

Taxonomic revision of the genus *Atopomesus* MYERS, 1927 (Characiformes: Characidae), with comments on its phylogenetic relationships

ANDRÉ L. H. ESGUÍCERO & RICARDO M. C. CASTRO

Laboratório de Ictiologia de Ribeirão Preto (LIRP), Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto (FFCLRP), Universidade de São Paulo. Avenida dos Bandeirantes, 3900, 14040-901, Ribeirão Preto, SP, Brazil. andre.esguicero@gmail.com; rmcastro@ffclrp.usp.br

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Abstract

The monotypic genus *Atopomesus*, a poorly known member of the family Characidae, is re-described. *Atopomesus pachyodus* is endemic to the Rio Negro basin, where it feeds on aquatic insect larvae, and seems to occur mostly in riverine sand banks and beaches. *A. pachyodus* was originally described as a member of the Characidae subfamily Cheirodontinae, but has been considered as an Characidae *incertae sedis* based on relatively superficial studies of its dentition and external morphology. However, according to the morphological analyses presented herein, a close relationship between *A. pachyodus* and the members the subfamily Aphyoditeinae is hypothesized. The inclusion of *A. pachyodus* in the Aphyoditeinae is based on the shared presence of a long posteriorly directed spiniform process on the posteroventral margin of the orbitosphenoid, the elongation of the transverse process of the neural arch of the third vertebra, and the elongation of the posterior process of the parasphenoid.

Resumo

O gênero monotípico *Atopomesus*, um membro pouco conhecido da família Characidae, é redescrito. *Atopomesus pachyodus* é endêmico da bacia do Rio Negro, onde se alimenta de larvas aquáticas de insetos, parecendo ocorrer principalmente em bancos de areia e praias fluviais. *A. pachyodus* foi descrito originalmente como um membro da subfamília Cheirodontinae, mas tem sido considerado um Characidae *incertae sedis* com base em estudos superficiais de sua dentição e morfologia externa. Entretanto, de acordo com a análise morfológica realizada no presente estudo, é apresentada uma hipótese de relação próxima de parentesco entre *A. pachyodus* e os membros da subfamília Aphyoditeinae. A inclusão de *A. pachyodus* em Aphyoditeinae é baseada na presença compartilhada por todos estes táxons de um longo processo em forma de espinho na margem posteroventral do orbitoesfenóide, no alongamento do processo transversal do arco neural associado à terceira vertebra, e no alongamento do processo posterior do paraesfenóide.

Key words

Amazon basin, blackwater rivers, freshwater fish, Neotropical ichthyofauna, Characidae systematics.

Introduction

In July 1927, GEORGE S. MYERS proposed the new Characidae genus *Atopomesus*. This new genus was described based on specimens deposited in the Indiana University, collected by CARL TERNETZ during an expedition to northern Brazil. The type material of *Atopomesus pachyodus* MYERS 1927 was collected in the Rio Negro drainage,

Amazon basin, nearby Cucuí Municipality, Amazonas State, Brazil, on the Colombian border. *Atopomesus* is still currently considered as a monotypic genus diagnosed by MYERS (1927) by being “unique in its massive retrorse dentition”.

MYERS (1927) considered *A. pachyodus* as a member of the Cheirodontinae, a subfamily of the Characidae established by EIGENMANN (1909, 1914, 1915, 1917), and GÉRY (1960) reported *A. pachyodus* as an “Aphyocharacidi” member, an artificial group belonging to the subfamily Cheirodontinae. Later on, in its compilation of the Characiformes of the world, GÉRY (1977) considered this species as a member of the Aphyoditeina, an artificial group belonging to the Grundulini, according to him, a tribe of small fish species belonging to the subfamily Cheirodontinae, primarily diagnosed by their dentition. In a revision of the subfamily Cheirodontinae, MALABARBA (1998) reported that *A. pachyodus* lacks one of the diagnostic synapomorphies of the Cheirodontinae, the possession of pedunculated teeth that are largely expanded and compressed distally, and, consequently, considered *A. pachyodus* as *incertae sedis* within the Characidae. Recently, in a more comprehensive morphological phylogeny of the Characidae, MIRANDE (2009, 2010) reached the same conclusions reported by MALABARBA (1998, 2003), maintaining the genus *Atopomesus* as *incertae sedis* in Characidae.

Although the cited studies have addressed the relationships of *A. pachyodus* with other characids, their hypothesis were based only on a superficial analysis of its dentition and external morphology. Thus, the present study aims to redescribe *A. pachyodus*, a poorly known species, and discuss its phylogenetic relationships within the Characidae, based on a wider comparative osteological analysis.

Material and methods

Measurements and counts follow FINK & WEITZMAN (1974), with the addition of the following measurements: snout to anus – measured from the snout tip to the anterior limit of the anus; dorsal-fin base length – measured from the dorsal-fin origin to the last dorsal-fin ray; anal-fin base length – measured from the anal-fin origin to the last anal-fin ray; dorsal-fin origin to adipose-fin origin; head depth – measured at vertical through the posterior end of supraoccipital spine; mouth length – measured as the internal distance between the anterodorsal region of the maxillary bones. Measurements were taken point to point with a digital caliper. The standard length (SL) is expressed in mm and all other measurements are expressed as a percentage of SL, except subunits of head, that are expressed as percentage of the head length (HL). Counts are followed by their occurrence in parentheses; asterisks indicate the counts of the holotype (reported values for the holotype were taken from the original description, high definition photographs and a radiograph graciously provided by the California Academy of Sciences Ichthyology Section).

Six specimens (MZUSP 29613, 17.3, 20.4, 22.7, 25.3, 28.3, and 32.4 mm SL) of *A. pachyodus* were cleared and

stained (CS) for cartilage and bone using the method of TAYLOR & VAN DYKE (1985). The analyses of the hyobranchial apparatus was based only in CS specimens. Vertebrae and supraneural bones counts were made in CS specimens and also in radiographs of all alcohol-preserved individuals. Total vertebral counts include four centra of the Weberian Apparatus and a single element for the terminal centrum. Osteological terminology follows WEITZMAN (1962) with modifications adopted by ZANATA & VARI (2005). Myological observations were made in a specimen (MZUSP 29613, 24.8 mm SL) prepared following DATOVO & BOCKMANN (2010); myological terminology follows WINTERBOTTOM (1974).

Institutional acronyms are as follows: California Academy of Sciences, Ichthyology Section, San Francisco (CAS), Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA) and Museu de Zoologia, Universidade de São Paulo, São Paulo (MZUSP).

Genus *Atopomesus* MYERS, 1927

Atopomesus MYERS, 1927: 112 [type species: *Atopomesus pachyodus* MYERS, 1927, by original designation (also monotypic). Gender masculine.

Diagnosis. The genus *Atopomesus* can be distinguished from all remaining characids genera by the possession of a uniquely massive retrorse dentition, with the first three to four medial premaxillary teeth extremely truncate, with rounded crests, and directed posteriorly. *Atopomesus pachyodus* can be also distinguished from all other members of the family Characidae by the absence of gill rakers on the trailing margins of the third and fourth ceratobranchials.

Atopomesus pachyodus MYERS, 1927

Fig. 1

Atopomesus pachyodus MYERS 1927:112 [type locality: Brazil: Cucuhy (= Amazonas State, São Gabriel da Cachoeira Municipality, Cucuí Township), Rio Negro, on the Colombian Border (approximately 1°12'N, 66°51'W)]. – GÉRY, 1960: 33 [as a member of “Aphyocharacidi” group, Cheirodontinae] – GÉRY, 1977: 582, 587, unnumbered fig. on page 587 [as a member of Grundulini tribe, Cheirodontinae; in key to genera of the Aphyoditeina]. – GOULDING *et al.*, 1988: 99, tab. 10.2 [as an endemic species of the Rio Negro drainage], 131, 168 [ecological notes]. – MALABARBA, 1998: 202 [as *incertae sedis* in Characidae]. – LIMA *et al.*, 2003: 113 [catalog]. – BUCKUP *et al.*, 2007: 47 [catalog]. – MIRANDE, 2009: 584, 2010: 545 [as *incertae sedis* in Characidae].

Material examined. CAS 41736 (ex IU17673), holotype (high definition photographs and a radiograph), 29.7 mm SL (holotype): Brazil: Amazonas State: Cucuhy (= São Gabriel da Cachoeira



Fig. 1. a: *Atopomesus pachyodus*, holotype, CAS 41736, 29.7 mm SL; Brazil: Amazonas: São Gabriel da Cachoeira: Cucuí. Image provided by the California Academy of Sciences, Ichthyology Section. **b:** *Atopomesus pachyodus*, MZUSP 29611, 25.5 mm SL; Brazil: Amazonas: Santa Isabel do Rio Negro. A more recently and better preserved specimen.

Table 1. Morphometric data of holotype and 51 non-type examined specimens of *Atopomesus pachyodus*. SD = Standard deviation.

	Holotype	Range	Mean	SD
Standard Length (mm)	29.5	17.3–35.6		
Percentages of standard length				
Depth at dorsal-fin origin	25.8	20.4–29.3	25.0	2.4
Snout to dorsal-fin origin	47.7	48.1–53.4	50.0	1.6
Snout to pectoral-fin origin	32.8	27.7–35.3	30.6	2.2
Snout to pelvic-fin origin	48.6	42.0–48.6	45.4	1.8
Snout to anal-fin origin	57.5	56.1–66.3	59.2	2.6
Snout to anus	55.8	50.2–55.9	52.9	1.8
Caudal-peduncle depth	10.0	7.6–11.1	9.3	1.0
Caudal-peduncle length	10.0	8.0–17.8	11.0	2.6
Pectoral-fin length	20.6	13.3–21.3	17.1	2.5
Pelvic-fin length	16.5	14.6–22.7	17.8	2.4
Pelvic-fin origin to anal-fin origin	17.0	11.2–18.1	14.6	2.1
Dorsal-fin base length	12.4	12.5–19.2	14.0	1.6
Dorsal-fin length	27.8	24.5–31.3	27.7	2.4
Anal-fin base length	26.5	26.0–32.7	28.4	1.7
Anal-fin length	20.4	20.4–27.5	23.2	2.0
Eye to dorsal-fin origin	35.9	31.6–36.6	33.5	1.7
Dorsal-fin origin to adipose-fin origin	37.5	33.6–40.0	35.4	1.8
Dorsal-fin origin to caudal-fin base	54.5	47.4–57.6	51.7	2.8
Head depth	19.6	18.5–22.4	19.7	1.1
Head length	30.4	27.1–31.6	29.6	2.2
Percents of head length				
Horizontal eye diameter	37.5	37.3–43.6	40.1	2.7
Post-orbital distance	32.9	35.4–47.4	40.0	5.0
Snout length	26.5	24.2–30.2	26.7	1.9
Interorbital width	24.8	22.7–33.3	25.6	3.1
Mouth length	21.4	19.0–26.7	23.1	3.1
Upper jaw length	32.1	29.8–40.5	33.3	2.7

Municipality, Cucuí Township): Rio Negro, sandbank near Colombian border; 1°11'N, 66°50'W; C. TERNETZ; 14 Feb 1925. – CAS 68805, 1, 26.4 mm SL: Brazil: Amazonas State: Rio Negro at Porto Castanho (= exact locality unknown, but presumably somewhere near Santa Isabel do Rio Negro Municipality; approximately 27°10'S, 64°58'W); C. TERNETZ; 8 Jan 1925. – CAS 68806, 1, 29.5 mm SL: Venezuela: Amazonas State: Rio Orinoco (= Rio Negro), Cassiquiare (river) at Isla del Guachaco; 2°0'21.66"N, 66°53'42.59"W; C. TERNETZ; 26 Feb 1925. – CAS 68807, 1, 27.0 mm SL: same data as holotype. – CAS 71628, 2, 26.8–27.4 mm SL: Venezuela: Amazonas State: Rio Negro, 1 day canoeing up river N. from Amanadona (= approximately 01°48'N, 67°02'W); C. TERNETZ; 22 Feb 1925. – INPA 9626, 4, 22.8–27.7 mm SL: Brazil: Amazonas State: Rio Negro, Lago Panema, em frente a boca do Rio Jaú (= approximately 1°52'S, 61°24'W); M. GARCIA & J.A. ZUANON; 8 Jul 1994. – MZUSP 29609, 7, 21.4–29.9 mm SL: Brazil: Amazonas State: Rio Negro, Paraná do Jacaré, beach (= Igarapé do Jacaré; approximately 2°01'S, 61°15'W); M. GOULDING; 17 Oct 1979. – MZUSP 29611, 6, 22.5–26.8 mm SL: Brazil: Amazonas State: Barcelos Municipality: Rio Negro; 0°58'S, 62°57'W (= based on notes by Michael Goulding, the real locality is: Santa Isabel do Rio Negro Municipality, Rio Negro, Praia (beach) de Umarani, two hours upriver from Barcelos; approximately 22°38'N, 65°19'W); M. GOULDING; 6 Sep 1979. – MZUSP 29613, 37, 17.1–27.4 mm SL, 6 CS, 17.3–32.4 mm SL: Brazil: Amazonas State: Rio Arirá, near the mouth; 0°31'S, 63°33'W; M. GOULDING; 6 Sep 1979. – MZUSP 17679, 1, 26.32 mm SL: Brazil: Roraima State: Rorainópolis Municipality: Rio Jauaperi, beach 30 km upriver from the mouth; 1°10'S, 61°35'W; T. ROBERTS; 19 Nov 1968.

Diagnosis. As for the genus.

Description. See Fig. 1 for general appearance. Morphometric data of holotype and 51 non-type specimens is given in Table 1. Body laterally compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of body convex from tip of the upper jaw to the anterior edge of nostril; slightly convex from snout to dorsal-fin origin;

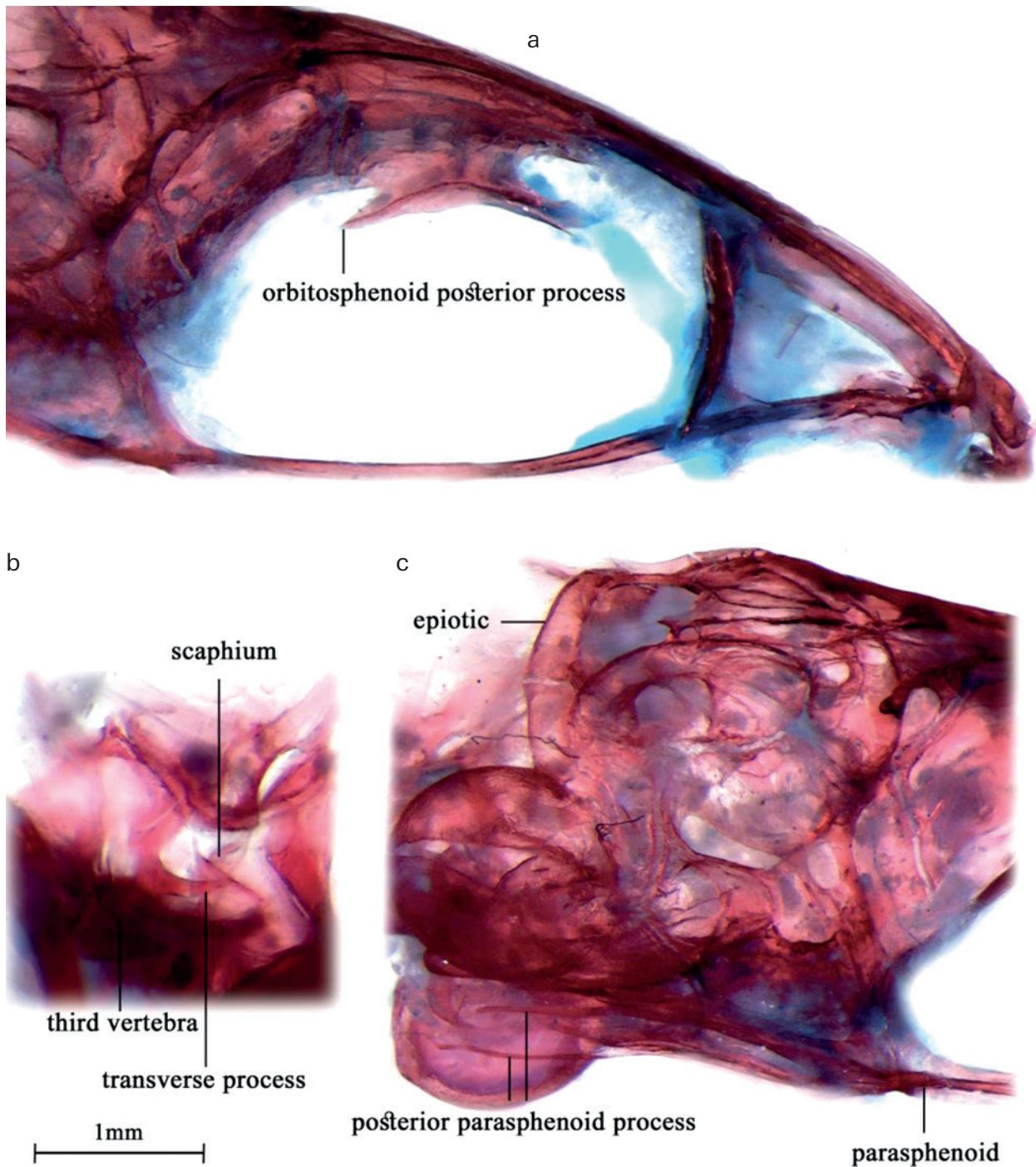


Fig. 2. a: Neurocranium, lateral view, anterior at right; b: detail of the weberian apparatus, lateral view, anterior at right; c: posterior region of the neurocranium, ventrolateral view, anterior at right, of *Atopomesus pachyodus*, MZUSP 29613, 32.4 mm SL.

straight and posteroventrally inclined along dorsal-fin base; straight and posteriorventrally inclined from posterior terminus of dorsal-fin base to adipose-fin origin; slightly concave along caudal peduncle. Ventral profile of body moderately convex from tip of lower jaw to anal-fin origin; straight and posterodorsally inclined along anal-fin base and concave along caudal peduncle.

Infraorbitals one to six present; sixth smallest and third biggest of infraorbital series. Frontals in contact anteriorly to frontal fontanel. Posteroventral margin of

orbitosphenoid with long posteriorly directed spiniform process (Fig. 2). Posterior process of parasphenoid long, extending posteriorly to vertical line through posterior margin of epiotic in lateral view (Fig. 2).

Mouth subterminal, ventrally oriented. Upper jaw slightly longer than, and overhanging, lower jaw. Anterior portion of snout fleshy, totally covering premaxillary teeth; papillae present along whole ventral margin of upper lip. Lower lip fleshy anteriorly, with papillae present along entire dorsal margin.

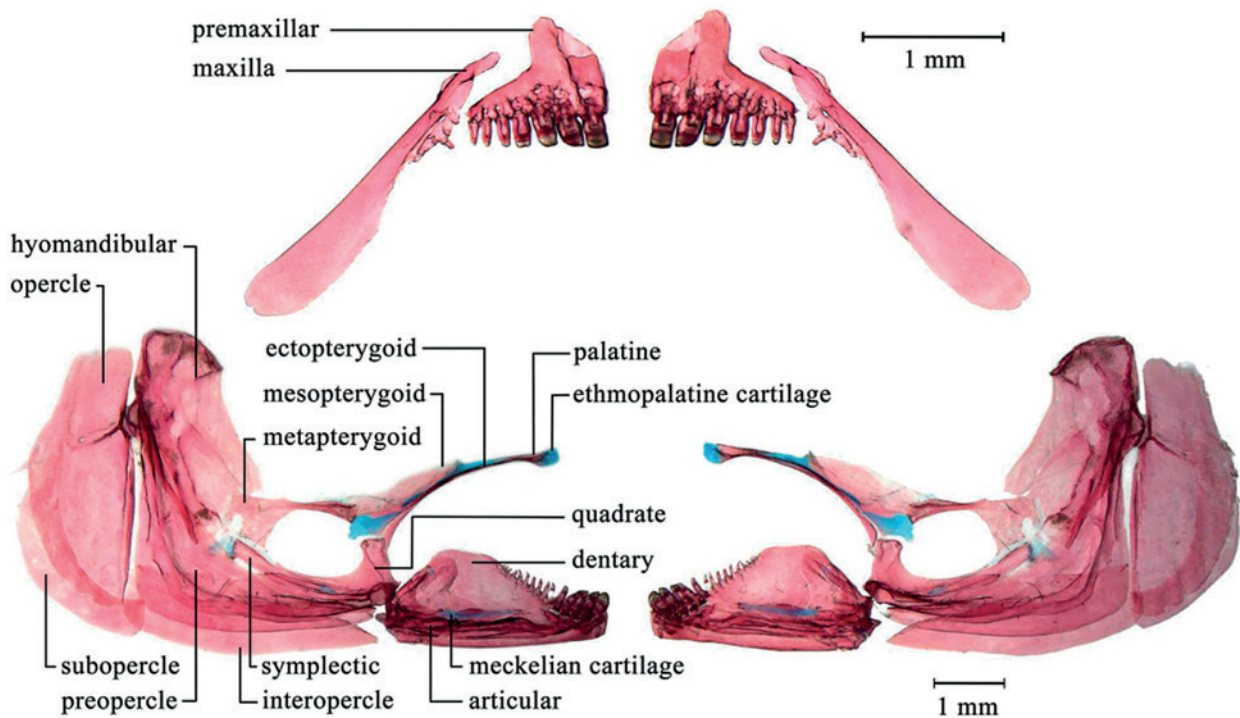


Fig. 3. Right upper jaw and suspensorium of *Atopomesus pachyodus*, MZUSP 29613, 32.4 mm SL. Lateral view at left, anterior at right. Medial view at right, anterior at left.

Teeth whitish, translucent to opaque, with brown distal portions. Premaxillary teeth in one row (Fig. 3), with seven aligned unicuspid teeth, gradually decreasing in size posteriorly; first three to four anterior premaxillary teeth incisiform, extremely truncate, anteroposteriorly compressed with rounded crest, posteromedially directed; last two or three teeth conical. Maxilla with 2(4), 3(4), 4(1), 5(27), 6*(9), 7(6) or 8(1) long and slender conical teeth (Fig. 3); toothed region straight, restricted to anterior region of maxilla. Dentary trapezoid, with 9(2), 10(5), 11(20), 12(22) or 13(2) unicuspid teeth (Fig. 3); first medial teeth incisiform, largest and robust, gradually decreasing posteriorly to the posterior most minute and slender conical teeth.

Palatine with no foramen, almost one-half length of ectopterygoid (Fig. 3). Ectopterygoid thin and elongated; mesopterygoid larger than ectopterygoid, contacting metapterygoid and quadrate. Metapterygoid contacting symplectic and hyomandibular; posteroventral metapterygoid fenestra, ventrally opened; posterior and ventral arms of metapterygoid separated.

Pectoral fin rays i, 12 (47). Pectoral fin pointed, reaching pelvic-fin origin when adpressed. Pelvic-fin rays i, 7. Pelvic-fin pointed, reaching anal-fin origin when adpressed. Anal-fin rays iii (first unbranched discernible only in CS specimens), 17(2), 18(2), 19(1) or 20*(47); last unbranched and first five branched anal-fin rays longer than remaining rays. First anal-fin pterygiophore inserted posterior to hemal spine of 15th vertebra; posteriormost anal-fin pterygiophore articulating with two last anal-fin rays. Dorsal-fin rays ii, 9; first unbranched dorsal-fin ray about half the length of second ray. Dorsal-fin

high and pointed, with origin slightly anterior midlength of body, and slightly posterior to pelvic-fin origin. First dorsal-fin pterygiophore posterior to neural spine of 8th vertebra. Adipose-fin origin situated approximately at vertical through the 16th branched anal-fin ray. Caudal-fin rays i, 17, i. Caudal-fin forked, lobes filiform, the upper lobe slightly longer than the lower one. Dorsal procurent rays 9(1), 10(2) to 12(3). Ventral procurent rays 10(2) or 11(4).

Scales cycloid. Lateral line complete, with 30(2), 31(4), 32*(7) or 33(1) perforated scales. Horizontal scale rows between dorsal-fin origin and lateral line 4*(12) or 5(2); horizontal scale rows between lateral line and pelvic-fin origin 3*(14). Single row of 6(1), 7(2), 8(4) or 9*(7) predorsal and 7(1), 8(6) or 9*(5) interdorsal scales, and 11(4) or 12*(10) circumpeduncular horizontal scale series. Single row of 2(7), 3(4), 4(1) or 5(1) scales overlying base of anterior portion of anal fin. Caudal fin naked, with no squamation on its lobes.

Presence of pseudotympanum (Fig. 4), exposing swim bladder anterolaterally at humeral region. Pseudotympanum with triangular shape, located immediately ventral to lateral-line nerve, delimited posteriorly by pleural rib of sixth vertebra, and extending anteriorly to pleural rib of fifth vertebrae, almost reaching tip of post-temporal. Dorsal margin of pseudotympanum anteriorly emarginated by *epaxialis*, medially by *lateralis superficialis* and posteriorly by *obliquus superioris*. Ventral margin of pseudotympanum emarginated by *obliquus superioris* (larger portion) and by *obliquus inferioris* at final portion of posterior end of pseudotympanum (smaller portion).

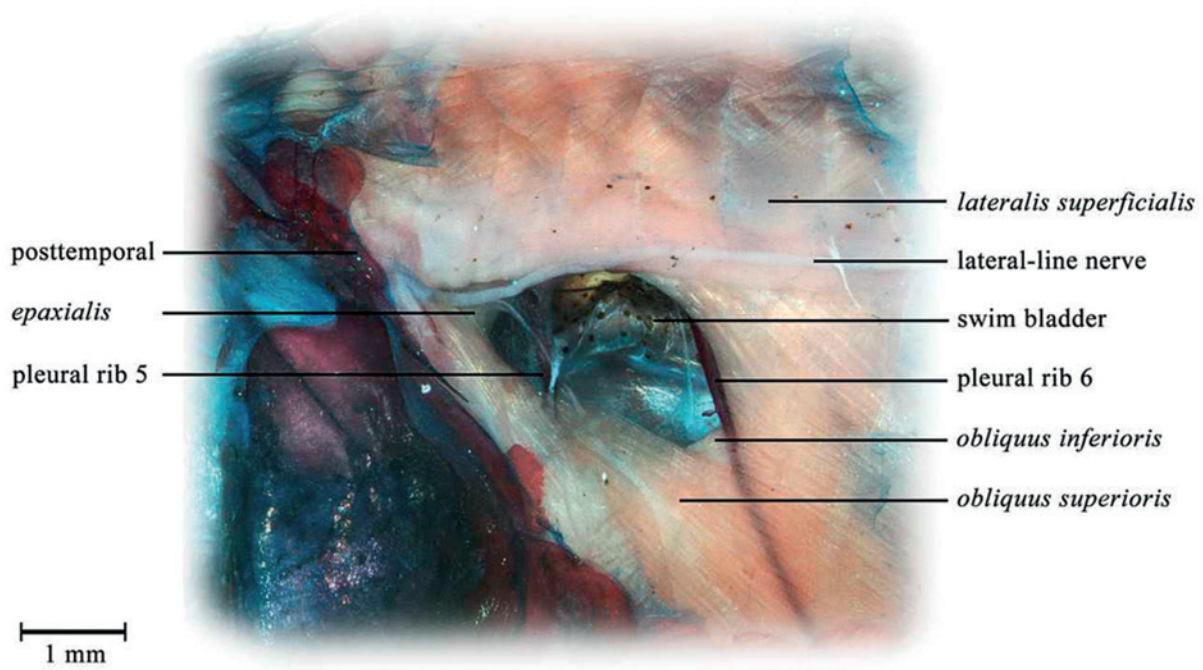


Fig. 4. Pseudotympanum of *Atopomesus pachyodus*, MZUSP 29613, 24.8 mm SL, lateral view, left side, anterior at left.

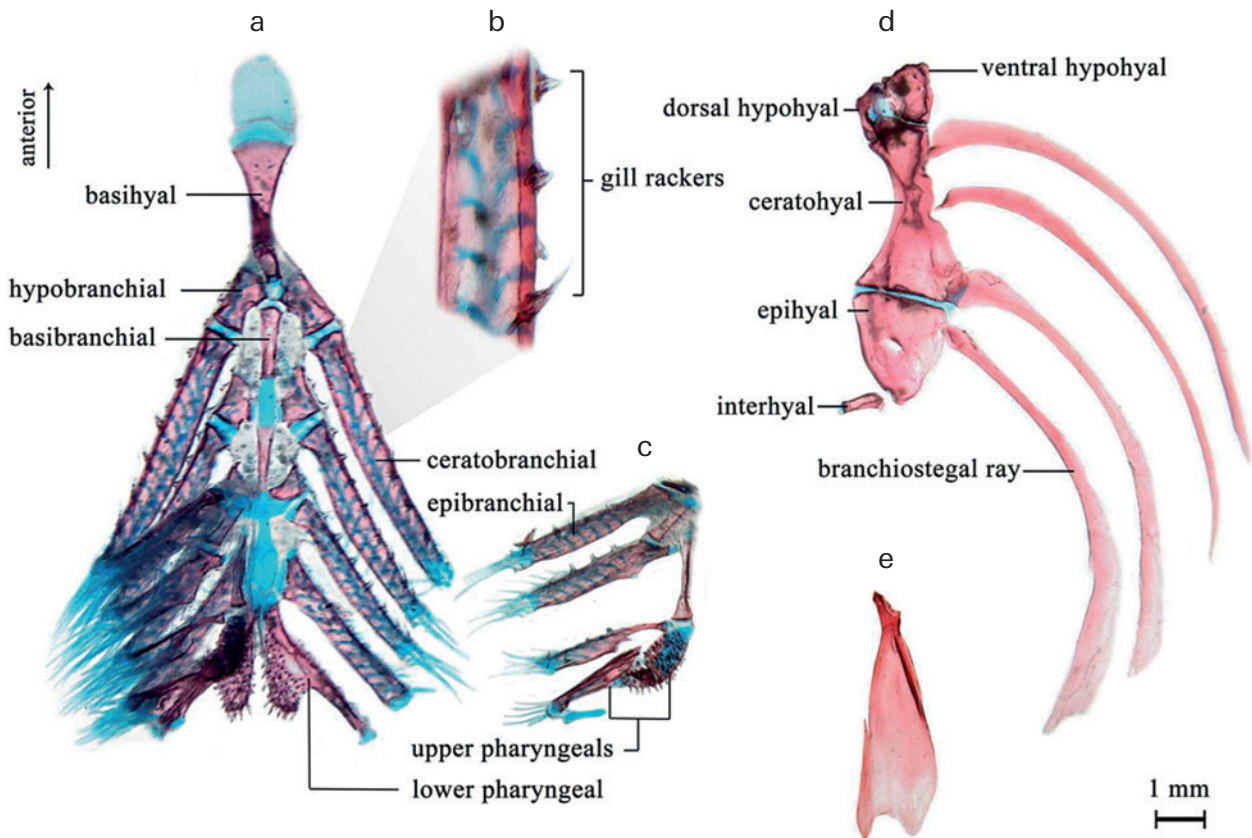


Fig. 5. Hyobranchial apparatus of *Atopomesus pachyodus*, MZUSP 29613, 32.4 mm SL. a- Branchial arches, dorsal view; b- Anterior region of the first ceratobranchial, right side, image magnified four times in relation to the others; c- Upper elements of right side, ventral view; d- Hyoid arch and branchiostegals, right side, lateral view; e- Urohyal, lateral view.

Precaudal vertebrae 14, caudal vertebrae 17(1) or 18* (51), totalizing 31(1) or 32*(51) vertebrae. Transverse process of third vertebra neural arch extending over scaphium (Fig. 2). Abdominal ribs 10. Supraneurals

4. Gill rakers small, shape varies from threadlike to arrow-like (Fig. 5). First gill arch with 3(6) gill rakers on hypobranchial, 7(6) on ceratobranchial, 4(6) on epibranchial, and 1 on cartilage between ceratobranchial

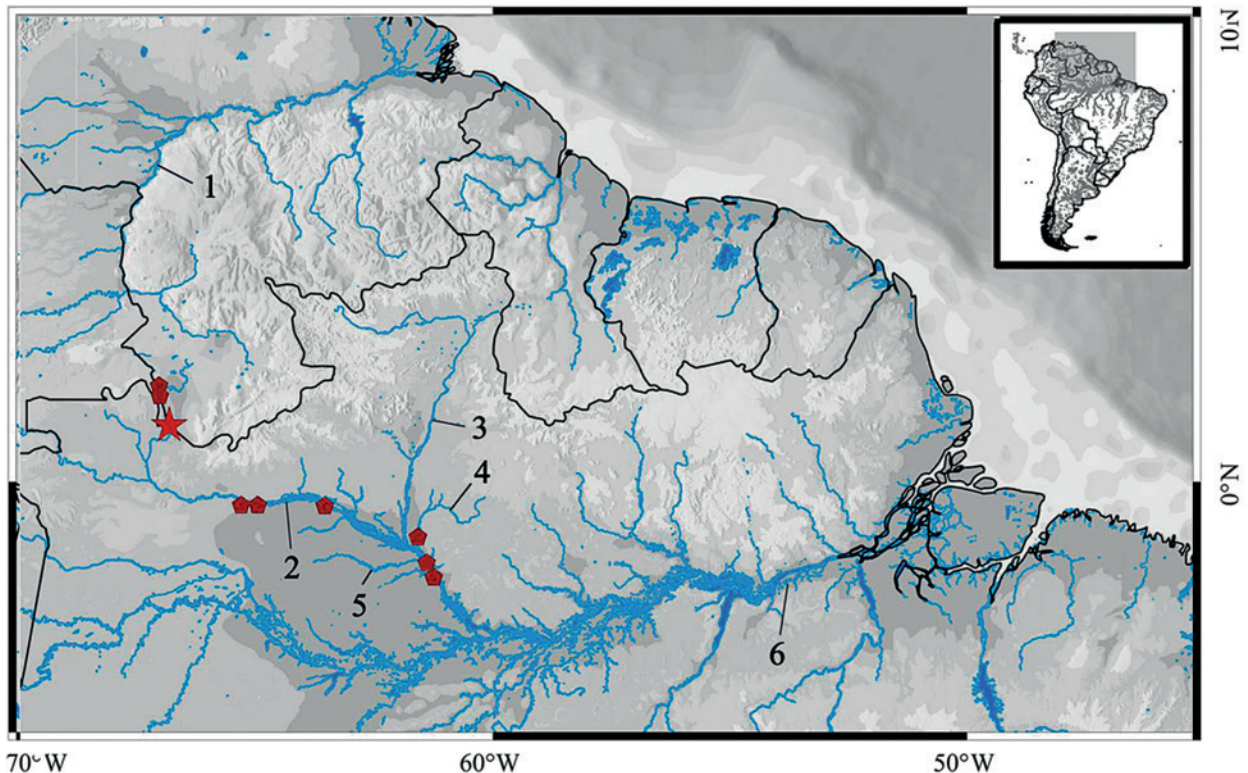


Fig. 6. Distribution of *Atopomesus pachyodus*, based on the examined material. Star indicates the type locality; 1: Rio Orinoco; 2: Rio Negro; 3: Rio Branco; 4: Rio Jauaperi; 5: Rio Jaú; 6: Rio Amazonas.

and epibranchial, totaling 15 gill rakers. Third and fourth ceratobranchials with no gill rakers on their trailing margins (Fig. 5). Branchiostegal rays 4(6), with 3(6) on anterior ceratohyal and 1(6) on posterior ceratohyal (Fig. 5).

Coloration in alcohol. Overall ground coloration yellowish (Fig. 1). Dorsal and anterior head portion with sparse dark chromatophores. Iris silver, with sparse dark chromatophores, more concentrated at upper region. Few dark-brown chromatophores sparsely distributed over body, more concentrated in mid-lateral region of body. All fins hyaline.

Distribution. All known samples of *Atopomesus pachyodus* were collected throughout the Rio Negro drainage, Amazon basin (Fig. 6). GOULDING *et al.* (1988) cited this species as endemic to an area that centers on the Rio Negro basin.

Ecological notes. The analysis of the stomach contents of two of the six CS individuals revealed a diet based mainly on aquatic insect larvae (mostly Chironomidae). Of the six examined individuals, four had the stomach empty and only two presented some food items. This species is known only from blackwater rivers with high acidity and low nutrient concentrations, occurring in marginal areas over sand banks, where it was frequently captured. GOULDING *et al.* (1988) reported *A. pachyodus* feeding on Diptera larvae and plant remains.

Discussion

Atopomesus pachyodus Myers, 1927 is a small size species of the family Characidae, with a distribution restricted to the acidic blackwaters of the Rio Negro drainage, Amazon basin. It feeds on aquatic insect larvae, probably in sand banks and beaches, where this species was frequently found, according to GOULDING *et al.* (1988). Its mouth, subterminal and ventrally oriented, also suggests a benthic feeding behavior (WINEMILLER *et al.*, 1995). The shape of the anteriormost premaxillary and dentary teeth, resembling the teeth of some Anostomidae species (see BIRINDELLI & BRITSKI, 2009, for an example), could be correlated with the invertivory diet of *A. pachyodus*, as reported by VARI (1983) for the family Anostomidae. In fact, the odd dentition of *A. pachyodus* readily distinguishes it from the remaining Characidae representatives, as also its lack of gill rakers on the trailing margins of the third and fourth ceratobranchials, a characteristic hitherto reported only for the genus *Boulengerella* EIGENMANN 1903 (VARI, 1995) and *Acestrorhynchus* EIGENMANN & KENNEDY 1903 (TOLEDO-PIZA, 2007).

Of the 51 non-type individuals analyzed, seven presented rayless pectoral fin. This pedomorphic feature was observed only in small specimens (17.3–20.4 mm SL). Indeed, only two (18.6 and 19.9 mm SL) of the nine analyzed specimens smaller than 20.5 mm SL presented pectoral fin with rays. In the family Characidae, the retention of the larval rayless pectoral fin was reported for

Hyphessobrycon catableptus (DURBIN 1909) and for species of the subfamily Characinae (LUCENA, 1998; LUCENA & MENEZES, 2003). Despite the presence of this paedomorphic feature, possibly related to ontogenetic truncations, *A. pachyodus* is not considered a miniaturized species, since presents none of the characteristics of a miniaturization process *sensu* MYERS (1958) and WEITZMAN & VARY (1988).

Since its description, *A. pachyodus* was considered closely related to the subfamilies Cheirodontinae and Aphyoditeinae, but these hypotheses were refuted by MALABARBA (1998) and MIRANDE (2010), based mainly on teeth morphology. MIRANDE (2010) reported that the strong teeth of *A. pachyodus* are quite different from the slender and small teeth of the Aphyoditeinae members. In fact, the teeth morphology of *A. pachyodus* is very different from any teeth morphology reported to these subfamilies. But, in the present analysis, other characters shared by *A. pachyodus* and members of the subfamily Aphyoditeinae (*sensu* MIRANDE, 2010) were found. *A. pachyodus* shares with *Parecbasis cyclolepis* EIGENMANN, 1914 and species of the genus *Microschemobrycon* EIGENMANN, 1915 an elongation of the posterior process of the parasphenoid, which extends posteriorly to a vertical line through the posterior margin of the epiotic in lateral view. This condition was also observed in *Macropsobrycon uruguaianae* EIGENMANN, 1915, a Cheirodontinae member, and *Thrissobrycon pectinifer* BOHLKE, 1953, considered as an Aphyoditeinae by GÉRY (1977), but as an *incertae sedis* Characidae by MIRANDE (2010). In the remaining Characidae representatives here analyzed, when present, the posterior process of the parasphenoid is short, not reaching the vertical line through the posterior margin of the epiotic in lateral view.

The length of the transverse process of the third neural arch was one of the characters successfully used by ZANATA & VARI (2005: 114) to establish phylogenetic relationships among various Alestidae groups. In *A. pachyodus*, the transverse process of the neural arch of the third vertebra extends over the scaphium, a condition also observed in all the genera of the subfamily Aphyoditeinae. This condition was also observed in *T. pectinifer*, *Macropsobrycon xinguensis* GÉRY, 1973, a Cheirodontinae member, and species of the genus *Brittanichthys* GÉRY, 1965, which were considered as Aphyoditeinae representatives by GÉRY (1977), but treated as *incertae sedis* Characidae by MIRANDE (2010). In the remaining Characidae representatives analyzed by us, the process of the neural arch of the third vertebra is proportionally smaller, with the anterior tip falling short to the posteroventral margin of the scaphium.

Another morphological feature shared by *A. pachyodus* and all the other members of the subfamily Aphyoditeinae is the presence of a long, posteriorly directed spiniform process, in the posteroventral margin of the orbitosphenoid. The joint possession of a long spiniform process as the one mentioned before was considered by MATTOX & TOLEDO-PIZA (2012: 43) as a synapomor-

phy of the Heterocharacinae, a subfamily of the family Acestrorhynchidae, and was also observed by them in *Cheirodon* GIRAD, 1855 and *Odontostilbe* COPE, 1870, both members of the subfamily Cheirodontinae. In the present study, a long posteriorly directed spiniform orbitosphenoid process was also observed in *T. pectinifer*, *Brittanichthys axelrodi* GÉRY, 1965, *M. uruguaianae* and *M. xinguensis*.

All mentioned shared characters of the present morphological analysis corroborate a close relationship between *A. pachyodus* and the other members of the subfamily Aphyoditeinae, as already proposed by GÉRY (1977). Consequently, the inclusion of *A. pachyodus* in the subfamily Aphyoditeinae (*sensu* Mirande, 2010) is recommended.

Acknowledgments

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