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## Research article

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# The identity of *Barbus capensis* Smith, 1841 and the generic status of southern African tetraploid cyprinids (Teleostei, Cyprinidae)

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**Abstract.** The identity of *Barbus capensis*, as described by Andrew Smith (1841), is reviewed following a careful examination of the lectotype in the Natural History Museum, London. Evidence shows clearly that it represents a specimen of the Berg-Breede River whitefish or ‘witvis’ and not the species known as the Clanwilliam yellowfish, to which it was attributed until recently. The original illustration of the species is shown to be a composite of these two different species. A replacement name for the Clanwilliam yellowfish is drawn from the earliest described synonym, *Labeobarbus seeberi* (Gilchrist & Thompson, 1913). Following widespread recognition that the genus *Barbus* Daudin, 1805 does not occur in sub-Saharan Africa, the generic status of the Berg-Breede River whitefish (witvis) and other tetraploid cyprinines of southern Africa is reviewed, taking genetic and morphological characters into account. Five distinct lineages, each representing a genus, are recognized, including the genera *Pseudobarbus* Smith, 1841 and *Cheilobarbus* Smith, 1841, and three new genera described herein: *Amatolacypris* gen. nov., *Sedercypris* gen. nov. and *Namaquacypris* gen. nov.

**Keywords.** Taxonomy, genera, mtDNA, tetraploids, Smiliogastrini.

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## Introduction

The advent of molecular phylogenetic analyses and genomics has rapidly improved the understanding of interrelationships of fishes in large diverse orders like the Cypriniformes (Mayden *et al.* 2008, 2009; Conway *et al.* 2010; Saitoh *et al.* 2011). At this time, the inter-familial relationships within the order are reaching consensus (Yang *et al.* 2015). Higher level intra-family relationships within the Cyprinidae, one of the largest and most complex vertebrate families in existence, have also received attention (Shunping *et al.* 2008; Wang *et al.* 2012). Cyprinids are widespread stream and river fishes that feature considerable convergent phenotypes across the continents. Early scientific explorations in colonial times often resulted in weak taxonomy and large genera that mask species relationships under a cover of general similarity. Outsized genera such as *Barbus*, for hundreds of species from Europe to Africa and even Asia, simply make no sense of the concept of a genus that seeks to portray the closest phylogenetic relationships of species. The type specimens and their attached African species names, derived from early colonial-era explorations, reside mostly in the large museums of European nations. This has obstructed the easy resolution of such outsized genera, as well as the identities and relationships of numerous species, by subsequent generations of researchers in home countries. The emergence of modern technologies for analytics and communication is helping to overcome these limitations, and the resultant taxonomic convulsions are now widespread. This situation is typical for a number of African freshwater fish genera, and in this study we seek to disentangle the deep-rooted and historical taxonomic confusion of a distinct clade of African cyprinids.

Andrew Smith (1841: unnumbered 2<sup>nd</sup> page of description) described and illustrated a large cyprinid fish that he named *Barbus capensis*, from the “rivers of the western coast of South Africa, more particularly the Breede and Oliphants rivers”. In the description Smith referred to “four grown specimens”, of which only one is known to survive, preserved in the Natural History Museum, London (NHMUK). The species was initially recognized as the Berg-Breede River whitefish or witvis (Afrikaans for whitefish) (Boulenger 1911; Gilchrist & Thompson 1913; Barnard 1937). However, on information that he received from J.R. Norman at the NHMUK about the form of the scales of the type specimen, Barnard (1937) attributed the name to the Clanwilliam yellowfish, a well-known species from the Olifants River system (Skelton 2001). He accordingly renamed the witvis as *Barbus andrewi*, for Sir Andrew Smith.

Upon re-examination of the type specimen, Vreven *et al.* (2016) reversed this action by concluding that the correct identity of the species is the witvis of the Berg and Breede rivers, and not the Clanwilliam yellowfish. Accordingly, they restored the name of the witvis to *Barbus capensis* (Smith, 1841) and that of the Clanwilliam yellowfish to *Labeobarbus seeberi* (Gilchrist & Thompson, 1913). As both the witvis and the Clanwilliam yellowfish are large and well-known species, these scientific name changes are undoubtedly disruptive to the community and need a clear explanation (Skelton 2016). This is especially relevant because, as reflected in the genera of both aforementioned species, the name *Barbus*, formally attributed to many African species, now has been restricted to a lineage of European species. The many African species that were formally part of this genus have been dispersed into different genera or left in a basket of unclassified ‘*Barbus*’ following the findings of Berrebi *et al.* (1996, 2014), Machordom & Doadrio (2001), Tsigenopoulos *et al.* (2002, 2010) and Yang *et al.* (2015). The taxonomic recommendations made by Yang *et al.* (2015) with regard to a lineage of tetraploid species from southern Africa, including species of the genus *Pseudobarbus*, was to place all species other than *Pseudobarbus* in a temporary genus ‘*Pseudobarbus*’. This suggestion was accepted by Skelton (2016) pending further analysis of the tetraploid clade. The witvis is a member of the tetraploid lineage, and therefore both its specific taxonomy and its generic status are in question.

This paper details the information that led Vreven *et al.* (2016) to re-identify Andrew Smith’s type of *Barbus capensis*, and reviews the generic placement of the witvis species and its allies.

## Material and methods

### Abbreviations

#### Institutions

- MRAC = Musée Royal de l'Afrique Centrale, Tervuren, Belgium  
NHMUK = Natural History Museum, London, UK  
SAIAB = South African Institute for Aquatic Biodiversity, National Research Foundation, Grahamstown, South Africa  
SAM = South African Museum, now the Iziko Museum, Cape Town  
ZMB = Museum für Naturkunde (formerly Zoologischen Museum), Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität, Berlin, Germany

#### Morphology

- HL = head length  
LL = lateral line  
SL = standard length

### Material examined

Comparative material, additional to specimens studied by Skelton (1980), used for determining the identity of the lectotype of *Barbus capensis* in this study is listed below. Morphological measures taken are based on Hubbs & Lagler (1964) as interpreted by Skelton (1988) and Armbruster (2012).

#### '*Pseudobarbus*' *serra* (Peters, 1864)

SOUTH AFRICA: holotype of '*Pseudobarbus*' *serra* (142 mm SL), Cape of Good Hope, Cape Colony, Krebs leg. (ZMB 3458); 1 specimen (132 mm SL), Krebs leg. (ZMB 3451); 4 specimens (53–184 mm SL), Olifants system, Olifants River, Visgat, National Heritage Site, -33.05189895, 19.2057991028, 10 Mar. 1998, R. Bills, D. Impson, D. Naran and E. Swartz leg. (SAIAB 58392); 2 specimens (160–184 mm SL), Olifants system, Driehoeks River, from aquarium Algeria Nature Conservation, -32.47999954, 19.2299995422, 12 Mar. 1998 (SAIAB 58397); 5 specimens (68–100 mm SL), Olifants system, Tra-tra River (big pool above Wuppertal), -32.28329849, 19.2105998993, 14 Nov. 1998, E. Swartz (SAIAB 59598); 2 specimens (71–158 mm SL), Olifants system, Lower Eselbank gorge, Tra-tra branch, -32.33610153, 19.2436008453, 15 Nov. 2015, R. Bills and E. Swartz leg. (SAIAB 59600); 1 specimen (65 mm SL), Olifants system, Biedouw River (below and at redfin limit), -32.16830062, 19.1618995667, 16 Nov. 1998, R. Bills and E. Swartz leg. (SAIAB 59606); 3 specimens (101–155 mm SL), Driehoeks River, Sanddrif falls, -32.4925003, 19.2803001404, 18 Nov. 1998, R. Bills and E. Swartz leg. (SAIAB 59611); 1 specimen (391 mm SL), Olifants River, Clanwilliam district, Bulshoek dam, -32.033333, 18.783333, 23 Sep. 1972, P. Skelton leg. (SAIAB 120947); 4 specimens (274–352 mm SL), Olifants system, Twee/Leeu River, -32.697778, 19.312222, 11 Oct. 1973, P. Skelton leg. (SAIAB 121205); 1 specimen (206 mm SL), Olifants system, Driehoeks River, Clanwilliam/Welbedacht road, -32.468333, 19.225278, 15 Mar. 1982, A. Scott, S. Thorne and K. Hamman leg. (SAIAB 128116); 3 specimens (221–336 mm SL), Olifants River, Clanwilliam, -32.7167, 19.0333, 10 Apr. 1937, K.H. Barnard, C.W. Thorne and A.C. Harrison leg. (SAIAB 135474).

#### '*Pseudobarbus*' *capensis* (Smith, 1841)

Specimens previously identified as '*Barbus*' *andrewi* Barnard, 1937, now a junior synonym of '*P.*' *capensis*.

SOUTH AFRICA: holotype of '*Pseudobarbus*' *capensis* (345 mm SL), west coast of Cape Colony, Dr. Andrew Smith leg. (NHMUK 1845.7.3.99); holotype of *B. andrewi* (140 mm SL), Burg River [= Berg River], Paarl Div., SW Cape, ± -32.766667, 18.150000, South African Museum leg. (NHMUK

1901.2.11.9); 2 specimens (85–125 mm SL), Berg River, Paarl Div., SW Cape, ± -32.766667, 18.150000, Sloggett leg. (NHMUK 1903.4.27.94–95); 1 specimen (135 mm SL), Berg River, near Paarl, ± -32.766667, 18.150000, Dr. J.D.F. Gilchrist leg. (NHMUK 1900.11.6.58); 4 specimens (172–232 mm SL), Western Cape, Jonkershoek Fisheries Station, -33.95000076, 18.9167003632, 4 Feb. 1987, L. Oellermann leg. (SAIAB 28427); 1 specimen (237 mm SL), Western Cape, Jonkershoek Fisheries Station, -33.95000076, 18.9167003632, 3 Feb. 1987, L. Oellermann leg. (SAIAB 28430); 1 specimen (136 mm SL), Breede River system, Breede River, ± -34.400000, 20.833333 (SAIAB 45061); 5 specimens (103–163 mm SL), Breede River, ± -34.400000, 20.833333, 1993, W. Haselaw leg. (SAIAB 52691); 5 specimens (289–363 mm SL), Breede River, Worcester, -33.678611, 19.426389, 3 Oct. 1973, P. Skelton and P. Burdett leg. (SAIAB 121204); 1 specimen (368 mm SL), Hex River, Breede River system, Worcester, -33.750000, 19.666667, 15 Oct. 1960, R. Jubb leg. (SAIAB 121289); 2 specimens (160–181 mm SL), McGregor, Langeberg (cement dam), -33.950000, 19.816667, 23 Sep. 1980, C. Stuart leg. (SAIAB 128191); 2 specimens (231–235 mm SL), Breede River system, Buffeljags River, Somerset Gift Farm, -34.000000, 20.601667, 6 Dec. 1986, S. Thorne leg. (SAIAB 130630); 1 specimen (304 mm SL), Berg River, ± -32.766667, 18.150000, 5 May 1972, Scarbow leg. (SAIAB 134671); 1 specimen (458 mm SL), Brandvlei, ± -32.950000, 20.483333, Oct. 1941, A.C. Harrison leg. (SAIAB 135679); 5 specimens (42–47 mm SL), Groot Drakenstein, Berg River, -32.900000, 18.316700, 25 Nov. 2004, A.C. Harrison leg. (SAIAB 135795).

#### ***Labeobarbus seeberi* (Gilchrist & Thompson, 1913)**

SOUTH AFRICA: 1 lectotype (185 mm SL), Olifants River, Clanwilliam, Cape Province, ± -31.700000, 18.200000, C.R. Seeber leg. (ex SAM), (NHMUK 1936.8.4.6); 2 paralectotypes (87–97 mm SL), same collecting data (SAIAB 134867); 1 specimen (165 mm SL), Olifants River, Clanwilliam, Cape, ± -31.700000, 18.200000, South African Museum leg. (NHMUK 1936.8.4.4); 5 specimens (1 examined: 188 mm SL), Olifants River, Clanwilliam, Cape Province, ± -31.700000, 18.200000, South African Museum leg. (NHMUK 1937.10.4.1–5); 1 specimen (380 mm SL), Olifants system, Middeldeer River, -32.750000, 19.216700, 20 Mar. 1996, R. Bills leg. (SAIAB 51534); 1 specimen (134 mm SL), Olifants system, Noordhoeks River, ± -32.720833, 19.065556, 22 Dec. 1996, R. Bills, M. da Pinna and D. Naran leg. (SAIAB 54113); 1 specimen (176 mm SL), Olifants system, Noordhoeks River (above road bridge), ± -32.720799, 19.065599, 22 Mar. 1997, M. Marriott and L. Randall leg. (SAIAB 54688); 1 specimen (179 mm SL), Boskloof River (50 m past the drilling site), Olifants system, ± -32.558102, 19.058901, 23 Feb. 1998, R. Bills, D. Naran and E. Swartz leg. (SAIAB 58362); 6 specimens (1 examined: 101 mm SL), Olifants system, Rondegat River, Upper Keurbos Farm, -32.294399, 18.996901, 23 Mar. 2002, R. Bills, M. Cunningham and E. Swartz leg. (SAIAB 65536); 2 specimens (1 examined: 442 mm SL), Olifants system, 15 Oct. 1960, R.A. Jubb leg. (SAIAB 121138); 7 specimens (1 examined: 435 mm SL), Olifants system, Tharahamina farm (Camp site), ± -32.862500, 19.090278, 28 Mar. 1980, G. Gabriels and S. Thorne leg. (SAIAB 126907); 4 specimens (186–273 mm SL), Olifants system, Kobee, Doring River, Boskraal Farm, -31.592778, 19.075833, 23 Nov. 1983, S. Thorne leg. (SAIAB 129144); 1 specimen (260 mm SL), Olifants system, Visgat, ± -33.055000, 19.208056, 17 Feb. 1987, S. Thorne leg. (SAIAB 130760); 8 specimens (1 examined: 354 mm SL), Olifants River, Clanwilliam, ± -32.716700, 19.033300, Mar. 1938, K.H. Barnard and C.W. Thorne leg. (SAIAB 135537); 13 specimens (6 examined: 74–103 mm SL), Olifants system, Jan Dissels River, Clanwilliam, ± -32.183300, 18.883301, 13 Nov. 1987, L. Oellermann leg. (SAIAB 28404).

#### **Molecular analysis**

Species sampled for DNA analysis include representatives of all the southern African cyprinine tetraploid genera as determined in this study: *Amatolicus trevelyani* (Günther, 1877) gen. et comb. nov., *Sedercypris calidus* (Barnard, 1938) gen. et comb. nov., *Sedercypris erubescens* (Skelton, 1974) gen. et comb. nov., *Cheilobarbus capensis* Smith, 1841, *Cheilobarbus serra* (Peters, 1864) comb. nov., *Namaquacypris*

*hospes* (Barnard, 1938) gen. et comb. nov., *Pseudobarbus afer* (Peters, 1864), *Pseudobarbus burchelli* Smith, 1841 and *Pseudobarbus quathlambae* (Barnard, 1938). *Enteromius* Cope, 1867, represented by *E. anoplus* (Weber, 1897), was used as an outgroup genus in this analysis.

We derived our phylogeny following methods of DNA extraction, amplification, mitochondrial DNA cytochrome *b* sequencing and analysis done in Swartz *et al.* (2009). Thirteen sequences, representing eight species, were sourced from Genbank (from Tsigenopoulos & Berrebi 2000; Machordom & Doadrio 2001; Tsigenopoulos *et al.* 2002; Durand *et al.* 2002) and a further 19 individuals were sequenced specifically for the present study (Appendix 1). The 32 sequences across a 1080 base pair region of cytochrome *b*, yielded 21 haplotypes. These were compared using Bayesian analyses performed in MrBayes v.3.0b4 (Huelsenbeck & Ronquist 2001). *Enteromius anoplus* (Weber, 1897) was used as an outgroup and *Pseudobarbus burchelli* Smith, 1841, *P. afer* (Peters, 1864) and *P. quathlambae* (Barnard, 1938) were included for comparison and to represent the three major *Pseudobarbus* sublineages identified by Swartz *et al.* (2009).

Bayesian posterior probabilities and branch lengths were estimated with the generalised time reversible model of DNA substitution with gamma-distributed rate variation across sites. One cold and three heated Monte Carlo Markov chains were run for a million generations. Resulting log-likelihood scores were plotted and showed that runs became stable before 5000 generations. To ensure that only optimal trees were being sampled, we discarded the first 10000 generations as burn-in. Optimal trees were sampled every 100 generations, yielding 10000 trees. Posterior probabilities and branch lengths were based on these optimal trees.

## Results

### Characters of the lectotype of *Barbus capensis* Smith, 1841

The type specimen of *Barbus capensis* (NHMUK 1845.7.3.99) (Fig. 1) was identified by Barnard (1937) as the lectotype of the species (see ICZN 1999: Art. 74.6). Smith (1841) indicated that he used four adult specimens for his original description of *B. capensis* but, apart from the type of *B. marequensis* (see Greenwood & Crass 1959), no other specimens of large cyprinids available to Smith in the 1830s are known to exist.

The evidence for identifying this specimen as a witvis is as follows. First, the scale striae pattern of the lectotype is difficult to determine accurately, because the scales are fixed and have been lacquered. As such, the striae cannot be inspected under a microscope. However, the pattern of striae on the witvis (SAIAB 52691, 165 mm SL) (Fig. 2A) is typically with few primary (reaching from the radial centre to the edge of the scale) radiate striae and more numerous secondary (not originating in the radial centre) striae in the posterior (exposed) field of the scale (Fig. 2A). These secondary striae could easily be interpreted as being parallel or longitudinal in form, especially in larger specimens where they are more numerous. This is evident in the scales of the lectotype (Fig. 2B), and was likely responsible for Norman's initial misleading advice to Barnard.

Second, the lectotype is uninformative regarding the form of the last unbranched dorsal-fin ray, or spine, as this ray is broken close to its base. In the witvis (e.g., Fig. 3A), this ray is bony and serrated, but relatively weakly so, at least in comparison with its sister species '*Pseudobarbus*' (formerly *Barbus*) *serra* (Peters, 1864) (Fig. 3C). The form of the ray in the Clanwilliam yellowfish is simple and non-spinous (Fig. 3B).

The lectotype is unambiguously informative with regard to a number of other significant diagnostic characters that identify it as a witvis, and separate the witvis from the Clanwilliam yellowfish. These characters are as follows (witvis values given first):

- (1) Number of branched dorsal-fin rays: eight (vs nine).
- (2) Number of branched anal-fin rays: six (vs five).
- (3) Shape of the anal fin in larger specimens ( $\pm \geq 300$  mm SL): square to moderately trapezoid vs extended anteriorly in larger specimens (see Barnard 1943: 164–165).
- (4) Length of the anal fin in larger specimens ( $\pm \geq 300$  mm SL): 11.5–15.6 (mean: 13.5) vs 15.7–18.9 (mean: 17.6) % SL. The divergent trend in the length of the anal fin between these species is clearly evident in the scatterplot (Fig. 4).
- (5) Head length: 26.3–30.9 (mean: 28.2) vs 23.7–25.6 (mean: 24.9) % SL.
- (6) Reach of the mouth: reaches to below the nostril vs reaches to below the anterior margin of the orbit
- (7) Length of the barbels: length of anterior and posterior barbels greater than orbit diameter vs less than orbit diameter.

### Molecular phylogeny

Our molecular phylogenetic analysis (Fig. 5) reflects a polytomy in the tetraploid species and indicates '*P.* trevelyani' as a distinct lineage, the sister group to all other southern African tetraploids. The sister clade to '*P.* trevelyani' presents a set of two sub-clades, each dichotomous, as follows: *Pseudobarbus* and '*P.* hospes' as a distinct lineage of its own, and a dichotomy with '*P.* capensis' and '*P.* serra' on the one hand, and '*P.* calidus' and '*P.* erubescens' on the other. Each of the sub-clades and their sub-lineages are strongly monophyletic and are recognized as new genera in the taxonomic descriptions below.

A summary of the morphological characters that further informs the clusters identified by the molecular phylogeny presented in Fig. 5, derived from Skelton (1980, 1988), is presented in Table 1.

### The identity of Andrew Smith's *Barbus capensis*

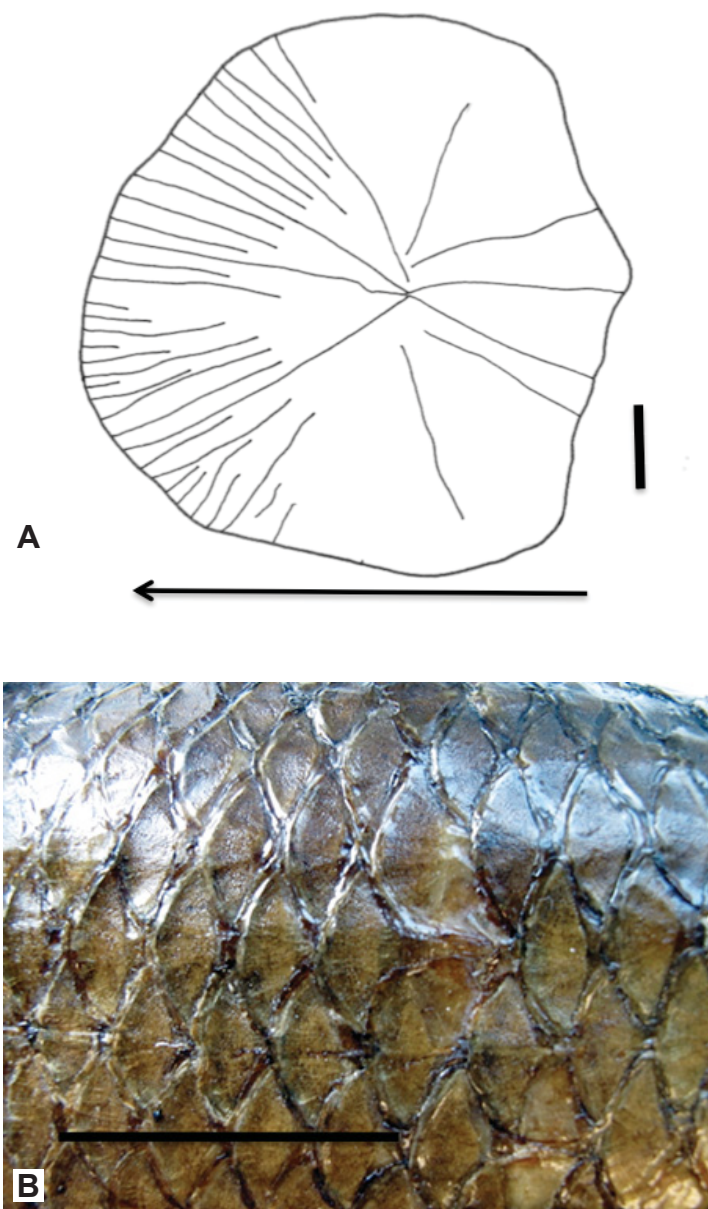
The lectotype of Andrew Smith's *Barbus capensis* (NHMUK 1845.7.3.99) is a mounted specimen of  $\pm 345$  mm SL (Fig. 1). While the NHMUK label only reports "Cape Colony" (no additional information in old NHMUK catalogue [James Maclaine: pers. comm., 2013]) as the type locality, Smith (1841: unnumbered 2<sup>nd</sup> page of description) indicated the species was found in "... rivers of the western coast of South Africa, more particularly the Breede and Oliphants rivers". Smith's statement was not correct concerning the Breede River as being of the "western coast", because it actually drains to the south coast and the Indian Ocean. The Berg River and Olifants River are the two largest systems draining to the west coast in the south-west Cape. Further, Smith (1841: Pisces, plate X, fig. 1) provided an illustration of the



**Fig. 1.** The type (lectotype) of *Barbus (Cheilobarbus) capensis* Smith, 1841 (NHMUK 1845.7.3.99). Photograph credit: Trustees of the Natural History Museum, London.

species (Fig. 6) that, in general, reflects the lectotype specimen but differs in two significant respects: (1) it shows many more and smaller scales (around 61 in the lateral line versus 37 on the lectotype); (2) the shape of the anal fin in the illustration is extended, as in a *Labeobarbus*, and not trapezoid as on the lectotype.

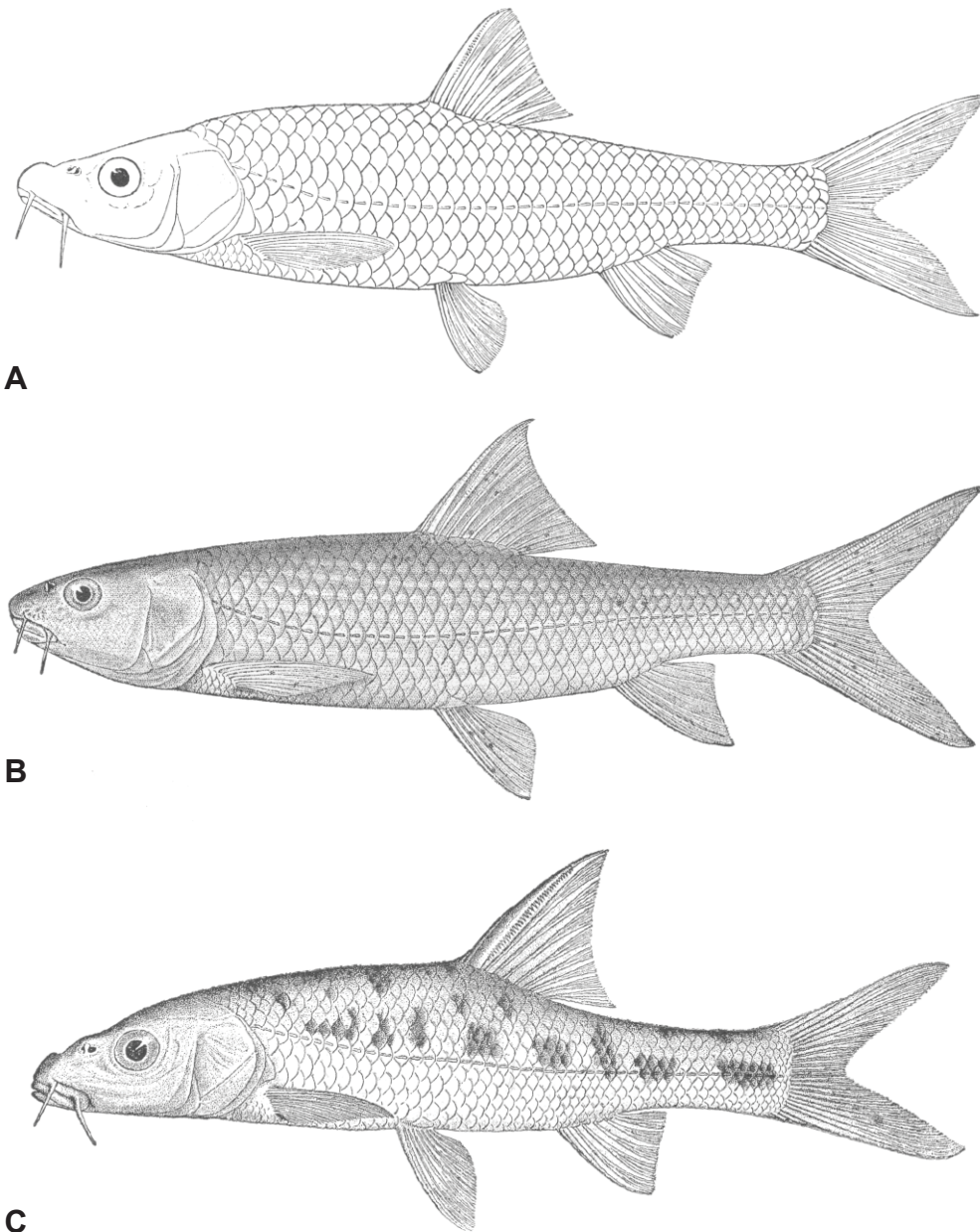
It is now known that there are four large cyprinid species (known colloquially as the witvis, sawfin, Clanwilliam yellowfish and Clanwilliam sandfish) in the rivers mentioned by Smith (1841) (see Skelton 2001). It is possible, therefore, that the four specimens mentioned in the original description of *Barbus*



**Fig. 2.** **A.** A scale of the witvis *Cheilobarbus capensis* Smith, 1841 (SAIAB 52691) drawn by camera lucida to show the pattern of striae. Scale bar = 1 mm. Arrow indicates anterior (embedded field) to posterior (exposed field) orientation. Primary radii reach from radial centre to scale edge; secondary radii do not reach radial centre. **B.** Close up of the scales from the right flank of the lectotype of *Barbus capensis* (NHMUK 1845.7.3.99). Scale bar = 5 cm. Photograph by E. Vreven.

*capensis* included at least two species and the illustration could be a composite drawing of the four specimens mentioned by Smith (1841) and not just of the existing lectotype.

Subsequent to the original description, Günther (1868: 98–99) reported *B. capensis* to be a species “without [a] strong osseous ray”. However, Boulenger (1911: 123, fig. 100) included *Barbus capensis* in his division of radially striated species with a serrated dorsal-fin ray, and provided an illustration of a non-type specimen from the Burg (sic) R. (Fig. 3A). The account given by Boulenger (1911)



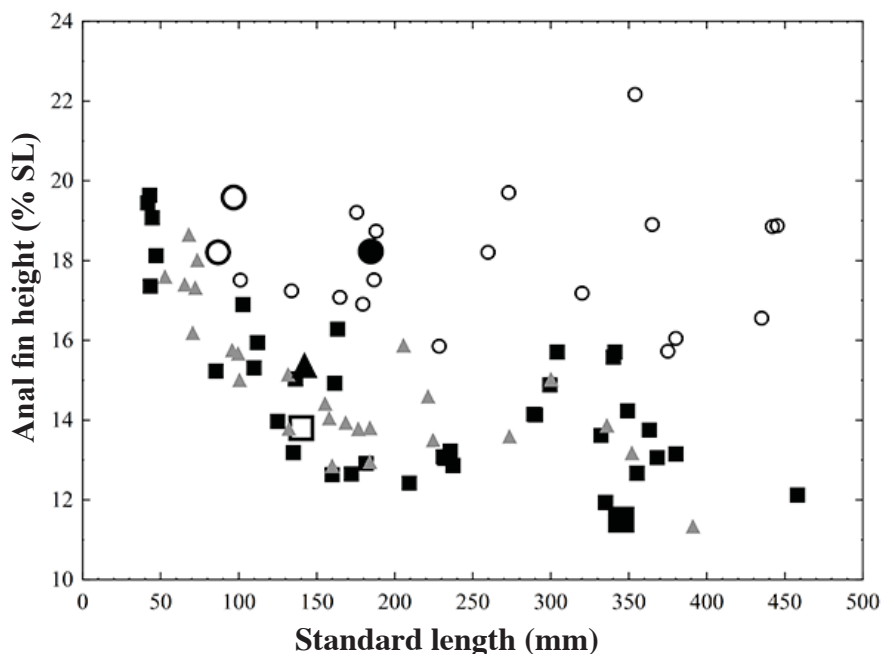
**Fig. 3.** **A.** Witvis, *Barbus capensis* now *Cheilobarbus capensis* Smith, 1841 (Gilchrist & Thompson 1913: fig. 70; Boulenger 1911: fig. 100). **B.** Clanwilliam yellowfish, *Labeobarbus seeberi* (Gilchrist & Thompson 1913: fig. 57; Boulenger 1916: fig. 150). **C.** Sawfin, *Barbus serra* now *Cheilobarbus serra* (Peters, 1864) (Gilchrist & Thompson 1913: fig. 61; Boulenger 1911: fig. 91), to show the overall body form and the form of the last unbranched dorsal-fin ray.



was repeated in the catalogue of Gilchrist & Thompson (1913), in which they also described a large “yellowfish” from the Olifants River system, *Barbus seeberi*, named for C.R. Seeber who collected the three syntypes (see Gilchrist & Thompson 1913: 399 and Barnard 1943:118). Gilchrist & Thompson lodged one of the three syntypes in the NHMUK (1936.8.4.6) while the other two are currently housed as SAIAB 134867 (ex SAM 10672).

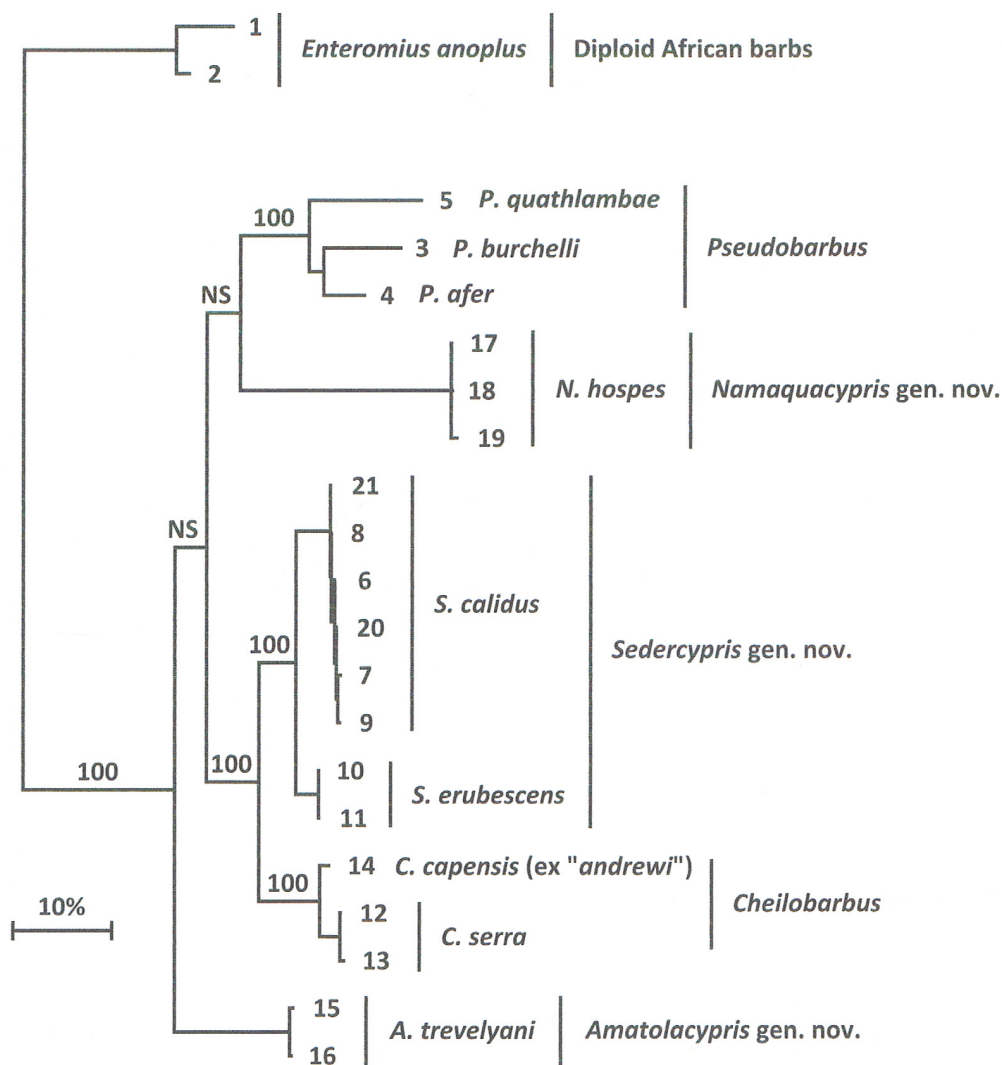
In the 1930s Dr. K.H. Barnard realized that Smith’s description of *Barbus capensis* could apply to at least two species: one, the Cape whitefish or witvis, in the Berg and Breede Rivers, the other the Clanwilliam yellowfish in the Olifants River system. He contacted Dr. J.R. Norman of the Natural History Museum, London, to resolve the identity of the type specimen. Barnard’s query directed Norman to the nature of the scales, whether they were striated in a longitudinal pattern, or with radiating striae as identified by Boulenger (1911). Norman responded that the striae of the scales on the type were longitudinal in form (Barnard 1937). This caused Barnard (1937) to re-assign the identity of Smith’s *Barbus capensis* to the Clanwilliam yellowfish and to rename the witvis from the Berg and Breede rivers, with the serrated dorsal spine and radiating striae on the scales, as *Barbus andrewi*. Barnard (1937) designated the specimen illustrated by Boulenger (1911: fig. 100) (Fig. 3A: NHMUK 1901.2.11.9), as the holotype of *Barbus andrewi*, the witvis. Barnard’s taxonomy has been followed since (e.g., Barnard 1943; Jubb 1965, 1967; Skelton 1993, 2001).

Skelton (2001), in his second edition of the freshwater fishes of Southern Africa, placed the Clanwilliam yellowfish, *B. capensis* (*sensu* Barnard 1937), with all other South-African longitudinally striated large barbs, into the genus *Labeobarbus* Rüppell, 1835. During a recent study visit to the NHMUK, however, one of us (EV 2013) re-examined the mounted lectotype of *B. capensis* and determined that it is, without doubt, not a *Labeobarbus*, and that it is not conspecific with *Labeobarbus seeberi* as previously established by Barnard (1937) (Vreven *et al.* 2016).



**Fig. 4.** Scatterplot of anal fin length (% SL) vs SL (mm) of the witvis, sawfin and Clanwilliam yellowfish to show the consistently longer anal fin of the latter. *Barbus andrewi*: □ = holotype; *B. capensis*: ■ = holotype, ■ = specimens; *B. serra*: ▲ = holotype, △ = specimens; *Labeobarbus seeberi*: ○ = lectotype and paralectotype, ○ = specimens.

Smith's (1841) illustration of the type (Fig. 6) indicates about 60 lateral line scales, 11 transverse body rows, 23 predorsal rows, and eight lateral rows around the caudal peduncle (i.e., about 16 caudal peduncle rows). The type specimen (Fig. 1) equivalently indicates about 38+2 lateral-line, 10 transverse body, 14 predorsal and eight lateral caudal peduncle scale rows. This marked difference and discrepancy in scale size has been discussed previously by Barnard (1943: 117) and by Greenwood & Crass (1959) in reference to the second illustration of *Barbus marequensis* by Smith (1841: Pisces, plate X) (Fig. 7). Furthermore, this illustration of *B. marequensis* does not reflect the type specimen of *B. marequensis* (NHMUK 1845.7.3.95) in details of scale size and other aspects. Greenwood & Crass (1959) concluded that the discrepancy in scale size between illustration and specimen was a case of artistic license, but further information on this matter is to be gleaned from an examination of the plate proofs as annotated by Smith, in the Günther portfolio at the University of Witwatersrand.



**Fig. 5.** Bayesian phylogram, showing the phylogenetic relationships among southern African tetraploid barbs based on the mitochondrial cytochrome *b* gene. Bayesian posterior probabilities are shown above branches. Allele codes are indicated at terminal branches. NS: Not significant. The Bayesian posterior probability at higher NS node is 53%; at the subsequent node 77%.

SKELTON P.H. *et al.*, Southern African tetraploid cyprinids**Table 1.** Summary of character states of tetraploid cyprinine genera from southern Africa. Data from Skelton (1980).

Character	<i>Pseudobarbus</i>	<i>Cheilobarbus</i>	<i>Sedercypris</i>	<i>Namaquacypris</i>	<i>Amatolacypris</i>
Suprapreopercular canal	absent	present	present	present	present
Mandibular canal	reduced/absent	present	present	present	present
Dorsal-fin unbranched ray	not serrated	serrated	serrated	serrated	Serrated (weak)
Anal-fin branched rays	5	5–6	6–7	5	5
total vertebrae	33–40	38–41	36–39	36–38	35–37
Predorsal vertebrae	10–15	10–13	11–14	13–15	10–12
Precaudal vertebrae	17–22	18–23	17–20	17–18	15–17
Caudal vertebrae	15–20	18–21	17–20	16–18	15–18
Supraneurals	0	5–8	5–9	8–10	3–6
Intramusculars (anterior)	cartilage	present	present	present	present
lachrymals	short	long	short	short	short
Mouth position	subterminal	subterminal	terminal	subterminal	subterminal
Barbels	1–2	2	2	2	1
Gut length:SL	1:1 >1:1	>1:1	1:1	1:1	>1:1
Tubercles on head	males, large, conical	males and females, small, erupted	males and females, small, erupted	males and females, small, erupted	males and females, small, erupted
Tubercles on fins	bands	1–2 rows	rows	band 2–3	single rows
Tubercles on scales	distal row	anterior scattered	anterior scattered	absent	anterior scattered
M:F dimorphism	marked	weak	weak	weak	weak
Red colour on fins	present	absent	present	absent	absent
Breeding behaviour	territorial	aggregations	aggregations	unknown	unknown
Max size (mm SL)	<150	>150	<150	<150	<150
Dorsal-fin base/pelvic base	dorsal over pelvic	dorsal over pelvic	dorsal behind pelvic	dorsal behind pelvic	dorsal over pelvic

Whilst there are no original illustrations of either of these species in the Günther portfolio of illustrations by George Ford and other artists in the Cullen Library, University of Witwatersrand, there is, however, a proof of Plate X, with Andrew Smith's annotations on it (Fig. 7). The annotation reveals that Smith intended to name the lower species as '*Barbus gariensis*' *nomen nudum* and not *B. marequensis* as it was published. 'Gariensis' is the early indigenous name for the Orange River. This seems to suggest that the specimen on which that illustration was based was an Orange-Vaal River yellowfish, *Labeobarbus aeneus* (Burchell, 1822), taken from the Orange River and not, as is currently considered, from the type of *Barbus marequensis* (NHMUK 1845.7.3.95) that is derived from the Limpopo River system. The illustration is more like a Vaal-Orange River smallmouth yellowfish (*Labeobarbus aeneus*) than it is to a large-scale yellowfish *Labeobarbus marequensis*.

If this deduction is correct, it would explain to a large extent the scale size discrepancy discussed by Greenwood & Crass (1959) for *Labeobarbus marequensis*. It also suggests that Smith, when finally compiling the fish volume with his illustrations, was aware of, and prepared to tolerate, discrepancies between the illustrations and the specimens he had on hand to describe the species. We have no further information as to when Andrew Smith reversed his decision to use the name *Barbus gariensis* (*n.n.*)

and published the illustration as *Barbus marequensis*, except that it must have been shortly before the plate was published in 1841. The conclusion to be reached from this observation is that Smith either did not crosscheck his descriptions closely with the illustrations and specimens he had deposited in the NHMUK, or, simply tolerated the discrepancies.

The Clanwilliam yellowfish is endemic to the Olifants River system (see Skelton 1993, 2001). There are two other large-sized cyprinids in the Olifants (but not in the Berg or the Breede). One is the Clanwilliam sandfish *Labeo seeberi* Gilchrist & Thompson, 1911 and the second is ‘*Pseudobarbus*’ *serra* (Peters, 1864), known as the sawfin (Skelton 1993, 2001). *Labeo seeberi* is distinct within that genus and need not be considered further. The sawfin is sister species to the witvis (Figs 5, 8) and therefore has relevance. Part of the argument put forward by Barnard (1937: 305–306) for erecting a new name, i.e., *B. andrewi*, for the Berg River witvis, lay in the fact that no large cyprinid with a simple, non-serrated dorsal-fin ray was known from the Berg River, whereas one such species, i.e., the Clanwilliam yellowfish, was known to occur in the Olifants River.

The similarities of the sawfin and the witvis such as radiately striated scales and characters of the head, including an elongated snout, is well illustrated in the scatterplot in Fig. 9. Although the last unbranched dorsal-fin ray is bony and serrated in both species, it is distinctly more heavily developed and serrated in the sawfin than in the witvis (see Fig. 3C and 3A, respectively). Moreover, the two species differ



**Fig. 6.** Andrew Smith's 1841 Plate X illustrating *Barbus capensis* (above) and *Barbus marequensis* (below). Photo credit: Cory Library, Rhodes University, Grahamstown.

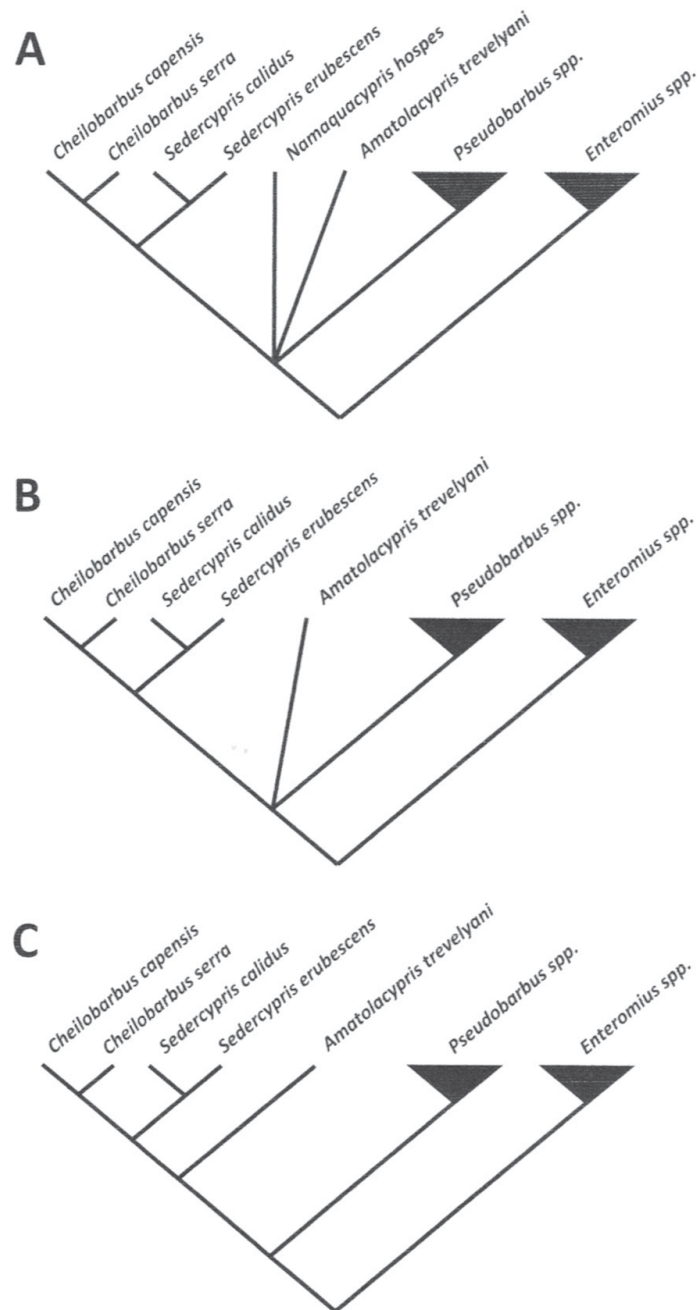
significantly in two diagnostic characters, firstly the number of branched rays in the anal fin (five in the sawfin vs six in the witvis) and the origin of the dorsal fin (behind the origin of the pelvic fins in the sawfin vs above the origin of the pelvic fins in the witvis). The lectotype of *Barbus capensis* reflects the witvis condition in both these characters and we therefore conclude that it is a witvis and not a sawfin derived from the Olifants River system.

Part of the existing confusion seems to have been due to the fact that the last unbranched dorsal-fin ray of the lectotype of *B. capensis* has, probably since it was mounted, been broken off almost at the base (see also Barnard 1937: 305–306), making it impossible to verify whether the specimen had a serrated dorsal spine as in both *B. andrewi* and *B. serra*. Smith (1841) is not clear on this point, as he does not make any mention on the possible serrations of the last unbranched dorsal-fin ray and neither does the drawing (Fig. 6) show this typical character. At the time when Smith (1841) wrote his account, no other cyprinid with a serrated dorsal-fin ray was known from Southern Africa. Apart from the witvis, all known cyprinid species with a serrated dorsal-fin ray from Southern Africa were described after Smith's (1841) paper.

The last unbranched dorsal-fin ray of Smith's *Barbus capensis* might have been broken at its base before he got the specimen in hand, as fishermen frequently break the spine of such species when it holds the specimen fast in a net. Smith (1841), for instance, reported that *B. capensis* is "frequently taken in



**Fig. 7.** Proof sheet of plate X, annotated by Andrew Smith in the R.T. Günther Collection (A649), Cullen Library, University of Witwatersrand. Photograph by P.H. Skelton.

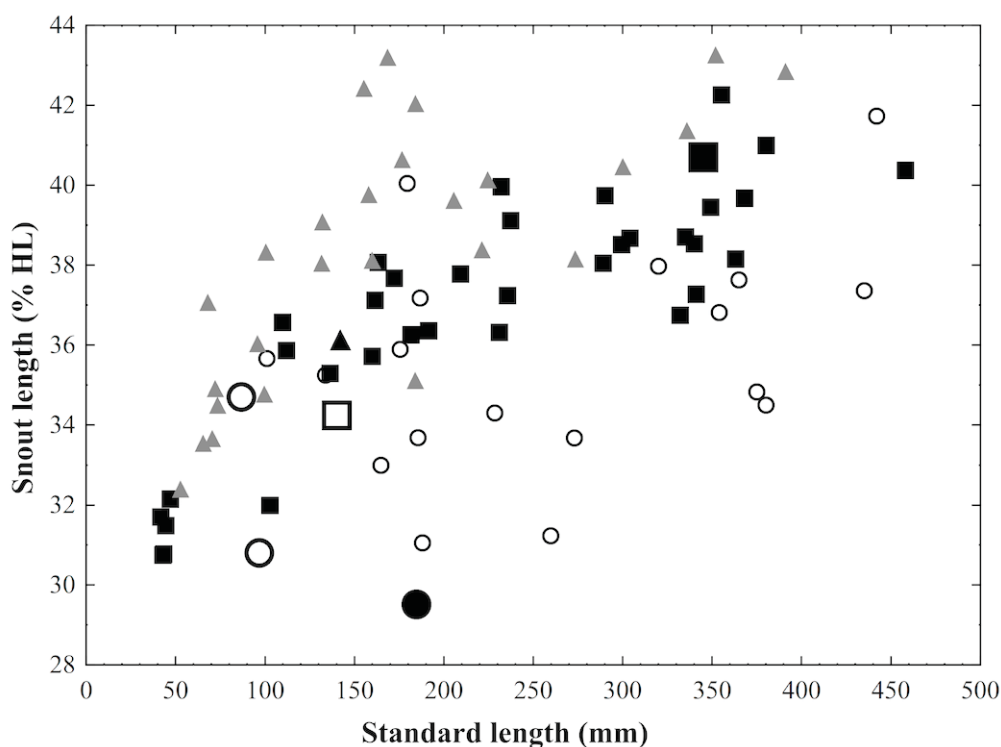


**Fig. 8.** Summary trees showing alternative phylogenies from the literature of the tetraploid cyprinines from southern Africa, using the nomenclature proposed by the present study. Only relationships with bootstrap support >80 or Bayesian posterior probability support greater than 95% were considered and all unsupported relationships were collapsed. **A.** The present study. **B.** Tsigenopoulos *et al.* (2002); de Graaf *et al.* (2007); neighbour-joining tree, De Graaf *et al.* (2010); Berrebi *et al.* (2014); Yang *et al.* (2015). **C.** Bayesian tree by de Graaf *et al.* (2007).

nets, and also occasionally by hooks”. This possibility is supported by the fact that the base of the last unbranched dorsal-fin spine of the lectotype is not mounted exactly parallel to the other rays, but rather, is clearly inclined to the left-hand side of the specimen, a feature that most probably would have been avoided by the taxidermist if the spine were still intact before mounting the specimen. This is the case, for instance, with the holotype of *B. marequensis*.

The lectotype of *B. capensis* has a dorsal-fin ray formula of IV + 8 (when the last two rays that meet at their base are counted as one) and an anal-fin ray formula of iii + 6 (when the last two rays that meet at their base are counted as one). Such a combination of fin-ray formulae, i.e., with a low number of branched dorsal-fin rays (eight) and more than five branched anal-fin rays, is unknown in *Labeobarbus*. These counts fit perfectly with that of the witvis. The number of branched anal-fin rays for this species (six), is considered specifically different from *B. serra*, which has five branched anal-fin rays. Furthermore, the lectotype of *B. capensis* has 40 lateral-line scales, fitting perfectly the range given for the witvis, i.e., 38–41 LL scales, but falls outside the range given for the sawfin, i.e., 41–44 LL scales (Skelton 1993, 2001). Finally, the lectotype of *B. capensis* ( $\pm$  345 mm SL, Fig. 1) has an unmistakably elongated snout (i.e., 56.0% HL), as reflected in Smith’s (1841) illustration (Fig. 6). This is a longer, more pointed, snout than that of the Clanwilliam yellowfish, as illustrated by Gilchrist & Thompson (1913: 398, fig. 57) (Fig. 3C) for the holotype of *B. seeberi* (NHMUK 1936.8.4.6, 185 mm SL). The Clanwilliam yellowfish has a clearly shorter and more rounded snout, i.e., 29.5% HL (Fig. 9), than the witvis.

The total evidence indicates unequivocally that the holotype of *B. andrewi* (NHMUK 1901.2.11.9), taken from the Berg River and illustrated by Boulenger (1911: 123, fig.100) (Fig. 3A), was correctly



**Fig. 9.** Scatterplot of snout length (% HL) vs SL (mm) of the witvis, sawfin and Clanwilliam yellowfish to show the consistently longer snout of the witvis and sawfin. Specimens of Clanwilliam yellowfish with ‘rubberlips’ have longer snouts than normal and these exceptions intrude into the scatterfield of the witvis and sawfin. *Barbus andrewi*: □ = holotype; *B. capensis*: ■ = holotype, ■ = specimens; *B. serra*: ▲ = holotype, △ = specimens; *Labeobarbus seeberi*: ○ = lectotype and paralectotype, ○ = specimens.

identified by Boulenger (1911) as a specimen of *B. capensis* (*sensu* Smith 1841). The evidence similarly indicates that *B. capensis* Smith, 1841 and *B. seeberi* Gilchrist & Thomson, 1913 are not conspecific as concluded by Barnard (1937).

### Key to southern African tetraploid cyprinid genera

1. Unbranched dorsal-fin ray without serrations; adult males with prominent conical tubercles on head, tubercle bands over the pectoral fin rays and single tubercle or single row of tubercles along edges of scales ..... *Pseudobarbus* Smith, 1841
  - Unbranched dorsal-fin flexible or bony, with serrations; adult males and females with scattered very small tubercles over head and body, simple row over anterior pectoral rays, scattered tubercles on exposed scale surfaces ..... 2
2. Lateral line with 38 or more scales ..... 3
  - Lateral line with less than 38 scales ..... 4
3. Adult size > 150 mm SL, dorsal fin base entirely before anal fin origin, snout more than 2 × orbit diameter ..... *Cheilobarbus* Smith, 1841
  - Adult size < 150 mm SL, dorsal fin base extends to above origin of anal fin, snout less than 2 × orbit diameter ..... *Namaquacypris* gen. nov.
4. Anal fin with 6 or 7 branched rays, mouth terminal, two pairs of barbels, length of barbels > 75% orbit diameter, base of fins red ..... *Sedercypris* gen. nov.
  - Anal fin with 5 branched rays, mouth subterminal, single (rarely two) pair of barbels, barbel length < 50% orbit diameter, base of fins without colour ..... *Amatolacypris* gen. nov.

### Taxonomy

Family Cyprinidae Rafinesque 1815  
 Subfamily Cyprininae Rafinesque 1815  
 Tribe Smiliogastrini Bleeker, 1863

Genus *Pseudobarbus* Smith, 1841

*Barbus* Daudin, 1805: 58 (in part, non-Cuvier: *Barbus* (*Pseudobarbus*) *burchelli* Smith, 1841).

*Pseudobarbus* – Skelton 1988: 263 (raised the subgenus of Smith (1841) to generic status).

### Type species

*Pseudobarbus burchelli* Smith, 1841.

### Included species

*Pseudobarbus burchelli* Smith, 1841; *Pseudobarbus afer* (Peters, 1864) (Fig. 10A); *Pseudobarbus asper* (Boulenger, 1911); *Pseudobarbus burgi* (Boulenger, 1911); *Pseudobarbus senticeps* (Smith, 1936); *Pseudobarbus phlegethon* (Barnard, 1938); *Pseudobarbus quathlambae* (Barnard, 1938); *Pseudobarbus tenuis* (Barnard, 1938); *Pseudobarbus skeltoni* Chakona & Swartz, 2013; *Pseudobarbus verloreani* Chakona, Swartz & Skelton, 2014; *Pseudobarbus swartzi* Chakona & Skelton, 2017.

### Diagnosis

*Pseudobarbus* is distinct from all other southern African tetraploid cyprinine genera in having a flexible, non-serrated dorsal-fin unbranched ray (vs serrated), in adults sexual dimorphism expressed in nuptial tubercle development and fin size and shape (*Pseudobarbus* males develop conical tubercles on the head



in a distinct pattern, on the scales in a row along the free edge, and in bands on the pectoral fins vs adults of both sexes having small erupted tubercles scattered over the head and scales; males of *Pseudobarbus* have longer and more expansive fins than females vs similar finnage in both sexes), a reduced or absent mandibular lateral line canal (vs normally developed mandibular canal), and in having weakly ossified characteristics of the skeleton, especially the supraneural and intra-muscular bones (vs regularly ossified supraneural and intramuscular bones). In addition to these characters *Pseudobarbus* differs from all these genera except *Sedercypris* gen. nov. in having red pigmentation at the base of the fins (vs no red pigmentation); from *Cheilobarbus* in adult size (< 150 mm SL vs > 150 mm SL); from *Amatolacypris* gen. nov. in having slender third and fourth infraorbital bones (vs broad third and fourth infraorbitals); and from *Namaquacypris* gen. nov. in the position of the dorsal fin (*Pseudobarbus* dorsal fin in mid-body, origin over or just behind the origin of the pelvic fins vs posteriorly, origin behind the pelvic fin), and in not having a membrane connecting the inner pelvic fin rays to the body (vs a membrane connecting the inner pelvic rays to the body). *Pseudobarbus* differs further from *Sedercypris* gen. nov. in the position of the mouth (subterminal vs terminal), and the number of anal-fin branched rays (five vs six or seven).

### Etymology

*Pseudobarbus* is derived from ‘*pseudes*’ (Greek) meaning false, deceptive, and ‘*barba*’ (Latin) a beard; in reference to a deceptive similarity with the genus *Barbus* from Europe.

### Description

Species of *Pseudobarbus* are moderate-sized (< 150 mm SL) fusiform or terete, tetraploid smiliogastrin minnows, with one or two pairs of simple circum-oral barbels; lips variably developed, pharyngeal teeth in two or three rows; tooth formulae 0-2,3,3,4+5-5-4,3,0-2; pharyngeal tooth crowns variable with off-set major cusp; intestine variable in length from 1:1 in SL to 3–4:1 SL; scales radially striated, from small to moderate in size, nape and breast scales reduced or embedded; no pectoral or pelvic axil scale; lateral line interrupted or complete, in mid-body; cephalic lateral line system with pre-opercular branch disconnected and reduced or absent on the mandible. Dorsal fin with simple flexible unbranched ray and normally seven branched rays. Anal fin with five branched rays. Pectoral fins sexually dimorphic in mature adults, males with longer more expansive pectorals. Adults with bright red patches at the base of the fins. Mature males develop conical tubercles on the head, in a distinctive pattern as illustrated in Skelton (1988: fig. 31), in single rows along the free edge of scales and in bands over anterior pectoral fins. Axial skeleton without ossified supraneural or intramuscular bones.

Genus *Cheilobarbus* Smith, 1841 stat. nov.

*Barbus* Daudin, 1805: 58 (in part, non-Daudin: *Barbus (Cheilobarbus) capensis* Smith, 1841).

*Barbus (Cheilobarbus)* Smith, 1841: description of pl. X., fig.1 (applied as a subgenus).

*Barbus* – Jordan 1919: 244.

‘*Pseudobarbus*’ – Yang *et al.* 2015: 99.

### Type species

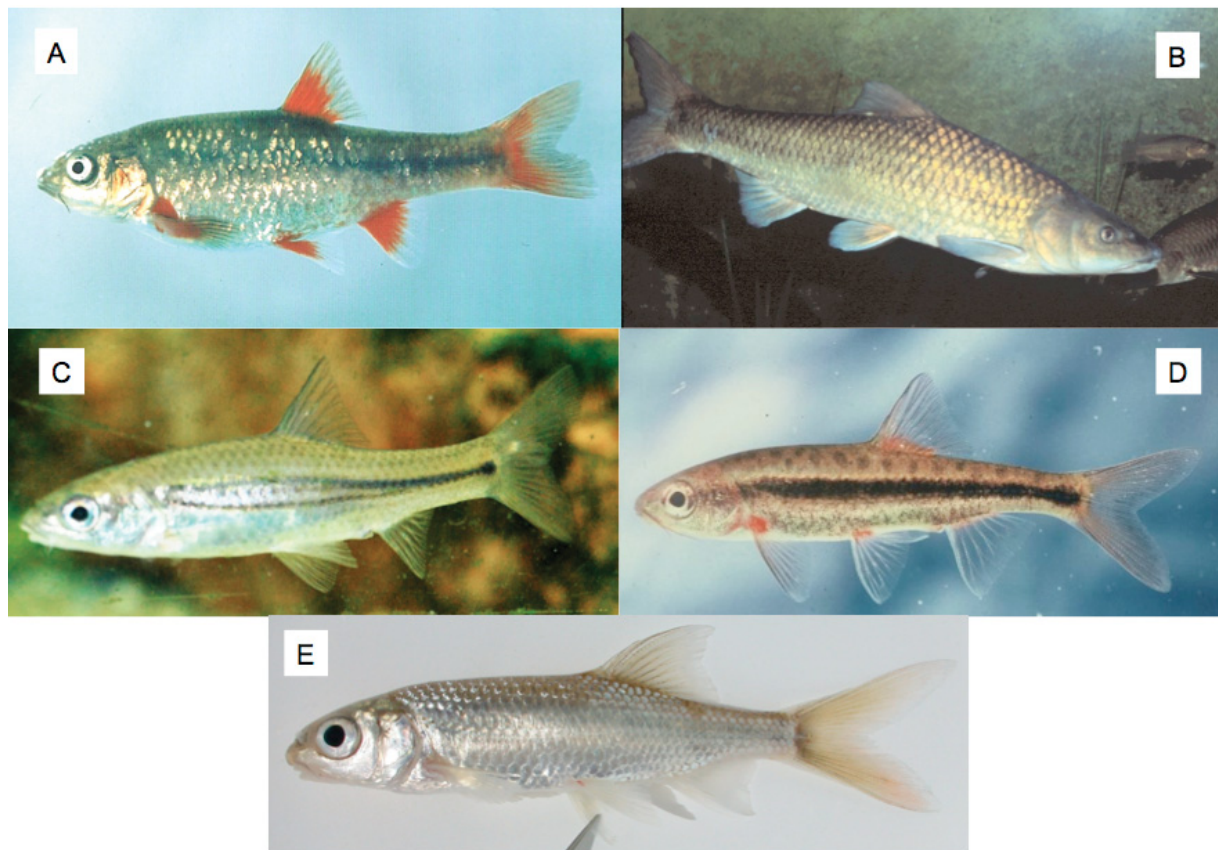
*Cheilobarbus capensis* Smith, 1841 (Fig. 10B)

### Included species

*Cheilobarbus capensis* Smith, 1841 (Fig. 10B), known as the witvis or Berg-Breede River whitefish, from the Berg (Atlantic drainage) and Breede Rivers (Indian Ocean drainage); *Cheilobarbus serra* (Peters, 1864) known as the sawfin or saagvin, from the Clanwilliam Olifants River (Atlantic drainage).

### Diagnosis

*Cheilobarbus* is distinguished from all other southern African tetraploid cyprinine genera by attaining a relatively large size (adult  $> 150$  mm SL vs  $< 150$  mm SL), and by having an extended snout as reflected in an elongated lachrymal bone (length  $3 \times$  depth vs rectangular-shaped lachrymal length  $2 \times$  depth). *Cheilobarbus* also differs from *Sedercypris* gen. nov. by an absence of red colour at the base of the fins, in the position of the mouth (subterminal vs terminal) and in the length of the gut ( $> 1.5 \times$  SL vs  $< 1.5 \times$  SL). *Cheilobarbus* differs from *Amatolacypris* gen. nov. in overall size, colour (silvery to olive-bronze vs grey with double black lateral stripe), number of barbels (two pairs vs one pair), number (five vs four) and form of the 3<sup>rd</sup> and 4<sup>th</sup> infraorbital bones (narrow and slender vs broad). *Cheilobarbus* differs from *Namaquacypris* gen. nov. in the position of the dorsal fin (entirely before anal fin base vs reaching above anal fin base), form of the scales (regular vs thin), and the lack of a membrane between the innermost pelvic rays and the body (vs present). *Cheilobarbus* differs from *Pseudobarbus* in having a serrated dorsal-fin unbranched ray (vs simple dorsal-fin unbranched ray), an absence of red patches at the base of the fins (vs presence), no sexual dimorphism in fin size and shape and in the form and expression of nuptial tubercles as adults (vs clear sexual dimorphism in fin size and shape [males with larger fins] and nuptial tubercles [males with large conical tubercles on snout and head, small tubercles on scales and fins]). *Cheilobarbus* can be separated from all other large sized southern African cyprinids by karyology



**Fig. 10.** Species representative of southern African tetraploid cyprinine genera. **A.** *Pseudobarbus afer* (Peters, 1864). **B.** *Cheilobarbus capensis* Smith, 1841. **C.** *Amatolacypris trevelyani* (Günther, 1877) gen. et comb. nov. **D.** *Sedercypris calidus* (Barnard, 1938) gen. et comb. nov. **E.** *Namaquacypris hospes* (Barnard, 1938) gen. et comb. nov. Photograph credits: A–D by P.H. Skelton (SAIAB); E by R.I. Bills (SAIAB).

(tetraploid vs diploid or hexaploid) the form of the scales (radiate striae vs parallel striae) and a serrated unbranched dorsal-fin ray (vs simple spinous unbranched dorsal-fin ray).

### Etymology

The name *Cheilobarbus* is derived from the Greek ‘*cheilos*’ meaning a margin, lip or brim, and the Latin ‘*barba*’ meaning a beard and referring to the oral barbels. Smith (1841) mentioned the “lips” of these species as being “full and firm”. Gender masculine.

### Description

*Cheilobarbus* is a genus of tetraploid cyprinine fishes with moderately sized, radiately striated scales; an elongated snout with elongated lacrymals, mouth subterminal with firm, well-developed lips, two pairs of simple oral barbels, pharyngeal bones with three rows of hooked pharyngeal teeth, tooth formula 5,3,2-2,3,5; intestine involuted and longer than the SL; dorsal fin positioned over or slightly behind the origin of the pelvic fins, the last simple ray bony weakly or strongly serrated, and eight branched rays; anal fin with three simple rays and five or six branched rays; mature breeding adults of both sexes develop small erupted nuptial tubercles densely scattered over head dorsum and in single rows over the pectoral fin rays; both species breed in male dominated nuptial shoals over gravel and cobbles.

### History

Smith (1841) attributed both the large *Barbus* species he described to a new subgenus *Cheilobarbus*, i.e., *Barbus (Cheilobarbus) capensis* and *Barbus (Cheilobarbus) marequensis*. While the latter species is identified as a *Labeobarbus*, the former, a tetraploid species, does not belong in *Labeobarbus*. The type species of the subgenus, *B. capensis*, was designated by monotypy by Jordan (1919: 244) as first revisor and, therefore, is not a junior synonym of *Labeobarbus*. The subgenus *Cheilobarbus* was described by Smith (1841) as follows: “Mouth opening forwards; lips full, and firm; intermaxillary bones slightly extensible; nostrils double; four cirri, two from snout, and one from each angle of mouth; lateral line consisting of a series of small tubes; scales large; dorsal fin short, and commencing slightly in front of base of ventral fins; commencement of anal fin about midway between ventral and caudal fins.” However this description is not diagnostic, e.g., it does not mention the nature of the unbranched dorsal-fin ray nor the nature of the scale radii. In order to institute *Cheilobarbus* as the genus for these species, an expanded diagnostic definition is required and the species to be included identified along phylogenetic grounds.

### *Sedercypris* gen. nov.

[urn:lsid:zoobank.org:act:09567CC9-7FF0-4054-BD36-CCCB26AB7F7D](http://urn:lsid:zoobank.org:act:09567CC9-7FF0-4054-BD36-CCCB26AB7F7D)

*Barbus* Daudin, 1805: 58 (*Barbus calidus* Barnard, 1938; *Barbus erubescens* Skelton, 1974).

‘*Pseudobarbus*’ – Yang *et al.* 2015: 99.

### Type species

*Sedercypris calidus* (Barnard, 1938) gen. et comb. nov. (Fig. 10D).

### Included species

*Sedercypris calidus* (Barnard, 1938) (Fig. 10D), distributed in the Clanwilliam Olifants River system, and *Sedercypris erubescens* (Skelton, 1974), endemic to the Twee River, a tributary of the Doring branch of the Clanwilliam Olifants River system.

### Diagnosis

Species of *Sedercypris* gen. nov. are distinct from all other southern African tetraploid genera in the combination of having six or seven branched rays in the anal fin (vs five – or six in *Cheilobarbus capensis*), and a red base to the fins (only *Pseudobarbus* also has a red base to the fins). The genus is further distinguished from *Cheilobarbus* in overall body size (adults  $\leq$  150 mm SL vs  $>$  150 mm SL); from *Namaquacypris* gen. nov. by fewer pre-dorsal vertebrae (11–14 vs 13–15) the position of the dorsal fin (in advance of the origin of the anal fin vs to over the origin of the anal fin), a difference in mouth position (terminal vs inferior), in not having a membrane between the inner pelvic rays and the body (vs presence of such a membrane *Namaquacypris* gen. nov.); from *Amatolacypris* gen. nov. in number and size of barbels (*Sedercypris* gen. nov. with two pairs of well developed barbels that equal the orbit diameter vs one pair that is less than half an orbit diameter), in the number and size and shape of the infraorbitals (five, all slender in *Sedercypris* gen. nov. vs four, 3<sup>rd</sup> and 4<sup>th</sup> broad in *Amatolacypris* gen. nov.); and from *Pseudobarbus* in a serrated unbranched dorsal-fin ray (*Pseudobarbus* has a simple unbranched dorsal-fin ray), the position of the mouth (terminal vs subterminal) and the absence of strong sexual dimorphism (vs sexual dimorphism with males having conical tubercles on the head, body and fins and larger fins compared to females).

### Etymology

Endemic to and named for the Sederberg (Cedarberg), Western Cape, South Africa, a Cape Fold mountain range in which rise streams and rivers tributary to the Olifants River system. The Afrikaans spelling of Sederberg is adopted for the name to avoid the possible confusion with the genus *Cheilobarbus* when the genus name is abbreviated to an initial in text. Masculine.

### Description

The genus *Sedercypris* gen. nov. includes medium sized (adults  $<$  120 mm SL) tetraploid cyprinine species from southern Africa with radiately striated scales; mouth terminal, lips slender, two pairs of well-developed simple oral barbels, pharyngeal bones with three rows of hooked teeth, formula 2,3,5 or 4-4 or 5,3,2; a simple s-folded intestine about equal to the SL in length; dorsal fin positioned over or behind the origin of the pelvic fins, with the last simple ray bony with posterior margin weakly or strongly serrated and 8 branched rays; anal fin with six or seven branched rays; mature adults with bright red flashes at the bases of fins. Breeding adults develop small erupted nuptial tubercles scattered over head dorsum and anterior body, single rows over anterior pectoral rays. Breeding takes place in male dominated nuptial schools over creviced rock faces.

### *Amatolacypris* gen. nov.

[urn:lsid:zoobank.org:act:0DD940C2-952C-4770-A0FC-C61104CD7599](http://urn:lsid:zoobank.org:act:0DD940C2-952C-4770-A0FC-C61104CD7599)

*Barbus* Daudin 1805: 58 (*Barbus trevelyani* Günther, 1877).

'*Pseudobarbus*' – Yang *et al.* 2015: 99.

### Type species

*Amatolacypris trevelyani* (Günther, 1877) gen. et comb. nov. (Fig. 10C).

### Included species

Type species only.

### Diagnosis

Among the southern African tetraploid cyprinine genera *Amatolacypris* gen. nov. is unique in colouration (silvery-grey with a thin double mid-lateral line) and in having only four infraorbitals, and broadly flanged 3<sup>rd</sup> and 4<sup>th</sup> infraorbital bones. It is further distinguished from *Cheilobarbus* on account of size (adults < 150 mm SL vs adults > 150mm SL), from *Pseudobarbus* and *Sedercypris* gen. nov. by an absence of red pigmentation at the base of the fins (vs red at the base of the fins); from *Pseudobarbus* by lacking clear sexual dimorphism in nuptial tubercles and fin size (vs strong sexual dimorphism in these characters); from *Sedercypris* gen. nov. by the position of the mouth (subterminal vs terminal) and barbels (one pair, short < 50% orbit diameter vs two pairs, long > 50% orbit diameter); from *Namaquacypris* gen. nov. by the number of predorsal vertebrae (10–12 vs 13–15) and position of the dorsal fin (origin above or slightly behind the origin of the pelvics vs well behind the origin of the pelvics), by the barbels (one pair, short, 50% orbit diameter vs two pairs, long > 50% orbit diameter) and by lacking a membrane between the inner pelvic rays and the body (vs presence of such a membrane in *Namaquacypris* gen. nov.).

### Etymology

Endemic to and named for the Amatola mountains in the Eastern Cape, South Africa. Masculine.

### Description

*Amatolacypris* gen. nov. is a monotypic genus of medium sized (< 120 mm SL) tetraploid smiliogastrin minnows from southern Africa, with radiately striated scales; four infraorbital bones, infraorbital three and four broadly flanged, covering space between orbit and preoperculum; mouth subterminal with one or two pairs of short oral barbels; pharyngeal bones with three rows of hooked teeth, formula 2,3,4 - 4,3,2; intestine involuted, longer than SL; dorsal fin origin over origin of pelvics, last simple dorsal-fin ray flexible, usually with small, weak serrations along posterior edge, seven branched rays; pelvic fin with reduced axillary scale; anal fin with five branched rays; mature adults of both sexes with minute erupted tubercles over head and body, single spaced rows over pectoral rays. Breeding biology not known.

### Etymology

Endemic to and named for the Amatola mountains in the Eastern Cape, South Africa. Masculine.

### *Namaquacypris* gen. nov.

[urn:lsid:zoobank.org:act:CD4D7A27-7BAC-4747-A128-6B94C8CEF3CF](http://urn:lsid:zoobank.org:act:CD4D7A27-7BAC-4747-A128-6B94C8CEF3CF)

*Barbus* Daudin, 1805: 58 (*Barbus hospes* Barnard, 1938).

'*Pseudobarbus*' – Yang *et al.* 2015: 99.

### Type species

*Namaquacypris hospes* (Barnard, 1938) gen. et comb. nov. (Fig. 10E).

### Included species

Type species only.

### Diagnosis

*Namaquacypris* gen. nov. may be separated from all other southern African tetraploid genera by the relatively posterior position of the dorsal fin (behind the pelvic fin and base to over the origin of the

anal fin vs over the pelvic fin and base before the origin of the anal fin), by a high number of predorsal vertebrae (13–15 vs 13 or fewer), the inner pelvic rays partly attached to the body by a membrane (vs an absence of such attachment), and by having a pair of barbels sub-equal in length (vs anterior barbels shorter than posterior barbels). *Namaquacypris* gen. nov. differs further from both *Pseudobarbus* and *Sedercypris* gen. nov. in an absence of red pigment at the base of the fins (vs bright red base to the fins), from *Pseudobarbus* in an absence of sexual dimorphism in fin length and nuptial tubercles (vs strong sexual dimorphism in fin length and nuptial tubercles), and from *Sedercypris* gen. nov. in the position of the mouth (subterminal vs terminal) and in having five branched anal-fin rays (vs six or seven branched anal-fin rays). *Namaquacypris* gen. nov. differs from *Amatolacypris* gen. nov. in colour and pigmentation (silvery, white below vs grey with a dark thin stripe and stripe over the lateral line), the number of infraorbitals (five vs four), the number and length of the barbels (two pairs, as long as the eye diameter vs one pair, shorter than half an eye diameter), and the size and shape of the 3<sup>rd</sup> and 4<sup>th</sup> infraorbital (slender vs broad). It differs from *Cheilobarbus* in size (< 150 mm SL vs > 150 mm SL), head shape (short snout vs long snout) and colour (adults plain silvery vs olive-bronze).

### Etymology

Named for Namaqualand, a semi-desert region of the Northern Cape, South Africa and Namibia through which the Lower Orange River flows. The genus is endemic to the lower Orange river below the Augrabies waterfall. Masculine.

### Description

*Namaquacypris* gen. nov. is a monotypic, tetraploid smiliogastrin genus of medium to small (< 100 mm SL) minnows from southern Africa, with small, light (thin) radiately striated scales; small, inferior mouth, with two pairs of equivalently long (equal or longer than the orbit diameter) oral barbels; pharyngeal bones with three rows of hooked teeth, formula 2,3,5, - 5,3,2; intestine with simple s-fold, short, slightly less than SL; a relatively high number (13–15) of predorsal-fin vertebrae; dorsal-fin origin nearer caudal base than tip of snout, entirely behind the pelvic fins, dorsal-fin unbranched ray serrated along posterior edge, basal serrations directed distally, seven branched rays; pelvic fins with inner rays attached to body by a membrane; anal fin origin below hind margin of dorsal base. Mature adults of both sexes develop minute nuptial tubercles scattered over head dorsum and upper body anterior to the dorsal fin, with bands 2–3 tubercles deep over pectoral fin rays. The breeding biology is not known.

### Discussion

#### Taxonomic implications and conclusions

This re-identification of the lectotype of *Barbus capensis* requires nomenclatural changes as made by Vreven *et al.* (2016), and elaborated on here as follows. Considering that *B. capensis* is, in fact, not a large hexaploid cyprinid, i.e., *Labeobarbus*, the species name *B. seeberi*, a junior synonym of *B. capensis* according to Barnard (1937), becomes available, and, as the earliest available name, is assigned to the Clanwilliam yellowfish as *Labeobarbus seeberi*. The name *Barbus andrewi* Barnard, 1937, becomes a junior synonym of *B. capensis*. Barnard (1937) subsequently identified the NHMUK syntype of *B. seeberi* that had been illustrated by Boulenger (1916: 241) as the “type”, leaving the two SAIAB (134867) specimens as “cotypes”. This decision holds as a correct lectotype designation (ICZN 1999: Art. 74.5) for the species. In addition, following Yang *et al.* (2015), the genus in which the witvis, *B. capensis* (= *B. andrewi*), is now placed recently changed to ‘*Pseudobarbus*’. This placement receives further discussion and taxonomic determination below.

#### Classification of tetraploid southern African cyprinids

Yang *et al.* (2015) recommended that the genus *Pseudobarbus* be expanded to embrace the entire lineage of tetraploid cyprinids in southern Africa using quotation marks, ‘*Pseudobarbus*’, until the situation

could be considered in detail. All *Pseudobarbus* and ‘*Pseudobarbus*’ species are tetraploid (Naran 1997; Naran *et al.* 2006). In addition to Yang *et al.* (2015) the phylogeny of the southern African tetraploid cyprinids was investigated, in part, by Tsigenopoulos *et al.* (2002), de Graaf *et al.* (2007, 2010) and Berrebi *et al.* (2014). All these studies consistently show that the genus *Pseudobarbus*, i.e., the redfins with a flexible, simple or unbranched dorsal-fin ray, is a strongly supported monophyletic lineage that is sister to the tetraploid species with a serrated last unbranched dorsal-fin ray species, here ‘*Pseudobarbus*’ (Figs 5, 8). All the aforementioned studies also show a strongly supported clade of serrated-rayed species that includes ‘*P.*’ *capensis*, ‘*P.*’ *serra*, ‘*P.*’ *calidus* and ‘*P.*’ *erubescens*. The position of ‘*P.*’ *trevelyani* (Günther, 1877) is, however, unsettled. ‘*Pseudobarbus*’ *trevelyani* is potentially linked as the sister species to the serrated-rayed clade (Fig. 8C, as in de Graaf *et al.* 2007), or, as an independent lineage in an unresolved polytomy with the other two lineages (Fig. 8B), as in Tsigenopoulos *et al.* (2002), de Graaf *et al.* (2007, 2010), Berrebi *et al.* (2014) and Yang *et al.* (2015).

It should be noted that the configuration of the lineages with respect to the position of ‘*P.*’ *trevelyani*, using the same data set, differs when analysed as a Neighbour joining tree (de Graaf *et al.* 2007; Fig. 8B) or using Bayesian analysis (de Graaf *et al.* 2007; Fig. 8C). Furthermore, none of the above-mentioned studies included samples of ‘*P.*’ *hospes* (Barnard, 1938). Thus the phyletic positions of ‘*P.*’ *trevelyani* and ‘*P.*’ *hospes* are currently uncertain.

From a morphological perspective, Skelton (1976) compared the post-cranial meristics of certain southern African cyprinids and drew tentative conclusions on relationships. He pointed to several possible links between species, including ‘*P.*’ *capensis* (as *Barbus andrewi*) and ‘*P.*’ *serra* (as *Barbus serra*), and these with ‘*P.*’ *calidus* and ‘*P.*’ *erubescens*, based on the high number of branched rays in the anal fin of all but ‘*P.*’ *serra*. In addition, Skelton (1976: 406) indicated that ‘*P.*’ *calidus* and ‘*P.*’ *erubescens* were similar to ‘*P.*’ *hospes* and ‘*P.*’ *trevelyani* by having the relatively high vertebral counts of all the smaller *Barbus* species examined. Skelton mentioned that both Farquharson (1962) and Gaigher & Pott (1973) regarded these species as derivatives of an early invasion of the Cape region, but cautioned that this did not necessarily indicate a common ancestry.

Skelton (1980) considered the morphology, osteology, and vertebral meristics of a wide range of southern African cyprinine species, in order to use the characters for a phylogenetic and taxonomic analysis of the redfin lineage. The genus *Pseudobarbus* was based on these data that, together with molecular data, were incorporated in the phylogenetic analysis by Swartz *et al.* (2009) of the redfin lineage. Several characters such as number of barbels, nature of the last simple dorsal-fin ray (serrated vs simple) were equivocally assigned, and therefore uninformative at the higher level of universality in terms of this lineage. Synapomorphies of the *Pseudobarbus* species, known as redfin minnows, include such prominent morphological characters as the development and pattern of nuptial tubercles, squamation, cephalic lateral line development, reductive osteology in both the cranial and post-cranial skeleton, pharyngeal teeth morphology and gut development (Skelton 1980; Swartz *et al.* 2009).

In contrast to *Pseudobarbus*, all other tetraploid smiliogastrin species are differentiated by having a serrated unbranched ray in the dorsal fin (Table 1). In ‘*P.*’ *trevelyani* and ‘*P.*’ *erubescens* the ray is generally weakly serrated and flexible and thus non-spinous. The soft-rayed redfin species of *Pseudobarbus* are sexually dimorphic, with males developing conical tubercles on the head, rows of small tubercles along the edge of scales and bands over the pectoral fins rays. The males establish and defend a nuptial territory, breeding one-on-one with individual females. Mature adults of other tetraploids in breeding condition all show small, scattered “pimple-like” tubercles over the head and body of both males and females (Skelton 1980). The differences in development and pattern of nuptial tubercles reflects a difference in the breeding biology of the lineages. The breeding behavior of ‘*P.*’ *trevelyani* and ‘*P.*’ *hospes* has not yet been reported, but all the other serrated rayed species are group spawners, with males and females

assembling in nuptial swarms and breeding over specific spawning beds or sites (Skelton 2001; Impson 2008; Paxton 2008; Paxton & King 2009).

These considerations together with the molecular phylogenetic results (Fig. 5) all indicate that a set of related genera is justified for the monophyletic clades of serrated-ray tetraploid cyprinids in southern Africa. The evidence favors a set of related genera because of the very distinctive and exclusive phenotype of each clade as defined by autapomorphies. Thus the large bodied sister species ‘*P.*’ *capensis* and ‘*P.*’ *serra* are sufficiently distinct on the grounds of attainable size, osteology and skeletal meristics from the other species to warrant their own genus. The sister clade to these large-bodied species, ‘*P.*’ *calidus* and ‘*P.*’ *erubescens*, are also sufficiently similar to each other but distinct, both morphologically and genetically, from other lineages, to warrant their own genus. ‘*Pseudobarbus*’ *trevelyani* and ‘*P.*’ *hospes* are each separate and independent lineages on morphological and genetic grounds, and each should be allocated a monospecific genus, justified by distinctive autapomorphies (Skelton 1980). Diagnoses of these new genera are provided in this paper.

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**Appendix 1** (continued on next page). Specimens and their origin analysed for the mitochondrial cytochrome *b* gene, using the nomenclature proposed in the present study.

Genus	Species	GenBank number/ sample code	Haplo- type	System	River	Locality description/source	Locality	Year	Author/collector
<i>Amatolacypris</i>	<i>trevelyani</i>	GenBank AF180847	16	–	–	–	–	–	Tsigenopoulos <i>et al.</i> , 2002
<i>Amatolacypris</i>	<i>trevelyani</i>	Sample BUTR1	15	Buffalo	Cwengcwe	SAIAB 52706	32°45'53" S, 27°22'22" E	1993	W. Haselau
<i>Amatolacypris</i>	<i>trevelyani</i>	Sample BUTR1	16	Buffalo	Cwengcwe	SAIAB 52706	32°45'53" S, 27°22'22" E	1993	W. Haselau
<i>Sedercypris</i>	<i>calidus</i>	GenBank AF287423	8	Olifants	–	–	–	–	Machordom & Doadrio, 2001
<i>Sedercypris</i>	<i>calidus</i>	GenBank AF287422	20	Olifants	–	–	–	–	Machordom & Doadrio, 2001
<i>Sedercypris</i>	<i>calidus</i>	GenBank AF180846	21	Olifants	–	–	–	–	Tsigenopoulos <i>et al.</i> , 2002
<i>Sedercypris</i>	<i>calidus</i>	Sample AC1	6	Olifants	Dassieboskloof	Deep pools in kloof near Wupperthal	32°17'00" S, 19°12'40" E	1998	E. Swartz & A. Flemming
<i>Sedercypris</i>	<i>calidus</i>	Sample KC1	7	Olifants	Boskloof	Below road crossing	32°33'35" S, 19°03'23" E	1998	E. Swartz, R. Bills & D. Naran
<i>Sedercypris</i>	<i>calidus</i>	Sample NC1	8	Olifants	Noordhoeks	Upstream of main road next to bedrock	32°43'13" S, 19°04'00" E	1998	E. Swartz, R. Bills & D. Naran
<i>Sedercypris</i>	<i>calidus</i>	Sample TC8	8	Olifants	Thee	Road crossing close to huils	32°47'38" S, 19°05'45" E	1998	E. Swartz
<i>Sedercypris</i>	<i>calidus</i>	Sample OP16	9	Olifants	Oudste	Upstream of orchards	32°49'37" S, 19°05'39" E	1998	E. Swartz
<i>Sedercypris</i>	<i>erubescens</i>	GenBank AF180845	10	Olifants	–	–	–	–	Durand <i>et al.</i> , 2002
<i>Sedercypris</i>	<i>erubescens</i>	Sample E1	10	Olifants	Twee	Above waterfall	32°41'37" S, 19°17'38.0" E	1998	E. Swartz
<i>Sedercypris</i>	<i>erubescens</i>	Sample HEBE1	11	Olifants	Heks	Bend in river	32°43'20" S, 19°13'09" E	2002	E. Swartz & M. Cunningham
<i>Sedercypris</i>	<i>erubescens</i>	Sample HEBE2	11	Olifants	Heks	Bend in river	32°43'20" S, 19°13'09" E	2002	E. Swartz & M. Cunningham
<i>Cheilobarbus</i>	<i>capensis</i>	GenBank AF180843	14	Breede	–	–	–	–	Durand <i>et al.</i> , 2002
<i>Cheilobarbus</i>	<i>capensis</i>	Sample AND1	14	Breede	Brandvlei Dam	Brandvlei Dam	33°40'42" S, 19°23'14" E	1999	E. Swartz, R. Bills & D. Naran

**Appendix 1** (continued). Specimens and their origin analysed for the mitochondrial cytochrome *b* gene, using the nomenclature proposed in the present study.

Genus	Species	GenBank number/ sample code	Haplo- type	System	River	Locality description/source	Locality	Year	Author/collector
<i>Cheilobarbus</i>	<i>capensis</i>	Sample AND2	14	Breede	Brandvlei Dam	Brandvlei Dam	33°40'42" S, 19°23'14" E	1999	E. Swartz, R. Bills & D. Naran
<i>Cheilobarbus</i>	<i>serra</i>	GenBank AF287447	12	Olifants	–	–	–	–	Machordom & Doadrio, 2001
<i>Cheilobarbus</i>	<i>serra</i>	GenBank AF287446	13	Olifants	–	–	–	–	Machordom & Doadrio, 2001
<i>Cheilobarbus</i>	<i>serra</i>	GenBank AF180844	12	Olifants	–	–	–	–	Tsigenopoulos <i>et al.</i> , 2002
<i>Cheilobarbus</i>	<i>serra</i>	Sample DS11	12	Olifants	Matjies	Downstream of waterfalls	32°29'51" S, 19°17'09" E	1998	E. Swartz & R. Bills
<i>Cheilobarbus</i>	<i>serra</i>	Sample OS1	12	Olifants	Olifants	Olifants gorge near track	32°58'18" S, 19°10'57" E	1998	E. Swartz, R. Bills, D. Naran & D. Impson
<i>Cheilobarbus</i>	<i>serra</i>	Sample TS1	13	Olifants	Dassieboskloof	Deep pools in kloof near Wupperthal	32°17'00" S, 19°12'40" E	1998	E. Swartz & R. Bills
<i>Enteromius</i>	<i>anoplus</i>	GenBank AF287417	1	–	–	–	–	–	Machordom & Doadrio, 2001
<i>Enteromius</i>	<i>anoplus</i>	GenBank AF112405	2	–	–	–	–	–	Tsigenopoulos & Berrebi, 2000
<i>Namaquacypris</i>	<i>hospes</i>	Sample HOS1	17	Orange	Orange	Violsdrif near border crossing	28°45'58" S, 17°37'12" E	1999	E. Swartz
<i>Namaquacypris</i>	<i>hospes</i>	Sample HOS2	18	Orange	Orange	Violsdrif near border crossing	28°45'58" S, 17°37'12" E	1999	E. Swartz
<i>Namaquacypris</i>	<i>hospes</i>	Sample HOS3	19	Orange	Orange	Violsdrif near border crossing	28°45'58" S, 17°37'12" E	1999	E. Swartz
<i>Pseudobarbus</i>	<i>afjer</i>	GenBank AF180851	4	–	–	–	–	–	Tsigenopoulos <i>et al.</i> , 2002
<i>Pseudobarbus</i>	<i>burchelli</i>	GenBank AF180848	3	–	–	–	–	–	Tsigenopoulos <i>et al.</i> , 2002
<i>Pseudobarbus</i>	<i>quathlambae</i>	GenBank AY791809	5	Orange	Matsoku	5 km above diversion weir	29°15'35" S, 28°33'29" E	2000	D. Tweedle

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