Seventy-five-million-year-old tropical tetra-like fish from Canada tracks Cretaceous global warming

M. G. Newbrey^{1,2,*}, A. M. Murray², M. V. H. Wilson²,
D. B. Brinkman¹ and A. G. Neuman¹

¹Royal Tyrrell Museum of Palaeontology, PO Box 7500, Drumheller, Alberta T0J 0Y0, Canada

²Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

Newly discovered fossil fish material from the Cretaceous Dinosaur Park Formation of Alberta, Canada, documents the presence of a tropical fish in this northern area about 75 million years ago (Ma). The living relatives of this fossil fish, members of the Characiformes including the piranha and neon tetras, are restricted to tropical and subtropical regions, being limited in their distribution by colder temperatures. Although characiform fossils are known from Cretaceous through to Cenozoic deposits, none has been reported previously from North America. The modern distribution of characiforms in Mexico and southern Texas in the southernmost United States is believed to have been the result of a relatively recent colonization less than 12 Ma. The new Canadian fossils document the presence of these fish in North America in the Late Cretaceous, a time of significantly warmer global temperatures than now. Global cooling after this time apparently extirpated them from the northern areas and these fishes only survived in more southern climes. The lack of early Cenozoic characiform fossils in North America suggests that marine barriers prevented recolonization during warmer times, unlike in Europe where Eocene characiform fossils occur during times of global warmth.

Keywords: biogeography; characiforms; Gondwana; Ostariophysi; Pangaea

1. INTRODUCTION

Characiform fishes, including the well-known neon tetras and piranhas, are an ancient and diverse order containing over 1600 extant species in 18 families (Nelson 2006). Living characiforms occur exclusively in fresh waters of Africa, South and Central America, Mexico and southernmost United States. Traditionally, characiforms have been considered a Gondwanan group that arose over 100 million years ago (Ma) on the western part of that landmass, which included present-day Africa and South America.

Ichthyologists and biogeographers still debate the time and place of origin of these fishes, as well as their palaeobiogeography (Lundberg 1998; Filleul & Maisey 2004; Briggs 2005; Peng *et al.* 2006; Otero *et al.* 2008). Although the characiform fossil record is poor compared with the diversity of living species, it is likely that much of the characiform diversification occurred between the Late Cretaceous and the Miocene when modern forms are found in the fossil record (Lundberg 1998). North America has never previously produced any characiform fossils, so it has not been considered as playing a role in the evolution of the group. Molecular analyses (Bermingham & Martin 1998) and the timing of the presence of a land bridge (Lundberg 1998) have indicated that characiforms did not disperse to Central America and southern North America before the late Miocene (Briggs 2005).

We report here the discovery of fossil characiform fish remains from freshwater deposits of the Campanian

Dinosaur Park Formation (75 Ma) near Onefour, southern Alberta. These fossils document that characiforms inhabited North America much earlier than previously believed, and our understanding of the early history of the group is therefore in need of revision. The presence of characiforms in the Cretaceous of Alberta suggests either that this group is older than previously thought and inhabited North America before its separation from Gondwana about 170 Ma, or that characiforms invaded North America much earlier than the Miocene, perhaps via a land bridge from South America or Europe about 80 Ma (Pitman *et al.* 1993; Martin *et al.* 2005).

The presence of these fishes in a northern latitude is surprising. However, global temperatures from this time period show that the area was much warmer in the Campanian (Frakes 1999; Zachos *et al.* 2001). Information from climate modelling studies indicates that precipitation levels were also higher in the Campanian than now (DeConto *et al.* 1999). We suggest that the warmer and probably moister global climate enabled these fishes to invade northern areas. In the early Cenozoic, decreased global temperatures likely extirpated the fishes from northern latitudes. The characins of Central America, Mexico and southern United States (New Mexico and Texas) are members of South American lineages, which were probably only able to reinvade millions of years later, using a new land bridge in the Miocene.

2. MATERIAL AND METHODS

The fossil material comprises 13 dentaries (TMP 1993.124.26, 1993.124.62, 1994.23.08, 1994.23.50, 1989.01.34,

* Author for correspondence (mike.newbrey@gov.ab.ca).

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1989.01.73, 2008.09.01, 2008.09.02, 2008.09.03, 2008.09.04, 2008.10.01, 2008.23.01, 2008.25.01), deposited in the collections of the Royal Tyrrell Museum of Palaeontology (TMP). Specimens were removed from surrounding matrix using underwater screen-washing techniques (Eberth & Brinkman 1997; Brinkman & Neuman 2002). Two of the specimens were sputter-coated with gold and imaged with a scanning electron microscope.

3. DESCRIPTION

The dentaries are small, less than 4 mm in height, and incomplete posteriorly (figure 1). Each dentary has the anterior symphyseal morphology unique to characiforms (Monod 1950; Gayet *et al.* 2003; Murray 2004) in which the left and right symphyseal lobes have four or five lobes that converge on the external side of the jaw but fan out towards the internal side and form an interdigitating bony hinge (figure 2).

The mandibular sensory canal is enclosed in bone as in other characiforms, and opens to the surface only through three large pores, one anterior and two lateral (figure 1*a,e*). Dorsal to the anterior end (the symphysis) is a triangular, edentulous area, and extending back from this is a single row of small, uniformly sized teeth (figure 1*b–d, f–h*). As in other characiforms, one or more foramina are associated with each round-to-subovate tooth base. The bases of most teeth contact the inner shelf, except the bases of the five or six anterior-most teeth, which, when resorbed, lose their contact with this shelf (figure 1*h*). These teeth remain in a functional position fused on their outer sides to the dentary, as in other characiforms.

Dentary replacement teeth in the majority of characiforms develop in a replacement trench or crypt and move from there into a functional position. However, in some characiforms replacement teeth form instead in the soft tissue, posteroventral to the functional tooth bases. This seems to be the case for the fossil dentaries, and may be primitive for the group.

4. DISCUSSION

Although many fossil characiforms have been reported, the vast majority of these records are based on teeth found in deposits of Africa and South America (Roberts 1975; Dutheil 1999; Stewart 2001, 2003), as well as a few isolated jaw bones (Stewart 1997; Gayet *et al.* 2003). Very few articulated fossil characiforms are known (Murray 2003).

Characiform fishes are currently restricted to fresh waters, and found in areas that were for the most part united in the western part of the Gondwanan land mass in the Early Cretaceous—that is, Africa and South America. This contemporary distribution has been interpreted as resulting from a Gondwanan origin, with modern distributions in Central and southernmost North America being the result of a much later (probably Miocene) dispersal from the south (Briggs 2005).

However, the known characiform fossil record indicates that the history of the group is more complex. The Characiformes have a geological range of over 100 Myr, with remains recovered from the Late Cretaceous of South America (Maastrichtian), Africa (Cenomanian)

and Europe (Maastrichtian; Werner 1993; Gayet *et al.* 2003; Otero *et al.* 2008). The fossil record may stretch back to the Early Cretaceous (Albian) if the fossil *Santanichthys diasii* is included in the order (Filleul & Maisey 2004). If *Santanichthys* is discounted from the order (as was suggested by Brito & Mayrinck 2008), the Canadian fossils represent some of the oldest Characiformes known; however, additional information on *Santanichthys* is needed before its relationships can be determined. In either case, they represent a significant geographic range extension for the order, being the first evidence for their former presence in northern North America.

Marine dispersal of characiform fishes was considered unlikely (Myers 1938; Bussing 1985; Bermingham & Martin 1998). Fossil evidence that some characiforms (e.g. *Sorbinicharax*) might have tolerated marine conditions (Otero *et al.* 2008) is debated, with the possibility that these taxa are either not from marine deposits or are not characiforms (Brito & Mayrinck 2008). Characiforms, fossil and extant, are absent from Asia, Madagascar and Australia, presumably because of ocean barriers. It is thus probable that characiform dispersals require land connections involving some combination of freshwater rivers and lakes or possibly shallow, coastal marine waters (Otero *et al.* 2008).

Other than a Gondwanan origin, two other scenarios have been proposed to explain characiform biogeographic patterns. Either the order arose much earlier and the breakup of Pangaea (Gondwana + North America and Eurasia) is responsible for the modern distribution (Peng *et al.* 2006), or a dispersal event from South America or Europe to North America occurred in the Late Cretaceous (figure 3), well before the Miocene (Bussing 1985).

A Pangaeian origin for characiforms, with their distribution resulting from the breakup of Pangaea in the Middle Jurassic (Peng *et al.* 2006), would require that the group be at least 170 million years old (Smith *et al.* 1994). This scenario has support from molecular clock calculations, which give an even older age (about 200 Ma) for the order (Peng *et al.* 2006). However, it is contradicted by the fact that the Jurassic fossil record of teleosts includes neither crown clupeocephalans (clupeomorphs plus ostariophysans including characiforms) nor crown members of their sister group, the euteleosts. Only the most basal, stem-group representatives of those clades are known from the Jurassic (Arratia 1997), despite a diverse and widely distributed teleostean fossil record. The Pangaeian origin is also contradicted by the lack of characiforms in Asia, India and Australia today, despite these regions also being derived from the Pangaeian continent.

A Late Cretaceous dispersal of characiforms from South America into North America is consistent with the presence of characiforms in South America during the Late Cretaceous. Their dispersal could have been accomplished through temporary connections between the two continents in the Panama-Caribbean region about 80 Ma (figure 3). Such a connection and vertebrate dispersal route for lizards, mammals and hadrosaurian dinosaurs (Estes 1983; Cifelli & Eaton 1987; Nydam 2002) has been posited previously, but remains poorly understood (Ross & Scotese 1988;

Figure 1. Scanning electron micrographs of two characiform dentaries from the Cretaceous Dinosaur Park Formation of Alberta. From left to right: lateral, medial, symphyseal and occlusal views. (a–d) TMP 1994.23.08; scale bars, 1 mm; (e–h) TMP 2008.09.01; scale bars, 0.5 mm.

Figure 2. Right dentary bones showing the unique morphology of the characiform symphysis in which four or five lobes form an interdigitating hinge. (a) The fossil TMP 2008.09.01; (b) *Charax gibbosus*, University of Michigan Museum of Zoology (UMMZ) 207313-5. The lobes are closer together on the external side of the jaw (the left side of the photographs), and fan out towards the internal side of the jaw (right side of the photographs). Scale bars, 0.2 mm.

Pindell & Barrett 1990; Pitman *et al.* 1993; Giunta *et al.* 2006; Pindell *et al.* 2006).

A Late Cretaceous dispersal of characiforms from Europe to North America is also plausible given the presence of characiforms in Europe during the Late Cretaceous (Otero *et al.* 2008). In this scenario, characiform dispersal could have occurred during the late Santonian/early Campanian (e.g. 80–85 Ma) via a land connection between Europe and North America. The fossil record indicates that such a route was used by duck-billed

Figure 3. Map of the Cretaceous palaeocoastline during the Campanian (~80 Ma). The location of the fossil locality is indicated by the star. The extant distribution of characiforms is indicated by the hatched shading. Cretaceous landmasses are indicated by solid shading. Arrows show two hypothesized directions of dispersal of Cretaceous characiforms in association with connections between South America or Europe and North America. (Continental outlines and positions based on Smith *et al.* 1994.)

dinosaurs during this time period, and later on in the Maastrichtian by marsupials, both times when sea levels were lower and temperatures warmer (Martin *et al.* 2005). This same route may have been available for characiforms.

The Canadian fossils do not prove or disprove either an older Pangaeian origin or a Late Cretaceous dispersal event from South America or Europe, but they do demonstrate that characiforms were more widely distributed in the Cretaceous than was previously recognized. However, the biology of living characiforms is consistent with the hypothesis of a Late Cretaceous dispersal from South America or Europe, assuming that the fishes were tracking a warming climate. Living characiforms are limited in their distribution by colder temperatures, as is evident from their modern distribution in tropical and subtropical regions. Before this time, the northern palaeo-position of the characiform fossil locality (see maps in Irving 1977; Smith *et al.* 1994; Hay *et al.* 1999) and cool Early Cretaceous global temperatures (e.g. Frakes 1999) would have barred characiforms from the more northerly latitudes. Under modern, cooler climatic conditions, characiforms do not reach north of central New Mexico. In a similar way, freshwater esocoids (pikes and mudminnows) have been found to shift their Cenozoic palaeodistribution with climate change, occurring at significantly higher northern latitudes during warmer periods of the Cenozoic (Newbrey *et al.* 2008a). Global mean annual temperature data likewise correlate generally with the fossil distribution of characiforms during the Cenozoic; during times of warmer climate (e.g. early Eocene, Miocene), characiforms were present in higher latitude areas of Europe (Newbrey *et al.* 2008b). The Late Cretaceous was also a time of warmer climate, with no continental glaciation (Frakes 1999). The Campanian, in particular, included times of considerable global warmth, followed by global cooling in the early Maastrichtian (Frakes 1999). We therefore suggest that the Canadian characiforms moved north from South America or northwest from Europe (figure 3) during the Late Cretaceous when the global climate was warm enough for them to invade higher latitudes. Future fossil finds may indicate which route is more probable. Later, we suggest they would have been extirpated from the north as temperatures decreased, possibly in the latest Cretaceous and early Palaeocene. Global temperatures were again warmer in the late Palaeocene to early Eocene (Zachos *et al.* 2001), and characiforms were present in the early Eocene of Europe (Otero *et al.* 2008). However, we suggest that characiforms were unable to re-enter North America from South America or Europe at this time, in view of their absence from the rich Eocene deposits of North America. Not until the Neogene did a land bridge between North and South America allow these fishes access to the northern continent once again, but cool global temperatures confined them to areas far south of their previous Cretaceous range.

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