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RICHARD P. VARI¹

ABSTRACT

Piabucus caudomaculatus is a new species of iguanodectine characoid from Bolivia and the first member of the subfamily Iguanodectinae reported from that country. The Iguanodectinae are shown to share a series of modifications of

the swimbladder, body wall, and anterior proximal pterygiophores, which distinguish them from other characoids and support the hypothesis of the monophyletic nature of the group.

INTRODUCTION

The subfamily Iguanodectinae is a small group of South American characoid fishes consisting of two genera, *Iguanodectes* and *Piabucus*, and six species according to the most recent systematic works on the group by Böhlke (1954) and Géry (1970). During examination of characoid material from the Rio Mamoré in the collection of the American Museum of Natural History, a new species of *Piabucus* was discovered and several unique characters were found separating the subfamily from other characoids.

The species of the subfamily Iguanodectinae have a distribution in the Atlantic drainages of South America from the Orinoco drainage in the north, through most of the rivers of the Amazon basin to the Paraguay drainage in the south. They are small fishes having a smeltlike form with an elongate, slender body, a moderate to long anal fin, and a short dorsal fin originating behind the

middle of the standard length. The mouth is small, terminal, and entirely in front of the eye with the lower jaw bearing one and the upper jaw one or two rows of teeth (when present the outer row consists of one or two teeth on the premaxillary external to the main tooth row). The teeth have a round base that expands outward to a flattened multicuspid edge. All species also have gill membranes that are free from the isthmus.

As pointed out by Géry (1970) all of these characters are found in isolation or various combinations in members of the subfamily Tetraopterinae, thereby raising doubts as to the monophyletic nature of the Iguanodectinae. However, in the course of this investigation three characters associated with the form and position of the swimbladder were discovered that appear to be unique to the Iguanodectinae.

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***Piabucus caudomaculatus*, new species**

Figure 1

Holotype. American Museum of Natural History (AMNH) 32490, a mature ?female 94 mm. standard length (SL), obtained by Sydney Anderson with rotenone, October 4, 1965, in the Rio Matucare, a small muddy stream (1 m. wide, flow .3m³ per sec.) just above its junction with the Rio Mamoré at Puerto Siles, Department of Beni, Bolivia (approx. lat. 12°49'S, long. 65°04'W).

Paratype. AMNH 32491, a mature ?female 96 mm. SL, obtained by W. P. MacLean, August 5, 1965, in the Rio Mamoré about 5 km. SE of Limoquiye, Department of Beni, Bolivia (approx. lat. 15°24'S, long. 64°46'W).

Etymology. The trivial name *caudomaculatus* is from the Latin *cauda*, tail, and *maculatus*, spot, and refers to the dark spot on the base of the middle caudal rays and center of the caudal peduncle.

Diagnosis. *Piabucus caudomaculatus* differs from other species of the subfamily with the exception of *P. melanostomus* in lacking a second row of teeth external to the main premaxillary row. Meristically it can be distinguished from *P. melanostomus* by differences in lateral line counts to the hypural joint (75-76 for *P. caudomaculatus* vs. 82-87 for *P. melanostomus*), dorsal rays (8 or 9 vs. 11), and anal rays (36-38 vs. 44-46). Morphometric characters separating the species include (measurements for *P. melanostomus* are for specimens of 50-110 mm. SL) head length in SL (4.8-4.9 vs. 5.5-6.0), and great-

est body depth in SL (4.45-4.55 vs. 4.0-4.1). In addition both the holotype and the paratype lack an adipose dorsal fin, a condition that is not found in any other species in the subfamily and which does not appear to vary within species (based on examination of several hundred specimens of different species).

Description. A slender, elongate, laterally compressed fish with a nearly straight dorsal profile only slightly convex between the rear of the skull and origin of the dorsal fin; interorbital region convex. Ventral profile strongly curved from tip of lower jaw to anus. Thoracic and pre-ventral region compressed; with compressed edge terminating in a flexible keel formed by a series of two or three scale rows. Keel originating slightly posterior to the vertical through base of the pectoral fin, continuing posteriorly to between pelvic fins where it terminates in a short process lacking dorsal attachment to ventral body wall. Mouth small, entirely in front of eye. Nares separated by a flap. The circumorbital series entirely covers cheek and overlaps center of vertical arm of preopercle and middle of preopercular sensory canal. Sensory canals present in all circumorbitals, a posteriorly directed side branch developed in circumorbital 4. Subopercle with a notch along its ventral border. Cleithrum with a deep notch surrounding the base of the pectoral fin.

Dorsal fin short, pointed, with second to fourth rays longest and origin of fin behind midpoint of standard length. Anal fin long with base and edge straight; base of anal with a sheath of

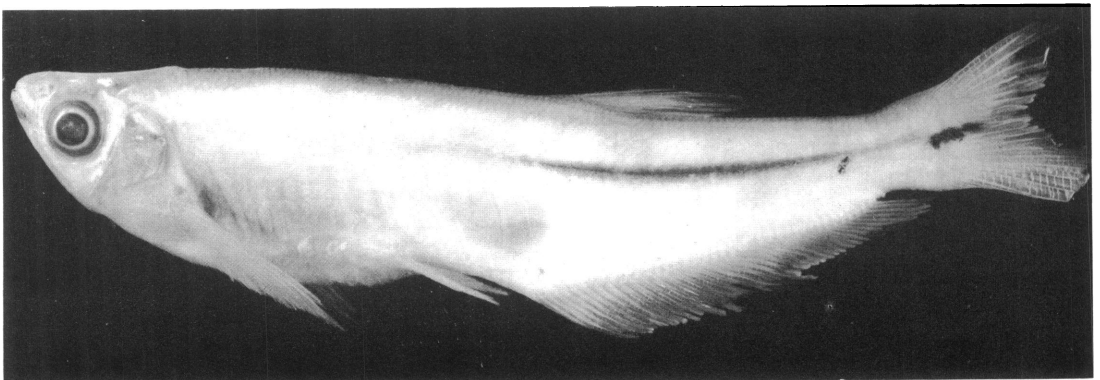


FIG. 1. Holotype of *Piabucus caudomaculatus*, AMNH 32490, 94 mm. SL.

scales one or two rows in height. Caudal emarginate; a triangular patch of scales extending out onto middle caudal rays. Pectoral fin pointed; tip falling slightly short of origin of pelvic fins. Pelvic fins pointed, tips reaching past anus but falling slightly short of origin of anal fin. Adipose fin lacking. Gill rakers slender, pointed, close set, shorter than the gill filaments; 6+1+13 on first arch. Lateral line complete, nearly straight; some rows of scales above lateral line merge together irregularly and some of rows below lateral line deflected toward anal fin. Scales cycloid, strongly adherent, with concentric striae.

Swimbladder of the *Piabucus* type (see below); thinning of the lateral body wall around the posterior chamber visible in figure 1 as the darker area dorsal and slightly anterior to the origin of the anal fin (form checked by X ray).

Scales 75 or 76 in lateral line from origin to hypural joint; 11 or 12 scales above lateral line to origin of dorsal fin; nine scales below to origin of anal fin. Head 4.8-4.9 SL (20-21% of SL); depth 4.45-4.55 in SL (22% of SL), distance from origin of dorsal fin to snout 1.65-1.67 in SL (60-61% of SL); distance from origin of anal fin to snout 1.67 in SL (60% of SL); length of base of anal fin 2.55-2.57 in SL (39% of SL); snout 3.3-3.55 in head length (HL); upper jaw 3.7-3.8 in HL; interorbital width 2.45-2.5 in HL; postorbital 2.05-2.10 in HL; width of eye 3.7-3.8 in HL, and 1.6-1.7 in interorbital width.

Fins. Dorsal 8 or 9, pectorals 13, pelvics 9, anal 36-38. No hooks or lappets on the anal fin as described for males of the Iguanodectinae by Böhlke (1954). The specimens do not have any of the other secondary sexual characters of the anal fin found in males of the genus *Piabucus*.

Vertebral Counts (from radiographs). 22 abdominal vertebrae including the four vertebrae of the Weberian apparatus; 25 caudal vertebrae including the fused first preural and ural centrum supporting the parahypural and hypurals as one element.

Teeth. Each jaw with one series of multi-cuspid teeth having a round base that expands outwards to a curved flattened edge. The teeth are colorless and the posterior edge of each tooth overlaps the anterior edge of the following tooth. Teeth in the upper jaw asymmetrical with 10-12 cusps, all of similar size; six or seven teeth on the

premaxillary, one tooth on the maxillary. Dentary with eight symmetrical teeth having 11-13 cusps, center cusp enlarged, about twice as large as the others. Lower jaw teeth inserting behind those of the upper jaw when mouth is closed.

Coloration. The overall color (in alcohol) is a pale yellow. A dark longitudinal stripe runs from a point slightly anterior to a vertical through the anal-fin origin posteriorly to the caudal peduncle. The stripe is widest and most intense above the middle of the anal fin and fades in both intensity and width anteriorly and posteriorly. The pigmentation of the stripe lies underneath the scales. In contrast, there are two darker spots of pigmentation in the epidermis. The larger is found at the base of the middle caudal-fin rays extending forward three or four scales anterior to the hypural joint. A smaller spot of pigmentation covers two or three scales slightly anterior of a vertical through the origin of the last anal-fin ray, and ventral to the lateral line and longitudinal pigment stripe. The rest of the body is unpigmented except for some dark pigmentation on the lower jaw.

Sex. These specimens are assumed to be female as they lack the secondary sexual characters found in males of other species of the genus *Piabucus*. However, it is possible that this species is not sexually dimorphic. It is presumed that these are mature individuals as specimens of *Piabucus dentatus* and *Iguanodectes spilurus* have been found mature at 60 to 70 mm.

Relationships. *Piabucus caudomaculatus* is assigned to the genus *Piabucus* based on its possession of a compressed thoracic and preentral region terminating ventrally in a keel formed of two or three rows of scales. Although similar ventral keels are found in the species of the genera *Triportheus*, *Pseudocorynopoma*, and *Rhaphiodon* among characoids, in none of these is the swimbladder of the form found in the Iguanodectinae and each of these genera share apomorphic characters with characoid groups other than the Iguanodectinae. Thus the ventral keel appears to have arisen more than once among characoids. However, within the subfamily Iguanodectinae it can be considered to be an apomorphic character uniting the species of the genus *Piabucus* into a monophyletic subgroup.

Within the genus *Piabucus*, *P. caudomaculatus*

appears to be most closely related to *P. melanostomus*, which shares a loss in the outer row of premaxillary dentition and the presence of pigmentation on the lower jaw, both characters unknown elsewhere in the subfamily.

Distribution. The material of *Piabucus caudomaculatus* was collected from two sites separated by 300 km. along the Rio Mamoré and its tributaries in the Bolivian Amazon. It represents the first report of a species of the Iguanodectinae from the rivers of Bolivia and also a large range extension for the genus *Piabucus*. This species is separated by about 1000 km. from the nearest reported locality for *P. melanostomus*, which appears to be its sister species. That species is limited to the Paraguay river drainage which is independent of the Amazon basin.

DISTINGUISHING CHARACTERS OF THE SUBFAMILY

The generalized swimbladder form in characoids consists of two chambers connected by a short narrow tube containing a muscular sphincter that prevents movement of air between the chambers. The rotund slightly elongate anterior chamber is attached dorsally by the peritoneum to the tripus and os suspensorium of the Weberian apparatus. The posterior chamber is elongate (at least twice the length of the anterior chamber) and as wide or slightly wider than the anterior chamber. The diameter of the posterior chamber is relatively constant for its entire

length but tapers slightly or is slightly expanded posteriorly in some species.

Whereas all species in the Iguanodectinae share the generalized form of the anterior chamber of the swimbladder, there are found in the subfamily two derived forms of the posterior chamber of the swimbladder. The species assigned to the genus *Piabucus* (*dentatus*, *melanostomus*, and *caudomaculatus* new species) share a posterior chamber with marked variation in its diameter (fig. 2) in contrast to the relatively uniform diameter of the chamber in the generalized form. The posterior chamber rather than being as wide as the anterior chamber, anteriorly, is very narrow for its anterior one-third (one-quarter the diameter of the anterior chamber) but expands posteriorly into a large bulbous region that is approximately six times the diameter of the anterior section of the chamber (one and one-half times the diameter of the anterior chamber).

The swimbladder in the genus *Iguanodectes* (fig. 3) is evidently a further modification of the type seen in *Piabucus* and appears to be unique among characoids (see also Eigenmann and Myers, 1929). The posterior chamber is divided into two subchambers of markedly different diameter by the development of a constriction at a point corresponding to the posterior limit of the anterior narrow section of the chamber in *Piabucus*. This constriction results in a narrow anterior section two-fifths the length of the entire posterior chamber and a rotund posterior section. The anterior section of the posterior chamber has

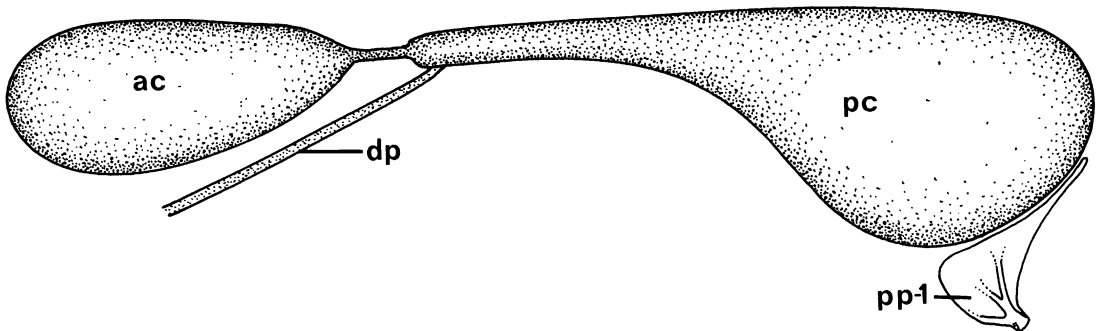


FIG. 2. Semidiagrammatic drawing showing the form of the swimbladder in the species of *Piabucus*. ac-anterior chamber of the swimbladder, dp-ductus pneumaticus, pc-posterior chamber of the swimbladder, pp-1-proximal anal pterygiophore-1.

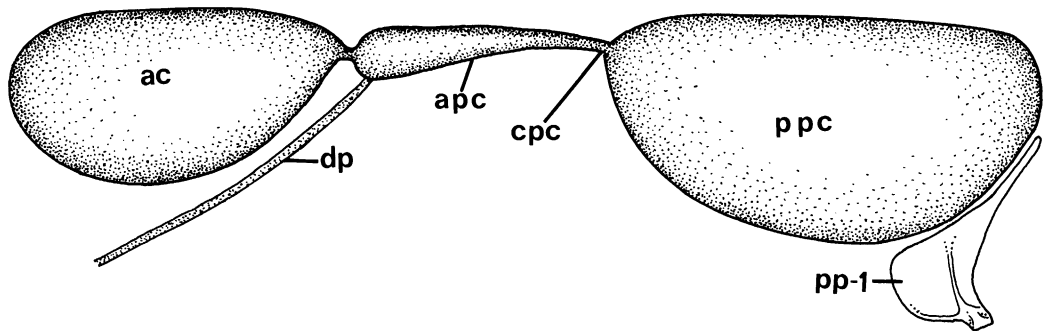


FIG. 3. Semidiagrammatic drawing showing the form of the swimbladder in *Iguanodectes spilurus*.

ac-anterior chamber of the swimbladder, apc-anterior section of the posterior chamber of the swimbladder, cpc-constriction in the posterior chamber of the swimbladder, dp-ductus pneumaticus, pp-1-proximal anal pterygiophore-1, ppc-posterior section of the posterior chamber of the swimbladder.

its thinnest, most distensible walls in the region where the ductus pneumaticus enters the swimbladder. Posteriorly the anterior chamber gradually narrows and there is an increase in the thickness of the connective tissue in the swimbladder wall. This combination results in a narrow non-distensible constriction that resembles the connection between the anterior and posterior chambers in the generalized swimbladder form. However, this constriction differs in being less distinct and in lacking a muscular sphincter as indicated by the movement of air between the sections of the posterior chamber. The posterior section of the posterior chamber in *Iguanodectes* is very slightly compressed, has thin walls, and is approximately one and one-third the diameter of the anterior chamber.

A second character distinguishing the subfamily is the reduction in the thickness of the myotomes in the region of the body wall where it contacts the lateral surface of the posterior chamber of the swimbladder. This reduction in the body wall thickness is shaped to fit the contours of the swimbladder wall and is most pronounced in the species of *Piabucus* where in the center of the reduced area the wall is one-half as thick as the unreduced sections. This modification in the thickness of the body wall allows the marked expansion of the posterior chamber of the swimbladder in the laterally compressed species of the Iguanodectinae. Although less pronounced, this thinning is similar to the lateral cutaneous area found lateral to the anterior

chamber of the swimbladder in many ostariophysans.

A third character separating the Iguanodectinae from the rest of the characoids is the form of the anterior proximal pterygiophores of the anal fin and their position with respect to the first hemal spine. In the generalized characoid condition the proximal pterygiophores of the anal fin are relatively straight, forward sloping elements inserting between or contacting the hemal spines (based on examination of the condition in approximately 150 species). The first pterygiophore is unexpanded or only slightly larger than the others and inserts posterior, or slightly anterior, to the first hemal spine. In both *Iguanodectes* and *Piabucus* however, the expanded posterior chamber of the swimbladder extends considerably beyond the anus and separates the anterior proximal pterygiophores from direct contact with the vertebral column (fig. 4). This results in modifications in the shape and orientation of the anterior proximal pterygiophores. The first proximal pterygiophore is greatly expanded anteriorly and slopes posterodorsally following the contour of the ventral surface of the posterior chamber of the swimbladder. The posterodorsal orientation of the first pterygiophore decreases successively in the more posterior five to seven elements. All the pterygiophores with this orientation differ from the generalized condition in characoids by inserting anterior to the first hemal spine.

Although similar large numbers of anterior

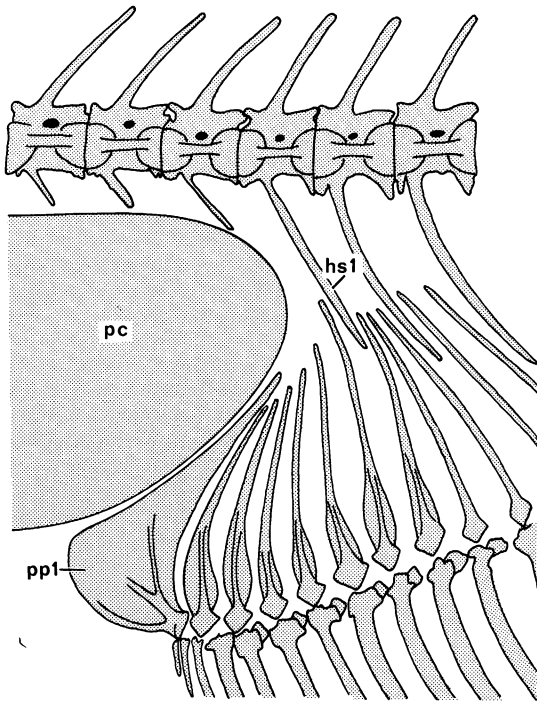


FIG. 4. Semidiagrammatic drawing of the rear of the posterior chamber of the swimbladder and the anterior proximal anal pterygiophores showing their relationships to the vertebral column.

hs-1-hemal spine-1, pc-posterior chamber of the swimbladder, pp-1-proximal anal pterygiophore-1.

proximal pterygiophores inserting anterior to the first hemal spine are found in some members of the Characinae (*Charax gibbosus*, *Roeboides dayi*, and *R. occidentalis*), where six or seven such elements are found, and in the Stethaprioniinae (*Stethaprion crenatus*) and Tetragonopterinae (*Parastremma sadina*, *Nematobrycon palmeri*, *Psellogrammus kennedyi*, *Pristella riddlei*, and *Ctenobrycon spilurus*), where four or five elements are found, in none of these species is the first proximal pterygiophore so greatly expanded. Neither do any of these species have the first and successive elements so markedly sloped.

The three characters above—the form of the anterior proximal pterygiophores, the reduction of the myotomes around the posterior chamber

of the swimbladder, and the distinctive shape of the swimbladder—appear to be unique to the Iguanodectinae and apomorphic for characoids. Thus the group can be separated from all other characoids based on these characters.

Géry (1970) in noting that the subfamily Iguanodectinae of Eigenmann and Myers (1929) was defined on the basis of a series of characters that were shared with members of the Tetragonopterinae, stated that as a consequence he believed that the subfamily should be reduced in rank to the level of a tribe, the Iguanodectini, in the subfamily Tetragonopterinae. Such shifts must be considered highly subjective and I prefer to maintain the subfamilial ranking for the group.

ACKNOWLEDGMENTS

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