,** Silvery, back dark, as also the fins.

Tor douronensis

Dorsal fin with 3 spines and 9 rays; anal fin with 3 spines and 5 rays; pectoral fin with 1 spine and 16 rays; ventral fin with 2 spines and 8 rays; linea leteralis with 21- 24 scales Height 3.2-3.3, 4.1 in length with caudal. Head 4- 4.2, 5-5.3 in length with caudal. Eye 4 1⁄2 – 5, 1 1⁄2 or more in snout, twice or somewhat more in interorbital space. Rostral barbels about 1 1⁄2 times, maxillary barbels about twice in eye. Lips thick, continuous, the lower one with median, more or **less developed square lobe, the hindborder of which does not reach the line connecting the corners of the mouth.** The **blunt snout** somewhat prominent, mouth inferior. Origin of dorsal opposite to 6th or 7th scale of lateral line and slightly before that of ventrals, separated by 8 scales from occiput, somewhat nearer to end of snout than to base of caudal. Dorsal concave, its third spine osseous, rather strong, slightly shorter than head, **its stiff part about equal to head without snout**. Anal truncate, slightly less high than dorsal, depressed not reaching caudal. Ventrals separated by 2 scales from lateral line, their length about equal to height of anal, distant from anus. Pectoral slightly shorter than height of dorsal. **Caudal deeply forked, its lobe pointed, about equal to head. Least height of caudal peduncle 1 1⁄2 or more in its length, surrounded by 12 scales.** Silvery, back darkish. Base of scales of back and sides darkish.

Tor tambra

Dorsal fin with 4 spines and 8-9 rays; anal fin with 3 spines and 5 rays; pectoral fin with 1 spine and 14-16 rays; ventral fin with 1 spines and 7-8 rays; linea leteralis with 22- 24 scales. Height 3 1⁄2-4, 4-4 1/5 in length with caudal. Head pointed, 3.3-4.2, 4.1-5.3 in length with caudal. Eye 5-6.6, 1 3⁄4 to more than twice in snout and about twice in slightly convex interorbital space. Maxillary barbels generally somewhat longer than the rostral ones and about equal to length of snout. **Snout prominent**, mouth inferior, **lips thick**, continuous, the lower one with a median **well developed free lobe**, the hindborder of which is convex or truncate, **but does not reach the line connecting the corners of the mouth**. Origin of dorsal opposite to 7th scale of lateral line and slightly before that of ventral, separated by 8 or 9 scales from occiput, nearer to end of snout than to base of caudal. Dorsal concave, its fourth ossified spine rather feeble, with its flexible portion equal to head without snout, **its stiff portion less than half length of head**. Anal truncate, its height somewhat more than that of dorsal, depressed reaching base of caudal or not so far. Ventrals separated by 2 scales from lateral line, their length equal to height of anal or somewhat less, distant from anus. Pectorals much longer than height of dorsal, somewhat less than length of head. **Caudal deeply forked, its lobe pointed, shorter than head. Less height of caudal peduncle 1 1⁄2 in its length, more or less than twice in length of head, surrounded by 12 scales.** Silvery, fins darkish.

Discussion

More recent descriptions of *T. tambroides, T. tambra* and *T. douronensis* are available (see FishBase 2015). However, these are largely based on material from the Mekong which are unlikely to be the same species as types from Indonesia. We therefore did not attempt to draw conclusions on taxonomic validity from comparisons of these descriptions. Recent descriptions of *T. soro* are not available due to its questionable validity (see Supplement 1 and later discussion). The key points contained in the descriptions of Valenciennes, Bleeker and Weber and de Beaufort are listed in Table S2.1

The original descriptions of Valenciennes are generally vague and ambiguous but there are subtle differences in the descriptions:

-*Soro* and *douronenis* have pointed anal fins whereas in *tambra* it is rounded.
-Soro has large ventral fins whereas in *tambra* they are small, no description of the ventral fins of *douronensis* is given.
-*Soro* is more elongate than other fish and has a high number of lateral line scales
-The lateral line in *tambra* is relatively straight but is described as curved in *soro* and marked with a series of large dots in *douronensis*.

However this is not sufficient to practically differentiate the species. The original descriptions of Valenciennes make no mention of lobes or mentum for any species in the descriptions. Bleeker (1854) only mentions lobe size in *tambroides*, stating “the lower (lip) extending into a wide fleshy projecting lobe” but does not offer this statement in a comparative context with other fish. In his accompanying notes, he adds “it is variable with age” but does not imply that *tambroides* has a larger lobe than *tambra* which is currently used as a diagnostic feature. It is only in his later descriptions, translated here, that the lobes are mentioned and used in the key to distinguish the 4 species. Using the lobe to differentiate the species therefore seems to be the invention of Bleeker (1863) and later authors. Bleeker differentiates *tambroides* from *tambra*, in his accompanying notes, using the shape and size of the head, stating “With

Labeobarbus tambra the snout is blunter, the neck more convex, the operculum considerably longer (wider)". However, there is no evidence of a difference in head size in the type material available and snout shape, as discussed in this paper, is affected by phenotypic plasticity. In his notes, Bleeker remarks "Labeobarbus tambra occurs all over Java, but avoids the turbid river mouths. It is often kept in ponds, and reaches a length of more than three foot." The culture of fish in lentic environments is now thought to stimulate the development of a "tambra like" appearance through phenotypic plasticity (Walton pers. obs.).

Furthermore, Bleeker also states in his notes that *tambroides* can be differentiated from *tambra* based on fin ray counts: with the dorsal fin of *tambroides* possessing one less ray than *tambra* and the pectoral fin has one or two less rays. However, there appears to be considerable within population variation in fin ray counts in this group of fishes (Walton pers. obs), indeed, both Bleeker and Weber and De Beaufort described a range of 1-2 rays within the same species in most cases so Bleeker's diagnosis wouldn't be a reliable method of distinguishing these fish. Javan Tor sp. within the same population also display significant variation in head shape. Given our current understanding of the complexities of Tor morphology, the morphological differences that Bleeker describes, therefore do not provide enough evidence to differentiate these two species.

Table S2 1. Summary of the morphological characteristics described in the descriptions of early workers namely Valenciennes (in Cuvier & Valenciennes, 1842), Bleeker (1863) and Weber Weber and de Beaufort (1916) who all examined Indonesian Tor material.

	Soro			***Tambroides***			***Douronensis***			***Tambra***		
	Val	**Bleeker**	**Web & de Be**	**Val**	**Bleeker**	**Web & de Be**	**Val**	**Bleeker**	**Web & de Be**	**Val**	**Bleeker**	**Web & de Be**
Dorsal Fin rays		4 Spines 8-10 Rays	3 Spines 8-9 Rays	NA	4 Spines 9-10 Rays	3 Spines 9-10 Rays		4 Spines 8-10 Rays	3 Spines 9 Rays		4 Spines 8-10 Rays	4 Spines 8-9 Rays
Pectoral Fin rays		1 Spine 14-15 Rays	1 Spine 14-16 Rays	NA	1 Spine 15-16 Rays	1 Spine 15-16 Rays		1 Spines 14-16 Rays	1 Spine 16 Rays		1 Spine 14-16 Rays	1 Spine 14-16 Rays
Anal Fin rays		3 Spines 5-6 Rays	3 Spines 5 Rays	NA	3 Spines 5-6 Rays	3 Spines 5 Rays		3 Spines 5-6 Rays	3 Spines 5 Rays		3 Spines 5-6 Rays	3 Spines 5 Rays
Ventral Fin		2 Spines 8 Rays	2 Spines 8 Rays	NA	2 Spines 8 Rays	2 Spines 8 Rays		2 Spines 8 Rays	2 Spines 8 Rays		2 Spines 7-8 Rays	1 Spine 8 Rays
Lateral line scales	25	26-28	24-28	NA	23-26	23-24	21	21-23	21-24	22	22-23	22-24
Length (x height)			3.4 – 3.8			3 – 3.4			3.2 – 3.3			3 1⁄2-4
Length with caudal	4 2/3	4 3/4-5	4.3 - 4.6	NA	5	-	4.5	4 1⁄4 - 4 3/5	4.1	4	4-5	4-4 1/5
Eye diameter		Head length/ 3 1⁄2 – 4	Head length/ 4	NA	Head length/ 3-4	Head length/ 4 – 5 ½		Head length/ 3 – 4 1/3	Head length/ 4 ½ - 5		Head length/ 3-4	Head length/ 5 – 6.6
Interorbital distance (x eye		1 1⁄4 - 1 2/3	2	NA	1 – 1 4/5	1 1⁄2 - 2		1 – 1 2/3	>2		1 1⁄4 -2 1⁄3	2

diameter)												
Lips		Bleeker (1854): “Fleshy” Bleeker (1863) “upper lip terete, not protracted, lower lip broad, simply back-sheathed for the total width, broad between lateral sheaths, behind the symphysis fused with lower jaw”	Moderately Thick. Median part of lower lip without lobe, but fixed to the skin.	NA	Bleeker (1854) “Very broad and very fleshy, with the lower (lip) extending into a wide fleshy projecting lobe.” Bleeker (1863) “Upper lip protracted into a lobe which generally is obtusely rounded, lower lip into a lobe, generally longer than that of the upper lip, obtusely or acutely rounded”	Swollen Thick Upper one with anterior lobe. Lower with a long free median lobe, which reaches to a line connecting the corners of the mouth		Bleeker (1854) “Fleshy” Bleeker (1863) “Upper lip terete, not prolonged, lower lip broad, not lobed or lobed only over a very short distance, between the lateral folds behind the symphysis rather broadly fused with the lower jaw”	Thick Lower with median, more or less developed square lobe, the hindborder of which does not reach the line connecting the corners of the mouth		Bleeker (1863): Upper lip not lobed, lower lip protracted into a medium-sized, broad, obtuse lobe.	Thick. lower one with a median well developed free lobe, the hindborder of which is convex or truncate, but does not reach the line connecting the corners of the mouth.

Barbels		Nasal (rostral) barbels not or slightly longer than the eye, upper jaw (maxillary) barbels much longer than the eye	Long as eye	NA	Upper jaw (maxillary) barbels slightly longer than nasal (rostral) barbels, slightly longer to considerably longer than the eye	Maxillary barbels somewhat longer than the rostral ones, slightly or much longer than eye.		Nasal (rostral) barbels not to slightly longer than the eye, upper jaw (maxillary) barbels slightly to much longer than the eye	Rostral 1 ½ times eye. maxillary Twice eye		Upper jaw (maxillary) barbels generally slightly longer than nasal (rostral) barbels, slightly to much longer than the eye	Maxillary longer than rostral and equal to snout length
Width of operculum		Operculum depth/ 1 1/2 - 1 3/4	11/2 – 13/4	NA	Operculum depth/ 1 2/3 – 1 3⁄4	-		Operculum depth/ 12⁄3 to 14⁄5	-		Operculum depth/ 12⁄3 - 2	-
Depth of operculum		11⁄2 to 13⁄4 x operculum width		NA	1⅔ to 1¾ x operculum width			12⁄3 to 14⁄5 x operculum width			12⁄3 to nearly 2 x operculum width	
Head length	1 1/3 – 1 1⁄4 x head width	3 1⁄2 – 4 x eye diameter	4.3 in SL	NA	3-4 x eye diameter. 1 1/3 – 1 1⁄4 x head depth. 1 3⁄4 - 1 3/5 x width	3.6 - 3.8 in SL		3 – 4 1/3 x eye diameter. 1 1/3 – 1 2/5 x head depth. 1 2/3 – 1 3⁄4 x width	4 - 4.2 in SL		31⁄2 - 51⁄2 x eye diameter. 11⁄3 - 12⁄5 x head depth. 13⁄4 - 13⁄5 x width	3.3 – 4.2 in SL
Snout		Snout slightly acutely convex, in younger animals shorter than the eye, in old animals longer than	-	NA	Snout acute, in younger animals shorter than the eye, in adults longer than the eye, not sticking out in front of the	-		Snout slightly acutely convex, not protruding anterior to the mouth, in younger animals shorter than the eye, in old	Blunt, NA somewhat prominent		Snout slightly acute, not to nearly twice as long as the eye, not sticking out in front of the	Prominent

	the eye, not sticking out in front of the mouth.		mouth, nearly straight or slightly convex.	animals longer than the eye	mouth.
Width	½ height	NA	½ height	½ height	Height/2 - 11/2
Height	2x width	NA	2x width	2x width	2 - 11⁄2 x width

Tor douronensis are widely differentiated by local people from other SE Asian *Tor* species by the size of the fins, with specimens with enlarged fins often reported as *douronensis*. However relative fin size of *douronensis* is not mentioned in any of the original descriptions or accompanying notes (*soro* is noted as having large ventral fins in Valenciennes (1842)). Bleeker describes how *douronensis* can be differentiated from *soro* in his accompanying notes stating it has a more laterally compressed body shape compared to the elongated *soro* and has fewer lateral line scales. This dichomotomy in body shapes can be observed in Javan specimens (see Fig. 2 in main document). However, Bleeker offers little explanation of the difference between *douronensis* and *tambra*.

The descriptions of *Tor soro*, combined with Bleekers drawing of the fish suggest this fish would be more appropriately placed in the genus *Neolissochilus*. Kottelat (2013) and Khaironizam et al. (2015) recommend fish described as *T. soro* should be reclassified as *N. soro* (only currently valid in Java), *N. soroides* (valid in mainland SE Asia) or *T. tambra* (valid in both areas). Despite this, *Tor soro* is currently identified throughout Indonesia and appears to be the most commonly used name for Indonesian mahseer species. Haryono (2006) demonstrated when using discriminant function analysis of morphometirc characteristics, *Tor soro* could be separated (100% grouping) from its cogeners (*Tor tambra, Tor tambroides* and *Tor douronensis*), whereas the other tor species showed considerable overlap. However, this paper is considered grey literature and the results should be treated with appropriate caution. This fish is often described as not possessing a lobe, which has probably led to much confusion of this species with others. On inspection of specimens classified as soro in the type location (MZB, Bogor, Java) it is apparent that they do have a lobe or at least the impression of a lobe, denoted by creases at the edges where the median portion of the lips meets the lips on either side. The reclassification of this fish as *Neolissochilus soro* may not therefore be necessary. If this fish is to be retained as a valid Tor species the description of it having “no lobe” should be revised to “having a very small lobe or two notches delineating presence of lobe” to avoid confusion and misinterpretation.

Kottelat (2013) was “not able to see real differences in the descriptions of *T. douronensis* and *T. tambra* by Valenciennes, Bleeker or Weber & de Beaufort” so tentatively follows the synonymy of the species suggested by Roberts (1993). We partially agree with this statement in that Valenciennes does not present enough evidence in isolation, to differentiate the species but this is not the case in Bleeker and Weber and de Beaufort. In the original descriptions it could also be said that there isn’t enough to see real similarities in the data presented either.
If we consider the descriptions of Bleeker and Weber and de Beaufort as primary texts we have more evidence from which to draw conclusions. According to these descriptions *douronensis* and *tambroides* only apparently differ in lobe size/ shape and subtle differences head length and head to eye size ratios (although the two authors contradict each other somewhat). The similarity in descriptions of these two species, coupled with the similarity of *tambroides* to *tambra* (as discussed previously) could therefore justify the synonymy of *douronensis, tambroides* and *tambra* however using Weber and de Beaufort’s evidence alone, synonomy between *tambra* and any other species described here does not seem acceptable given distinct differences in

spine and ray counts (Dorsal: 4 vs 3, Ventral: 2 vs 1 in *tambra* vs *douronensis, tambroides, soro* respectively) and lateral line scale counts (Table S2). The distinction between species in these description is perhaps most significant between *tambra* and *soro*, with clear differences in body shape, lateral line (scale counts and appearance), ventral fin size and fin ray counts, undermining the current synonymy of *Tor soro* with *Tor tambra*. The designation of these fish as synonymous was probably based on secondary evidence with little reference to these early descriptions. Roberts (1999) erroneously states "In the key to species, he [Bleeker] gives 26-28 scales in lateral series for *T. tambra*." If this were true it would make the scale counts of *tambra* and *soro* comparable, possibly influencing the authors decision to consider the two synonymous. In fact, Bleeker records 22-23 scales on the lateral line in *tambra*, which is quite different to *soro's* 26-28 scales.

References

Bleeker, P. Overzigt der ichthyologische fauna van Sumatra, met beschrijving van eenige nieuwe soorten. Natuurkd. Tijdschr. Neder.-Indië 7:49-108 (1854).

Bleeker, P. *Atlas ichthyologique des Indes Orientales Neerlandaises. Tome Ill. Cyprins.* Frederic Muller, Amsterdam. 150 pp. tabs. CII-CXLIV (1863).

Cuvier, G. and A. Valenciennes. *Histoire naturelle des Poissons. Vol.* 16. Paris. xx+472 pp., pIs. 456-487 (1842).

Froese, R. and D. Pauly (eds). FishBase. World Wide Web electronic publication version (11/2014). http://www.fishbase.org. Accessed 17 June 2015 (2015).

Haryono, H. and A.H. Tjakrawidjaja. Morphological study for identification improvement of Tambra Fish (Tor spp.: Cyprinidae) from Indonesia. Biodiversitas 7(1) 59-62 (2006).

Roberts, T.R. The freshwater fishes of Java, as observed by Kuhl and van Hasselt in 1820–23. Zoologische Verhandelingen 285: 1–94 (1993).

Khaironizam, M.Z., M. Zakaria-Ismail, and J.W. Armbruster. Cyprinid fishes of the genus *Neolissochilus* in Peninsular Malaysia. Zootaxa **3962** (1) 139-157 (2015).

Kottelat, M. The fishes of the inland waters of Southeast Asia: a catalogue and core bibliography of the fishes known to occur in freshwaters, mangroves and estuaries. Raffles B Zool (Suppl. 27):1-663 (2013).

Oijen, M.J.P van, and G.M.P. Loots. An illustrated translation of Bleeker's Fishes of the Indian Archipelago Part II Cyprini. Zool. Med. Leiden 86 (1), 8.vi.2012: 1-469, figs 1-131 (2012).

Weber, M., and L.F. de Beaufort. The fishes of the Indo-Australian Archipelago. Ill. Ostariophysi: II Cyprinoidea, Apodes, Synbranchi. E. J. Brill, Leiden. xv+455 pp (1916).

SUPPLEMENT 3

Morphological characteristics of fish sampled by Wibowo et al. (unpublished). Fish reported in this table are known to relate to the GenBank accession numbers KC905001-24 (Figure 7) but unfortunately, it is not known which sequences correspond to each voucher specimen as this was not recorded.

Total length (mm)	180	149	177	150	217	167	114	256
Standard length	146	120	140	137	178	133	93	210
Head length	33.28	26.39	32.01	25.6	40.65 *(operculum removed)	29.43	20.54	38.24 *(operculum removed)
Head depth	24.04	20.38	22.18	20.54	28.47	21.78	14.58	29.54
Head width	17.87	15.58	17.28	16.44	22.02	16.86	10.97	24.36
Pre-orbital distance	10.2	9.62	11.39	10.16	13.57	10.77	6.11	13.58
Post-orbital distance	14.23	11.45	13.86	11.26	17.26 *	12.66	8.9	22.22
Eye diameter	7.96	6.7	6.87	7.04	8.4	7.01	5.37	10.29
Inter orbital width	11.27	9.79	11.27	9.99	16.01	9.85	7.41	18.06
Pre-dorsal distance	65.36	47	62.53	53.29	70.63	55.53	38.37	83.96
Post-dorsal distance	51.87	44.59	44.98	34.75	64.81	41.34	28.21	73.38
Dorsal-fin base length	19.07	15.2	17	17.13	25.69	15.7	12	20.3
Dorsal-fin depressed length	broken	27.73	29.96	23.85	38.17	25.66	broken 22	40.68
Anal-fin base length	9.28	8.65	9.33	9.33	12.43	8.21	6.55	13.47
Anal-fin depressed length	24.37	19.34	21.19	17.7	28.19	23.92	15.57	34.86
Pre-anal distance	97.45	76.6	95.03	84.18	129	89.4	60.02	161
Pectoral-fin length	27.85	21.41	24.83	20.41	33.78	25.16	15.14	37.71
Pelvic-fin length	23.58	21.42	24.84	20.34	29.61	21.61	14.13	32.8
Body width	17.84	14.25	18.09	15.4	22.39	16.46	11.62	27.9
Body depth	39.57	30.38	36.84	34.52	52.71	35.21	23.36	52.46
Distance between pectoral & anal fins	61.89	46.76	64.56	51.5	70.61	56.33	37.26	94.36
Distance between pelvic & anal fins	35.42	19.51	32.61	27.27	31.04	30.93	16.73	48.67

Length of caudal fin	41.36	28.01	34.7	29.68	39.47	35.12	22.19	50.55
Length of caudal peduncle	20.09	18.13	22.86	17.32	35.2	20.18	14.99	33.06
Caudal peduncle depth	17.06	15.08	15.3	13.58	21.27	16.26	10.15	22.97
Meristic analysis								
Lateral scale count	24	22	25	22	23	23	23	24
Predorsal scales	10	10	9	9	9	8	9	8
Circumpeduncle scales	10	10	10	10	10	10	10	10
Scales above the lateral line (DLL)	4.5	4.5	3.5	4.5	4.5	4.5	4.5	4.5
Scales below the lateral line (VLL)	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5
Dorsal fin rays count	IV, 8	IV, 8	IV, 8	IV, 8	IV, 8	IV, 8	IV, 9	IV, 8
Pelvic fin rays count	II, 8	II, 8	II, 8	II, 8	II, 8	II, 8	II, 8	II, 8
Pectoral fin rays count	I, 16	I, 15	I, 15	I, 14	I, 14	I, 14	I, 15	I, 15
Anal fin rays count	III, 6	III, 6	III, 5	III, 5	III, 5	III, 5	III, 5	III, 5
Trophic morphology characteristics								
Lips description	Relatively thin lips.	Relatively thin lips.	Relarively thick lips	Relarively thick lips	Relatively thin lips.	Relarively thick lips	Relatively thin lips.	Relatively thin lips.
Lips width (middle of top lip)	2	1.72	3.61	3.26	2.71	2.7	1.2	1.9
Lobe description	Short and blunt. Does not extend past an imagined line between the corners of the mouth sqaure in shape	Short and blunt. Does not extend past an imagined line between the corners of the mouth sqaure in shape	Not very long, rounded. extends level to the corners of the mouth.	Not very long, rounded. Does not extend to below the corner of the mouth.	Short and blunt. Does not extend past an imagined line between the corners of the mouth sqaure in shape	Not very long, rounded. Does not extend to below the corner of the mouth.	Only discernable by notches on the corners of the jaw	Short and blunt. Does not extend past an imagined line between the corners of the mouth sqaure in shape
Lobe length	3.35	1.99	3.82	3.4	4.41	3.69	1.9	4.13
Snout description	Blunt, rounded	Blunt, rounded	Pointed, more triangulur in ventral view profile	Pointed, more triangulur in ventral view profile	Blunt, rounded	Pointed, more triangulur in ventral view profile	Pointed, more triangulur in ventral view profile	Blunt, rounded
Snout length	14.89	14.26	16.18	14.38	19.92	13.71	10.16	22.67

Maxillary barbel length	12.97	8.49	11.36	8.62	15.76	8.57	5.3	15.17
Rostral barbel length	9.11	5.9	6.31	5.05	11.78	7.62	4.69	12.3
maxilla width	7.83	6.24	7.73	6.36	9.4	7.24	4.78	8.94
Additional notes	Maxillary barbel extends past the eye. Tambra morph type. Tambra/ Douro	Maxillary barbel extends past the eye. Tambra morph type. Tambra/ Douro	Tambroides morph type. Maxillary barbel extends past the eye	Tambroides morph type. Maxillary barbel extends past the eye	The guts have been removed Maxillary barbel extends past the eye. Tambra morph type. Tambra/ Douro	The guts have been removed Tambroides (apart from lobe) morph type. Maxillary barbell extends past the eye	Tambroides (apart from lobe) morph type. Maxillary Barbel extends past the eye	Maxillary barbel extends past the eye. Tambra morph type. Tambra/ Douro