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Phylogeny and biogeography of the genus *Pseudobarbus* (Cyprinidae): Shedding light on the drainage history of rivers associated with the Cape Floristic Region

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ABSTRACT

Relationships among the historically isolated lineages of *Pseudobarbus* were reconstructed using molecular and morphological data. Contradictions between the molecular and morphological phylogenies suggest convergent evolution and homoplasy in some morphological characters. The earliest divergence in *Pseudobarbus* was between *P. quathlambae* in Lesotho and the rest of the genus associated with the Cape Foristic Region in South Africa. A close relationship between *P. phlegethon* from the Olifants River system on the west coast of South Africa and a lineage of *P. afer* from small river systems in Afrotemperate Forests on the south coast, can only be explained through previous occurrence and subsequent extinction of ancestral populations in the Gourits River system. Several river systems had confluences before reaching lower sea levels, most notably during the last glacial maximum about 18,000 years ago, explaining closely related populations across different river systems. Mainly river capture explains shared lineages across river systems that did not share a common confluence during lower sea levels.

1. Introduction

The Cape Floristic Region (CFR) is the only floral kingdom that is located entirely within the geographical confines of one country and known for its high levels of plant diversity (Goldblatt and Manning, 2002). In contrast, the freshwater fish diversity is low (Skelton, 1986), despite the region being characterised by many river systems of various sizes. The evolutionary history of primary freshwater fish often reflects drainage evolution, due to limited opportunities for dispersal between different river systems (Brito et al., 1997; Waters and Wallis, 2000; Mesquita et al., 2001). However, since there are only two to 10 primary freshwater fish species per river system and only three widespread genera (*Pseudobarbus*, *Galaxias* and *Sandelia*) across the CFR, prospects of using freshwater fish to study the biogeography of this region's rivers are limited. Of the three widespread CFR fish genera, *Pseudobarbus* is the most species rich with six currently described species occurring in the CFR and one in Lesotho compared to one species each for *Galaxias* and *Sandelia*. The distribution of the *Pseudobarbus* species is relatively well known and is also the freshwater genus in the CFR that has been revised taxonomically most recently (Skelton, 1988), making it the ideal group with which to investigate the drainage evolution of the CFR.

Pseudobarbus occur in all the major river systems and most of the smaller river systems of the CFR and in the neighbouring Orange River system. The latter river system has its origins in the highlands of Lesotho, is the largest river system in South Africa and once shared a mouth with the Olifants River system in the north-western CFR (De Wit, 1993). The Olifants, Berg, Breede, Gourits, Gamtoos and Sundays River systems are the larger systems in and bordering the CFR and drain from interior regions of the Western Cape and Eastern Cape provinces associated with the semi-arid Karoo region. The Keurbooms and Swartkops River systems penetrate coastal mountain ranges, but originate within the CFR. There are also several small coastal river systems that do not penetrate coastal mountain ranges, especially along the southern coastline (Fig. 1).

Several river captures are evident from the current drainage patterns of rivers in the CFR. During lower sea levels most of the rivers of the CFR would have had common confluences before reaching the sea, forming palaeoriver systems that are currently drowned. During the last glacial maximum (LGM) about 18,000 years ago, the sea level along the south coast of the CFR was about 130 m below present levels (Tankard, 1976; Rogers, 1985; Ramsay and Cooper, 2002). Probably, only about nine to 10 major palaeoriver systems that has not been completely drowned in subsequent

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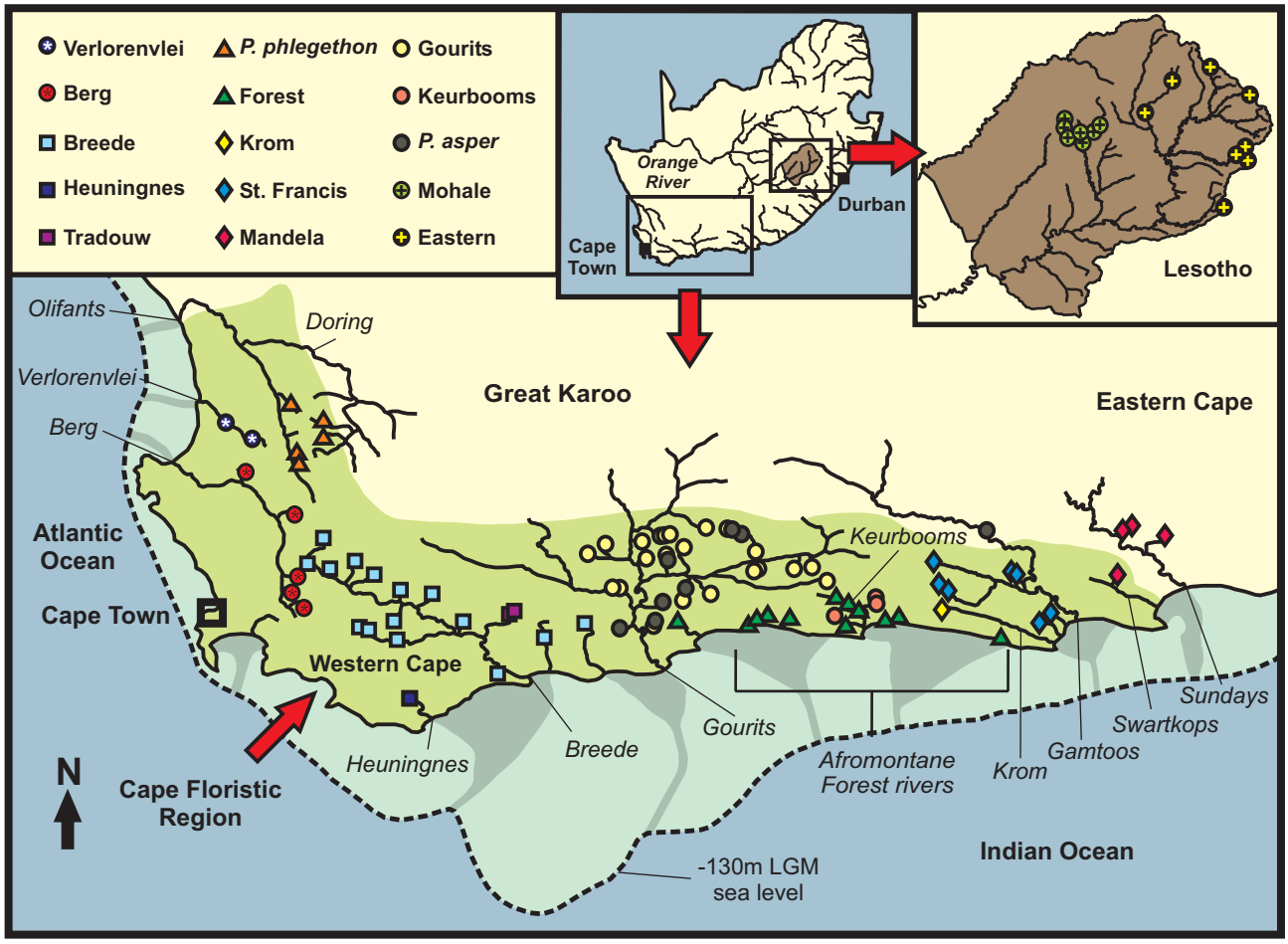

Fig. 1. Regions and river systems referred to in the text and the sampling sites for the present study, which indicate the distribution of historically isolated lineages of *Pseudobarbus* in the Cape Floristic Region and Lesotho. All these sites were analysed using control region, whilst selected sites from each of the lineages were analysed using cytochrome *b* and 16S (see Supplementary data S1 and S2).

sea level transgression, based on reconstructions by Swartz et al. (2007 and unpublished), are relevant to the biogeography of *Pseudobarbus* (Figs. 1 and 6). It cannot, however, be assumed that known river captures, confluence of rivers during lower sea levels or other climatic and geological events influenced the evolution of *Pseudobarbus* without testing congruence with the latter's population history.

Pseudobarbus originate from the southern African region with historical links to the rest of the African continent. *Pseudobarbus* species are all tetraploid (Naran et al., 2006) and closely related to the tetraploid '*Barbus*' species that are endemic to southern Africa (Machordom and Doadrio, 2001b; Tsigenopoulos et al., 2002). *Pseudobarbus* and the southern African tetraploid '*Barbus*' are the sister group to the pan-African diploid '*Barbus*' (Machordom and Doadrio, 2001b; Tsigenopoulos et al., 2002). When Skelton (1980, 1988) reviewed the taxonomy and established morphological relationships within *Pseudobarbus*, he found that several morphological characters are shared between the Maloti Minnow (*P. quathlambae*) in the upper reaches of the Orange River system in Lesotho and *P. tenuis* from southern parts of the CFR (Gourits and Keurbooms River systems), which suggested a sister species relationship. The latter was surprising given the large geographic distance between these two species. Based on the morphological characters, *P. phlegethon* from the Olifants River system in the western parts of the CFR was inferred as the sister species to *P. quathlambae* and *P. tenuis*. *Pseudobarbus afer*, which is the most widespread redfin species (southern CFR), and the Karoo adapted *P. asper* (Gourits and Gamtoos River systems) were inferred as sister species. Skelton (1980, 1988) suggested that *P. afer* is a polytypic species because of large variation in several morphological characters. The two *Pseudobarbus* species with two pairs of barbels (*P. burgi* and *P. burchelli*) that occur in the Berg, Breede and associated river systems (western CFR) have always been regarded as sister taxa (Jubb, 1965; Skelton, 1980, 1988), compared to all the other *Pseudobarbus* species that have only one pair of barbels.

These morphological relationships were easily explained through differentiation between adjacent river systems, except for the large geographic distance between *P. quathlambae* and *P. tenuis*. Skelton (1980) suggested that an ancestor of the latter species must have occurred in Karoo tributaries of the Orange River system (north of the CFR in Fig. 1). These populations would have given rise to *P. tenuis* in the Gourits River system where they now occur in sympatry with *P. asper*. Sympatry between *P. tenuis* and *P. asper* was therefore likely the result of secondary contact. Redfins do not currently occur in the area of the Orange River system where Skelton (1980) proposed an exchange between the Orange and Gourits River systems. Extinction of the proposed ancestral populations in Karoo tributaries of the Orange River system therefore had to be assumed.

Skelton (1980, 1988) noted morphological variation between populations within species, but the differences were not clear or consistent enough to warrant full species status for these unique populations. However, mtDNA evidence suggests that 15 historically isolated lineages can be identified within the seven