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Miocene Characid Fishes from Colombia: Evolutionary Stasis and Extirpation

JOHN G. LUNDBERG, ANTONIO MACHADO-ALLISON, RICHARD F. KAY

Fossil fishes from the Miocene La Venta fauna of the Magdalena River Valley, Colombia, are identified as *Colossoma macropomum* (Characidae), a living species from the Orinoco and Amazon basins. The fossils document a long and conservative history for a species that is highly specialized for feeding on streamside plants. The phylogenetically advanced position of *Colossoma* in the subfamily Serrasalminae implies that six related genera and other higher characid taxa originated well before 15 million years ago. This discovery also corroborates neontological evidence for a vicariance event that contributed species from Miocene Orinoco-Amazon faunas to the original Magdalena region fauna. The fossils suggest a formerly diverse Magdalena fauna that has suffered local extinction, perhaps associated with late Cenozoic tectonism. This new evidence may help explain the depauperate nature of the modern Magdalena River.

"IT IS QUITE OUT OF THE QUESTION to transport all of these genera over the present barrier formed by the Cordilleras of Bogotá . . ." [C. H. Eigenmann, 1920 (*1*)]. The tremendous richness of the South American fish fauna is concentrated in the Amazon and Orinoco rivers. Beyond these basins, into northwestern Colombia and then lower Central America, the number of fish species falls sharply. This diversity pattern exists in spite of suitable habitat in faunistically depauperate rivers and requires a historical explanation. Such explanation has been frustrated by incomplete phylogenetic and distributional data for living fishes and a very poor paleontological record (*2*).

The Magdalena River, lying between the Andean Cordilleras Oriental (Bogotá) and Central, drains about 241,000 km^2 of central Colombia. The modern Magdalena fish fauna comprises about 150 species, far fewer than estimates for the adjacent Orinoco and Amazon faunas (*3*). On the basis of the high proportion of shared taxa, Eigenmann (*1*) proposed that the Andean Cordillera Oriental is younger than the lowland Magdalena region, thus allowing for direct capture of widespread Orinoco and Amazon fishes when the Magdalena Basin formed as the mountains rose. If this is so, why are there not more Orinoco and Amazon elements in the Magdalena fauna? An alternative hypothesis considered by Eigenmann involves chance dispersal of species into the Magdalena from elsewhere. The dispersal of freshwater fishes is severely constrained by the evolution of landform and watersheds. Fishes may not have had enough opportunities and time to reach relatively young or remote waters. If Eigenmann's vicariance hypothesis is correct, we would expect greater faunistic similarity in the past, before local extinction and divergence obscured the similarity between faunas that were once one.

Paleontological investigations in Colombia have recovered jaw elements and teeth of a large characid fish from Miocene deposits in the Magdalena Basin. This material is indistinguishable from the extant *Colossoma macropomum*. Today this species occurs in the Orinoco and Amazon systems: it is absent from the Magdalena. Given their age and extralimital locality, these fossils bear noteworthy implications for the history of fishes in South America.

The specimens come from the upper Magdalena River Valley northwest of Villavieja, about 3°15′N, 75°13′W, Huila Department, Colombia. Stratigraphically, the fossils occur in clays, called the "Monkey Unit" (*4*), of the Villavieja Formation (Honda Group). These fishes are part of the La Venta fauna (*5*) that is approximately 15 million years old. The precise dating of this fauna is problematic (*6*), but variation in age estimates does not affect our conclusions. The strata are composed of continental deposits derived from the Cordillera Central. The area presently incorporated into the Magdalena Valley was then a piedmont fluvial plain sloping to the east and southeast and running parallel to the Cordillera Central (*7*). There was no major uplift in the Cordillera Oriental during Honda time although local blocks along the range may have been uplifted.

We report the following fossil specimens now deposited in the Museo Geológico of the Colombian Instituto Nacional de Investigaciones Geológica-Mineras (INGEOMINAS) at Bogotá: (i) partial mandible (Fig. 1A), including fragments of both jaws

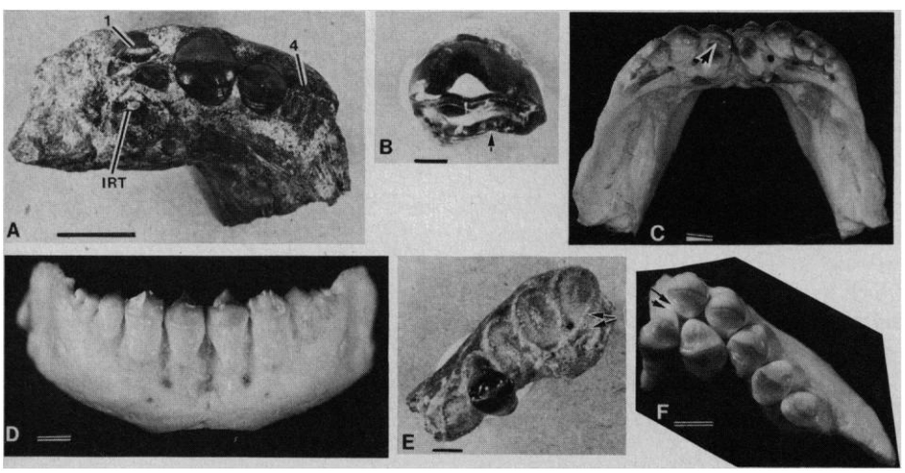

Fig. 1. Jawbones and teeth of *Colossoma macropomum*. (A) Fossil right mandible, dorsal view. Scale bar, 10 mm. (B) Isolated first outer row tooth. Scale bar, 2 mm. In (B) and (C), arrows point to a notch on the posterior side of the outer tooth for reception of the inner row tooth. (C) Modern mandible, dorsal view. (D) Same as (C), anterior view. Scale bars for (C) and (D), 5 mm. (E) Fossil right premaxilla, ventral view. Scale bar, 3 mm. In (E) and (F), arrows indicate facing margins of symphyseal outer and inner row teeth. (F) Modern left premaxilla, ventral view. Scale bar, 5 mm. Abbreviations: 1, first outer row tooth base; 4, fourth outer row tooth base; and IRT, inner row tooth base.

J. G. Lundberg, Department of Zoology, Duke University, Durham, NC 27706.
A. Machado-Allison, Instituto de Zoologia Tropical, Universidad Central de Venezuela, Apartado 47058, Caracas, 1041-A, Venezuela.
R. F. Kay, Department of Anatomy, Duke University Medical Center, Durham, NC 27706.

and teeth in two rows; (ii) first mandibular, outer row tooth (Fig. 1B); (iii) seven large teeth in a block of matrix of which six are associated; (iv) fragmentary left premaxilla, bearing a complete second inner-row tooth; and (v) partial right premaxilla (Fig. 1E) with indications of seven teeth.

The fossils are identified thus: Order Characiformes, Family Characidae, Subfamily Serrasalminae, *Colossoma macropomum* (Cuvier), 1818.

On the basis of the hypothesis of relationships of the Serrasalminae (Fig. 2) (*8*), representative species of all related genera were compared to the fossils to confirm the identification. The fossils do not differ detectably from corresponding elements in modern *C. macropomum* (Fig. 1, C, D, and F). Among all taxa the fossils and modern *Colossoma* are characterized by the position of the mandibular inner row tooth adjacent to the middle of the first outer row tooth and the corresponding concavity on the rear margin of the latter and the lack of a gap between the inner and outer symphyseal teeth of the premaxilla. It is noteworthy that in *Piaractus brachypomum*, the most similar and closely related species of *C. macropomum*, the mandibular inner row tooth contacts the medial corner of the outer row tooth, and the facing margins of the symphyseal teeth are separated by a hiatus. *Colossoma macropomum* is also unusual among living serrasalmines from Colombia and Venezuela in its large size. Individuals commonly approach 1 m in length and the largest fossil mandible is from a fish of about that size.

Following from their strong resemblance to a specialized extant species, their Miocene age, and their location on the other side of what is now an absolutely limiting barrier for modern *C. macropomum*, these fossils bear three important implications for the history of South American fishes.

First, the fossil *Colossoma* demonstrate that some South American fishes have remained morphologically conservative for at least 15 million years. This appears long in relation to estimates of species longevity based on other fishes or mammals (*9*). However, evolutionary stasis of similar duration is known for some North and South American fish and turtle species (*10*). Further, the dental morphologies of serrasalmine fishes, especially those of the "A" lineage (Fig. 2), are diagnostic of genera and often species. This diversity indicates past evolutionary lability of the trophic apparatus in this group. *Colossoma* are herbivorous fishes (*11*) that eat shoreline herbaceous plants and fallen fruits and seeds. These plant materials are sheared with their unusual teeth before swallowing (*12*). The fossil

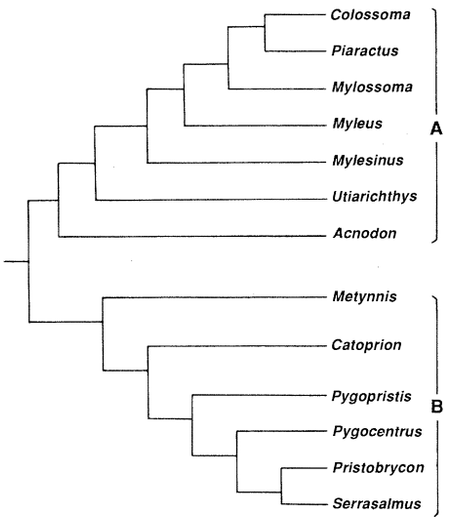

Fig. 2. Phylogenetic relationships among the genera of the characid subfamily Serrasalminae from Machado-Allison (*8*).

Colossoma give a significant historical perspective for establishing a minimum age of origin of this ecological specialization.

Second, the Miocene-aged *Colossoma* provide a minimum date for "modernization" of the Serrasalminae, a prominent lineage in the South American ichthyofauna (*13*). Given the phylogenetic framework (Fig. 2) and the principle of equal age for phylogenetic sister groups, it follows that lineages leading to each genus in the "A" clade existed by the mid-Miocene, as did at least the basal stem of the "B" clade, which includes the piranhas. Fossil evidence is needed to determine whether other modern serrasalmine species had differentiated by mid-Miocene.

Third, the fossil *Colossoma* are consistent with the vicariance hypothesis for the Magdalena region. They indicate that, before the Cordillera Oriental arose (*7*) to complete the Magdalena River Valley, the Amazon or Orinoco systems extended farther westward. This is confirmed by additional La Venta faunal elements, such as lungfishes (*Lepidosiren*) and pelomedusid turtles (*Podocnemis*) (*14*) which, like *Colossoma*, presently occur in the Amazon or Orinoco but not in the Magdalena. The Miocene aquatic fauna that the fossils represent was available for vicariant fragmentation with development of the mountain barrier and new river basin.

The modern Magdalena fauna is depauperate by an order of magnitude compared to those of the Orinoco and Amazon (*3*). The Magdalena is a large and ecologically diverse river system. Any Orinoco or Amazon fish species of large waters could likely survive today in at least the lower Magdalena system. Why is this river poor in fish diversity now, when originally it may have contained a richer fauna derived directly from the Orinoco or Amazon? Surely there has been a large element of catastrophism in the history of the Magdalena ichthyofauna. Habitat disturbance caused by severe tectonic activity in the walls of the Magdalena Valley, especially during later uplift of the Cordillera Oriental and vulcanism in the Cordillera Central (*15*), may have extirpated some species. Once isolated from the Orinoco, Amazon, and Maracaibo faunas, the Magdalena fish fauna could increase in species richness by occasional fortuitous immigration or through speciation in situ. Neither process has occurred to any great extent, although there are two dozen or so endemic forms in the fauna. Thus, the picture suggested for the modernization of the Magdalena fish fauna includes erosion of diversity during the late Cenozoic.

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