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Sistemática de *Odontostilbe* Cope, 1870 com a proposição de uma nova tribo Odontostilbini e redefinição dos gêneros *incertae sedis* de Cheirodontinae (Ostariophysi: Characiformes: Characidae)

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SUMÁRIO

Dedicatória

Ao meu pai Paulo F. Bührnheim in memoriam.
A minha querida mãe Catarina S. Motta.
Ao amado Valdely F. Kinupp.
Todos encantados pela diversidade da vida.

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Resumo

A subfamília Cheirodontinae compreende cerca de 50 espécies válidas, sendo um grupo de caracídeos de ampla distribuição geográfica nas Américas do Sul e Central, presente em todas as bacias hidrográficas maiores da América do Sul (Amazônica, Orinoco, Paraná-Paraguay e São Francisco) e ainda com representantes do gênero *Cheirodon* transandinos no Chile. Dentre 15 gêneros reconhecidos na subfamília monofilética Cheirodontinae por Malabarba (1998), cinco permaneceram *incertae sedis*: *Odontostilbe* Cope (1870) com *Holoshesthes* Eigenmann, 1903 como sinônimo, *Aphyocheirodon* Eigenmann, 1915, *Pseudocheirodon* Meek & Hildebrand, 1916, *Prodontocharax* Pearson, 1924 com *Amblystilbe* Fowler, 1940 como sinônimo, e *Cheirodontops* Schultz, 1944. *Odontostilbe* destacava-se com cerca de dez espécies consideradas válidas (Malabarba, 2003), o maior número de espécies entre todos os gêneros de Cheirodontinae (seguido de *Serrapinnus* com sete espécies). A situação taxonômica de *Odontostilbe* era confusa, com o holótipo da espécie tipo *Odontostilbe fugitiva* referido como perdido e esta espécie fracamente definida por linha lateral completa e dentes multicúspides. No presente estudo, o objetivo principal foi a revisão taxonômica e filogenia de *Odontostilbe*, que juntamente levou às revisões de *Holoshesthes, Aphyocheirodon* e *Cheirodontops*. No total, *Odontostilbe* Cope (1870) é redefinido com o reconhecimento de 15 espécies para o gênero, 10 novas. A análise filogenética com 53 táxons, 28 espécies de Cheirodontinae e 15 espécies de *Odontostilbe*, resultou na definição de uma nova tribo Odontostilbini com 26 espécies reconhecidos nos gêneros *Odontostilbe*, *Holoshesthes*, *Prodontocharax*, *Amblystilbe*, *Pseudocheirodon*, e *Lobodeuterodon* Fowler, 1945. A nova tribo é sustentada por treze sinapomorfias relacionadas a modificações dos canais sensoriais do parietal e do primeiro infraorbital, a forma do segundo e sexto infraorbitais, do palatino, do bordo anterodorsal da maxila, da protuberância lateral da maxila inferior, da parte lateral exposta do ramo inferior do ângulo-articular, do branquiostegal mais posterior, ao comprimento do raio não ramificado da nadadeira pélvica, ao perfil da nadadeira anal e a extensão da linha lateral. No entanto, inter-relações dos gêneros de Odontostilbini não são esclarecidas e *Odontostilbe* não tem sua monofilia estabelecida. Mesmo assim, três linhagens monofiléticas foram distinguidas em Odontostilbini: clado correspondente a *Holoshesthes* com seis espécies e *Aphyocheirodon* e *Cheirodontops* como seus sinônimos; clado *Pseudocheirodon* com duas espécies; e clado *Lobodeuterodon* + (*Prodontocharax* + *Amblystilbe*) com três espécies. Os gêneros *Holoshesthes* e *Lobodeuterodon* são removidos da sinonímia de *Odontostilbe* e *Amblystilbe* é removido da sinonímia de *Prodontocharax*. *Holoshesthes* é revalidado. *Odontostilbe* é válido e em uma posição conservadora inclui várias espécies em uma politomia basal da tribo, incluindo a espécie-tipo do gênero. Um novo membro para a tribo Cheirodontini foi encontrado, *Axelrodia lindeae*.

Abstract

The subfamily Cheirodontinae comprises about 50 valid species, being a group of characids widely distributed in South and Central Americas, occurring in the major hydrographic basins of South America (Amazon, Orinoco, Paraná-Paraguay and São Francisco basins), besides including representatives of the transandinean genus *Cheirodon* from Chile. Among 15 genera recognized to the monophyletic subfamily Cheirodontinae by Malabarba (1998), five remained *incertae sedis*: *Odontostilbe* Cope (1870) with *Holoshesthes* Eigenmann, 1903 as synonym, *Aphyocheirodon* Eigenmann, 1915, *Pseudocheirodon* Meek & Hildebrand, 1916, *Prodontocharax* Pearson, 1924 with *Amblystilbe* Fowler, 1940 as synonym, and *Cheirodontops* Schultz, 1944. *Odontostilbe* was notable containing about ten valid species (Malabarba, 2003), the highest number of species among all the remaining Cheirodontinae (followed by *Serrapinnus* with seven species). The taxonomic status of *Odontostilbe* was confusing, with the holotype of the type species *Odontostilbe fugitiva* referred as lost, and this species being weakly defined by lateral line complete and multicuspid teeth. In this study, the main goal was the taxonomic revision and phylogeny of the *Odontostilbe*, which jointly leaded to the revisions of the *Holoshesthes*, *Aphyocheirodon* and *Cheirodontops*. In all, *Odontostilbe* Cope (1870) is redefined with 15 species recognized to the genus, 10 new species. The phylogenetic analysis with 53 taxa, 28 species of Cheirodontinae and 15 species of *Odontostilbe*, resulted in the definition of a new tribe Odontostilbini with 26 species recognized in the genera *Odontostilbe*, *Holoshesthes*, *Prodontocharax*, *Amblystilbe*, *Pseudocheirodon*, and *Lobodeuterodon* Fowler, 1945. The new tribe is supported by thirteen synapomorphies related to modifications of the sensory canals of the parietal and first infraorbital and the shape of the second and sixth infraorbitals, palatine, anterodorsal border of maxilla, a ridge laterally on lower jaw, exposed lateral portion of lower branch of angulo-articular, posteriormost branchiostegal, to the length of the unbranched pelvic-fin ray, to the anal-fin profile and extent of the lateral line. However, the interrelationships of the species and genera of Odontostilbini are not clear and the monophyly of *Odontostilbe* is not established. Even though, three monophyletic lineages are distinguished in Odontostilbini: the clade corresponding to *Holoshesthes* with six species and *Aphyocheirodon* and *Cheirodontops* as its junior synonyms; the clade *Pseudocheirodon* with two species; and the clade *Lobodeuterodon* + (*Prodontocharax* + *Amblystilbe*) with three species. *Holoshesthes* is revalidated. *Odontostilbe* is valid and conservatively includes several species in a basal polytomy of the tribe, including the type species of the genus. A new member to the Cheirodontini tribe was found, *Axelrodia lindeae*.

Apresentação

A presente tese reúne resultados da revisão taxonômica e filogenia do gênero *Odontostilbe* em quatro capítulos, um publicado e três a serem submetidos à revista científica "Neotropical Ichthyology", na qual foi publicado o Capítulo 3. Inicialmente o objetivo foi resolver o complexo de espécies relacionadas a espécie tipo *Odontostilbe fugitiva*, com ênfase nas bacias dos rios Amazonas e do rio Orinoco, pois as espécies das Bacias dos rios Paraná e Paraguai tinham sido anteriormente revisadas pelo presente orientador. O estudo foi ampliado com a descoberta de novas espécies relacionadas a *Odontostilbe* e a *Holoshesthes*, então considerado sinônimo deste. Desta forma, foi necessária a revisão dos gêneros *Cheirodontops* e *Aphyocheirodon*, ambos monotípicos e hipoteticamente relacionados a *Odontostilbe* e a *Holoshesthes*. O Capítulo I compreende a análise filogenética com representantes de todos os gêneros de Cheirodontinae, incluindo 10 espécies novas de *Odontostilbe* e três outras espécies novas formando um clado com a espécie tipo de *Holoshesthes*, assim revalidado. Neste capítulo o resultado principal inclui a proposta de uma nova tribo Odontostilbini para os Cheirodontinae, em adição às tribos conhecidas Cheirodontinae e Compsurini. Odontostilbini contém todos os gêneros anteriormente considerados *incertae sedis* em Cheirodontinae, *Odontostilbe*, *Holoshesthes*, *Aphyocheirodon*, *Prodontocharax*, *Amblystilbe*, *Lobodeuterodon* e *Cheirodontops*. Entretanto, a monofilia de *Odontostilbe* não é constatada e apenas três linhagens monofiléticas em Odontostilbini de posição incerta podem ser propostas. Em uma posição conservadora todas as espécies que formam uma politomia basal na tribo são alocadas em *Odontostilbe*, junto com a espécie-tipo do gênero. Vale destacar no Capítulo I a descoberta de um novo membro de Cheirodontinae na tribo Cheirodontini, *Axelrodia lindeae*. No Capítulo II, a revisão taxonômica e revalidação de *Holoshesthes* são apresentadas em uma abordagem filogenética, destacando *Aphyocheirodon* e *Cheirodontops* como seus sinônimos juniores. Três espécies são redescritas, duas das Bacias dos rios Paraná-Paraguay e uma da Bacia do rio Orinoco, e três novas são descritas para as Bacias dos rios Orinoco e alto rio Amazonas. Em seguida, no Capítulo III a redescrição da espécie tipo de *Odontostilbe fugitiva* é fornecida em conjunto com a descrição de três das espécies novas para o gênero, todas da Bacia Amazônica. No Capítulo IV é apresentada a redescrição de *Odontostilbe pulchra*, amplamente distribuída na Bacia do rio Orinoco e ilha de Trinidad, com a descrição de duas espécies novas, também da Bacia do rio Orinoco. Quatro espécies novas das Bacias dos rios Paraná e Paraguai foram confirmadas e duas espécies do alto rio Madeira (uma redescrição e uma nova) serão tratadas em trabalhos futuros, bem como a revisão de *Lobodeuterodon euspilurus*.

CAPÍTULO I

Phylogeny of the new tribe Odontostilbini, with a redefinition of the *incertae sedis* genera of the Cheirodontinae (Ostariophysi: Characiformes: Characidae)

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Abstract.

The phylogenetic relationships of the genera *Odontostilbe* (Cope, 1870), *Holoshesthes* Eigenmann, 1903, *Aphyocheirodon* Eigenmann, 1915, *Pseudocheirodon* Meek & Hildebrand, 1916 , *Prodontocharax*, Pearson, 1924, *Amblystilbe* Fowler, 1940, and *Cheirodontops* Schultz, 1944 are reviewed, with the proposition of a new tribe Odontostilbini in the subfamily Cheirodontinae. The new tribe is sustained by thirteen synapomorphies related to modifications of the sensory canals of the parietal and first infraorbital and the shape of the second and sixth infraorbitals, palatine, anterodorsal border of maxilla, a ridge laterally on lower jaw, exposed lateral portion of lower branch of angulo-articular, posteriormost branchiostegal, and by the elongation of the unbranched pelvic-fin ray, anal-fin profile not dimorphic, extent of the lateral line canal on caudal-peduncle, and lateral line complete. It comprises three monophyletic lineages. However, the relationships among these monophyletic groups of the Odontostilbini remain to be elucidated, containing an unresolved polytomy with fifteen *Odontostilbe* species and three monophyletic lineages. The genus *Odontostilbe* is conservatively maintained as a valid genus, though none synapomorphies were found to sustain it as monophyletic. The three monophyletic groups in the Odontostilbini are: a clade formed by six species of *Holoshesthes,* containing the monotypic *Aphyocheirodon* and *Cheirodontops* as synonyms; a clade formed by two *Pseudocheirodon* species; and a clade formed by *Lobodeuterodon* Fowler, 1945, *Prodontocharax,* and *Amblystilbe*. The genera *Holoshesthes* and *Lobodeuterodon* are removed from the synonymy of *Odontostilbe*, and the genus *Amblystilbe* is removed from the synonymy of *Prodontocharax*. A new member to the Cheirodontini tribe was found, *Axelrodia lindeae*.

Key words: Systematics, *Odontostilbe*, *Holoshesthes*, *Aphyocheirodon*, *Pseudocheirodon*, *Prodontocharax*, *Cheirodontops*, *Lobodeuterodon*.

Introduction

Characidae is the most speciose family of Neotropical fishes, showing the widest distribution among recent freshwater fish taxa in South and Central America, with the genus *Astyanax* present in North America. The Cheirodontinae is the most widespread subfamily of the Characidae, occurring from Costa Rica to central Chile and Argentina, in both slopes of the Andes. A total of 15 genera are recognized in the subfamily (Malabarba, 1998; Malabarba & Weitzman, 1999; 2000), with approximately 50 valid species (Malabarba, 2003; Malabarba *et al.*, 2004; Bührnheim & Malabarba, 2006). An extent historical review of the classification of the subfamily is provided by Malabarba (1998), and is not repeated here.

Malabarba (1998) proposed the monophyly of Cheirodontinae, shortening the subfamily to contain only 13 genera (plus two undescribed genera described in Malabarba & Weitzman, 1999; 2000) and removing several genera previously assigned to this subfamily mostly by Eigenmann (1915: 21 genera) and Géry (1977: 35 genera). Taxa included in the Cheirodontinae were arranged by Malabarba (1998) in two tribes in the cladogram reproduced here in Fig. 1: the Cheirodontini, containing the genera *Cheirodon, Nanocheirodon, Serrapinnus*, *Heterocheirodon*, *Spintherobolus*, the fossil †*Megacheirodon*, and one still undescribed genus; and the Compsurini, containing *Compsura*, *Saccoderma*, *Macropsobrycon* and two new genera latter described as *Acinocheirodon* and *Kolpotocheirodon*. Five genera were found basal in the Cheirodontinae and not referred to any of the two tribes proposed. These genera, called *incertae sedis* in Cheirodontinae by Malabarba (1998) were *Odontostilbe* Cope, 1870 (*Holoshesthes* Eigenmann, 1903, and *Lobodeuterodon* Fowler, 1945, as synonyms), *Aphyocheirodon* Eigenmann, 1915, *Pseudocheirodon* Meek & Hildebrand, 1916, *Prodontocharax* Pearson, 1924 (*Amblystilbe* Fowler, 1940 as synonym), and *Cheirodontops* Schultz, 1944.

Odontostilbe was erected to include a single species, *O. fugitiva* Cope, 1870, characterized by teeth in a single series on the premaxillary and dentary bones, broadly spatulate and crenate, and chiefly by a complete lateral line (Cope, 1870). As this latter character would be the unique difference between *Cheirodon* Girard, 1855 (lateral line incomplete) and *Odontostilbe*, the validity of *Odontostilbe* was questioned repeatedly, and the genus was put in the synonymy of *Cheirodon* more than once (Ulrey, 1895; Fink & Weitzman, 1974), or as a subgenus of it, *Cheirodon* (*Odontostilbe*) by Lüken (1875). However, *Odontostilbe* usually has been considered valid (Eigenmann, 1915; Eigenmann & Kennedy, 1903; Eigenmann & Ogle, 1907; Fowler, 1913, 1940, 1943, 1948; Géry, 1964, 1972a, 1972b, 1977; López, 1972; Uj, 1987). Recently, Bührnheim & Malabarba (2006) provided the review of the type species *O. fugitiva*, considering the genus valid with nine species, and 10 additional species of cheirodontines related to it delaying a phylogenetic analysis to clear its relationships. In the phylogenetic analysis of the Cheirodontinae by Malabarba (1998), *Odontostilbe* was considered valid with *Holoshesthes* in synonym. This synonym, based on the finding of *O. fugitiva* as sister species of *Holoshesthes pequira* was discussed by Bührnheim & Malabarba (2006) that warned to possible relationships between *Holoshesthes* and *Cheirodontops*, and even with new species discovered in a comprehensive taxonomic revision of *Odontostilbe*.

Holoshesthes was defined by Eigenmann (1903) on the presence of a single series of “many-pointed incisors” on premaxillaries and mandible, and on maxillaries “along its entire length” (actually, on anterior edge of maxillaries, Bührnheim & Malabarba, in manuscript). The monotypic genus contained only *H. pequira* (Steindachner, 1882), removed from the genus *Chirodon* [*Cheirodon*, Girard, 1854]. The genus was completely redefined by Eigenmann (1915:83-84) in the proposition of the new subfamily Cheirodontinae, mainly based on characters of dentition. It had been considered valid since its creation (Fowler, 1948; Böhlke, 1954; Géry, 1977; Uj, 1987) until 1998's with the phylogenetic analysis of the Cheirodontinae by Malabarba, in which *Holoshesthes* was put in synonym of *Odontostilbe*. Eigenmann (1915) described *Holoshesthes heterodon*, but this was removed to *Serrapinnus* by Malabarba (1998).

Eigenmann (1915) also erected *Aphyocheirodon* diagnosed mainly on dentition characters, a monotypic genus with *A. hemigrammus*. The genus has been considered valid (Fowler, 1948; Géry, 1977), and rare in collections, "not being recorded since its original description" (Böhlke, 1954:123). An apparent similar dentition between *Cheirodon microdon* (valid as *Serrapinnus microdon*) and *A. hemigrammus* leaded Böhlke (1954), and Géry (1977) suggest them as synonyms. However, Malabarba (1998) redefined *Aphyocheirodon* on three synapomorphies, including a unique modification in the orientation of dentary cusps.

Another currently recognized *incertae sedis* genera in the Cheirodontinae *Pseudocheirodon* was erected by Meek & Hildebrand (1916), which differed it from *Cheirodon* by the “absence of the protruding interhemal spines on caudal peduncle”, from *Odontostilbe* by the “incomplete lateral line”, and from *Compsura* by the “scaling on the base of the caudal in the male normal”. The genus was monotypic with *P. affinis* from Panamá.

Böhlke (1954) considered the diagnostic characters of Meek & Hildebrand (1916) insufficient and left *Pseudocheirodon* as a synonym of *Cheirodon*. On contrary, Bussing (1967) considered *Pseudocheirodon* valid and described *P. terrabae* from Costa Rica. López (1972) also retained *Pseudocheirodon,* but showed the remarkably interspecific variation on lateral line, incomplete to complete, in *P. affinis*. Both authors, Bussing (1967) and López (1972), diagnosed *Pseudocheirodon* from *Cheirodon* by an even cutting edge of the dentary teeth, the lack of fin hooks and low number of interhemals (= ventral procurrent caudal-fin rays) in the former. These diagnostic features were contested by Fink & Weitzman (1974) that proved the presence of anal-fin hooks in males of *Pseudocheirodon species* and argued that the number of ventral procurrent caudal-fin rays was largely varying in *Cheirodon*. Furthermore, the even cutting edge could be found in some undescribed species of *Cheirodon*. Thus, *Pseudocheirodon* was considered a synonym of *Cheirodon* by Fink & Weitzman (1974), comprising *Cheirodon affinis* and *C. terrabae*. However, Géry (1977: 566) proposed *Pseudocheirodon* as a subgenus of *Cheirodo*n keeping the diagnostic "absence of no interhaemal spines". Noteworhty, Fink & Miller (1985) assigned *Cheirodon arnoldi* Boulenger, 1909, mistakenly assigned from Mexico, as a senior synonym of *C. affinis*. Currently the genus is considered valid with *P. arnoldi* and *P. terrabae*. This was established in the phylogenetic analysis of the Cheirodontinae by Malabarba (1998), in which *Pseudocheirodon* was redefined by three new derived characters, two related to maxillary modifications, and one to the dentary symphyseal joint, which is conspicuously round, smooth.

Subsequently, Pearson (1924) used the overall “teeth mostly tridentate”, the complete lateral line, and the “anal short” to diagnose another cheirodontine genus, *Prodontocharax* with the type species *P. melanotus*. The genus has been considered valid as a cheirodontine, *e.g.* listed by Fowler (1948). Böhlke (1953) reviewed the genus, designating a lectotype and paralectotypes to *P. melanotus,* and remarking the diagnostic mouth distinctly inferior to the genus. He also described *P. alleni*. Furthermore, he reinforced *Amblystilbe* Fowler, 1940 as being different from *Prodontocharax*. Soon later, Böhlke (1954) treated *Prodontocharax* and *Amblystilbe* as nearly related, proposing a tribe Prodontocharacini, though he did not examined specimens of *Amblystilbe*. Géry (1977) considered *Prodontocharax* with *Amblystilbe* in synonym in his *Aphyodite*-group, a group comprising *Aphyodite* and 14 genera of "puzzling" characids. Géry (1977: 590), in a key commented that *Prodontocharax* was "possibly descendent from some *Odontostilbe*-like ancestor", and with asterisks notation alerted "*A. howesi,* the type species of *Amblystilbe* [sic], may be a distinct species". In the phylogenetic analysis of Cheirodontinae, Malabarba (1998) presented four synapomorphies to *Prodontocharax*, with *Amblystilbe* in synonym: the "tridentate", tricuspid teeth, but only on dentary, "the jaw teeth are elongate and conical or tricuspid", the dorsal-fin with a black spot, and the maxilla curved, with tooth portion continuous with the premaxilla and angled relative to the non-tooth-bearing portion of maxilla. The junior synonym of *Amblystilbe* with *Prodontocharax* is also admitted by Malabarba (2003), but a phylogenetic reanalysis of these two genera with the discovery of a new related species suggested these are not synonyms (Bertaco, pers. comm.). *Amblystilbe* with an inferior mouth as *Prodontocharax* was proposed by Fowler (1940) as a Cheirodontinae with the type *A. howesi*, being only especially differed from *Othonocheirodon* [sic]= *Othonocheirodus*, not a Cheirodontinae by Malabarba (1998).

Also considered a cheirodontine, *Cheirodontops*, with similar dentary teeth of *Holoshesthes*, was diagnosed by Schultz (1944) on the "lacking of all traces of teeth on the maxillaries". The genus was put in synonym of *Holoshesthes* by Böhlke (1954), but retained by Géry (1977) on the lacking of maxillary teeth. Malabarba (1998) considered two synapomorphies sustaining *Cheirodontops*, the dentary teeth shape considered ambiguously present in *Odontostilbe pequira*, in *Serrapinnus heterodon*, and in *Acinocheirodon melanogramma*, and the presence of three larger dentary teeth independently acquired in "*Odontostilbe*" *mitoptera*. Bührnheim & Malabarba (2006) pointed out that after the taxonomic revision of *Cheirodontops* (Bührnheim & Malabarba, in manuscript), it shares with the *Odontostilbe* synapomorphies defined by Malabarba (1998), then deserving phylogenetic analysis.

At all, Malabarba (1998) redefined *Odontostilbe*, *Aphyocheirodon*, *Pseudocheirodon*, *Prodontocharax*, and *Cheirodontops* as monophyletic, but his analyses were made without the taxonomical revision of these genera. Subsequently, an increasing number of new species were found, especially in the more specious genus *Odontostilbe*, which now includes about sixteen species (Bührnheim & Malabarba, 2006). The only alternative phylogenetic hypothesis of the relationships among these *incertae sedis* genus was presented by Calcagnotto *et al.* (2005) based on molecular analysis, in which *Aphyocheirodon*, *Cheirodon*, *Cheirodontops*, and *Prodontocharax* forms a clade, with *Aphyocheirodon* and *Cheirodon* as sister species. However, all the genera are erroneously referred because the material examined is from upper río Mamoré basin, río Amazonas basin in Bolivia, where *Aphyocheirodon*, *Cheirodon*, and *Cheirodontops* did not occur (probably the species are *Serrapinnus*, or *Odontostilbe*), and this is the drainage of *Amblystilbe* occurrence (not treated as synonym of *Prodontocharax* here). Thus, a new phylogenetic analysis of the Cheirodontinae is presented here encompassing 58 species of all representative genera in contrast to 21 species analyzed by Malabarba (1998). The main objective of this paper is to resolve the relationships of the *incertae sedis* genera, and discuss new cladistic hypothesis to Cheirodontinae and its tribes.

Material and Methods

Phylogenetic Procedures. The frame concepts of phylogenetic systematics are those of Hennig (1966) and subsequent authors. The most parcimonious overall hypothesis of character distribution is the principle to generate the cladogram. Phylogenetic analysis was performed with TNT 1.0, 2005 by P. Goloboff, J. S. Farris & K. Nixon, and Winclada 1.00.08, 1999-2002 by K. Nixon. The algorithms used were the traditional heuristic search and the new technology with sectorial searches and tree fusing (Goloboff, 1999). Since none differences were found between the results of these algorithms, the heuristic results are presented. Weighting or addictive characters were not applied in the initial analyses. Subsequently, additional cladograms with implicit weights, k value 3, were obtained in order to downweight homoplastic characters as in Kullander (1998). In each analysis 100 replications were used to minimize error rate as the strict consensus is done for more trees (Goloboff & Farris, 2001). This number of replicates was found when the topology of the strict consensus tree was stable. Increasing the number of replications gradually to 200, 500, or 1000 replications did not change the topology of the strict consensus tree obtained and minimum length of trees. Collapsing trees during TBR (tree bisection reconnection) swapping were applied to eliminate unsupported groups without greatly reduce the number of correct groups (Goloboff & Farris, 2001). ACCTRAN optimization was preferred following de Pinna (1991), in which ambiguous character distributions are resolved by the optimization that maximizes reversals rather than parallelisms. Terminal autapomorphies were excluded from analyses, but present in multistate characters. The bootstrap values (Felsenstein, 1985) were calculated using 1000 replicates to the node support.

A total of 58 taxa and 169 characters were analyzed (Appendix II), including 27 autapomorphies. Ingroup taxa comprised the species of the *incertae sedis* cheirodontine genera of Malabarba (1998), including *Amblystilbe alleni*, *Aphyocheirodon hemigrammus*, *Cheirodontops geayi*, *Prodontocharax melanotus*, *Pseudocheirodon terrabae* and *P. arnoldi*, and 19 species of *Odontostilbe* or basal cheirodontines, including *O. fugitiva* (type species of *Odontostilbe*), *O. pequira* (type species of *Holoshesthes*), *O. euspilurus* (type species of

Lobodeuterodon), *O. paraguayensis, O. ecuadorensis, O. nareuda, O. parecis, O. microcephala, O. splendida, O. pao* and 8 new species. Outgroup cheirodontines (44 species) includes representatives of all genera defined in the phylogenetic analysis of Malabarba (1998), except †*Megacheirodon*. Representatives of the genus *Serrapinnus* were chosen according to putative different lineages recognized by modifications of tooth shape, verified in *Serrapinnus heterodon, S. microdon*, and *S. micropterus* (Malabarba, 1988, 1994, 1998). *Cheirodon* representatives were restricted to the cisandinean species, *Cheirodon ibicuhiensis* and *C. interruptus*. The Compsurini representatives included species of all genera, *Compsura heterura*, *Saccoderma hastata*, *Kolpotocheirodon theloura*, *Acinocheirodon melanogramma*, and *Macropsobrycon uruguayanae*. The compsurini species referred as "*Odontostilbe" dialeptura*, and *"Odontostilbe" mitoptera* in Malabarba & Weitzman (1999, 2000), (Malabarba, 2003), both originally described in *Cheirodon* and reviewed by Fink & Weitzman (1974), were not included in this study.

Fourteen outgroup species were chosen to include representatives of the main lineages of the Characidae, following Malabarba & Weitzman (2003) and Weitzman *et al.* (2005): the basal genera *Brycon* and *Bryconops*; representatives of the Characinae, Aphyocharacinae, and Rhoadsinae genera, plus the *incertae sedis Astyanax*,; and components of the putative monophyletic Clade A of Malabarba & Weitzman (2003), *Hemibrycon* and the Stevardiinae *Diapoma*.

Five Characinae species were chosen in order to test a possible relationship between Cheirodontinae and Characinae as suggested by Malabarba & Lucena (1995), and by the molecular data of Ortí & Meyer (1997) and Calcagnotto *et al.* (2005). These included basal species of the main lineages of Characinae identified by Lucena (1998), represented by the genera *Priocharax*, *Gnathocharax*, *Phenacogaster*, *Cynopotamus*, and *Charax*.

Aphyocharax was also included in the analysis based on the previous suggestion of close relationships between Aphyocharacinae of Eigenmann (1909) and the old sense Cheirodontinae of Eigenmann (1915).

An effort was made in choosing putative basal species for the outgroup taxa. *Brycon pesu* was chosen based on the phylogeny of *Brycon* obtained by Zanata (2000), and *Diapoma speculiferum* considering Glandulocaudinae (Weitzman & Menezes, 1998), and Stervadiinae (Weitzman *et al.*, 2005) phylogenies. *Carlana*, previously considered closely related to the Cheirodontinae (Fink & Weitzman (1974), was found the most basal in the Rhoadsiinae (Cardoso, 2003). However, in the lack of clear phylogenetic relationships, the availability of specimens was considered in defining outgroup species of *Astyanax*, *Bryconops*, *Hemibrycon*, and *Aphyocharax*..

Other currently *incertae sedis* characid species included in our study are *Aphyocharacidium bolivianum* Géry, 1973 and *Axelrodia lindeae* Géry, 1973. The genus *Aphyocharacidium* was described by Géry (1960) to accommodate *Odontostilbe melandetus* Eigenmann 1912. This species, along with *Aphyocharacidium bolivianum*, were not considered cheirodontines by Malabarba (1998), despite they share a similar pseudotympanum. Considering the finding of mature males of *A. bolivianum*, unknown before to the genus (Géry, 1973), this species was included in the outgroup taxa to test possible relationships with cheirodontines. New availiable mature males of *Axelrodia lindeae* were also decisive to include the species in the analysis. Mature males of *A. lindeae* were found to share some of the secondary sexually dimorphic synapomorphies described for Cheirodontini and *Serrapinnus*, and thus its relationships must be tested regarding those taxa. *Axelrodia* comprises three species, in need of taxonomic revision. Noteworthy, *Aphyocharacidium* Géry, 1960 and *Axelrodia* Géry 1965a, belong to the group named Aphyoditeina proposed by Géry (1965b, 1973) in Characidae.

Osteological preparations and Terminology. Clearing and staining procedures (c&s) followed Taylor & Van Dyke (1985). The gill raker at the junction of the ceratobranchial and the epibranchial was counted as the posteriormost gill raker of the lower branch (Bührnheim & Malabarba, 2006). Scanning electronic images of the teeth and first branchial arches were obtained from dissected or cleared and stained specimens. Osteological terminology follows Weitzman (1962), except mesethmoid instead of ethmoid and epioccipital instead of epiotic, following Fink & Fink (1981) and Weitzman & Fink (1983). The caudal-fin skeleton terminology follows Weitzman & Fink (1985). Scanning electron micrographs (SEM) were obtained from teeth and gill rakers.

Institutional abbreviations. The following institutions provided material for the study: ANSP - Academy of Natural Sciences, Philadelphia, USA; CAS - California Academy of Sciences, San Francisco, USA; CPULRA (UMSS) - Universidade de San Simón, Cochabamba, Bolivia; FMNH - Field Museum of Natural History, Chicago, USA; INHS - Illinois Natural History survey, Illinois, USA; ICNMNH - Universidad Nacional de Colombia, Museu de Historia Natural, Bogotá, Colombia; KU - University Kansas, Kansas, USA; KU - University Kansas, Kansas, USA; LACMNH - Los Angeles County Museum of

Natural History, Los Angeles, USA; MCNG - Museo de Ciencias Naturales de Guanare, Guanare, Venezuela; MCP - Museu de Ciências e Tecnologia, Porto Alegre, Brazil; MEPN - Museo de la Escuela Politécnica Nacional, Quito, Ecuador; MHNG - Muséum d'histoire naturelle, Geneva, Switzerland, MNHN - Muséum d'historie naturelle, Paris, French; MNRJ - Museu Nacional, Rio de Janeiro, Brazil; MPEG - Museu Paranaense Emílio Goeldi, Belém, Brazil; MUSM - Museo de Historia Natural de la Universidad Nacional Mayor de San Marcus, Lima, Peru; MZUSP - Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; NRM - (Naturhistoriska Riksmuseet) Swedish Museum of Natural History, Stockholm, Sweden; ROM - Royal Ontario Museum, Toronto, Canada; UMMZ - University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA; USNM - National Museum of Natural History, Washington D.C., USA.

Results

Cladogram presentation. The clades are assigned with alphabetical letters and numbers at nodes in the strict consensus trees, the weighted and unweighted tree (Figs. 2, 3), excepting for the recognized major tribes of Cheirodontinae. The number presented below the node is the bootstrap value. The limit of 40 to the bootstrap value presentation is applied considering the Cheirodontinae reached 41 in the weighted tree (Fig. 3). Matrix of characters and overall statistics of characters are respectively in Appendixes II and III. The consistency index (CI) of the weighted tree is presented jointly with the character description.

Character description and analysis. Characters are referred *a priori* to the weighed cladrogram, unless noted.

Cranium

Character 1 (CI = 0.14) - Anteromedial process of the mesethmoid (Ch. 20, modified of Zanata & Vari, 2005): (0) well-developed, extending between premaxillae and reaching anterior tooth bearing border of the premaxillae (Fig. 4a, b); (1) short, not extending or partially extending between premaxillae, not reaching anterior tooth bearing border of the premaxillae (Fig. 4c-f).

The mesethmoidal spine, named "ethmoidal spine" by Weitzman (1962), contacts the anterior region of the premaxillae, serving as a joint surface for these bones, as in *Hemibrycon* sp. (Fig. 4a). It separates the contralateral premaxillae at different degrees (Zanata & Vari, 2005: figs. 5-8). Most cheirodontines, as *Odontostilbe fugitiva*, *Heterocheirodon jacuiensis*, and *Spintherobolus ankoseion* (Fig. 4c-d, f), have a short anteromedial process of the mesethmoid not extending or partially extending between the premaxillae, and it is considered by parsimony a synapomorphy of the clade K formed by *Carlana* + Cheirodontinae, independently acquired in *Phenacogaster*. *Macropsobrycon* is coded as state 1, though having a different modification of the anteromedial border of the mesethmoid treated in the next Ch. 5 (Fig. 4e).

The well-developed anteromedial process of the mesethmoid practically reaching the anterior border of the premaxillae (state 0) is observed in *Acinocheirodon*, *Holoshesthes geayi*, and *Odontostilbe* n. sp. "e". While *Holoshesthes pequira*, *Holoshesthes* n. sp. "p", *Holoshesthes* n. sp. "k" (Fig. 4e), and *Serrapinnus heterodon* have some variation in the degree of development of the mesethmoidal spine, but the larger specimens usually have larger ethmoidal spines and are coded as state 1. It is noteworthy that among cheirodontines the presence of a larger mesethmoidal spine is usually associated with massive dentary teeth, and by parsimony it is admitted as independently acquired in the compsurin *Acinocheirodon*, the cheirodontin *S. heterodon*, and in the clade A12 formed by *Holoshesthes* species. The exceptions among these cheirodontines with massive dentary teeth are *Holoshesthes geayi*, *Holoshesthes* n. sp. "b" and *Holoshesthes hemigrammus*, forming clade A15. In these two latter species, actually the premaxilla is reduced in depth, and the process of the mesethmoid are not extending between most of the contralateral premaxillary joint (somewhat more developed in *H. hemigrammus* than *Holoshesthes*. n. sp. "b").

Gnathocharax and *Aphyocharax* have the anteromedial process of the mesethmoid relatively short in comparison with other species, but it extends farther between the premaxillae that are reduced in depth, being coded as state 0. The miniature *Priocharax* totally lacks the anteromedial process of the mesethmoid, having the anterior border in a smooth convex line, a condition not seen in any other examined taxa, and coded as state 0.

Zanata (2000: Ch. 4) remarked that the development of interdigitations between contralateral premaxillae and the degree of contact with the mesethmoid seems to be somewhat correlated, but with exceptions. Premaxillae completely or almost completely separated by the anteromedial process of the mesethmoid do not present interdigitations along adjoining surfaces of the premaxillae, whereas premaxillae not separated by the anteromedial process of the mesethmoid have the interdigitations connecting the premaxillae. The examined specimen of *Brycon pesu* is an exception to these statements, having the interdigitations and a well-developed anteromedial process of the mesethmoid extending between most contralateral premaxillary joint, and then coded state 0 here. As noted by Zanata (2000: 69), the premaxillary interdigitations are absent in cheirodontines even with the anteromedial mesethmoid process being short, not between the premaxillae, denoting no correlation of the presence of interdigitations with the development of the mesethmoidal spine.

Zanata & Vari (2005: Ch. 19, fig. 5) noticed that the abbreviated anteromedial process of the mesethmoid in *Cheirodon* is different of the reduced process found in african alestids *Clupeocharax*, *Lepidarchus*, and *Tricuspidalestes*, because it exclusively extends over anterodorsal surface of the median portions of the contralateral premaxillae in the latter taxa.

Character 2 (CI = 0.20) - Shape of the anteromedial process of the mesethmoid (Ch. 20, modified of Zanata & Vari, 2005): (0) pointed, or different from state 1 (Fig. 5a-b, e-f); (1) forming a short projection, wide at its base and narrower at its tip, with slightly sinusoidal lateral borders, similar to brackets contour (Fig. 5c-d).

The pointed anteromedial process of the mesethmoid, the "ethmoidal spine" of *Brycon meeki* by Weitzman (1962), is plesiomorphic in our analysis, present in most outgroup taxa (*Hemibrycon* sp., Fig. 5a). Among cheirodontines, only *Pseudocheirodon* retains a pointed anteromedial process of the mesethmoid (state 0) (Fig. 5b). The state 1, a brackets like contour of the anteromedial process of the mesethmoid, is a new unique synapomorphy to the Cheirodontinae (*Odontostilbe fugitiva*, *Holoshesthes* n. sp. "k", Fig. 5c-d). *Heterocheirodon*, *Spintherobolus*, and *Macropsobrycon* are coded as state 0, bearing different modifications of the anteromedial border of the mesethmoid, treated in the next characters.

Character 3 (CI = 1.00) - Shape of the anteromedial process of the mesethmoid (Ch. 20, modified of Zanata & Vari, 2005): (0) pointed, or different from state 1 (Fig. 5a-d, f); (1) presence of a thick small medial process, somewhat round and more developed ventrally, on anterior tip of mesethmoid (Fig. 5e)

The derived state 1 (Fig. 5e) is unique to *Spintherobolus*, possibly another reductive condition to these miniature characids (except *S. papilliferus*, not a miniature). The thick small central process serves as a partial joint surface to contralateral premaxillae (Fig. 4f).

Priocharax, as formerly referred, lacks the anteromedial process of the mesethmoid, coded as state 0. A different truncate anterior portion of mesethmoid lacking the anteromedial process is described in *Hydrocynus*, among Alestids (Brewster, 1986: fig. 1; Zanata & Vari, Ch. 20, 2005).

Character 4 (CI = 1.00) - Shape of the anteromedial process of the mesethmoid (Ch. 20, modified of Zanata & Vari, 2005): (0) pointed, or different from state 1 (Fig. 4a-c); (1) anterior border with a small truncate central projection (Fig. 5f).

A reduced truncate anteromedial process of the mesethmoid (mesethmoidal spine) is unique to *Heterocheirodon* (Fig. 5f). This reduction implies in a somewhat different articulation with the premaxillae. In cheirodontines and outgroup taxa examined the mesethmoidal spine or/and the lateral wings of the mesethmoid (in the next Ch.) bear the articulation with contralateral premaxillae (Fig. 4a-c). In *Heterocheirodon*, the reduced and truncate anteromedial process of the mesethmoid, and the reduced lateral wings of the mesethmoid, do not bear the articulation with contralateral premaxillae; instead the entire truncate anterior portion of the mesethmoid contact the premaxillae (Fig. 4d).

Character 5 (CI=1.00) - Anterior portion of the mesethmoid (Ch. 20, modified of Zanata & Vari, 2005): (0) pointed, or different from state 1 (Fig. 5a-f); (1) bifurcated (Fig. 4e).

This is an autapomorphy of *Macropsobrycon uruguayanae*. The ascendent processes of the premaxillae are located between the two branches of the bifurcated anterior portion of the mesethmoid (Fig. 4e).

A greatly modified anterior portion of the mesethmoid, trifurcate anteriorly and with a pair of lateral processes projecting towards the articular surface of the premaxillae (Ch. 1, Buckup, 1998) is found in *Characidium* (Buckup, 1993: fig. 4), *Crenuchus*, *Xenocharax*, *Citharinus*, *Distichodus* (Vari, 1979: fig. 6, supraethmoids), *Parodon, Steindachnerina*, but it is not found in other cheirodontines.

Character 6 (CI = 0.20) - Lateral wings of the mesethmoid (Ch. 13, modified of Malabarba, 1998; Ch. 2, modified of Buckup, 1998; Ch. 11, modified of Zanata, 2000; Ch. 23, modified Zanata & Vari, 2005; Netto-Ferreira, modified of 2006): (0) distinct (Fig. 5c-d); (1) almost indistinct or absent (Fig. 5c-d).

These lateral expansions are termed as lateral ethmoid wings by Weitzman (1962: fig. 2). The wings usually support the posterior tip of the ascendent process of the premaxilla, being well-developed in all *Brycon* species (Zanata & Vari, 2005). Malabarba (1998: fig. 7A-B) illustrated the well-developed lateral mesethmoid wings of *Triportheus* sp. (Fig. 7B), and the inconspicuous ones of *Lignobrycon myersi* (Fig. 7A) [note: figs. 7A and 7B were mistakenly referred in reverse along the character 13 description by Malabarba, 1998)]. Buckup (1998) refers to a well-developed lateral ethmoidal wing as one of the synapomorphies of Crenuchinae. Netto-Ferreira (2006) named the lateral wings as articular processes of the mesethmoid, noting that they not only usually support the ascending process of the premaxilla in Characiforms, but contact the maxilla, endopterygoid (mesopterygoid), and ectopterygoid in Lebiasinids.

Usually, cheirodontines have distinct lateral wings with different shapes (*e.g.* small in *Odontostilbe fugitiva*, and *Heterocheirodon yatai* (Fig. 5c, f), developed in *Holoshesthes* n. sp. "k" (Fig. 5d). Indistinct or absent wings are present in compsurins, in clade M (*Kolpotocheirodon* + (*Acinocheirodon* + *Macropsobrycon*). However, in *Macropsobrycon* the modified anterior portion of the mesethmoid seems to lack the lateral wings (Fig. 4e), being uncoded to the present character because the uncertain homology of the bifurcated projection of mesethmoid treated in previous Ch. 5. State 1 is also three times acquired in other lineages of the Cheirodontinae: in the Cheirodontini *Spintherobolus* clade X (Fig. 5e), in the Odontostilbini *Pseudocheirodon* clade A3 (Fig. 5b), and in *Holoshesthes hemigrammus*.

In *Kolpotocheirodon* and *Spintherobolus* (Fig. 5e) the wings seem to be lacking, while in *Acinocheirodon, Pseudocheirodon* (Fig. 5b), and *Holoshesthes hemigrammus* the wings seem to be very reduced. In the outgroup, *Aphyocharax* also seems to lack lateral wings.

Cynopotamus, *Charax*, and *Priocharax* (see Ch. 3) are coded as inapplicable to this character following Zanata & Vari (Ch. 23, 2000), that considered the overall form of mesethmoid significantly different from the morphology of the group in analysis, in our case the cheirodontine. In *Cynopotamus* and *Charax* the wings seem to be lacking (Zanata, 2000 considered state 0, Ch. 11, absence to *Charax*). However, there is a convex lateral expansion of the mesethmoid that supports the ascendent process of the premaxillae in both *Cynopotamus* and *Charax*. In *Carlana*, the character is also considered inapplicable. This rhoadsiine has a reduced mesethmoidal spine in the wide and convex anterior portion of the mesethmoid that supports the contralateral premaxillae along practically all their anterodorsal border. It is difficult to state if the lateral wings are absent or extremely developed and fused with the anterolateral portions of the mesethmoid forming such a wide anterior mesethmoid portion.

Character 7 (IC = 0.33) - Epioccipital bridge (Ch. 6, modified of Weitzman & Fink, 1983): (0) present (Fig. 6a); (1) absent (Fig. 6b).

The epioccipital bridge usually bisects the posttemporal fossa in its mid portion or lies just dorsal to it in most characids (Weitzman & Fink, 1983: figs. 10-13) (*Odontostilbe fugitiva*,

Fig. 6a). In *Paracheirodon*, the epioccipital bridge lies at the dorsal border of the posttemporal fossa, or occasionally is absent in *P. simulans*, being a synapomorphy to the genus (Weitzman & Fink, 1983: Ch. 6, figs. 6-8). Among cheirodontines, the epioccipital bridge is absent and a synapomorphy to clade X formed by *Spintherobolus* species (*S. ankoseion*, Fig. 6b), but reversed (present) in *S. papilliferus*.

By parsimony, the lack of the epioccipital bridge is a synapomorphy independently derived in a clade E containing *Charax* + (*Cynopotamus* + *Priocharax*). In the unweighted tree, this clade correspond to the clade H, but with the addition of *Gnathocharax*, reversed to state 0.

Epioccipital bridge is also lacking in all specimens of *Tyttocharax* and *Xenurobrycon*, but it is not a synapomorphy to them according to the most parcimonious hypothesis to Xenurobryconini phylogeny (Weitzman & Fink, 1985).

Character 8 (CI = 0.33) - Rhinosphenoid (Ch. 11, Malabarba, 1998; Ch. 7, Buckup, 1998; Ch. 16, Zanata, 2000; Ch. 31, Zanata & Vari, 2005): (0) present (Fig. 7a-c),; (1) absent (Fig. 7d).

In contrast to the presence of the rhinosphenoid in all other cheirodontines (Fig. 7a-c), it is absent in *Spintherobolus* (Fig. 7d), in the outgroup genus *Aphyocharax*, and in the clade E1 formed by *Cynopotamus + Priocharax*. Basal characiforms as citharinids, distichodontids, and alestids lack the rhinosphenoid (Vari, 1979: figs. 7-9; Zanata & Vari, 2005: Ch. 31, fig. 9). The taxa grouped in the Clade 21 in Buckup's (1998) phylogeny, including *Boulengerella*, *Ctenolucius*, *Hepsetus*, *Hoplias*, and the lebiasinids *Lebiasina*, *Pyrrhulina*, and *Nannostomus*, also lack the rhinosphenoid. *Gnathocharax steindachneri* has a partially cartilaginous rhinosphenoid with a somewhat central osseous piece, coded as having the rhinosphenoid as Lucena (1993).

The rhinosphenoid in *Carlana eigenmanni* is unique among all the specimens examined, being not only connected posteriorly with the orbitosphenoid, but also dorsally to the ventral surface of frontals.

Uj (1987) tentatively defined *Cheirodon* by the reduction or sometimes the total loss of the rhinosphenoid. The relative size of the rhinosphenoid was not evaluated, but the species of *Cheirodon* examined here have the rhinosphenoid.

Character 9 (CI = 0.33) - Orbitosphenoid (Ch. 1, Lucena, 1998; Ch. 25, Benine, 2000, Ch. 18 modified of Zanata, 2000): (0) not contacting the parasphenoid (Fig. 7a-c).; (1) contacting the parasphenoid (Fig. 7d).

In most cheirodontine the orbitosphenoid is not contacting the parasphenoid (*Cheirodon interruptus*, *Odontostilbe fugitiva*, *Odontostilbe* n. sp. "e", Fig. 7a-c). The orbitosphenoid contacts the parasphenoid exclusively in *Spintherobolus* (*S. papilliferus,* Fig. 7d), and in the outgroup taxa *Aphyocharax, Cynopotamus* (an extensive portion), and *Priocharax,* all the species that lack the rhinosphenoid (previous Ch. 8). Thus probably these modifications are related.

In a taxonomic review of *Charax*, Lucena (1987) criticized the consistence of the two characters, the rhinosphenoid presence-absence and the contact between the orbitosphenoid and parasphenoid, showing intraspecific variation and concluding they would be of low phylogenetic value. Lucena (1987) found both characters varying in most *Charax* species, but in *C. stenopterus* (the species examined here) the contact between orbitosphenoid and parasphenoid is always lacking, though rhinosphenoid presence varied. Furthermore, Lucena (1987) reinforced a suggestion of Menezes (1976) that these modifications are correlated with feeding habits, in which the large size of the preys requires a strong connection between the parasphenoid and roof cranial bones. Latter, Lucena (1998) evaluated the orbitosphenoid-parasphenoid connection in his phylogenetic analysis of *Roeboides*, but did not discuss the character in detail since was not useful in defining a clade in *Roeboides*. However, the orbitosphenoid-parasphenoid connection was found in the characines *Acestrocephalus*, *Charax gibbosus*, *C. stenopterus*, *C. tectifer*, *Cynopotamus*, *Galeocharax*, *Roeboides bonariensis*, and *R. myersi* (Lucena, 1998).

Noteworthy, *Priocharax ariel*, another characine species examined here, was coded as state 0 by Lucena (1998). Probably, Lucena (1998) did not consider the cartilage in the connection orbitosphenoid-parasphenoid because the two c&s specimens examined by him (and re-examined here) were lightly stained. An additional c&s specimen prepared from the same lot examined by Lucena (MCP 9953) revealed the cartilage connecting the orbitosphenoid and parasphenoid, then *P. ariel* is herein coded as state 1. Cartilage is present in the connection between orbitosphenoid and parasphenoid in *Priocharax ariel,* all *Spintherobolus* species (reduced cartilage portion in one specimen of *S. broccae,* and in one specimens of *S. papilliferus* examined). It is also probably present in a minor amount in *Cynopotamus kincaidi* (the c&s specimen examined was not stained with alcian blue, but there is a space between the orbitosphenoid-parasphenoid connection) and present in *C. amazonicus*.

Aphyocharax nattereri almost does not have this cartilage, and there is a dorsal osseous lamellar extension of the parasphenoid, where the orbitosphenoid is connected. This is similar to that described to *Hepsetus odoe* (Roberts, 1969: fig. 11), but the "dorsally-projecting process" of the parasphenoid is posteriorly positioned in comparison to that of *A. nattereri*.

Zanata (2000) distinguished four states relative to the position of the connection orbitosphenoid-parasphenoid. She did not consider cartilage between osseous structures, but two states of that character (Ch. 18) were defined by the existence of different size gaps in that connection, and the others by the posteriorly positioned or anteriorly positioned connection. *Charax pauciradiatus* and *Salminus* were recognized to present the shorter gap, the orbitosphenoid and parasphenoid proximate but not in contact. Benine (2004) disagree with that description of the character, noticing that *C. pauciradiatus* has a close contact between the orbitosphenoid-parasphenoid, but did not evaluate the cartilage joint. Roberts (1969) describes an endochondral joint in *Salminus*. Thus, the cartilage joint in the connection orbitosphenoid-parasphenoid is a potentially informative structure to be considered in the analysis of this character. Furthermore, orbitosphenoid contact with parasphenoid seems to change ontogenetically, as suggested by Lucena (1998: Ch. 1) in restricting the state 1 to adults.

Benine (2004) found *Markiana nigripinnis* also has the orbitosphenoid contacting the parasphenoid.

Character 10 (CI = 0.16) - Posteroventral process of the orbitosphenoid (Ch. 9, modified of Lucena, 1993; Ch. 5, modified of Lucena, 1998; Ch. 17, modified of Lucena & Menezes, 1998): (0) absent, or presence of a tiny posteroventral process associated to a small posterior concavity in the orbitosphenoid (Fig. 7a-b); (1) present, a short spine-like projection associated to a well-developed posterior concavity in the orbitosphenoid (Fig. 7c); (2) present, a long and spine-like projection extending backward, associated to a small posterior concavity in the orbitosphenoid (Fig. 7d); (3) present, a long spine-like projection associated to a posterior well-developed concavity in the orbitosphenoid.

A long spine-like posteroventral process of the orbitosphenoid is a synapomorphy of *Lonchogenys, Gnathocharax, Hoplocharax,* and *Heterocharax* (Lucena, 1993), all of them composing the Clade 2 of the Characinae in the phylogenetic analysis of *Roeboides* (Lucena, 1998). In his doctoral dissertation, Lucena (1993) referred the character as a "spine-like process", but in posterior works (Lucena, 1998; Lucena & Menezes, 1998) he defined the character as "concavity on posteroventral region of orbitosphenoid". Here, the long spine-like projection associated to a posterior well-developed concavity (state 3) corresponds to his state 2 of Ch. 9 (Lucena, 1993), state 1 in Ch. 5 (Lucena, 1998), and state 2 in Ch. 17 (Lucena &

Menezes, 1998). Furthermore, the uniquely derived state 2 is added as an autapomorphy of *Spintherobolus papilliferus* (Fig. 7d).

Most cheirodontines share a derived short spine-like projection associated to a posterior well-developed concavity, state 1 (*Odontostilbe fugitiva*, Fig. 7c), a modification acquired in clade K comprising *Carlana* and the Cheirodontinae. Among the outgroup taxa *Aphyocharacidium* and *Diapoma* independently have state 1 too. The lack or small spine-like projection (state 0) is independently manifested in *Cheirodon interruptus* (Fig. 7a), clade R with *Heterocheirodon*, in clade M in *Macropsobrycon* and *Kolpotocheirodon*, reversed in *Acinocheirodon*, in clade X with *Spintherobolus* species (except *Spintherobolus papilliferus*, state 2, Fig. 7d), and in *Amblystilbe* and *Holoshesthes hemigrammus*. The clade A9 with *O. microcephala*, *Odontostilbe* n. sp. "e" (Fig. 7b), and *Odontostilbe* n. sp. "p",also have tiny pointed posteroventral corner of orbitosphenoid formed by a small posterior concavity, all of them coded as state 0. *Odontostilbe* n. sp. "b" independently reversed to state 0 among Odontostilbini species.

Character 11 (CI = 0.15) - Laterosensory canals of parietal (Uj, 1987; Chs. 18, 19 modified of Lucena, 1993; Ch. 16, modified of Buckup, 1998; Ch. 156, 157, 158 modified of Zanata & Vari, 2005; Ch. 185, modified of Netto-Ferreira, 2006): (0) longitudinal branch of the laterosensory canal of parietal posteriorly contiguous to the transverse laterosensory canal of parietal (the "supratemporal canal" of Uj, 1987), and anteriorly contiguous to the laterosensory canal of frontal (Fig. 6a); (1) longitudinal branch of the laterosensory canal of parietal posteriorly not contiguous to the transverse laterosensory canal of the parietal, divided by a gap, and anteriorly contiguous to the laterosensory canal of frontal (Fig. 6c);
(2) all the canals on parietal lacking (Fig. 6b).

The reductions of the laterosensory canal of the postocular cranium and shoulder girdle in characids were discussed by Weitzman & Fink (1983). They described the complete laterosensory canal systems of *Astyanax* and *Gymnocorymbus* as the primitive arrangement in characids (Weitzman & Fink, 1983: figs. 9, 28A, 29 for *Astyanax* and figs. 10, 30 for *Gymnocorymbus*), and a relatively little laterosensory canal loss in *Cheirodon interruptus*. Uj (1987) tentatively separated two groups of cheirodontines, based in some of these reductions, including *Cheirodon* in the "group A", with reduced postocular laterosensory canals, and "*Odontostilbe*" species plus *Holoshesthes pequira* in a "group B" (actually comprising *Odontostilbe* and species currently recognized as belonging to *Serrapinnus*), all of them with complete postocular laterosensory canals. Uj (1987) did not make an accurate taxonomic review of *Cheirodon* and *Odontostilbe*, incurring in errors such as the use of a broad concept for "*Odontostilbe piaba*". Actually, his "*O. piaba*" probably included at least *Serrapinnus calliurus*, and none *Serrapinnus piaba*. Thus, it is difficult to affirm to which species belong Uj's illustrations of "*O. piaba*" (*e.g.* Uj, 1987: figs. 2 and 4). These two cranial drawings show both states of the character presented here, complete and reduced, in his "*O. piaba*", leading to a possible erroneous view that the character varies intraspecifically, besides that it would not support groups A and B proposed by Uj.

We found the laterosensory canal of the parietal highly homoplastic on the relationships of the cheirodontines. The clade J (*Aphyocharax* + (*Carlana* + (Cheirodontinae))) has the state 1 as derived, the longitudinal branch of the laterosensory canal of parietal posteriorly not contiguous to the transverse laterosensory canal of the parietal, divided by a gap, and anteriorly contiguous to the laterosensory canal of frontal, *Heterocheirodon* species (Fig. 6c). Noteworthy, the laterosensory canal of the parietal of all examined species of *Cheirodon* and *Serrapinnus* did not vary intraspecifically as it would be expected by Uj's illustrations (1987). Consistently these species have the interrupted laterosensory canal of parietal.

Remarkably, among Cheirodontinae the state 0 is by parsimony a reversed synapomorphy to Odontostilbini (*Odontostilbe fugitiva*, Fig. 6a), but state 1 is present independently three times in *Lobodeuterodon*, *Odontostilbe* n. sp. "b", and *Holoshesthes hemigrammus* (Fig. 6d) . The seven specimens examined of *Lobodeuterodon* had some variation in the character, but all of them had the interrupted laterosensory canal of parietal at least at one side of the skull, then coded as state 1. Ontogenetic intraspecific variation was found in the character to *Holoshesthes pequira*, in which juveniles present a gap on the canal and adult specimens have the entire laterosensory canal of parietal.

Among the Compsurini, the interrupted laterosensory canal of parietal, state 0, is reversed in *Acinocheirodon*. Actually, in one examined specimen of *A. melanogramma* from the rio Jequitinhonha basin the laterosensory canal of parietal was interrupted, differing from the specimens from the rio São Francisco basin, with a complete laterosensory canal. Malabarba & Weitzman (1999) suggested that these two populations from separate drainages would be probably two different species as they showed some differences, *e.g.* in caudal peduncle depth, but they conservatively admitted an *A.* cf. *melanogramma* because of small sampling of rio Jequitinhonha basin.

Total lack of the laterosensory canals of parietal, corresponding to state 2, is a feature of *Spintherobolus* (*S. ankoseion*, Fig. 6b), and of the outgroup genus *Priocharax,* all miniature characid fishes (except *Spintherobolus papilliferus*). Generally small sized cheirodontines have the gap in the laterosensory canal of parietal, which supports the hypothesis of paedomorphic reduction of the character along with miniaturization (Weitzman & Fink, 1983; Weitzman & Vari, 1988). Mid-sized *S. papilliferus* seems to contrary this trend as *Phenacogrammus aurantiacus* among alestids (Zanata & Vari, 2005).

The lebiasinids *Pyrrhulina* and *Nannostomus* (Weitzman, 1964; Lucena, 1993; Netto-Ferreira, 2006) also lack of the laterosensory canals of the parietal, corresponding to state 2. The outgroup taxa *Aphyocharax, Gnathocharax,* and *Axelrodia lindeae* were coded as state 1, because they lack the entire longitudinal laterosensory canal of parietal (including contiguous anterior portion of the canal along frontal), but they have the vertical supratemporal canal on posterior portion of parietal.

Character 12 (0.20) - Laterosensory canal of frontal (Uj, 1987; Ch. 159, modified of Zanata & Vari, 2005): (0) posteroventral branch of the laterosensory canal of frontal contiguous to the laterosensory canal of pterotic (Fig. 6a,c); (1) posteroventral branch of the laterosensory canal of frontal interrupted, or absent, not contiguous to the laterosensory canal of pterotic (Fig. 6d); (2) all the canals lacking on frontal, including the supraorbital (Fig. 6b).

The lack of the posteroventral branch of the laterosensory canal of frontal, hypothesized as unique in *Cheirodon* by Uj (1987), is by parsimony absent or partially reduced in the cheirdodontines: *Cheirodon interruptus* (but not in *C. ibicuhiensis*); the clade M with *Kolpotocheirodon* + (Acinocheirodon + *Macropsobrycon*), but reversed to state 0 in *Acinocheirodon*; and in *Holoshesthes hemigrammus* (Fig. 6d). Total lack of the laterosensory canals of frontal is a feature observed in *Spintherobolus* (*S. ankoseion*, Fig. 6b) among Cheirodontinae, but also in the outgroup genus *Priocharax*, which seems to be related with miniaturization (see discussion under Ch. 11). In clade E formed by species of the Characinae, state 1 is a derived condition, reversed to state 0 in *Cynopotamus*, and modified to state 2 in *Priocharax*. In *Aphyocharax* state state 1 is also derived. .

Circumorbital bones

Character 13 (0.33) - Shape of antorbital: (0) elongate (Fig. 8a); (1) short (Fig. 8b),.

The short antorbital is a synapomorphy of *Spintherobolus* (Fig. 8b), independently acquired in *Gnathocharax*. In *Priocharax* the antorbital is present as a tiny piece of bone and viewed as a red dot after alizarin stained.

Character 14 (CI = 0.50) - Shape of the first infraorbital (Ch.5 modified of Zanata, 2000): (0) not as in state 1 (Fig. 8b-d); (1) subrectangular with anteroventral portion extended (Fig. 8a).

The first infraorbital, subrectangular in shape, is a new synapomorphy to the Cheirodontinae. The extended anteroventral portion serves as a joint surface to the ventral portion of the antorbital (*Cheirodon interruptus*, Fig. 8a). Some variation in the extended anteroventral portion is found mainly in *Holoshesthes* species, in *Serrapinnus heterodon, Holoshesthes hemigrammus*, *Holoshesthes* n. sp. "b", *Prodontocharax*, *Amblystilbe, Odontostilbe* sp. "e", and *Odontostilbe* n. sp. "b", in which the anteroventral extension anteroventral is more discrete. The only cheirodontines lacking this subrectangular first infraorbital are *Spintherobolus* (Fig. 8b), and *Axelrodia lindeae* (Fig. 8c).

Noteworthy, among the outgroup taxa, a nearly squared first infraorbital is found only in *Phenacogaster* (Fig. 8d). A different leaf-shaped first infraorbital, in which the posteroventral portion extends under the second infraorbital, is a synapomorphy of *Triportheus* and *Lignobrycon* (Malabarba, 1998: Ch.3, fig. 5), also observed in *Brycon pesu*, and *Salminus*. Zanata (2000) partially agree with Malabarba's (1998) results, but found that *Agoniates* shares this character and forms a clade with *Triportheus* and *Lignobrycon*, and that *Brycon pesu* (plus all the *Brycon* species) does not have the leaf-shaped first infraorbital.

Character 15 (CI = 0.11) - Laterosensory canal of the first infraorbital (Ch. 10, modified of Malabarba 1998; Ch. 23, Serra, 2003): (0) along almost the entire length of the longest axis of the first infraorbital or reaching to about half length of the longest axis (Fig. 9a-b); (1) absent or nearly absent at the posterior portion of the first infraorbital, never reaching to about half length of the longest axis (Fig. 9c-d).

The laterosensory canal entire or along half length of the first infraorbital longer axis is plesiomorphic in our analysis, with its lack or near absence derived in clade K with *Carlana* and the cheirodontines , but reversed to state 0 in clade L with *Compsura* + *Saccoderma*, in clade S with New genus n. sp. C + (*Serrapinnus* + (*Axelrodia lindeae* + *Spintherobolus*), and in the Odontostilbini (*Odontostilbe* n. sp. "e", *O. pulchra*, Fig. 9a-b). However, among the Odontostilbini, state is independently derived to in *Holoshesthes hemigrammus, Odontostilbe* n. sp. "b" and *Odontostilbe* n. sp. "h".

Here, the recognition of intraspecific variation in the character (*e.g.* total lack or the presence of a short posterior portion of the canal in specimens of *H. hemigrammus*), leaded to the redescription of the state 1 of the Ch. 10 defined by Malabarba (1998). However, *Cheirodon* and *Nanocheirodon* included in state 1 totally lack the laterosensory canal of the first infraorbital in all specimens examined (*Cheirodon interruptus*, Fig. 9c);. Besides, all specimens of *Kolpotocheirodon*, and *Macropsobrycon* (Fig. 9c); examined lack the sensory canal of the first infraorbital, differently from Malabarba (1998), where they are coded as state 0 (having the canal).

The outgroup taxa *Charax* and *Carlana* independently share the state 1 (absence of laterosensory canal in the first infraorbital). Serra (2003, fig. 5A-B,) found the absence or reduction of this canal as one of the synapomorphies of *Hasemania*.

Spintherobolus and *Priocharax* have extreme reductions of the laterosensory canal on head and circumorbital series, which makes difficult the assumption of a total lack of the first infraorbital or its fusion with other infraorbitals (following Ch. 16, state 1). Thus, they were uncoded for the present character. *Axelrodia lindeae* has the first infraorbital almost reduced to the canal (Fig. 8c), with a small anteroventral lamella, and *Aphyocharax* has only the sensory canal of the first infraorbital; both species are coded as state 0.

Character 16 (CI = 0.50) - Infraorbitals (Ch. 12, Malabarba, 1994; Ch. 9, Malabarba, 1998; Ch. 18, Weitzman & Malabarba, 1999): (0) infraorbitals 1 to 6 present (Fig. 8a, c-d); (1) first infraorbital absent or fused with the second infraorbital (Fig. 8b),. One large bony element located in the usual position of the second infraorbital. Another infraorbital, extremely reduced in size placed in the position of the third infraorbital (absent in *Spintherobolus broccae*). Infraorbitals 4 thorough 6 absent, at least as ossifications.

State 1 is a known synapomorphy of *Spintherobolus* (Weitzman & Malabarba, 1999). *Priocharax ariel* was coded as state 1 because a new c&s specimen (paratype, 14.3 mm SL, MCP 9953) has two distinct small ossified circumorbital bones, probably corresponding to reduced second and third infraorbital. Weitzman & Vari (1987) described for both *P. ariel* and *P. pygmaeus* an incomplete infraorbital series, with the presence of just the antorbital bone ossified. The antorbital is present in *Priocharax*, and viewed as a tiny red dot in one alizarin stained specimen. In two other c&s specimens from the same lot (MCP 9953), the reduced second and third infraorbitals are present on the left side of one specimen, and just the third infraorbital on the right side.

Character 17 (CI = 0.12) - Shape of the second infraorbital (Ch. 8, modified of Lucena & Menezes, 1998): (0) ventral border slightly convex to nearly straight (Fig. 10a); (1) ventral border with a slight concavity near its half length, close to the posterior tip of the maxilla (Fig. 10b).

The sinuosity of the ventral border of the second infraorbital is described to *Roestes* and *Lonchogenys* (Lucena & Menezes, 1998). In *Roestes* (Fig. 4 in Lucena & Menezes, 1998) the sinuosity is more accentuated. The following cheirodontines were coded as state 1, being this character highly homoplastic (CI = 0.12) and little informative on the relationships of these genera: *Cheirodon*, *Heterocheirodon*, *Serrapinnus*, *Acinocheirodon*, *Kolpotocheirodon*, *Macropsobrycon* (Fig. 9d), *Odontostilbe paraguayensis* (Fig. 11b), and *O. parecis*. However, state 1 is a synapomorphy to clade A12 formed by all species of *Holoshesthes* (Fig. 10b). Noteworthy, state 1 also sustains the clade N formed by *Kolpotocheirodon* + (*Acinocheirodon* + *Macropsobrycon*). In the outgroup, just *Phenacogaster* shares this derived condition (Fig. 8d).

Although having the first and second infraorbitals possibly fused (Fig. 8b), *Spintherobolus* species are coded in state 0, considering the absence of a concavity similar to that described in state 1 in this "fused infraorbital".

Character 18 (CI = 0.08) - Shape of the second infraorbital: (0) anterodorsal border without pointed projection or not as state 1 (Figs. 8c-d; 9c); (1) anterodorsal border with a small to well-developed pointed projection, underneath the posterodorsal portion of the first infraorbital (Figs. 9a-b, d; 10a-c).

State 1 is a synapomorphy to the Odontostilbini, though homoplastic being present in other cheirodontines, in the clade U with *Serrapinnus* species and independently in clade P in *Cheirodon ibicuhiensis*, and in the clade N with *Acinocheirodon* + *Macropsobrycon* (Figs. 9d; 10c).. Among the own Odontostilbini, the clade A4 formed by *Odontostilbe* n. sp. "h" + (*Lobodeuterodon* + (*Amblystilbe* + *Prodontocharax*)), and independently *Odontostilbe* n. sp. "b" have the character reversed to state 0.

Among the outgroup only *Aphyocharacidium* presents state 1. Other outgroup taxa, *Astyanax*, *Hemibrycon*, *Diapoma*, *Cynopotamus*, and *Gnathocharax* have a small to well-developed pointed projection on anterodorsal border, but just dorsal to the anterior portion of the laterosensory canal, and not underneath the posterodorsal portion of the first infraorbital, then coded as state 0.

Serrapinnus micropterus, and *Cheirodon ibicuhiensis* are coded as state 1, but a tiny pointed projection is not always distinct; the same to *Odontostilbe ecuadorensis, O. dierythrura*, *O. parecis*, *O. pulchra* and *O. fugitiva* (Figs. 9b; 10a)., and to the outgroup genus *Aphyocharacidium*. Among cheirodontines, *Cheirodon interruptus* (Fig. 9c), *Nanocheirodon,* New genus n. sp. C., *Axelrodia lindeae* (Fig. 8c), *Compsura*, *Kolpotocheirodon*, *Amblystilbe*, *Prodontocharax*, *Pseudocheirodon terrabae*, and *Holoshesthes hemigrammus* (Fig. 11a), totally do not have a distinct pointed projection, all coded as state 0, though *e.g. H. hemigrammus* can have the anterodorsal border of the second infraorbital underneath ventral to the posterodorsal portion of the first infraorbital (Fig. 11a). *Spintherobolus* species have fused infraorbitals 1 and 2 fused or lack infraorbital 1, coded as state 0. In *Axelrodia lindeae* the anterior portion of the second infraobital is reduced to the canal (Fig. 8c), and also coded as state 0.

Lucena & Menezes (1998: Ch. 6, fig. 4) referred to an interlocking mechanism formed by a small process extending from the anteroventral portion of the laterosensory canal in the second infraorbital which extends over the dorsal border of the first infraorbital, as an apomorphy of Roestinae, independently derived in *Heterocharax*, *Lignobrycon*, and *Triportheus*. This interlocking mechanism is different from the present character described for the anterodorsal border of the second infraorbital, and is not observed in the cheirodontines.

Character 19 (CI = 0.16) - Posteroventral border of the third infraorbital relative to the laterosensory canal of preopercle: (0) contacting the laterosensory canal of preopercle; (1) ventrally contacting the laterosensory canal of preopercle, but leaving a posterior naked area between border of the third infraorbital and the laterosensory canal of preopercle; (2) not contacting the laterosensory canal of preopercle, leaving a naked area between the posterolateral border of the third infraorbital and the laterosensory canal of preopercle.

This is a highly homoplastic character. In most taxa examined, the posterior border of third the infraorbital contacts the laterosensory canal of preopercle. By parsimony state 1 appears as a synapomorphy to the broad clade D, modified to state 2 in the clade E (*Charax* + (*Cynopotamus* + *Priocharax*)), excepting *Cynopotamus* with state 1, and reversed to state 0 in the clade G (*Hemibrycon* + *Diapoma*) and in the clade J (*Aphyocharax* + (*Carlana* + Cheirodontinae). Among the Cheirodontinae, again a posterior naked area (state 1) appears in the clade P formed by *Cheirodon ibicuhiensis* and *C. interruptus*. Among Odontostilbini, state 1 is found independently in *Odontostilbe microcephala* and state 2 in *Holoshesthes hemigrammus*.

In other cheirodontines, a large naked area (state 2) is exclusive of clade W with *Spintherobolus* and *Axelrodia lindeae*, being related to the general reduction of the infraorbitals. Similarly, *Priocharax*, not a cheirodontinae, have a large naked area (state 2) in clade E. *Holoshesthes hemigrammus*, *Charax*, and *Phenacogaster*, with third infraorbital somewhat reduced, were coded as state 2, but the naked area is smaller than in *Spintherobolus* and *Priocharax*.

Uj (1987) remarked the third infraorbital is well-developed in the osteological description of *Odontostilbe fugitiva*. The third infraorbital, referred as a large suborbital or an almost entire suborbital, leaving or not a naked area on cheek, is a character traditionally used in keys to distinguish species of the Characidae (*e.g. Aphyocharax* by Eigenmann, 1915, and *Hyphessobrycon* or *Hemigrammus* species by Géry, 1977).

Character 20 (CI = 0.11) - Shape of the fourth infraorbital (Ch. 2, Benine, 2004): (0) squarish, similar in width and height, or reduced (Fig. 11a); (1) somewhat deeper, rectangular or irregularly shaped, height longer than width (Fig. 11b, d).

Cheirodontines have the forth infraorbital usually somewhat rectangular (Fig. 11b, d). By parsimony, the state 1 is a modification firstly appearing in the clade I (*Astyanax* + (*Aphyocharax* + (*Carlana* + Cheirodontinae), then reversed to state 0 in clade N (*Acinocheirodon* + *Macropsobrycon* (reduced, Fig. 10c)), in *Cheirodon* (reduced) (Fig. 8a), *Odontostilbe* n. sp. "e", *Odontostilbe* n. sp. "h", *Amblystilbe*, and *Holoshesthes hemigrammus* (Fig. 11a). In *Axelrodia lindeae*, the fourth infraorbital is only formed by a short sensory tube, sometimes with the lamella (Fig. 8c), and not coded for this character. *Spintherobolus* are also uncoded, lacking the fourth infraorbital (Fig. 8b).

Benine (2004) remarked the polymorphism in the shape of the forth infraorbital, but recognized the same variation herein described. Most *Moenkhausia* species in his clade 12 has the forth infraorbital elongate (state 1), with a few reversions. The forth infraorbital has intraspecific variation in the development of the lamellae, but not in the relative length and width.

Character 21 (CI = 0.10) - Shape of the fifth infraorbital (Ch. 4, Benine, 2004): (0) broad, with expanded lateral laminas from the laterosensory canal (Fig. 11c); (1) narrow, lateral laminas absent and reduced to the laterosensory canal, or lateral laminas small and irregularly expanded, not wider than the canal width (Figs. 11a-b).

By parsimony, the reduced fifth infraorbital is a synapomorphy to the comprehensive clade J (*Aphyocharax* + (*Carlana* + Cheirodontinae)), being present in most cheirodontines, but with several reversals and reacquisitions. Among Odontostilbini, reversions to state 0 occur three times: in the clade A3 formed by the two species of *Pseudocheirodon*, in the clade A5 *Lobodeuterodon* + *Prodontocharax* + *Amblystilbe*, and in *O. microcephala* (Fig. 11c). Among

Compsurini, the reversion to state 0 occur in the clade M formed by *Kolpotocheirodon* + (*Acinocheirodon* + *Macropsobrycon*), but again modified to state 1 in the last genus. Reversion to state 0 also occurs in the New genus n. sp. C, a cheirodontin. The Cheirodontini *Spintherobolus* and *Priocharax* (Figs. 8b-c) are uncoded, lacking the fifth infraorbital.

Benine (2004) in a phylogenetic analysis of *Moenkhausia* found the narrow fifth infraorbital as a synapomorphy of the large Clade 23 containing 25 species of *Moenkhausia*, among other characids, with reversions to broad fifth infraorbital in four *Moenkhausia* species.

Character 22 (CI = 0.14) - Shape of the anterior border of the sixth infraorbital (Ch. 11, modified of Malabarba, 1994): (0) anterior lamella absent (Figs. 8b-c); (1) anterior lamella small, reduced, once in laterosensory tube width, in a somewhat small lingual-like shape (Figs. 8d; 11a); (2) anterior lamella expanded in a lingual-like shape (Figs. 11b-d).

This character has been modified several times along Cheirodontinae lineages, but by parsimony state 2 is a synapomorphy to Odontostilbini. The state 2, a well-developed anterior lingual-shaped lamella is found in most *Odontostilbe* species (*O. paraguayensis*, *O. microcephala*, Fig. 11b-c), in most *Holoshesthes* species (*Holoshesthes* n. sp. "k", Fig. 11d), and in the clade A1. The exceptions in Odontostilbini having a smaller lingual-shaped lamella (state 1) are *Odontostilbe* n. sp. "h, *Odontostilbe* n. sp. "b", and *Holoshesthes hemigrammus* (Fig. 11a).

However, state 2 is present in the clade U with *Serrapinnus* species, and in the outgroup genus *Astyanax*. While state 1 is present in *Compsura*, *Macropsobrycon*, New genus n. sp. C, and the outgroup genus *Phenacogaster* (Fig. 8d). New genus n. sp. C was coded as having a small anterior lamella of sixth infraorbital by Malabarba (1994). Here, we consider the same, but one from 7 specimens examined has a somewhat lingual-like shaped sixth infraorbital.

In *Cheirodon* (Fig. 8b), *Axelrodia lindeae* (Fig. 8c), and *Saccoderma* the sixth infraorbital is formed only by the sensory tube. In *Nanocheirodon*, *Heterocheirodon,* and *Kolpotocheirodon* it can be only a sensory tube or with reduced lateral lamellas. All of them are coded as state 0. *Spintherobolus* (Fig. 8b), and the outgroup taxa *Aphyocharax*, *Charax*, *Gnathocharax*, and *Priocharax* totally lack the sixth infraorbital, coded as state 0 to this character.

Character 23 (CI = 1.00) - Laterosensory canal of the sixth infraorbital: (0) unbranched, restricted to the posterior portion of the sixth infraorbital or not as state 1 (Figs. 11a-b, d); (1)

branched, anterior branch extended along the expanded lingual-like shape anterior lamella of the sixth infraorbital (Fig. 11c).

The development of the anterior branch of the sensory canal of the sixth infraorbital has some intraspecific variation. *Odontostilbe fugitiva, O. ecuadorensis*, *Odontostilbe* n. sp. "p", and *Odontostilbe* n. sp. "e" include specimens with both conditions of the character. All specimens of *Odontostilbe* n. sp. "m" (6 specimens examined), and *O. microcephala* (6 spec. examined) (Fig. 11c), have the branched canal of the sixth infraorbital. By parsimony, it represents a unique synapomorphy to these species of *Odontostilb*e grouped in clade A8.

Among outgroup species, *Brycon pesu* and *Cynopotamus kincaidi* have a branched canal of the sixth infraorbital, but it is considered non homologous, since the canal bifurcation is at mid portion of the infraorbital, while in *Odontostilbe* species the bifurcation is at the posterior portion of the infraorbital.

Spintherobolus, and the outgroup taxa *Aphyocharax*, *Charax*, *Gnathocharax*, and *Priocharax* lack the sixth infraorbital, coded as state 0 to this character.

Opercular Apparatus

Character 24 (CI = 0.33) - Posterior border of opercle (Chs. 11, 12, 13, 14, modified of Lucena, 1998; Ch. 48, modified of Benine, 2004): (0) convex (Fig. 12a); (1) posterodorsal border nearly straight to concave and posteroventral border convex to pointed (Fig. 12b-h).

The state 1 is seen in most cheirodontines (Fig. 12b-h). Only *Kolpotocheirodon* (Fig. 12a) has the posterior border of opercle convex, also observed in the outgroup taxa *Brycon* and *Cynopotamus*.

Benine (2004: Ch. 48) referred only to the posteroventral border of opercle. His plesiomorphic less accentuated posteroventral border of opercle (State 0, *Astyanax altiparanae* in Benine, 2004: fig. 45) corresponds to our state 1. Benine’s state 2 - accentuated posteroventral border of opercle, (*Hyphessobrycon eques* in Benine, 2004: fig. 46.) is also included here in state 1. We refrain to consider the accentuated posteroventral border of opercle as a separate state because intraspecific variation was found in the sinusoidal posterior border of the opercle in cheirodontines. His state 1, a practically straight posteroventral border of opercle (Benine, 2004: fig. 44, *Moenkhausia barbouri*) described in *Oligosarcus pintoi*, *Markiana nigripinnis*, *Piabina argentea*, *Tetragonopterus argenteus*, and seven species of *Moenkhausia*, was not observed in our analysis.

Diapoma is uncoded, because it has an extremely pointed posteroventral border of the opercle. Different shapes of the posterior border of opercle were described by Lucena (1998) to the characines *Roeboides*, *Lonchogenys*, *Heterocharax*, and *Hoplocharax*. He identified a pointed projection of the posterior border of opercle as a synapomorphy of *Roeboides xenodon*, *R. affinis*, and *R. descalvadensis* (Lucena, 1998: fig. 7). *Lonchogenys*, *Heterocharax*, and *Hoplocharax* also have a similar pointed projection, but the dorsoposterior border of opercle is concave (Lucena, 1998: fig. 8).

Character 25 (CI = 0.21) - Dorsal border of opercle (Ch. 47, modified of Benine, 2004): (0) convex; (1) nearly straight or with a slight posterior elevation (Fig. 12a, c-f); (2) ascendant, posterior portion elevated, protruded (Fig. 12b, g); (3) concave, forming a posterodorsal pointed projection (Fig. 12h).

By parsimony, state 1 is considered a synapomorphy of *Carlana* + Cheirodontinae, with further character changes to state 2 in *Macropsobrycon* (Fig. 12g), *Axelrodia lindeae*, *Holoshesthes hemigrammus* (Fig. 12b), and *Odontostilbe* n. sp. "h". The concave dorsal border of opercle (Fig. 12h), state 3, is a synapomorphy of *Spintherobolus* (reversed in *S. papilliferus*), similar but non-homologous to that found in *Priocharax*. A similar depression on anterodorsal border of opercle is a synapomorphy of Hemiodontidae (Langeani, 1998: figs. 5, 7-9).

Benine stated the straight dorsal border of opercle as plesiomorphic in characiforms, based on Vari's (1979) work with the africans Citharinidae and Dischodontidae. Here, and considering the Characidae, the convex dorsal border of opercle is hypothesized as plesiomorphic, as observed in the outgroup *Brycon pesu*, *Bryconops caudomaculatus*, *Astyanax* aff. *fasciatus*, *Hemibrycon sp.*, *Diapoma speculiferum*, *Aphyocharax nattereri*, *Aphyocharacidium bolivianum*, *Cynopotamus kincaidi*, *and Charax stenopterus*..

Character 26 (CI = 0.50) - Anterodorsal portion of the subopercle: (0) protruded, forming a pointed projection (distinguishable in Fig. 12e-f); (1) convex and not protruded (Fig. 12h).

The convex, not protruded, anterodorsal portion of the subopercle is a synapomorphy of *Spintherobolus* (Fig. 12h), among cheirodontines, and independently is present in the characine *Priocharax*. In *Odontostilbe pao* the anterodorsal portion of the subopercle is not convex, but also there is no pointed projection. Considering that only one c&s specimen is available and that the pointed projection may vary somewhat intraspecifically, *O. pao* is coded as state 0.

Character 27 (CI = 0.17) - Preopercular sensory canal (Ch. 66, modified of Lucena, 1993; Ch. 26, modified of Buckup, 1998; Ch. 107, modified Zanata & Vari, 2005; Ch. 197, modified of Netto-Ferreira, 2006): (0) long, preopercular canal reaching the anterodorsal corner of opercle (Fig. 13a); (1) short, preopercular canal reaching the posterior condylar articular surface of hyomandybular (Fig. 13b); (2) without preopercle sensory canal; (3) short, preopercular canal reaching the posterior condylar articular surface of hyomandybular, and above it an autogenous preopercular canal, not contiguous with the preopercle canal.

This character was described as the preopercle bony sensory tube by Weitzman (1962). Most cheirodontines have the long preopercular tube (Fig. 13a) reaching the anterodorsal corner of opercle, similarly observed in outgroup taxa *Brycon*, *Bryconops*, *Hemibrycon*, *Diapoma*, *Carlana*, and *Aphyocharacidium*.

The shorter preopercular canal reaching the posterior condylar articular surface of hyomandybular is restricted to some cheirodontines, the clade O with *Cheirodon* (Fig. 13b) + *Nanocheirodon*, *Serrapinnus microdon*, *Axelrodia lindeae*, *Kolpotocheirodon*, *Macropsobrycon*, *Odontostilbe* n. sp. "b", and *Holoshesthes hemigrammus*, and outgroup taxa *Astyanax* and *Aphyocharax*.

A third condition is seen in *Spintherobolus* that has a total loss of laterosensory canal of preopercle, the same was independently observed in the miniature *Priocharax*. The lack of preopercle sensory canal is a derived condition of some Alestidae genera - *Clupeocharax*, *Ladigesia*, *Lepidarchus* and *Tricuspidalestes* (Zanata & Vari, 2005: Ch. 106).

Among characines, *Charax*, and *Gnathocharax* are coded as state 1, and *Phenacogaster*, and *Cynopotamus* are coded as state 3 by the presence of an autogenous preopercular canal bone (Roberts, 1969), or suprapreopercle (Menezes, 1976), not contiguous with the preopercle tube, treated independently as another character by Lucena (1993: Ch. 64), and Benine (2004: Ch. 49). Lucena (1993) found the suprapreopercle in *Charax gibbous*, but we found it absent in *Charax stenopterus*. Benine (2004) found the suprapreopercle in *Charax pauciradiatus*, and describes its presence as a synapomorphy to his Clade 14 including *Oligosarcus*, *Charax*, and *Markiana*. Regarding the extension of preopercle sensory tube in Characinae, Lucena (1993: Ch. 66) found the long preopercle sensory tube, surpassing the apex of the anterodorsal border of the opercle derived in *Phenacogaster* and part of the Clade 97 (including Clade 94 with *Acanthocharax*, *Acestrocephalus*, *Galeocharax*, *Cynopotamus*, *Charax*, *Roeboides*, and *Eucynopotamus* syn. *Roeboides*, plus separately *Hemibrycon*). However, he did not evaluate this character in his posterior phylogenetic analysis of *Roeboides* (Lucena, 1998), or Cynodontidae (Lucena & Menezes, 1998). Furthermore, Lucena (1993) also found the presence of suprapreopercle as a synapomorphy to his Clade 94, with the characine genera cited above , excepting *Phenacogaster*. The examination of the same *Phenacogaster* specimens of Lucena (1993) (MCP 16129, now *P. jancupa* Malabarba & Lucena, 1995), showed this species actually has the autogenous suprapreopercle. Similarly, the *Phenacogaster franciscoensis* used in our data matrix has the suprapreopercle, but smaller than that of *P. jancupa*. Besides having the suprapreopercle, both species have a short preopercular canal reaching the posterior condylar articular surface of hyomandybular (state 1 of Ch. 27 herein). Differently, Lucena (1993) considered the *Phenacogaster* preopercular canal long, surpassing the apex of the anterodorsal border of the opercle. This is because he did not notice the separate suprapreopercle in *Phenacogaster*. Furthermore, the difficult in distinguishing the separate suprapreopercle is remarked by him, and was not considered in his Character 64 (Lucena, 1993:52).

Buckup (1998) hypothesized a monophyletic Clade 13 in his characiforms phylogeny defined, among other characters, by a short preopercular canal, not crossing over the anterodorsal corner of opercular bone. His Clade 13 includes the characines *Cynopotamus*, *Charax*, and *Phenacogaster*, besides several other genera as *Brycon* and *Bryconops*. On the contrary, *Brycon* and *Bryconops* are coded here as state (0) having a long, preopercular canal reaching the anterodorsal corner of opercle. This is explained probably by the different species of *Brycon* and *Bryconops* used in each phylogenetic analysis; Zanata & Vari (2005) used *Brycon pesu* and *B. falcatus*, and *B. pesu* has a long preopercular canal, but not *B. falcatus*. Buckup used *Brycon guatemalensis*. Here we use *B. pesu*. This is the same that probably happened with *Bryconops*, *B. caudomaculatus* here different from *B. affinis* of Buckup (1998) or *B. alburnoides* of Zanata & Vari (2005). A large lamellar supraopercle, an exclusive feature of *Hepsetus* and *Hoplias*, constitutes another modification of the suprapreopercle in characiforms (Lucena, 1993, Ch. 67; Buckup, 1998, Ch. 27), even though the homology between this large laminar ossification with the supraopercle is questionable (Zanata & Vari, 2005).

Suspensorium

Character 28 (CI = 1.00) - Ectopterygoid teeth (Ch. 56, Lucena, 1993; Ch. 22, Buckup, 1998; Ch. 30, modified of Toledo-Piza, 2000; Ch. 41, Benine, 2004): (0) absent; (1) present (Fig. 12b).

Only one specimen of *H. hemigrammus* has two teeth just on the left side of the ectopterygoid, among three available c&s specimens, and it is an autapomorphy of the species among cheirodontines (Fig. 12b). In the Characinae, Lucena (1993) reported ectopterygoid teeth in *Charax*, *e.g. Charax gibbosus* has teeth in a row or grouped in the posterior portion of the ectopterygoid (Lucena, 1987). *Charax stenopterus*, the outgroup species of *Charax* in this study, does not have ectopterygoid teeth. Despite *Charax* is putatively monophyletic (Lucena, 1987; Lucena, 1998), the relationships among its species remain unclear. Other species reported to have ectopterygoid teeth, among a total of 16 species considered valid in *Charax* by Lucena & Menezes (2003), are *C. condei, C. hemigrammus, C. rupununi*, *C. metae,* and *C. tectifer* (Lucena, 1987; Lucena, 1989).

Presence of ectopterygoid teeth has been known as variable in characoids, appearing in highly specialized genera as *Acestrorhynchus, Boulengerella* (Roberts, 1969), or variable within a given species, appearing in some specimens or just in one of the ectopterygoids (as noted for *Nannostomus eques* by Weitzman, 1964). However, the taxa of the Clade 20 of Buckup (1998) comprising *Boulengerella, Ctenolucius, Hepsetus, Lebiasina, Pyrrhulina, Nannostomus*, *Hoplias*, and *Acestrorhynchus,* share the presence of ectopterygoid teeth, independently acquired in the Crenuchidae.

Presence of a narrow laminar extension from dorsolateral border of the ectopterygoid bearing numerous teeth (Lucena & Menezes, 1998: Ch. 25, fig. 3) is another character different from the discussed above, and unique to the Cynodontinae.

Character 29 (CI = 0.40) - Mesopterygoid teeth (Ch. 55, modified of Lucena, 1993; Ch. 23, modified of Buckup, 1998; Ch. 31, modified of Lucena, 1998; Ch. 24, modified of Lucena & Menezes, 1998;Ch. 29, modified of Toledo-Piza, 2000;): (0) absent; (1) present, teeth grouped on median portion of the mesopterygoid (Fig. 14a-b, e-f); (2) present, conical teeth in two separate groups on median portion of the mesopterygoid (Fig. 14c-d).

A group of teeth on mid portion of the mesopterygoid is shared by *Odontostilbe* n. sp. "p" (conical to tricuspid teeth, Fig. 14a-b), *Odontostilbe* n. sp. "e", and *Acinocheirodon melanogramma*. Two groups of such teeth is uniquely found in *Odontostilbe* n. sp. "b" (Fig. 14c-d). Only one juvenile of *Holoshesthes pequira,* 21.4 mm SL (MZUSP 21067) has the group of teeth on mid portion of the mesopterygoid (Fig. 14e-f). Among remaining examined specimens, six c&s juveniles and eight c&s adults (including one adult, 31.0 mm SL, also from the same lot of the juvenile bearing teeth - MZUSP 21067) do not have these teeth. Besides this absence in most of the examined specimens, *H. pequira* was coded as state 1.

Lucena (1993) found the presence of mesopterygoid teeth supports a clade formed by *Rhaphiodon*, *Cynodon* and *Acestrorhynchus*, being independently acquired in *Hoplerythrinus*.

In a further study among *Roeboides* species (Lucena, 1998), the presence of mesopterygoid teeth supported the Subclade A, composed of *Roeboides* sp. A, latter described as *Roeboides dispar* Lucena, 2001.

In Cynodontinae and Acestrorhynchidae the character was found to be ambiguous, evolving independently in *Acestrorhynchus* and Cynodontinae or appearing in the ancestor of the *Acestrorhynchus* + Cynodontinae clade with reversal a in the nearly related Roestinae (Lucena & Menezes , 1998). Among other characiforms, two species of *Boulengerella* also have mesopterygoid teeth (Vari, 1995).

Character 30 (CI = 0.13) - Shape of the palatine (Ch. 38, modified of Serra, 2003): (0) nearly rectangular, irregular, posterior portion somewhat narrow, or not as states 1 to 4 (Fig. 12b, d); (1) regular rectangular, well developed (Fig. 12c); (2) slender rectangular, uniformly narrower than state 1 in longitudinal axis (Fig. 12a); (3) spherical (Fig. 12f); (4) squarish or ovoid (Fig. 12e).

The regular rectangular palatine is a synapomorphy for the new tribe Odontostibini (state 1 (Fig. 12c), also observed in *Spintherobolus ankoseion*, with further changes to a squarish or ovoid palatine (state 4) in the clade A6 with *Prodontocharax* + *Amblystilbe* (Fig. 12d), reversed to state 0 in the *Holoshesthes* clade A12 (Fig. 12b, d), and in *Odontostilbe* n. sp. "e".

By parsimony, the slender rectangular palatine, state2 appears independently twice in clade N, in *Kolpotocheirodon* and in *Macropsobrycon* (Fig. 12g), but not in *Acinocheirodon,* state 0. State 2 is also a synapomorphy for the clade R with the two species of *Heterocheirodon* (although it is not too slender as that of *Kolpotocheirodon*), and as autapomorphies for *Axelrodia lindeae* and the outgroup *Bryconops.*

The spherical palatine is a synapomorphy of clade A3 *Pseudocheirodon* (state 3) (Fig. 12f). The New genus n. sp. C has a rectangular palatine smaller than that of *Odontostilbe*, but considered as state 1.

Outgroup taxa with squared palatine are *Hemibrycon* sp., *Diapoma speculiferum*, and *Aphyocharax*. Remarkably, *Hemibrycon* sp. and *Diapoma* have a conspicuous central fenestra on palatine. *Priocharax* is coded as state 0, but has a totally cartilaginous palatine.

Serra (2003) distinguished in her phylogenetic analysis of *Hasemania* just two shapes of the palatine: nearly squared or nearly rectangular, in which most *Hasemania* species share the nearly rectangular palatine. Examination of *H. bilineata* having a nearly rectangular palatine by Serra (2003) revealed it has an irregular palatine that would be coded here as state 0.

Character 31 (CI = 1.00) - Metapterygoid-quadrate fenestra (Ch. 61, Lucena, 1993; Ch. 24, modified of Buckup, 1998; Ch. 124, Netto-Ferreira, 2006): (0) present; (1) absent, quadrate dorsally contacting the mesopterygoid and posteriorly contacting the metapterygoid.

A large quadrate and a nearly rectangular metapterygoid are found in all *Spintherobolus* species obliterating the metapterygoid-quadrate fenestra. Absence of the metapterygoid-quadrate fenestra is known in *Lebiasina*, *Pyrrhulina* and *Nannostomus* (Weitzman, 1964; Buckup, 1998). However, in these Lebiasinidae genera the obliteration of the fenestra is independently caused by different modifications of associated bones. The metapterygoid is elongate in *Nannostomus harrisoni* (Weitzman, 1964: fig. 7) compared to a rectangular metapterygoid in *Spintherobolus* (Fig. 12h).

Buckup (1998: Ch. 24) admitted two states for this fenestra, state 0, well developed, usually circular or oval in shape, and state 1, absent or greatly reduced.

Premaxilla

Character 32 (CI = 0.33) - Ascending process of the premaxilla (Ch. 35, Lucena, 1993; Ch. 31, Buckup, 1998; Ch. 39, Zanata, 2000; Ch. 54, Zanata & Vari, 2005; Ch. 78, Netto-Ferreira, 2006): (0) ascending process projected, pointed (Fig. 15a-b); (1) ascending process absent or with small point on dorsal border of the premaxilla (Fig. 15c-d).

In the Cheirodontinae, the absence or nearly absence of the ascending process of the maxilla is parsimoniously accepted as independently derived in the clade A3 with *Pseudocheirodon* species, in the clade A5 with *Lobodeuterodon* + (*Prodontocharax* + *Amblystilbe*), and independently in *Odontostilbe parecis*. This short ascending process of the premaxilla is known in basal characiform groups Distichodontidae and Citharinidae (Vari, 1979), and also in many other lineages *Boulengerella*, *Ctenolucius*, *Crenuchus*, *Characidium*, *Nannostomus*, *Pyrrhulina*, *Parodon*, *Prochilodus* and *Steindachnerina* (Buckup, 1998).

Character 33 (CI = 1.00) - Shape of the premaxilla: (0) triangular, or nearly triangular (Figs. a-b, d) (1) cap-like shape, with an well-arched rounded dorsal border (Fig. 15c).

The usual shape of the premaxilla in cheirodontines is the plesiomorphic triangular premaxilla. *Prodontocharax* and *Amblystilbe* (Fig. 15c) (state 1) share a derived premaxilla, rounded dorsally. In *Lobodeuterodon* the dorsal border of premaxilla is somewhat rounded, but the premaxilla is not as deep as that of *Prodontocharax*, and *Amblystilbe* (Fig. 15c)

Character 34 (CI = 0.50) - Laminas of the medial border of the premaxilla that articulate with the mesethmoid: (0) almost absent, not pronounced, forming a shallow oval articular fossa along dorsomedial portion of the premaxilla (Fig. 16a); (1) slightly pronounced, forming a V-shaped bifurcation, the posteromedial lamina oblique to anteromedial lamina (Fig. 16b); (2) slightly pronounced, the posteromedial lamina at the coronal plane and perpendicular to the anteromedial lamina (Fig. 16c).

Zanata & Vari (2005: Ch. 56, state 0) referred the presence of a shallow articular fossa along dorsomedial portion of the premaxilla articulating with the process of the mesethmoid as plesiomorphic, contrasting with an apomorphic deep articular fossa with a second more lateral fossa unique to *Hydrocynus*. They coded *Brycon pesu* and *Cheirodon interruptus* as state 0. Here, almost all cheirodontines, including *C. interruptus*, are distinguished by an articular fossa formed by slightly pronounced laminas forming a V-shaped bifurcation (state 1, Fig. 16b), differently from *B. pesu* and most outgroup taxa (state 0, Fig. 16a). This is a new synapomorphy to the Cheirodontinae, but that is also present in the outgroup genera *Charax* and *Phenacogaster*. Among cheirodontines, two species of *Pseudocheirodon* forming the clade A3 share the uniquely derived laminas slightly pronounced with the posteromedial lamina disposed at the coronal plane and perpendicular to the anteromedial lamina laminas (state 2, Fig. 16c). *Heterocheirodon* has a different articulation between contralateral premaxillae and the mesethmoid (Fig. 4d, Ch. 4), but the laminas of the anterior border of the premaxilla are similar to those of most cheirodontines.

Two genera of cheirodontines are uncoded for the character. *Macropsobrycon uruguayanae* totally lack the anteromedial laminas of the premaxilla, having an extended contralateral contact between premaxillae without interdigitations, and forming a different articulation with the mesethmoid (Fig. 4e, former Ch. 5.). In *Spintherobolus*, the laminas of the premaxillae are also indistinct and with extended contralateral contact between the premaxillae, but there is an articulation between premaxillae and the thick small medial process, more developed ventrally, on anterior tip of mesethmoid (Fig. 4f, former Ch. 3). *Priocharax* has an extreme reduction of the contact area between contralateral premaxillae, without visible laminas, and is uncoded to this character.

The presence or absence of interdigitations between contralateral premaxillae (Zanata & Vari, 2005: Ch. 55) were not considered in this study. The lack of these interdigitations in all cheirodontines and most outgroup taxa examined (except *Brycon*) seems to be related to development of the laminas of the medial border of the premaxilla to articulate with the mesethmoid. Zanata (2000) commented the presence or absence of the interdigitations could be related to the level of separation between the premaxillae by the mesethmoid, being present when the mesethmoid is short anteriorly, partially or not placed between premaxillae. However, the cheirodontinae with short anterior projection of the mesethmoid do not have these interdigitations. Zanata (2000) concluded the absence of interdigitations in cheirodontines is then not related to absence of the mesethmoid between premaxilla.

Character 35 (CI = 0.33) - Number and arrangement of the tooth rows of the premaxillae (Ch. 38, Lucena, 1993; Ch. 32, Buckup, 1998; Ch. 55, Malabarba, 1998; Ch. 42. modified of Zanata, 2000; Ch. 27, modified of Benine, 2004; Ch. 57, modified of Zanata & Vari, 2005; Ch. 83, modified of Netto-Ferreira, 2006): (0) two tooth rows or different from state 1; (1) a single regular row in the premaxilla with teeth perfectly aligned and similar in shape and cusp number (Fig. 15a-d).

This was a putative synapomorphy of the Cheirodontinae extensively discussed by Malabarba (1998), and before considered the basic character that defined the Cheirodontinae *sensu* Eigenmann (1915) and *sensu* Géry (1977). Here, by parsimony the single regular row in the premaxilla with teeth perfectly aligned and similar in shape and cusp number is shared in the clade J by *Aphyocharax* + (*Carlana* + Cheirodontinae), and is present independently in *Priocharax*, and *Aphyocharacidium*.

The Rhoadsiinae have typically a single series in young specimens and two premaxillary tooth series in adults. *Carlana eigenmanni* is an exception, with one tooth series during all life, and coded as state 1 in the present analysis.

At present, three tooth rows were coded as state 0, only appearing in *Brycon* among all taxa examined, although it is recognized as a derived condition to most *Brycon*, independently acquired in *Chalceus* and *Triportheus* (Zanata, 2000).

Character 36 (CI = 1.00) - Size of the medial tooth in the single tooth row of the premaxilla (Ch. 40, modified of Lucena, 1993; Ch. 84, modified of Netto-Ferreira, 2006): (0) same size of following teeth (Figs. 15a-b, d; 17a); (1) markedly larger than the following posterior teeth (Fig. 17b-f).

This is a unique synapomorphy to the clade A14 comprising *Holoshesthes* n. sp. "p" + (*Holoshesthes*. n. sp. "k" + (*Holoshesthes geayi* + (*H. hemigrammus* + *Holoshesthes* n. sp. "b"))) (Fig. 17b-f), excepting *H. pequira* (Fig. 17a). This character was initially included in the analysis of Malabarba (1994: Ch. 64), but excluded of his published Cheirodontinae phylogeny (Malabarba, 1998).

The presence of one markedly larger medial tooth on the premaxilla is seen in many predatory characid taxa, as *Hoplias*, *Acestrorhynchus*, *Oligosarcus*, (Roberts, 1969: figs. 3, 5; Menezes, 1969), Cynodontidae (Lucena & Menezes, 1998: fig. 5), and Cynopotaminae (Menezes, 1976: figs. 2-4) (currently in Characinae), but this is not the case in the cheirodontines that are mostly herbivorous. *Cynopotamus kincaidi* and *Charax stenopterus* were examined and have such medial teeth, but these species also have an inner tooth row, being uncoded for the present character as the homology between the outer row of these species and the unique row of Cheirodontinae is unclear. The same uncertain homology between tooth rows in the premaxilla is considered to other outgroup taxa with two or even three tooth rows in the premaxilla.

Lucena (1993: Ch. 40) refers to the medial distinct teeth in the premaxilla, but he defined an overall premaxillary teeth arrangement, in which the posteriormost tooth is also larger than the intermediate ones. This is a synapomorphy to his Clade 94 including most Characinae taxa (*Acanthocharax*, *Galeocharax*, *Cynopotamus*, *Charax* and *Roeboides*), and independently apomorphic to Cynodontidae (*Cynodon*, *Rhaphiodon*). In his more recent phylogeny of *Roeboides*, Lucena (1998: Ch. 21) presents a modified description of the character, and the derived state 1 is the presence of two rows of premaxillary teeth, the outer row with the medial and the posteriormost teeth larger than the intermediate ones, plus an inner row with two conical teeth, which is found in *Acestrocephalus*, *Galeocharax*, and *Cynopotamus* (Menezes, 1976: figs. 8-10).

Character 37 (CI = 1.00) - Size of 1-3 posteriormost teeth in the single tooth row of the premaxilla: (0) posterior teeth of similar size or gradually smaller of the preceding teeth (Fig. 15a, b-d); (1) 1-3 posteriormost teeth larger than the preceding teeth (Fig. 17d).

This is an autapomorphy of *Holoshesthes geayi*, among cheirodontines (Fig. 17d). As in the former Ch. 37, the questionable homology of tooth rows of the premaxilla among taxa is considered and most outgroup taxa are uncoded to the present character.

Character 38 (CI = 0.50) - Position of the main cusps of the posteriormost teeth in the single tooth row of the premaxilla: (0) cusps almost perpendicular to the ventral border of premaxilla (Fig. 15a, b-d); (1) cusps slightly oblique to the ventral border of the premaxilla, curved posteriorly (Fig. 17d).

This is a unique synapomorphy of the clade A13 containing *Holoshesthes* n. sp. "p" + (*Holoshesthes*. n. sp. "k" + (*Holoshesthes geayi* + (*H. hemigrammus* + *Holoshesthes* n. sp.

"b"))), excepting *H. pequira*. In *Holoshesthes* n. sp. "p", some specimens did not have the posteriorly curved main cusp, but others have (Fig. 17b, see separate tooth of another specimen). We found impossible to code this character in taxa with more than one tooth row on premaxilla.

Character 39 (CI = 0.40) - Shape and size of the cusps in the single tooth row of the premaxilla: (0) central cusp notably larger than lateral ones (Fig. 17b-f); (1) central cusp slightly larger than lateral ones, usually three mid cusps somewhat larger than lateral ones (Figs. 17a, 15a-d); (2) all cusps similar in form.

The central cusp remarkably large, pointed (state 0), is another synapomorphy of the clade A13 containing *Holoshesthes* n. sp. "p" + (*Holoshesthes*. n. sp. "k" + (*Holoshesthes geayi* + (*H. hemigrammus* + *Holoshesthes* n. sp. "b"))), excepting *H. pequira*, and independently present in the Compsurini *Acinocheirodon.* While the premaxillary teeth cusps similar in shape and size, state 2, is a synapomorphy to the clade A3 formed by the two species of *Pseudocheirodon*, but that is also present in the Compsurini *Kolpotocheirodon* and in the Cheirodontini *Serrapinnus micropterus*. This character was initially included in the analysis of Malabarba (1994: Ch. 69), but excluded of his published Cheirodontinae phylogeny (Malabarba, 1998).

In *Amblystilbe* (Fig. 15c) and *Prodontocharax* the tricuspid teeth are coded as state 1, with the mid cusp slightly larger than lateral ones. All species with unicuspid teeth on the premaxilla are coded as inapplicable to the character, but *Holoshesthes* n. sp. "b" that sometimes has a smaller lateral cusp to the larger conic one (Fig. 17f) is coded as state 0. The outgroup taxa with more than one tooth row in premaxilla are not coded to the character, due to the possible non homology of comparable tooth rows and the variation in shape and size of tooth cusps among different rows.

Character 40 (CI = 0.16) - Tooth cusp number of the first to third medial teeth in the single tooth row of the premaxilla (Ch. 72 modified of Malabarba, 1998): (0) usually conical tooth or conical tooth with a small lateral cusp (Fig. 17f); (1) 3-6 cusps, usually 3-5; (2) 5-7 cusps, usually 5-6 (Fig. 17b-e); (3) 7-13 cusps, usually 9-11 (Fig. 15a-b,d).

The higher number of cusps, 8-13 cusps, usually 9-11 cusps in the premaxillary teeth, state 3, is most parsimoniously considered a synapomorphy for *Carlana* + Cheirodontinae with further several changes to states 0, 1 or 2 among included clades. Among the Odontostilbini, state 1 is apomorphic to the clade A6 formed by *Prodontocharax* + *Amblystilbe*; and the state

2 is apomorphic to the clade A11 including *Odontostilbe* n. sp. "b" and all species of *Holoshesthes*, but modified to state 1 in the clade A14 and reversed to state 0 in *Holoshesthes* n. sp. "b". State 2 is also present in *Odontostilbe* n. sp. "p", in clade A10 of the Odontostilbini. Among the Cheirodontini, state 2 is a synapomorphy to the clade P with the two species of *Cheirodon*, and to the clade T that includes *Serrapinnus micropterus* presenting state 3, *S. microdon* coded as state1, and the clade W with *Axelrodia lindeae* + *Spintherobolus* species presenting state 0. This means that in the clade T, the clade W (*Axelrodia lindeae* + *Spintherobolus* species) shows a tendency to reduction of the cusp number in the premaxillary row. This tendency of reduction is similar among the Odontostilbini in the clade A12 in which the basal *H. pequira* and *Holoshesthes* n. sp. "p" have 5-7 cusps, usually 5-6 (Fig. 17a), and the remaining *Holoshesthes* species have 3-6 cusps, usually 3-5 cusps in the premaxillary teeth (Fig. 17b-e), and then *Holoshesthes* n. sp. "b" has the reduced conical tooth or conical tooth with a small lateral cusp (Fig. 17f).

State 1, 3-6 cusps, usually 3-5 cusps in the premaxillary teeth, is by parsimony assumed to support the broad clade F which includes several outgroup taxa coded as uninformed because the possible non-homology between the unique premaxillary tooth row of the cheirodontines and the two premaxillary tooth rows of them. These outgroup taxa with two tooth rows in the premaxilla include *Hemibrycon*, *Diapoma*, *Phenacogaster*, and *Astyanax*. Actually, all of these genera have 3-6 cusps, usually 3-5 cusps in the outer premaxillary tooth row, which is also present in the examined *Brycon* and *Bryconops*.

In *Aphyocharax* conical or tricuspid premaxillary teeth are present, but the species is coded as state 1. Overall tooth cusp morphology, not only on the premaxilla, but also on maxilla and dentary, is treated by Buckup (1998: Ch. 72), and Zanata (2000: Ch. 36).

Character 41 (CI = 0.18) - Number of teeth in the single tooth row of the premaxilla: (0) more than 8, usually more than 10 (Fig. 17e); (1) usually 6-8 teeth (Fig. 17a-f), (2) usually 4 teeth; (3) usually 5 teeth (Fig. 15a-b, d).

By parsimony state 3 is a synapomorphy to the clade k formed by Carlana + Cheirodontinae, with most of the cheirodontines presenting usually 5 premaxillary teeth (Fig. 15a-b, d).. The higher number of teeth in a unique tooth row in the premaxilla is only present in *Holoshesthes hemigrammus* (Fig. 17e), and *Axelrodia lindeae*, and in the outgroup *Aphyocharacidium*, *Aphyocharax*, and *Priocharax*.

Among Odontostilbini, state 1 is a synapomorphy of the clade A12 containing the six species of *Holoshesthes* (Fig. 17a-f), reversed to state 0 in *H. hemigrammus* (Fig. 17e), and to the clade A6 with *Amblystilbe* + *Prodontocharax* (Fig. 15c, about four teeth lacking). However, state 1 is present in other cheirodontines lineages, in Cheirodontini taxa *Serrapinnus heterodon*, *Serrapinnus microdon*, *Spintherobolus*, and in Compsurini, the clade N *Acinocheirodon* + *Macropsobrycon*.

State 2 is unique to the clade R with the two species of *Heterocheirodon*. A new synapomorphy to *Heterocheirodon*, not reported before by Malabarba (1998) and Bertaco & Malabarba (1999).

Character 42 (CI = 0.20) - Space between teeth in the single tooth row of the premaxilla: (0) teeth juxtaposed, practically without space between teeth (Fig. 17d, f); (1) teeth spaced, space between teeth nearly equal to one tooth (Fig. 15c).

State 1 is a synapomorphy to *Prodontocharax* + *Amblystilbe*, but independently appearing in *Serrapinnus microdon*, *Holoshesthes* n. sp. "b" (Fig. 17f), and *Macropsobrycon*. *Holoshesthes geayi* has a somewhat spaced maxillary teeth coded as state 1 (Fig. 17d). This character was initially included in the analysis of Malabarba (1994: Ch. 65), but excluded of his published Cheirodontinae phylogeny (Malabarba, 1998).

Character 43 (CI = 0.14) - Overlapping teeth in the single tooth row of the premaxilla (Ch. 61, modified of Malabarba, 1994): (0) absent (Figs. 15c, 17b-f); (1) present, 1-4 tooth cusps overlapping between adjacent teeth, usually between posteriormost teeth or in all of teeth (Figs. 15a-b, d, 17a).

This character was initially included in the analysis of Malabarba (1994: Ch. 61), considering state 1 as lateral cusps extensively overlapping median cusps of adjacent teeth (up to 3 cusps), but it is excluded of his published Cheirodontinae phylogeny (Malabarba, 1998). Here, overlapping between premaxillary teeth is considered regardless the number of cusps involved even the case when only one cusp is overlapping another cusp of the adjacent tooth.

State 1 is a synapomorphy to the clade k with Carlana + Cheirodontinae, with reversions to state 0 and reacquisions. Among Odontostilbini, the reversions occur in the clade A6 with *Prodontocharax* + *Amblystilbe*, and in the clade A11 with *Odontostilbe* n. sp. "b" + *Holoshesthes* (clade A12), except in *H. pequira* that reacquires state 1. Other reversions to state 0 are found in cheirodontins *Nanocheirodon*, *Serrapinnus*, *Axelrodia lindeae*, *Spintherobolus*, and the compsurines *Acinocheirodon*, *Compsura*, and *Macropsobrycon*.

Maxilla

Character 44 (CI = 0.12) - Extent of anterodorsal ascending rod-like process of the maxilla, articulated to the premaxilla (Ch. 91, modified of Netto-Ferreira, 2006): (0) short, around 4-5 times in the total length of the maxilla (Fig. 18d-h); (1) long, around 3.5 times or less in the total length of the maxilla; (2) very short, more than 6 times in the total length of the maxilla (Fig. 18a-c).

Relatively long ascending rod-like process of the maxilla is only seen in the outgroup *Bryconops*, *Astyanax*, *Aphyocharacidium*, and *Hemibrycon*. Thus, by parsimony the short of anterodorsal ascending rod-like process of the maxilla, state 0 is a synapomorphy to the clade J including *Aphyocharax* + (*Carlana* + Cheirodontinae), but also is present in *Diapoma*. The very short process, state 2, is apomorphic to clade A15 formed by *Holoshesthes geayi* + (*H. hemigrammus* + *Holoshesthes n*. sp. "b"). However, this condition of the state 2 is present in other cheirodontines, *Macropsobrycon*, *Heterocheirodon*, and *Axelrodia lindeae*, besides present in the outgroup clade E (*Charax* + *Cynopotamus* + *Priocharax*), in *Phenacogaster* and *Gnathocharax*. Noteworthy these outgroup taxa belongs to the putative Characinae (Lucena, 1998).

Gnathocharax has an ascending process not in a rod-like shape, but wider and with the anterior tip expanded laterally which contacts a cartilage anterior to the palatine, coded as state 2. *Spintherobolus* n. sp. has a similar lateral expanded anterior tip of the rod-like ascending process. *Spintherobolus* species have the ascending rod-like process of the maxilla around 5 times in the total length of the maxilla, coded as state 0, because it is not too short as seen in state 2. In *Lobodeuterodon* the ascending rod-like process of the maxilla is short, around 4-5 times in the total length of the maxilla, but in Fig. 18e it looks like shorter because the angle of the piece in the micrograph.

Netto-Ferreira (2006) described two states for this character - the ascending process of the maxilla reaching to the ascending process of the premaxilla or not and described most Lebiasinidae as having the short ascending process.

Character 45 (CI = 0.08) - Flange on anterodorsal portion of the maxilla, posterior to rod-like ascending process of the maxilla: (0) present (Fig. 18d-f); (1) absent (Fig. 18a-c, e-h).

This flange is a synapomorphy to the Odontostilbini, being present in 10 species, reversed in the clade A9 formed by *Odontostilbe microcephala* + (*Odontostilbe* n. sp. "e" + *Odontostilbe* n. sp. "p"), in the clade A2 with *Odontostilbe pao* + *Pseudocheirodon*, and in *O. nareuda*, and *O. pulchra* (Fig. 18g). Among Compsurini, *Saccoderma* is the only species with the flange, and among Cheirodontini, it is only present in *Nanocheirodon* and *Serrapinnus micropterus*. Similar flange on anterodorsal portion of the maxilla is indicated as a synapomorphy of *Attonitus ephimerus* and *A. irisae* by Vari & Ortega (2000: fig. 1).

Amblystilbe and *Prodontocharax* have an elevated mid portion of the maxilla, not equivalent to the dorsal flange referred here, and coded as state 1. *Spintherobolus* species have a different dorsal border of the maxilla, in which the mid portion is also elevated (even forming a spine-like projection in one specimen of *Spintherobolus* n. sp., but followed by a slight concave depression, also coded as state 1.

Character 46 (CI = 0.16) - Longitudinal groove just below dorsolateral border of the maxilla: (0) absent (Fig. 18c-h); (1) present (Fig. 18a-b).

This is a synapomorphy of the clade A12 formed by *Holoshesthes pequira*, *Holoshesthes* n. sp. "p", *Holoshesthes* n. sp. "p", *H. geayi*, and *Holoshesthes* n. sp. "b", but reversed in *H. hemigrammus*, and independently appearing in cheirodontines *Acinocheirodon*, *Serrapinnus heterodon*, and *Serrapinnus microdon*. *Macropsobrycon* has a longitudinal groove along the maxilla, but not well-marked, being coded as state 0. Among outgroup taxa, *Astyanax*, *Hemibrycon*, *Aphyocharacidium*, *Diapoma*, and *Phenacogaster* have this longitudinal groove along the maxilla. *Gnathocharax* has a longitudinal groove only on the posterior portion of the maxilla.

Character 47 (CI = 1.00) - Protruding spine-like projection on the ventral border of the maxilla, just ahead anteriormost teeth: (0) absent; (1) present.

This is unique in the clade A3 with the two species of *Pseudocheirodon*.

Character 48 (CI = 1.00) - Shape of the posterior portion of the maxilla (Ch. 6, modified of Malabarba, 1998; Ch. 3, modified of Lucena & Lucena, 2002): (0) somewhat spatula-like shaped, short or elongate, with a slightly deep mid region and then narrowing to the posterior tip, or different from state 1 (Fig. 18a-g); (1) somewhat triangular, short, median portion deeper and gradually narrowing to the posterior tip (Fig. 18h).

The state 1 was found uniquely derived in *Pseudocheirodon* by Malabarba (1998), and the character described as “posterior tip of maxilla”, enlarged or narrow. Here, this condition is also observed in *Odontostilbe pao*.

Brycon, *Hemibrycon*, *Phenacogaster, Carlana, Aphyocharax* are coded as state 0, but they have numerous teeth on the maxilla with a reduced edentulous posterior portion, a different condition from that observed in the Cheirodontinae. *Macropsobrycon uruguayanae* and *Holoshesthes* n. sp. "b" lack teeth on the maxilla, but have the spatula-like posterior portion of the maxilla, state 0. Similarly, the examined *Bryconops caudomaculatus* does not have maxillary teeth, but other species of the genus have maxillary teeth, such *B. magoi* of Chernoff & Machado-Allison (2005: fig. 5) and the spatula-like posterior portion of the maxilla.

A short edentulous posterior portion of the maxilla has been hypothesized as a synapomorphy of *Deuterodon* (Lucena & Lucena, 2002: Ch. 3, figs. 1-3). They interpret this similarity, and other similar modifications in maxillary shape between *Pseudocheirodon* (*P. arnoldi*, and *P. terrabae*) and *Deuterodon* as independent acquisitions. Actually, a somewhat triangular shape of edentulous posterior portion of the maxilla is similar between *Pseudocheirodon* and *Deuterodon,* but the portion with teeth of the maxilla is not as deep as that of *Deuterodon*, defined in Ch. 1 of Lucena & Lucena (2002). *Deuterodon* also do not share other modifications in the maxilla found in *Pseudocheirodon*, as the torsion of the maxilla described in Ch. 52.

Character 49 (CI = 1.00) - Shape of the maxilla (Ch. 7, Malabarba, 1998; Ch. 2, Lucena & Lucena, 2002): (0) maxilla nearly straight, with tooth-bearing portion angled ventrally relative to the premaxillary tooth-bearing portion; (1) maxilla curved, with tooth-bearing portion continuous with premaxillary tooth-bearing portion and angled relative to edentulous portion of the maxilla.

As previously commented in Ch. 48, this is hypothesized to appear homoplastically only in *Pseudocheirodon* and *Deuterodon*, an *incertae sedis* genus of the Characidae (Lucena & Lucena, 2002: Ch. 2, fig. 3.).

Character 50 (CI = 0.14) - Relative size of the posterior edentulous portion of the maxilla (Ch. 3, modified of Lucena & Lucena, 2002, Ch. 51, modified of Serra, 2003): (0) short, smaller than the anterior tooth bearing portion of the maxilla; (1) with approximately the same length of the anterior tooth bearing portion of the maxilla (Fig. 18d-h); (2) extended, longer than the anterior tooth bearing portion of the maxilla (Fig. 18a-c).

State 1 is new uniquely derived feature for the Cheirodontinae. In the Odontostilbini it occurs in all species of *Odontostilbe* and in *Lobodeuterodon* (Fig. 18d-h). Exceptions to that condition are found in the clade A12 formed by all species of *Holoshesthes* presenting state 2, a long posterior edentulous portion of the maxilla (Fig. 18a-c), and in the clade A1 where independently *Prodontocharax* and *Pseudocheirodon* have state 0, a short posterior edentulous portion of the maxilla. This latter condition is similar in the short maxilla of *Deuterodon* (Lucena & Lucena, 2002: figs. 1-3), and his Ch. 3, the length of posterior edentulous portion at maximum twice in length of the tooth bearing portion of maxilla, is equivalent to the present state 1.

State 2 occurs in some Cheirodontini, the *Cheirodon, Heterocheirodon yatai, Serrapinnus heterodon,* and *S. microdon,* and in the Compsurini *Acinocheirodon*. *Macropsobrycon* and the outgroup genus *Bryconops* lacks maxillary teeth, being uncoded for the character, though other *Bryconops* species have maxillary teeth (Chernoff, 2005).

Another characters correlated to the size of posterior edentulous portion of maxilla are those considering maxillary teeth distribution (Lucena, 1993: Ch. 44; Zanata, 2000: Ch. 53; Netto-Ferreira, 2006: Ch. 93). In these characters those authors coded as having teeth along almost all extent of maxilla the same species here coded as having a short posterior edentulous portion of maxilla.

Character 51 (CI = 0.25) **-** Posterior portion of the maxilla: (0) ventral margin of posterior portion of the maxilla not extended ventrally beyond maxillary tooth bases (Fig. 19); (1) ventral margin of the posterior portion of the maxilla extended ventrally beyond maxillary tooth tips (Fig. 18a-h).

The deeper edentulous posterior portion of the maxilla is a new synapomorphy of the Cheirodontinae, reversed to the plesiomorphic narrow maxilla in the clade W with *Axelrodia lindeae* + *Spintherobolus*.

Macropsobrycon lacks maxillary teeth, but the overall shape of the posterior portion of the maxilla is similar to the cheirodontines then coded as state 1. *Bryconops caudomaculatus* does not have maxillary teeth, but other species of the genus as *B. colaroja* have maxillary teeth (Chernoff & Machado-Allison, 1999: fig. 2a, c), corresponding to state 0.

Character 52 [CI = 0.50] - Posterior edentulous lamina of the maxilla: (0) flat and plane; (1) posteroventral portion of the posterior edentulous lamina of the maxilla turned medially, being settled in a different plane regarding anterior portion of the maxilla.

A torsion of the posterior edentulous lamina of the maxilla is a uniquely derived character supporting the clade A1 in Odontostilbini. This clade is formed by a polytomy with *Odontostilbe splendida,* the clade A2 (*O. pao* + *Pseudocheirodon*), and the clade A4

(*Odontostilbe* n. sp. "h" + (*Lobodeuterodon* + (*Prodontocharax* + *Amblystilbe*). However, a reversion occurs in *Amblystilbe*.

Character 53 (CI = 0.25) - Length of the maxilla (Ch. 42, modified of Lucena, 1993; Ch. 34, modified of Buckup, 1998; Ch. 8, modified of Malabarba, 1998; Ch. 45, modified of Zanata, 2000; Ch. 54 modified of Serra, 2003; Ch. 72, modified of Zanata & Vari, 2005; Ch. 87, modified of Netto-Ferreira, 2006): (0) long, almost reaching the posterior border of lower jaw, contacting the posteroventral portion of the angulo-articular, below anterodorsal extension of the angulo-articular, and beyond vertical through the mid-distal portion of the infraorbital 2; (1) short, terminating at mid portion of lower jaw, contacting the anterodorsal extension of the angulo-articular or at mid portion of the angulo-articular, and reaching beyond the vertical through the contact area between the infraorbitals 1 and 2 or up to the mid portion of the infraorbital 2.

The long maxilla is plesiomorphic in the analysis, present in most of the outgroup taxa. Almost all cheirodontines have the maxilla short, except *Holoshesthes geayi* and *H. hemigrammus* that have a relative long maxilla that practically reaches the posterior border of the lower jaw, slightly beyond mid portion of the infraorbital 2 (coded as state 0).

State 1 partially corresponds to Ch. 8 of Malabarba (1998) in which the maxilla should be reaching the area of contact between the infraorbitals 1 and 2, an autapomorphy of *Prodontocharax melanotus*. Here, the examination of additional specimens of *P. melanotus* revealed the posterior tip of the maxilla is posterior to the contact area between the infraorbitals 1 and 2. The perfect occlusion of mouth is needed to check the character. Anyway, overall observation of the character in cheirodontines showed intraspecific variation, and the posterior tip of the maxilla reaches beyond vertical through the contact area between the infraorbitals 1 and 2 or up to mid portion of the infraorbital 2.

Zanata (2000: Ch. 45) described cheirodontines as having a short maxilla, at maximum reaching the vertical at anterior border of eye orbit. She and Lucena (1993) recognized another condition to the present character, not used here, and equivalent to the split of the present long maxilla in relative long maxilla and the truly long maxilla. Both authors situated the length of maxilla relative to eye orbit, differently as stated here. Therefore, different results are obtained here, with *Charax* having truly long maxilla, and *Brycon* having a relatively long maxilla, both under the same state 0.

Character 54 (CI = 0.21) - Number of teeth in the maxilla (Chs. 44, 45, modified of Lucena, 1993; Ch. 52, modified of Zanata, 2000; Ch. 50, modified of Serra, 2003; Ch. 78, modified of Zanata & Vari, 2005; Ch. 92, modified of Netto-Ferreira, 2006): (0) numerous, more than seven; (1) usually five or six (Fig. 18c); (2) usually two or three, up to four (Fig. 18d-h); (3) usually one or none (Fig. 18a-b); (4) always none.

State 2, usually two or three up to four maxillary teeth is a synapomorphy to the Cheirodontinae. However, usually one or none maxillary teeth (state 3) is found in the clade A14 including *Holoshesthes* n. sp. "k" + *H. geayi* + (*H. hemigrammus* + *Holoshesthes* n. sp. "b"), excepting in *H. hemigrammus* that usually five or six maxillary teeth (state 1). Indeed, *Holoshesthes* n. sp. "k" has usually one and rarely two maxillary teeth, being coded as state 3. State 3 is also present in the Cheirodontini *Cheirodon interruptus*, and in the outgroup *Astyanax*.

State 1, usually five or six maxillary teeth, is not unique to *H. hemigrammus* and occurs in the clade A6 with *Prodontocharax* + *Amblystilbe*, and in the clade W with *Axelrodia lindeae* + *Spintherobolus*.

The edentulous maxilla is known in some characids, *e.g.* several *Bryconops* species (Chernoff, 2005). Among cheirodontines, *Macropsobrycon* totally lacks the maxillary teeth. The absence of maxillary teeth is also found in *Hasemania melanura* and *H. bilineata* (Serra, 2003: Ch. 46).

Previous phylogenetic studies of Zanata (2000: Ch.52), Serra (2003: Ch. 50), Zanata & Vari (2005: Ch. 78), and Netto-Ferreira (2006: Ch. 92), have considered only the absence or presence of maxillary teeth. However, Lucena (1993) considered in his Ch. 44 the absence of maxillary teeth as one state of the character that refers to the extent of tooth bearing portion on maxilla, and in his Ch. 45 the presence of less than 29 maxillary teeth *versus* more than 30 maxillary teeth.

Character 55 (CI = 0.22) - Number of cusps of the anterior maxillary teeth (Ch. 46, modified of Lucena, 1993, Ch. 48, modified of Serra, 2003): (0) teeth with four cusps or more (Fig. 18d-h); (1) tricuspid teeth (Fig. 18c); (2) unicuspid (Fig. 18a).

Tricuspid teeth are present in the clade A6 with *Prodontocharax* + *Amblystilbe*, and independently in *Holoshesthes hemigrammus*. In the clade A16 with *H. hemigrammus* + *Holoshesthes* n. sp. "b", the tricuspid teeth is most parsimoniously hypothesized appearing in the ancestral of the clade then reduced to the unicuspid condition in the latter species. In *H. geayi* tricuspid or tetracuspid teeth are equally found (Fig. 18b), then it is coded as state 0.

The unicuspid teeth are apomorphic to the clade W containing *Axelrodia lindeae* + *Spintherobolus*. Among outgroup taxa all genera of the Characinae have unicuspid teeth, but this feature was not found supporting a clade with them. *Aphyocharax* has the larger anterior maxillary teeth tri to unicuspid, but it was coded as state 1 considering the anteriormost larger maxillary teeth. *Macropsobrycon* and *Bryconops caudomaculatus* lack the maxillary teeth, being uncoded to this character.

Dentary (*Ch. 70 is not limited to dentary)

Character 56 (CI = 0.33) - Shape of tooth bearing portion of the dentary in lateral view: (0) the posterior tooth bearing portion of the dentary, with smaller teeth, continuous, almost straight or slightly elevated relative to the anterior portion bearing larger teeth; (1) the posterior tooth bearing portion of dentary, with smaller teeth, elevated, forming a marked convexity (Fig. 20a-f); (2) all tooth bearing portion of the dentary nearly straight and forming an angle of approximately 120° relative to the posterior edentulous dorsal border of dentary (Fig. 20g-h); (3) two sections with teeth, the horizontal anterior section with 5-6 large teeth, and an oblique and ascending posterior section with smaller teeth. Teeth of the posterior section sometimes disposed in an almost perpendicular axis in relation to the longer axis of teeth of anterior section (Fig. 20i-j).

State 2 is a new synapomorphy to the Cheirodontinae, but it is also present in the outgroup genera *Phenacogaster* and *Aphyocharacidium*. State 1 is found in the clade A12 with the six species of *Holoshesthes*, and independently in the Cheirodontini *Serrapinnus heterodon*, *S. microdon*, and in the Compsurini *Acinocheirodon* (coded as state 2 because it has just 1-2 smaller teeth on the posterior tooth bearing portion of dentary). State 3 is a synapomorphy to the clade A5 including *Lobodeuterodon* + (*Prodontocharax* + *Amblystilbe*), also acquired more two times in Odontostilbini, in *Pseudocheirodon arnoldi* and in *Odontostilbe microcephala*.

Character 57 (CI = 0.13) - Lateral ridge of the upper portion of the angulo-articular, on posterolateral portion of the lower jaw, near the posterior portion of the maxilla, observed in dorsal view: (0) ridge absent or almost absent; (1) short ridge with a somewhat straight surface; (2) thick ridge with a slightly convex surface, well-marked in dorsal view and discernible in not dissected specimens; (3) laminar ridge with a straight surface, well-marked in dorsal view.

State 1 is a synapomorphy to the Cheirodontinae, admitting some reversions to state 0 (the plesiomorphic state), modifications to states 2 and 3, and further reacquisitions. It is not uniquely derived because it is present in the outgroup genus *Phenacogaster*. The laminar ridge with a straight surface, state 3, is a derived condition in the Odontostilbini, but modified to state 1 in *Odontostilbe microcephala*, and in the clade A12 formed by the species of *Holoshesthes* (except *H. hemigrammus* reversed to state 0). Among the Compsurini state 3 is found in *Saccoderma* and state 2 in *Compsura*.

State 2 is also apomorphic in the clade A4 formed by *Odontostilbe* n. sp. "h" + (*Lobodeuterodon* + (*Prodontocharax* + *Amblystilbe*), excepting in *Amblystilbe* that presents state 3. Among the Cheirodontini, independently state 2 is present in *Nanocheirodon*, and reversions to the plesiomorphic state 0 appear in the clade W formed by *Axelrodia lindeae* + *Spintherobolus*.

Character 58 (CI = 0.11) - Lower border of the dentary: (0) approximately straight (Fig. 20a, f-j); (1) slightly convex (Fig. 20b-e).

The slightly convex lower border of the dentary is present in the cheirodontines *Nanocheirodon*, *Serrapinnus heterodon*, *Serrapinnus microdon*, *Macropsobrycon*, and is a synapomorphy to the clade A13 including most of the species of *Holoshesthes* (except *H. pequira* and *H. hemigrammus*). In *H. pequira* (Fig. 20a) the lower border of the dentary is not convex as those remaining species of *Holoshesthes*, then coded as state 0.

Character 59 (CI = 0.20) - Anteriormost teeth of the dentary: (0) longer axis of the anteriormost teeth perpendicular to the longer axis of the dentary (Fig. 20a-f); (1) longer axis of the anteriormost teeth oblique to the longer axis of the dentary, forwardly projected (Fig. 20g-j).

The dentary teeth projected is a synapomorphy grouping *Carlana* to Cheirodontinae (but also present in *Phenacogaster*), with reversions to the state 0 in *Acinocheirodon*, *Serrapinnus heterodon*, *S. microdon*, and the clade A12 formed by the species of *Holoshesthes*.

Character 60 (CI = 0.09) - Upper branch of the angulo-articular: (0) short, not extended anteriorly or slightly extended, anterior border pointed or slightly pointed, 4-5 times in the longitudinal length of the dentary (Fig. 20 a-f, i); (1) elongate, anteriorly extended, anterior border pointed or slightly pointed, 2-3 times in the longitudinal length of the dentary (Fig. 20g-h, j).

This character is highly variable among examined taxa. Most cheirodontines and several outgroup taxa have the upper branch of angulo-articular elongate (state 1), being short (state 0) in the clade R including two species of *Heterocheirodon*, in the clade V including *Serrapinnus heterodon* + *Serrapinnus microdon*, and in the clade M including *Kolpotocheirodon* + (*Acinocheirodon* + *Macropsobrycon*), and in several species of Odontostilbini, in *Odontostilbe parecis, Odontostilbe* n. sp. "h", in the clade A9 formed by *O. microcephala* (Fig. i) + (*Odontostilbe* n. sp. "e" + *Odontostilbe* n. sp. "p"), and in the clade A12 formed by all species of *Holoshesthes* (Fig. 20 a-f).

Brycon has a short upper branch of the angulo-articular, practically restricted to the base of the angulo-articular, and shorter than the upper branch of the angulo-articular in all other taxa examined, coded as state 0.

Character 61 (CI = 0.11) - Lower branch of the angulo-articular on lateral surface of dentary: (0) short, not extended anteriorly or slightly extended, anterior border forming a slight convexity, 4-5 times in the longitudinal length of the dentary (Fig. 20j); (1) elongate, extended anteriorly, anterior border pointed or slightly pointed, 2-3 times in the longitudinal length of the dentary (Fig. 20a-i).

This is also a highly homoplastic character. Most cheirodontines share state 1 (present in most outgroup taxa, except *Charax* and *Brycon*). The state 0 is apomorphic for the Odontostilbini. However, among the odontostilbins the clade A3 formed by the species of *Pseudocheirodon*, the clade A7 formed by a polytomy with several species of *Odontostilbe* (*O. dierythrura*, *O. paraguayensis*, *O. ecuadorensis*, *O. fugitiva*, *Odontostilbe* n. sp. "m", + (*O. microcephala* + (*Odontostilbe* n. sp. "e" + *Odontostilbe* n. sp. "p"))) + clade A12 (including all *Holoshesthes* species), retain the state 1, the same to *O. pulchra*.

*Lobodeuterodon (*Fig. 20j) is coded as state 0, the anterior border of the lower branch of the angulo-articular is not pointed or slightly pointed, but can exceed 4-5 times in the longitudinal length of the dentary.

Among the Cheirodontini, state 0 is apomorphic to the clade R containing *Heterocheirodon*, and also present in *Spintherobolus papilliferus*. In *Cheirodon interruptus* some specimens show a less pointed anterior border of the lower branch of the angulo-articular exposed on lateral surface of the dentary, but it is coded as state 1. This is the same for *Hemibrycon*.

Character 62 (CI = 0.20) - Extent of dentary with teeth: (0) more than half length of the dorsal border of the dentary (Fig. 20 a-f, i); (1) approximately the third anterior portion of the dorsal border of the dentary (Fig. 20g-h, j).

State 1 is a synapomorphy to the Cheirodontinae, also present in the clade H formed by *Aphyocharacidium* + *Phenacogaster*, and in *Astyanax*. State 0 appears in *Odontostilbe microcephala* (Fig. 20i), and supporting the clade A12 formed by all species of the *Holoshesthes* (Fig. 20a-f). *Macropsobrycon* is as coded state 1, but it has about the quarter portion of the dorsal border of the dentary with teeth.

Character 63 (CI = 0.33) - Protruding spine-like projection upwardly directed in anterodorsal portion of the dentary symphysis: (0) lacking; (1) well-formed.

In *Spintherobolus* this projection is much reduced, and its absence is an autapomorphy for *Axelrodia lindeae*. Among outgroup taxa, it is lacking only in *Cynopotamus* that do not have interdigitations in the symphyseal dentary joint, as observed in *A. lindeae*, and this could be related to the lack of the spine-like projection on anterodorsal portion of dentary. However, *Spintherobolus, Priocharax,* and *Pseudocheirodon* that similarly do not have these interdigitations on symphyseal dentary joint, have the spine-like projection. In *Brycon* this projection seems to be almost indistinct, being coded as state 0, possibly related to the presence of the inner symphyseal teeth.

Character 64 (CI = 0.33) - Anteriormost portion of dentary, at the symphyseal joint, in lateral view: (0) deep, 2-3 times in the height of the middle portion of dentary (Fig. 20a-f); (1) narrow, 4-5 times in the height of the middle portion of dentary (Fig. 20g-j); (2) narrow, 7 times or more the height of the middle portion of dentary (Fig. 19).

Spintherobolus species have a narrow anteriormost portion of dentary, 5-6 times in the height of the middle portion of dentary (Fig. 19) and is coded as state 1, not too delicate as that of *Amblystilbe* (state 2). Most cheirodontines have state 1, but *Acinocheirodon,* and the clade A12 including all species of *Holoshesthes* have state 0. Characines also shares state 1, except *Gnathocharax* state 0. In *Odontostilbe pulchra* the anteriormost portion of dentary is narrow, 4-5 times in the height of the middle portion of dentary, but in Fig. 20h the angle of dentary in the micrograph misleads that.

Character 65 (CI = 0.33) - Posterior small unicuspid teeth of the dentary (Ch. 67, modified of Serra, 2003; Ch. 37, modified of Benine, 2004; Ch. 85, modified of Zanata & Vari, 2005): (0) absent or if present, nearly vertical and perpendicular to the longitudinal axis of the dentary, some cusp tips posteriorly directed (Fig. 20g-j) ; (1) present, lingually turned (Fig. 20b-d).

State 1 is present in the clade A12 formed by the species of *Holoshesthes*, and independently in *Serrapinnus heterodon,* and *Serrapinnus microdon*. (plus *Gnathocharax,* and *Bryconops*). In Fig. 20a, e-f, respectively the *Holoshesthes pequira*, *Holoshesthes* n. sp. "b", and *H. hemigrammus* species lost some of the delicate posterior small unicuspid teeth of the dentary, but all have such teeth.

Acinocheirodon has just 1 posterior unicuspid tooth in the dentary, that is curved lingually, but posterior unicuspid teeth of dentary are numerous in the species coded as state 1. Thus, *Acinocheirodon* is coded as state 0, the same for all the other cheirodontines without these posterior unicuspid teeth.

Differently, Benine (2004) referred to the presence or absence of the posterior small unicuspid teeth of dentary, while Serra (2003) and Zanata & Vari (2005) distinguished them regarding an abrupt reduction in size of posteriormost teeth, against the presence of gradually smaller posteriormost teeth.

Character 66 (CI = 0.33) - Flange in the dorsolateral border of the dentary: (0) absent (Fig. 21d); (1) present, forming a concavity in the dorsolateral surface of the dentary, at vertical after the posteriormost teeth of the dentary (Fig. 21a-c).

State 1 is a unique synapomorphy to the clade A2 formed by *Odontostilbe pao* + (*Pseudocheirodon terrabae* + *Pseudocheirodon arnoldi*).

Character 67 (CI = 1.00) - Ontogenetic change in the shape and tooth cusp number between juveniles and adults: (0) absent, or different from state 1; (1) present, teeth of juveniles usually with 7 cusps, central cusp longer and slightly larger with lateral cusps decreasing in size; teeth of adults with 3 central cusps larger, compressed and in row forming a sharp cutting edge.

The ontogenetic shift of the dentary teeth shape is uniquely derived in *Holoshesthes pequira*. Among outgroup species examined, the juveniles of the rhoadsiine *Carlana eigenmanni* are known to have a "cheirodontine" like dentition, changing in adults. Basically, this change is reported to the teeth on the maxilla (not dentary), which increases in size along maturation and gains up to 8 unicuspid teeth posterior to the two anterior multicuspid teeth

(Fink & Weitzman, 1974). However, caniniform posteriormost unicuspid teeth on the dentary seems to gradually develop from juveniles (a juvenile 28.0 mm SL lacks these teeth, LACNMNH 9230-20) to adults (an adult 55.9 mm SL, with 4 caniniform teeth), a feature not commented by Meek (1912) or Fink & Weitzman (1974). Meek (1912) described the species with only one adult specimen, noticing the development of posterior unicuspid dentary teeth, which he described as "canine".

Character 68 (CI = 0.50) - Symphyseal dentary joint (Ch. 47, Lucena, 1993; Ch. 35, Buckup, 1998; Ch. 9, Malabarba, 1994; Ch. 4 Malabarba, 1998; Ch. 82, Zanata & Vari, 2005): (0) articulates through intercalated bony folds; (1) articulates through rounded bony surfaces joined by tough ligamentous tissue.

The lack of intercalated bony folds at symphyseal dentary joint is homoplastic and a synapomorphy for *Spintherobolus* independently derived in *Pseudocheiron*. Vari (Fig. 2, 1979) found the lack of interdigitating dentary symphyseal hinge in most basal Distichodontidae and Citharinidae. Otherwise, the hinge-like complex formed by the contralateral dentaries is present in most Alestids, except *Lepidarchus* (Fig. 22, Zanata & Vari, 2005), and Characids. Curimatidae, Prochilodontidae, Chilodontidae and Anostomidae also lack these folds (Ch. 37, Buckup, 1998).

Character 69 (CI = 0.50) - Anterior fenestra of dentary (Ch. 5, modified of Malabarba, 1998): (0) absent; (1) presence of a small oval fenestra, more than five times in the total length of the dentary; (2) presence of a large, about twice in the total length of the dentary (Fig. 19).

This fenestra is a synapomorphy of *Spintherobolus* (Fig. 19) (Malabarba, 1998; Weitzman & Malabarba, 1999, fig. 12). It is situated on the anteroventral portion of dentary, similarly to the smaller fenestra found in *Phenacogaster* and *Priocharax*.

Character 70 (CI = 0.40) - Tooth shape (Ch. 56, modified of Malabarba, 1998; Ch. 3, modified of Weitzman & Malabarba, 1999): (0) not pedunculated, tooth base enlarged; (1) sligthly pedunculated, forming a slight constriction in middle portion (Fig. 19); (2) pedunculated, largely expanded, and compressed distally; (3) pedunculated, largely expanded, and compressed distally, only on dentary (Figs. 16-18, 20-21).

The pedunculate tooth shape (state 3) is present in all cheirodontines and *Carlana* forming the clade K, by parsimony only modified to state 1 in the clade W including *Axelrodia lindeae* + *Spintherobolus* species. However, it is reversed to state 0, not pedunculate teeth in

Axelrodia lindeae, and to state 2, the pedunculate teeth in *Spintherobolus* n. sp. This new species of *Spintherobolus* sp. n. was coded as state 3 based on its pedunculated teeth of the dentary, though it has slightly pedunculated in the premaxilla and maxilla (Fig. 19).

The overall presence of teeth pedunculated, largely expanded, and compressed distally on the premaxilla, maxilla, and dentary was considered by Malabarba (1998) and Weitzman & Malabarba (1999), a synapomorphy of the Cheirodontinae, reversed in *Spintherobolus*. Weitzman & Malabarba (1999) already noticed the slightly pedunculation of the teeth in *Spintherobolus*, describing it to *S. papilliferus* "all jaw teeth with expanded basal pedicle and more or less conical along their length, but with slightly expanded tip.", or to *S. ankoseion*, *S. broccae*, and *S. leptoura* "all jaw teeth with basal pedicle and somewhat laterally expanded distal conical cusp". However, they did not consider the slight pedunculation as a separate state in its analysis.

Although pedunculate teeth occur in species of other genera, as *Carlana*, *Deuterodon*, some species of *Jupiaba* (*e.g. J. pinnata* in Zanata, 1997), or *Myxiops aphos* (Zanata & Akama, 2004: fig. 5).), these are hypothesized to be non-homologous and independently acquired since they do not share other synapomorphies with the Cheirodontinae.

Character 71 (CI = 0.66) - Tooth cusp arrangement of the anterior large dentary teeth (Ch. 57 modified of Malabarba, 1998; Ch. 68, modified of Serra, 2003): (0) unicuspid to multicuspid teeth with one to three central cusps noticeable prominent relative to lateral cusps (Fig. 20a-j); (1) each tooth with 7 cusps, being 5 central cusps larger, similar in size, and in a row forming a sharp cutting edge; (2) each tooth with 8-9 cusps, being 6-7 central cusps larger, similar in size, and in a row forming a sharp cutting edge.

States 1 and 2 are respectively synapomorphies of *Saccoderma* and *Pseudocheirodon*.

Carlana eigenmanni has similar cusp arrangement of the large and anterior dentary teeth, but with slightly prominent central cusp, and larger teeth have 8-12 cusps followed by posterior 2-4 unicuspid to tricuspid teeth, or with up to 5 cusps (Fink & Weitzman, 1974). These posterior dentary teeth of *C. eigenmanni* are large, similar in size to the anterior teeth or even longer, and different from the decreasing in size posterior teeth observed in the cheirodontines.

Character 72 (CI = 0.42) - Tooth cusp arrangement of the anterior larger dentary teeth (Ch. 58, modified of Malabarba, 1998: (0) teeth unicuspid to multicuspid with central cusp larger, not compressed; (1) 3 central cusps larger, nearly equal in size, somewhat compressed; (2) 3 central cusps larger, nearly equal in size, compressed and aligned at their distal tips in a row forming a sharp cutting edge; cusp tips distal (Fig. 20 a-e); (3) 3 central cusps larger, nearly equal in size, compressed and aligned at their distal tips in a row forming a sharp cutting edge; cusp tips of lateral cusps lateral (Fig. 20f).

Serrapinnus microdon has the three central cusps larger and somewhat compressed, but not as developed as in states 2 or 3, and not aligned distally in sharp cutting edge being coded as state 1. The state 2 is a synapomorphy to the clade A12 with the species of *Holoshesthes*, further modified to state 3 in *Holoshesthes hemigrammus*. However, state 2 occurs in the cheirodontin *Serrapinnus heterodon* and the compsurin *Acinocheirodon*. State 3 was before recognized by Malabarba (1998) as unique to *Holoshesthes hemigrammus*, but maintained in the monotypic genus *Aphyocheirodon*.

Character 73 (CI = 0.50) - Dentary teeth (Ch. 59, Malabarba, 1998): (0) 5 to 6 anteriormost teeth larger and following teeth decreasing in size posteriorly (Fig. 20g-j); (1) 3-4 anteriormost teeth larger and following teeth decreasing in size posteriorly (Fig. 20a-e); (2) 8 to 10 anteriormost teeth larger and following teeth decreasing in size posteriorly (Fig. 20f).

State 1 is present in *Serrapinnus heterodon*, *S. microdon*, *Acinocheirodon*, and most species of *Holoshesthes*, except *H. hemigrammus* that uniquely has state 2.

Character 74 (CI = 0.18) - Tooth cusp number of larger anterior dentary teeth (Ch. 51 modified of Lucena, 1993): (0) teeth with four cusps or more (Fig. 20a-j); (1) teeth tricuspid (Fig. 19); (2) unicuspid teeth.

Among cheirodontines, state 1 is a derived character to *Spintherobolus* and to the clade A6 (*Amblystilbe* + *Prodontocharax*), while state 2 to *Axelrodia lindeae* and *Macropsobrycon*. In the outgroup taxa, *Aphyocharax*, and *Aphyocharacidium* also have tricuspid dentary teeth, state 1. Notably all species of the Chararacinae share state 2, except *Phenacogaster* with the larger anterior dentary teeth tricuspid.

Dentition

Character 75 (CI = 0.28) - Mouth position (Ch. 73, modified of Netto-Ferreira, 2006): (0) terminal, mouth slit nearly at horizontal through the middle of eye, or different from states 1 and 2; (1) slightly subterminal, mouth slit at horizontal below the middle of eye; (2) subterminal, mouth slit at horizontal with the lower edge of eye.

In the Cheirodontinae, three mouth positions are recognized. The terminal mouth is found in most taxa, the slightly subterminal in *Odontostilbe dierythrura*, *Odontostilbe* n. sp. "m", and *Odontostilbe pao*, and the subterminal that supports the clade A4 formed by *Odontostilbe* n. sp. "h" + (*Lobodeuterodon*, + (*Prodontocharax* + *Amblystilbe*)), and independently present in *O. microcephala*.

Netto-Ferreira (2006) remarked that Lebiasinidae other than *Copeina*, *Copella*, *Derhamia*, and *Pyrrhulina*, have a somewhat subsuperior mouth, sligthly up turned but not visible in dorsal view. In Cheirodontinae, this subsuperior mouth would correspond to a mouth slit position slightly oblique at horizontal through middle of eye, here included in state 0. This is seen in *Macropsobrycon*, and other species that have a lower jaw projected beyond the upper jaw, here recognized to have terminal mouths, coded as state 0.

Aphyocharax and *Gnathocharax* show a superior mouth, but are assigned as State 0.

Character 76 (CI = 0.16) - Lower jaw profile: (0) not projected on head profile; (1) slightly projected on head profile.

State 1 is a synapomorphy to the clade A12 formed by all species of *Holoshesthes*, but independently appearing among the Compsurini in the clade N formed by *Acinocheirodon* + *Macropsobrycon*, and among the Cheirodontini in the clade V formed by *Serrapinnus heterodon* + *S. microdon*. In the outgroup, *Aphyocharacidium* similarly has state 1, and *Aphyocharax* and *Gnathocharax* were coded as state 1, but present a more projected lower jaw on head profile.

Hyoid Arch

Character 77 (CI = 0.28) - Shape of the posteriormost branchiostegal ray in males: (0) ventral border nearly straight (Fig.22a); (1) ventral border slightly concave on the anterior to median length of the ventral border (Fig. 22b); (2) ventral border deeply concave on the anterior to median length of the ventral border (Fig. 22c).

The concavity of the posteriormost branchiostegal ray forms a hole ventrally on head exactly near the most ventral portion of the gill gland of the first gill arch. Thus, this osseous modification of the posteriormost branchiostegal ray could be related to the gill gland, functioning as an opening to facilitate excretion. This gill gland is present in all of the Cheirodontinae examined with available mature males (Fig. 23a-b) (excepting *Spintherobolus* n. sp., and *Amblystilbe alleni*, none mature males). However, not all Cheirodontinae with the gill gland have the modified posteriormost branchiostegal ray in males. Thus, the association between these structures seems to be not as simple as hypothesized here.

The gill gland is formed by glandular tissue and modified gill filaments, being first reported to *Corynopoma riisei* (Burns & Weitzman, 1996), and later described to other glandulocaudine genera (Bushman *et al*., 2002), also to the Cheirodontinae *Compsura heterura* and *Odontostilbe* sp. (actually *Holoshesthes pequira*) (Oliveira, 2003), and to four *Odontostilbe* species (Bührnheim & Malabarba, 2006). *Aphyocharax anisitsi* (Gonçalves *et al*., 2005) also has the gill gland, and many of the present outgroup taxa here examined (*Phenacogaster franciscoensis*, *Aphyocharacidium bolivianum*, *Hemibrycon* sp.). The gill gland was not included in the present matrix of characters, because it has been found to differ in structure among Cheirodontinae taxa (Oliveira, 2003). In all Odontostilbini the gill gland comprises about 10 gill filaments of the first gill arch, while in Compsurini, *e.g. Macropsobrycon*, it comprises practically all gill fiaments.

State 1 is a synapomorphy to the Odontostilbini, just reversed to state 0 in *Pseudocheirodon*. While in the Cheirodontini, state 1 is a new synapomorphy to *Heterocheirodon*, and in the Compsurini, the state 1 is uniquely present in *Compsura*. Remarkably, among the outgroup taxa, *Hemibrycon* has similar modification of the posteriormost branchiostegal in males, state 1, and have the gill gland. The branchial gland is present in all members of the Odontostilbini (Fig. 23a-b), and in present in the Compsurini *Compsura*. The concave ventral border condition of the posteriormost branchiostegal ray in males, state 2, is a new autapomorphy of *Kolpotocheirodon* (Fig. 22c), not reported before by Malabarba (1998), Malabarba & Weitzman (2000), and Malabarba *et al.* (2004). Notably, *Kolpotocheirodon* has a well-developed gill gland among cheirodontines, practically comprising all gill filaments in the lower branch of the first gill arch.

Brycon, and *Amblystilbe* are uncoded to this character, considering that mature males were not examined. Thus, *Amblystilbe* is hypothesized to have state 1 in the *Odontostilbini*.

Character 78 (CI = 0.11) - Posterior border of the branchiostegals rays: (0) all branchiostegals rays somewhat smooth, or with few irregular indentations; (1) all branchiostegals rays or at least the two posteriormost branchiostegals rays markedly crenulated.

State 1 is a synapomorphy to the Cheirodontini, shared by most of the its representatives, excepting New gen. n. sp. "C", the clade V formed by *Serrapinnus heterodon* + *S. microdon*, and the *Spintherobolus* n. sp., all reversed to state 0. In the Odontostilbini, independently *Odontostilbe* n. sp "h" in the clade A4 and *Amblystilbe* in the clade A6 have the crenulate posterior border of the branchiostegals rays. In the outgroup taxa, state 1 is found in *Diapoma*, *Aphyocharax* and *Phenacogaster*.

Character 79 (CI = 0.50) - Lower border of the anterior ceratohyal where branchiostegals attach (Ch. 68, modified of Lucena; Ch. 70, modified of Zanata, 2000): (0) almost smooth, with one or two slight marked concavities where branchiostegals 1 or 1 and 2 are attached; (1) two conspicuous concavities where branchiostegals 1 and 2 are attached.

The presence of two conspicuous concavities on lower border of the anterior ceratohyal where branchiostegals 1 and 2 are attached is a new synapomorphy to Cheirodontinae, reversed in clade W with *Axelrodia lindeae* and *Spintherobolus* species. However, this is a derived condition also present in the outgroup taxa *Carlana*, *Aphyocharax*, and *Astyanax*. Zanata (2000) remarked the presence of well-defined concavities in the lower border of the anterior ceratohyal in cheirodontines, tetragonopterines, *Roeboexodon*, *Lignobrycon*, *Brycon atrocaudatus* and *B. alburnus*.

Branchial apparatus

Character 80 (CI = 1.00) - Shape of the basihyal: (0) smooth; (1) with two small processes on the anteroventral portion of the basihyal.

State 1 is a unique synapomorphy of the clade Y containing most of the *Spintherobolus* species, except *Spintherobolus* n. sp.

Character 81 (CI = 0.35) - Basibranchial 1: (0) elongate, located between and somewhat separating the paired hypobranchial 1 elements; (1) short, located anteriorly between paired hypohyals; partially extending posteriorly between the paired hypobranchial 1 elements, but not totally separating them that are placed posteriorly.

The elongate basibranchial 1 seems to be plesiomorphic in characids, being found in the basal outgroup taxa *Brycon,* and in the clade C formed by *Bryconops* + *Gnathocharax*. The short basibranchial 1 is a derived character sustaining the comprehensive clade D including outgroup taxa *Charax, Cynopotamus, Priocharax, Astyanax, Aphyocharacidium, Phenacogaster,* and the Cheirodontinae. Reversions to state 0 occur in the clade G formed by *Hemibrycon* + *Diapoma*, and also in *Aphyocharax*. Among the cheirodontines, reversions to state 0 are present in some elements of the Odontostilbini, in the clade A9 formed by *Odontostilbe microcephala* + (*Odontostilbe* n. sp. "e" + *Odontostilbe* n. sp. "p"), but state 1 is reacquired in *Odontostilbe* n. sp. "e", and in Odontostilbe n. sp. "h", *Odontostilbe* n. sp. "b", and in the Cheirodontin clade X with all *Spintherobolus* species. In *Spintherobolus broccae* the character is uncoded because the c&s specimen is not entire, but by parsimony it shares state 0 with the remaining *Spintherobolus* species.

Priocharax, *Gnathocharax*, and *Aphyocharax* comparatively have a somewhat short basibranchial 1 separating the paired hypobranchial 1 elements, and considered as state 1. *Priocharax* has the basibranchial 1 totally cartilaginous.

Character 82 (CI = 0.33) - Basibranchial 4 (Ch. 74, Lucena, 1993; Ch. 78, Zanata, 2000; Ch. 53, Benine, 2004; Ch. 157, Netto-Ferreira, 2006): (0) totally cartilaginous; (1) partially ossified, central piece osseous.

The partially ossified basibranchial 4 with central piece osseous is a unique synapomorphy supporting the broad clade F, containing the clade G (*Hemibrycon* + *Diapoma*), the clade H (*Aphyocharacidium* + *Phenacogaster*), *Astyanax*, *Aphyocharax*, *Carlana* and the Cheirodontinae (reversed to state 0 in *Axelrodia lindeae*). A cartilaginous basibranchial 4 is found in the basal taxa *Brycon*, *Bryconops*, and in the characines *Cynopotamus*, *Gnathocharax*, *Charax*, and *Priocharax*. However, the present analysis did not group the Characinae in a monophyletic clade, and *Gnathocharax* is with *Bryconops* in clade C.

The character is coded as uninformed in *Spintherobolus broccae*, since the c&s specimen examined is not entire, and then assumed to share the state 1 in the strict consensus cladogram obtained.

Zanata (2000) remarked that the basibranchial 4 totally cartilaginous seems to be plesiomorphic, and the partially ossified basibranchial 4 in *Agoniates*, *Lignobrycon*, *Triportheus*, and three *Brycon* species (not *B. pesu* in the present study) seems to be derived. However, Zanata (2000) reported a totally cartilaginous basibranchial 4 to the cheirodontines *Cheirodon interruptus*, *Odontostilbe* aff. *paraguayensis* (not *Odontostilbe*, probably *Serrapinnus* sp., see Ch. 114), and *Serrapinnus heterodon*. None of the *Cheirodon*, *Odontostilbe*, and *Serrapinnus* specimens examined have the basibranchial 4 totally cartilaginous, but instead the central piece is osseous. Lucena's (1993) observations of the basibranchial 4 in the Cheirodontinae agree with the present study.

Character 83 (CI = 0.25) - Teeth on the suspensory pharyngeal 2 (Ch. 72, Lucena, 1993; Ch. 36, Lucena, 1998; Ch. 155, Netto-Ferreira, 2006): (0) with teeth; (1) edentulous.

The edentulous suspensory pharyngeal 2 observed in clade W with *Axelrodia lindeae* + *Spintherobolus* is apomorphic to these cheirodontines, but it is also observed in *Priocharax* and *Gnathocharax*. Lucena (1993) coded *Phenacogaster* and *Diapoma* as state 1, lacking teeth in the suspensory pharyngeals 2, but these teeth were found present in the same genera in the present study. Lucena (1993) used *Phenacogaster jancupa*, and here we used *P. franciscoensis*. The exam of the same specimen of the same lot of *P. jancupa* (MCP 16129) that Lucena examined confirmed that this species has an edentulous suspensory pharyngeal 2, different from *P. franciscoensis* that has the teeth. This interspecific variation of the character possibly occurs in *Diapoma*: *Diapoma speculiferum* examined here has these teeth, while *D. terofali* examined by Lucena is reported as not possessing these teeth. Lucena (1998) report an edentulous suspensory pharyngeal 2 to *Priocharax* and *Acanthocharax*, but not to *Gnathocharax*.

Character 84 (CI = 0.50) - Teeth on the suspensory pharyngeal 3 (Ch. 37, Lucena, 1998): (0) with teeth; (1) edentulous.

The edentulous suspensory pharyngeal 3 is derived in *Spintherobolus*. Among the Characinae, it was already noted as uniquely derived in *Gnathocharax* by Lucena (1998), confirmed here.

Character 85 (CI = 0.12) - Gill rakers in the ceratobranchial 1 (Ch. 73, Lucena, 1993; Ch. 34, Lucena, 1998; Ch. 154, Netto-Ferreira, 2004): (0) in one row along the lateral border of the ceratobranchial 1; (1) in two rows, one row along the lateral border of the ceratobranchial 1, and one row along the medial border of the ceratobranchial 1.

The medial row of gill rakers is formed by diminute gill rakers, usually smaller than the lateral ones. Among the Cheirodontini, the two rows of gill rakers on ceratobranchial 1 is a derived character to the *Spintherobolus* clade X, and independently to the *Heterocheirodon* clade R. While among the Odontostilbini, this derived condition, state 1, is present in *Odontostilbe microcephala*, in the clade A4 only in *Odontostilbe* n. sp. "h", and in the terminal *Prodontocharax*.

State 1 is also observed in *Carlana* and *Cynopotamus* (this latter uncoded by Lucena, 1998). The medial row with gill rakers is found in the Lebiasinidae (Netto-Ferreira, 2004), in *Raphiodon*, *Serrasalmus*, *Hoplias*, *Erythrinus*, *Hoplerythrinus*, *Iguanodectes*, *Othonocheirodus*, *Parecbasis*, *Acanthocharax*, *Bryconamericus*, and *Cynodon* (Lucena, 1993), and *Hoplocharax* (Lucena, 1998).

Character 86 (CI = 0.14) - Length of the gill rakers of the first gill arch relative to the branchial cavity: (0) short to mid-sized, occupying less than half of the branchial cavity between the cranium base and the gill branches; (1) elongate, proportionally occupying more than half or half of the branchial cavity between the cranium base and the gill branches.

The elongate gill rakers are conspicuous in the cheirodontines *Macropsobrycon* and *Serrapinnus microdon* that practically have most of the branchial cavity below cranium base occupied by the long gill rakers (Figs. 23c). Other cheirodontines such as *Heterocheirodon*, *Holoshesthes* (Fig. 23d), and *Acinocheirodon*, and the characine *Priocharax* (Fig. 23e), have less elongate gill rakers, but occupying half of the branchial cavity between the cranium base and the gill branches. *Spintherobolus* has very short gill rakers (Fi. 23f). *Aphyocharax* (Fig, 23g) and *Gnathocharax* have only the gill rakers of the lower branch elongate, but coded as state 1 as its gill rakers occupy more than half or half of the branchial cavity between the cranium base and the gill branches.

Acinocheirodon melanogramma is coded as state 1, based on the specimens from the rio São Francisco. The specimens of *Acinocheirodon* cf. *melanogramma* from the rio Jequitinhonha have shorter gill rakers and should be coded as state 0, being possibly a separate species from the population of the rio São Francisco (see previous comments on Ch. 11, and Malabarba & Weitzman, 1999).

The strict consensus tree obtained shows state 1 as a synapomorphy to the clade N with *Acinocheirodon* + *Macropsobrycon*, among the Compsurini, to the clade V with *Serrapinnus heterodon* + *S. microdon*, and to the clade A12 with all *Holoshesthes* species, among the Odontostilbini. In *Aphyocharax* and *Gnathocharax* the derived state 1 is independently acquired, and these species are not nearly related.

Character 87 (CI = 1.00) - Length of the gill rakers on upper branch relative to the length of the gill rakers on the lower branch of the first gill arch: (0) gill rakers of dissimilar length; those of the lower branch longer than those of the upper branch; (1) gill rakers of similar length in the upper and lower branches (Fig. 23g).

The gill rakers of similar length in the upper and lower branches of the first gill arch is a unique synapomorphy to the clade A6 formed by *Amblystilbe* and *Prodontocharax*. Menezes (1976) referred most characoids having elongate gill rakers, tending to become gradually reduced in size towards the ends of the gill arches, and exemplified this pattern in *Brycon* of Weitzman (1962), *Astyanax*, *Paroligosarcus* (currently synonym of *Oligosarcus*), and

Oligosarcus, and many other genera. The increasing elongation of gill rakers is oriented from the anteriormost to the posteriormost gill rakers (Fig. 23a-h).

Character 88 (CI = 0.33) - Length of the gill rakers of the upper branch, of the first gill arch: (0) most or all gill rakers short, gill rakers length nearly equal or smaller than the epibranchial width (Fig. 23h); (1) most or all gill rakers mid-sized to elongate, surpassing the anterior border of the epibranchial, gill rakers length twice or more than epibranchial width (Fig. 23a-e, g).

The gill rakers mid-sized to elongate is a unique synapomorphy defining the broad clade D, including the clade E (*Charax*, *Cynopotamus* + *Priocharax*), clade G (*Hemibrycon* + *Diapoma*), clade H *Aphyocharacidium* + *Phenacogaster*, *Aphyocharax*, *Astyanax*, *Carlana* and the Cheirodontinae. Short gill rakers in the upper branch, state 0, are found in the outgroup taxa *Brycon*, *Bryconops*, *Hemibrycon*, *Gnathocharax*, and among cheirodontines it is a derived condition only present in *Spintherobolus* (with extreme reduction on gill rakers, see Ch. 91, 92) (Fig. 23f). *Amblystilbe* is coded as state 1, because is has several gill rakers surpassing the epibranchial width (Fi. 23g).

Aphyocharax (Fig. 23h) and *Phenacogaster* have short anterior gill rakers on upper branch of the first gill arch, but they are coded as state 1 because the posteriormost gill rakers are have equal or more than the epibranchial width.

Character 89 (CI = 0.25) - Number of gill rakers in the upper branch of the first gill arch: (0) 10 or more; (1) 4-9; (2) 1-3.

Most outgroup taxa (except *Brycon*) and cheirodontines have 4-9 gill rakers in the upper branch of the first gill arch. State 0, the high number of gill rakers is a feature found in the outgroup *Brycon*, and in some representatives of the Odontostilbini: *Odontostilbe microcephala*, and the clade A6 (*Amblystilbe* + *Prodontocharax*). Among the Cheirodontini, *Heterocheirodon* and *Cheirodon interruptus* are coded as state 0, because they usually have 10-11 gill rakers on the upper branch, then showing indepedent acquisitions of this character condition. State 2, the lower number of gill rakers is exclusive to clade W, present in *Axelrodia lindeae*, *Spintherobolus* sp. n., and in clade Y reversed to state 1 in *S. papilliferus*, and *S. ankoseion* (Fig. 23f), but not in S. *broccae*.

Benine (2004: Ch. 55) jointly considered length and number of gill rakers as a single character in his phylogenetic analysis of *Moenkhausia*. The presence of long and numerous gill rakers defined his Clade 54, including *Moenkhausia costae*, *M. dichoura*, and *M. intermedia*, and were found homoplastic in *Stichonodon insignis*.

Character 90 (CI = 0.18) - Number of gill rakers in the lower branch of the first gill arch (Ch. 77, modified of Zanata, 2000): (0) 13-16 gill rakers, rarely 12; (1) less than 12 (except *Odontostilbe* n.sp. "m" with 12-13); (2) usually 17 or more.

This is another highly homoplastic character with conditions evolving repeatedly in the present cladogram. State 1, less than 12 gill rakers in the lower branch of the first gill arch, is present defining the comprehensive clade B, including all outgroup taxa (except *Brycon*, state 0), and the Cheirodontinae.

In Compsurini, state 1 is present in *Saccoderma*, and a derived condition to clade N with *Acinocheirodon* + *Macropsobrycon*, but modified to state 2 in *Macropsobrycon* (with 16-17 gill rakers on lower branch and considered as state 2) (Fig. 23c).

Among the Cheirodontini, the state 0 appears in *Cheirodon interruptus*, and in clade V with *Serrapinnus heterodon* + *S. microdon*, ranging 13-16 lower gill rakers. While state 2 define the clade R with *Heterocheirodon jacuiensis* + *H. yatai* that share an elevated number of lower gill rakers, 17-18. *Spintherobolus* is uncoded for the character, considering the different and unusual absence of gill raker in the lower branch of the first gill arch, treated in the Ch. 95.

In Odontostilbini state 0, 13-16 lower gill rakers, is a synapomorphy to clade A12 (*Holosheshes* species, except *H. hemigrammus*, state 1), and state 2 to the clade A6 formed by *Amblystilbe* + *Prodontocharax* having numerous lower gill rakers 17 to 19 (fig. 23g).

Zanata (2000), defined her Ch. 77 only with two states, less than 20 lower gill rakers or more than 20. The high number of lower gill rakers, more than 20, was considered a synapomorphy to *Triportheus* and *Lignobrycon* by Zanata (2000), which can reach up to 90 in *Triportheus*, and 40 in *Lignobrycon myersi* (Malabarba, 1998). This condition was not observed here. The present examined *Brycon pesu* has 13-14 lower gill rakers, and as it is the most primitive taxon in the analysis, this is the plesiomorphic state of the character here.

Character 91 (CI = 1.00) - Shape of the gill rakers on the first gill arch (Ch. 35, modified of Lucena & Menezes, 1998): (0) elongate and lanceolate (Fig. 23a-e, g-h); (1) short and conical (Fig. 23f).

This a new unique synapomorphy to *Spintherobolus*, the clade X, not in Malabarba (1998) and Weitzman & Malabarba (1999), and including the *Spintherobolus* n. sp. These conical gill rakers do not have similar shape in Characiformes. However, short gill rakers with spines, acute denticles, are known in Acestrorhynchidae and Cynodontinae (Roberts, 1969; Menezes, 1969: figs, 23, 36, 38, 42-43, 50, 54, 57-60; Lucena & Menezes, 1998; Toledo-Piza, 2000). Roberts (1969: 423, fig. 37) commented that possibly gill rakers were secondarily reduced in some characids, *Acestrorhynchus* and *Rhaphiodon*.

Character 92 (CI = 1.00) - Gill rakers on the lower branch of the first gill arch: (0) present (Fig. 23a-e, g-h; (1) absent or with only one posteriormost gill raker at the junction of the ceratobranchial with the epibranchial (Fig. 23f).

This a new unique synapomorphy to *Spintherobolus*, the clade X, not in Malabarba (1998) and Weitzman & Malabarba (1999), and including the *Spintherobolus* n. sp.

Character 93 (CI = 0.50) - Denticles on the gill rakers of the first gill arch: (0) present (Fig. 23a, h) ; (1) absent (Fig. 23f).

Roberts (1969: 423, figs. 33-37) commented the presence of tooth-bearing gill rakers in *Hoplias*, *Acestrorhynchus*, *Raphiodon*, and *Salminus* (in fig. 36), but toothless in *Hepsetus* and *Ctenolucius,* which would present a specialized condition. Weitzman (1962) described these gill raker structures as conical spicules of bone in *Brycon meeki*. In *Acestrorhynchus* these teeth are acute, and the gill rakers are referred as flat spiny bony plates by Menezes (1969), or laminar and spiny by Lucena & Menezes (1998). Reviewing the Cynodontinae, Toledo-Piza (2000: fig. 12) also referred to spines on gill rakers in *Cynodon* and *Raphiodon*. These small structures were also called as the gill raker denticles and have been used to distinguish *Bryconops* species by Machado-Allison *et al.* (1993: figs. 4, 7, 10-11, 15), and Chernoff (1999: fig.3a-b), or *Odontostilbe* species by Bührnheim & Malabarba (2006).

Here, the denticles are lacking in *Priocharax* and in clade W with *Axelrodia lindeae* + *Spintherobolus* (Fig. 23f), being a synapomorphy to the clade W. These denticles are present in all other taxa examined in different numbers and arrangements (Fig. 23a, h). The accurate checking of the denticles was obtained through scanning electronic micrographs of each species; at least two specimens (a male and a female) in most outgroup species, and more than two, usually four specimens, in the ingroup species. The denticulation in cheirodontines seems to be restricted to the basal portion of the gill rakers, distributed mostly on the anterolateral border of the upper and lower gill rakers (Fig. 23a). This is different in a particular outgroup species, *Aphyocharax nattereri,* that has denticles along all the lower gill rakers on the anterolateral and posterolateral borders (Fig. 23h. As this pattern was only found in *A. nattereri*, it is not considered an additional character in the present analysis. A gill raker of *Aphyocharax anisitsi* was checked in SEM, and not showed this unusual denticle distribution.

Girdle

Character 94 (CI = 0.66) **-** Position of the posttemporal bone relative to the posttemporal fossa (Ch. 67, modified of Benine, 2004): (0) posttemporal placed over posttemporal fossa, partially over epioccipital (Weitzman & Fink, 1983: figs. 10-11); (1) posttemporal placed posterior to the posttemporal fossa, and over epioccipital (Weitzman & Fink, 1983: figs. 5, 7-8) ; (2) posttemporal placed posterior to the posttemporal fossa, and practically not over epioccipital, crossing only the dorsal portion of the epioccipital.

Spintherobolus ankoseion and *S. broccae*, clade Z, uniquely share the posttemporal placed posteriorly to the posttemporal fossa, state 1, which is similar in *Paracheirodon*. However, the joint between the posttemporal and supracleithrum in *Spintherobolus* lies at the ventral border of the posttemporal fossa, below to the derived position of *Paracheirodon* that is at or dorsal to the midpoint of the vertical length of the posterior border of the posttemporal fossa (Weitzman & Fink, 1983, Ch. 5 and figs. 6-8). In *Charax*, *Cynopotamus*, and *Priocharax*, clade E, the posttemporal position is backward to the epioccipital, a uniquely derived condition, state 2.

Benine (2004: Ch. 67) found four states to this character, not illustrating them. His state 1, the posttemporal anterior to the epioccipital was not observed here (probably similar to fig. 12 of *Hemigrammus erythrozonus* in Weitzman & Fink, 1983), being a synapomorphy of two clades formed by several *Moenkhausia* species. His state 0, the posttemporal over epioccipital, is not equivalent to the present state 1, but probably to our state 0. This is because he did not have any species with similar pattern of *Spintherobolus* or *Paracheirodon*, and considered *e.g. Gymnocorymbus thayeri* (Weitzman & Fink, 1983, fig. 30) as having the posttemporal over the epioccipital, but actually this is placed slightly oblique to the epioccipital and only partially over it, not over epioccipital as seen in *Spintherobolus*. His state 2, posttemporal posterior to the epioccipital with slight overlap, is not correspondent to our state 2, and was not observed here. His state 3, posttemporal totally posterior to the epioccipital, described to *Charax*, is treated here in state 2.

Character 95 (CI =0.50) - Laterosensory canal of the supracleithrum (Ch. 91, Lucena, 1993; Ch. 54, Buckup, 1998; Ch. 161, Zanata & Vari, 2005; Ch. 202, Netto-Ferreira, 2006): (0) present; (1) absent.

The loss of the laterosensory canal of the supracleithrum is observed in *Spintherobolus ankoseion*, *S. papilliferus*, *S. broccae*, forming clade Y, and independently in *Priocharax*, clade E1. *Spintherobolus* sp. n. has some reduction of the canal, but a small portion is present dorsally, being coded as state 0.

Lucena (1993) and Buckup (1998) found the absence of this sensory canal as a synapomorphy to a clade formed by *Nannostomus* and *Pyrrhulina*, but this canal is a also lacking in *Copella* (Netto-Ferreira, 2006), supporting a broader clade in Lebiasinidae (reversed in *Copeina*).

Character 96 (CI =0.33) - Postcleithrum 1: (0) somewhat oval, anteroposteriorly expanded; (1) slender, not anteroposteriorly expanded.

The slender postcleithrum 1 is derived to clade R with *Heterocheirodon jacuiensis* + *H. yatai* and independently appearing in *Macropsobrycon.* Two taxa are uncoded for the character, *Diapoma* and *Priocharax* lacking the postcleithrum 1, and *Gnathocharax*. In the latter there are several modifications of the pectoral girdle, as the loss of the postcleithrum 3 (next Ch. 97), and the presence of a small plate-like postcleithrum near the pectoral-fin rays that probably correspond to the postcleithrum 2 or even to the postcleithrum 1.

The Gasteropelecinae (Weitzman, 1964) and the alestid *Lepidarchus* (Zanata & Vari, 2005), *e.g.* lack the entire poscleithrum 1.

Character 97 (CI =0.33) - Postcleithrum 3 (Ch. 90, Lucena, 1993; Ch. 31, Lucena & Menezes, 1998; Ch. 59, Buckup, 1998; Ch. 134, Zanata & Vari, 2005): (0) present; (1) absent.

Absence of postcleithrum 3 is a derived condition in all *Spintherobolus* species (clade X), and in the characines *Gnathocharax* (clade C) and *Priocharax* (clade E1).
Zanata & Vari (2005) report absence of postcleithrum 3 in alestids *Clupeocharax*, *Hemmigrammopetersius barnardi* and *Rhabdalestes rhodeiensis*. Also absent in many other characiforms, *e.g.* Gasteropelecinae (Weitzman, 1954; 1960), *Ctenolucius* (Vari, 1995), *Chilodus* (Vari *et al.*, 1995), *Triportheus* and *Lignobrycon* (Malabarba, 1998), *Gnathocharax*, *Lignobrycon*, and supporting a clade with Cynodontinae, *Gilbertolus*, and *Roestes* (Lucena & Menezes, 1998; in matrix of Toledo-Piza, 2000).

Character 98 (CI = 0.25) - Shape of the postcleithrum 3 (Ch. 69, Benine, 2004; Ch. 135, Zanata & Vari, 2005): (0) without lamella; (1) bearing a posterior lamella.

The presence of a posterior lamella on the postcleithrum 3 is a unique synapomorphy in the broad clade D with most outgroup taxa (except *Brycon*, *Bryconops*, *Diapoma* and *Aphyocharax*) and the Cheirodontinae. Only *Macropsobrycon* has a relatively rod-like shape of postcleithrum 3, without the posterior lamella among cheirodontines. This character is coded as inapplicable in *Spintherobolus* species, and in the characines *Gnathocharax* and *Priocharax* due to the absence of postcleithrum 3.

The presence of the lamella was one of the characters defining the "group A" proposed by Uj (1987) and formerly discussed here in Chs. 8, 11-12. This "group A" with the lamella comprised the *Cheirodon* species *versus* the "group B" lacking the lamella containing *Odontostilbe* and *Serrapinnus* species, and *Holoshesthes pequira* (see Ch. 8). Here, all species examined of *Odontostilbe*, *Serrapinnus*, and *Holoshesthes pequira* have the lamella.

The lamella of the postcleithrum 3 has a significant intraspecific variation in size and shape. Casciotta *et al.* (1992, fig. 9a, b) noted that and illustrated the postcleithrum 3 of "*Odontostilbe piaba*" (probably *Serrapinnus* sp.) and *Heterocheirodon yatai*. They briefly commented Uj's (1987) Characters 1-6, considering them inappropriate as diagnostic features, and a pointed out the presence of the lamella in *Odontostilbe yatai* (valid as *Heterocheirodon yatai*), not present in Uj's *Odontostilbe* species.

Benine (2004) found the presence of the lamella as a synapomorphy for his broad Clade 4, comprising almost all *Moenkhausia* species and several characid genera, *Bario, Astyanax, Phenacogaster, Charax, Oligosarcus, Markiana, Tetragonopterus, Ctenobrycon, Gymonocorymbus, Poptella, Stichonodon,* and *Hemigrammus.* Meanwhile, the reversion to state 0 was a synapomorphy for his Clade 7, including *Piabina, Creagutus, Knodus, Moenkhausia crisneja*, and *Bryconamericus*.

Character 99 (CI = 0.50) - Extrascapular (Ch. 52, Buckup, 1998; Ch. 93, Lucena, 1993; Ch. 127, Zanata & Vari, 2005; Ch. 163, Netto-Ferreia, 2006): (0) present; (1) absent.

We found the extrascapular absent in *Spintherobolus* and *Axelrodia lindeae*, forming clade W, and independently in the miniature characine *Priocharax*. *Aphyocharax* has a reduced extrascapular. Loss of extrascapular is discussed in Weitzman & Fink (1983) regarding *Paracheirodon* reductions, and by Weitzman & Fink (1985) in the Xenurobryconini genera *Xenurobrycon*, and *Tyttocharax*. They also reported the absence of the extrascapular as derived in the characids *Axelrodia riesei*, *Brittanichthys axelrodi*, and *Tyttocharax madeirae* (respectively Figs. 13, 14, 15 in Weitzman & Fink, 1983). The primitive extrascapular was exemplified in *Astyanax* and *Gymnocorymbus* in Weitzman & Fink (1983: figs. 10, 30).

The absent extrascapular is a feature found in many Lebiasinidae, as *Nannostomus* and *Pyrrhulina* (Lucena, 1993; Buckup, 1998), and discussed by Netto-Ferreira (2006) that found this modification not in all species of *Nannostomus*, and *Copeina* as previously reported by Weitzman (1964) and Weitzman & Cobb (1975). Zanata & Vari (2005) the extrascapular is absent in some alestids, *Lepidarchus*, *Ladigesia*, and *Tricuspidalestes*.

Character 100 (CI = 0.25) - Posteroventral border of the coracoid: (0) large and pointed or different of state 1; (1) posterior and ventral borders nearly forming an angle of 90° or slight extended, forming a small point or a truncate corner

State 1 is a new synapomorphy to the Cheirodontinae, but also apomorphic in the clade G formed by *Hemibrycon* + *Diapoma*, in the clade H formed by *Aphyocharacidium* + *Phenacogaster*, and in *Astyanax*.

Cynopotamus and *Charax* are coded as state 0 because they have and angle larger than 90° formed by the posterior and ventral borders of the coracoid. *Spintherobolus* has a reduced coracoid (next Ch. 101), not forming the posteroventral corner, coded as state 0. *Carlana* has an extended posteroventral border of the coracoid different from states 0 and 1, and *Priocharax* a vertically elongate cartilaginous coracoscapular plate (Weitzman & Vari, 1987: Fig. 4), both also coded as state 0.

An expanded coracoid is unique in *Gnathocharax* (here state 0) among Characinae (Lucena, 1998), but also reported to *Lignobrycon* and *Triportheus*. The round posteroventral border of the coracoid is unique to *Gnathocharax*, and different to that illustrated by Malabarba (Fig. 10B-D, 1998) to *Lignobrycon* and *Triportheus.*

Character 101 (CI = 1.00) - Coracoid (Ch. 13, Malabarba, 1998; Ch. 26, Weitzman & Malabarba, 1999): (0) elongate; (1) reduced in length, nearly discoid in shape.

This is a known synapomorphy of *Spintherobolus*, clade X, found by Malabarba (1998) and in Weitzman & Malabarba (1999, fig. 18), here including *Spintherobulus* n. sp.

Fins

Characters of sexual dimorphism relative to fins need fully mature males for a precise description, and are treated as uncoded when males were not available, or coded based on information of nearly related species. This is the case of *Brycon*, *Cynopotamus*, *Gnathocharax*, and *Spintherobolus* n. sp. In *Priocharax*, there were no mature males available of *P. ariel*, but only one fully mature male of *P. pigmaeus*. Information of males of *P. ariel* from Weitzman & Vari (1987), and from mature males of *P. pigmaeus* were also used to code the characters of sexual dimorphism in *Priocharax*. In *Amblystilbe*, *Odontostilbe* n. sp. "e", *Odontostilbe* n. sp. "p", and *Odontostilbe nareuda*, the available males are not fully mature and without well-developed hooks on fins, and then are not coded for most sexually dimorphic characters (unless noted).

Character 102 (CI = 0.33) - Elongation of second dorsal-fin ray of males (Ch. 11, modified of Malabarba, 1998): (0) absent; (1) second unbranched dorsal-fin ray elongate and surpassing the first unbranched dorsal-fin ray, forming a short to long filament.

This elongation was before proposed as a synapomorphy to *Odontostilbe* with *Holoshesthes* in synonym (Malabarba, 1998). Here, the elongate second unbranched dorsal-fin ray is a synapomorphy to the clade A7 containing a polytomy with *Odontostilbe dierythrura*, *O. paraguayensis*, the clade A8 (with the type species *Odontostilbe fugitiva*), and the clade A11 (mostly *Holoshesthes* species). In the clade A11 the terminal clade A16 formed by *H. hemigrammus* and *Holoshesthes* n. sp. "b" do not have any elongate dorsal-fin rays.

Almost all mature males of *Odontostilbe* species share the elongate unbranched dorsal-fin ray, except *O. pulchra* and *O. parecis*. The lack of elongation in dorsal-fin is a derived condition to the clade A12 (*Odontostilbe* n. sp. "h", *Lobodeuterodon* + Clade A14 (*Amblystilbe* + *Prodontocharax*)). However, *Amblystilbe*, in the lack of fully mature males is uncoded for the character. *Odontostilbe nareuda, Odontostilbe* n. sp. "e", and *Odontostilbe* n. sp. "p" are also uncoded to the character, considering the lack of fully mature males.

Similar elongation of the second unbranched dorsal-fin ray, and the unbranched pelvic-fin ray (Ch. 107) in males maybe is a diagnostic feature of *Astyanax fasciatus sensu* Melo & Buckup (2006, fig. 5). Different and non homologous elongations of the dorsal-fin rays are known in other characids, as the second to fourth branched dorsal-fin rays in *Hyphessobrycon elachys* described by Weitzman (1985), or the first, second, third or fourth branched dorsal-fin rays in the rhoadsiines *Carlana* and *Rhoadsia*.

The outgroup taxa *Brycon*, *Cynopotamus*, *Gnathocharax*, and the cheirodontine *Spintherobolus* n. sp are coded as state 0 here and for the next Chs. 106-107, considering the lack of the elongate dorsal-fin rays forming a filament in nearly related species.

A long filament reaching to the adipose fin is present in some males of *O. microcephala*, *Odontostilbe pao*, *Holoshesthes geayi*, and *H. pequira*, all of them coded as state 1. This condition of elongation is not treated in another state because it has considerable intraspecific variation, and the more elongate filaments are more susceptible to be broken.

Character 103 (CI = 0.25) - Elongation of the unbranched pelvic-fin ray of males (Ch. 15, modified of Malabarba, 1998): (0) absent; (1) present.

The presence of this elongation on the pelvic fin is a unique synapomorphy to the Odontostilbini. Exceptions in having the elongate pelvic-fin ray, among the Odontostilbini, are the same species uncoded in the previous Ch. 102, without available fully mature males. *Odontostilbe parecis* is coded as state 0, based on two mature males, the holotype and a paratype. Noteworthy, *Prodontocharax* is coded as state 1, based on a fully mature male with elongate unbranched pelvic-fin ray (USNM 326941). *Amblystilbe*, in the lack of fully mature males is uncoded for this character, and most parcimoniously assumed to have the elongate pelvic-fin ray.

Character 104 (CI = 1.00) - Elongation of fin rays in females: (0) absent; (1) present, elongate unbranched dorsal-, pectoral-, pelvic- and anal-fin rays in mature females.

This is an autapomorphy of *Holoshesthes* n. sp. "p", detailed in Bührnheim & Malabarba (in manuscript), and with a notably elongation of the unbranched pectoral-fin ray. Elongation of fin rays of females seems to be unique in Characids. Females are ordinarily lacking derived features of sexual dimorphism as hooks on fin rays, and usually just showing high body depth measures caused by the belly expansion related the maturation of ovocytes, as in the *Odontostilbe* species (Bührnheim & Malabarba, 1998). Among the markedly sexually dimorphic characid genera, the males usually manifest elongate dorsal fin-rays as *Hyphessobrycon* species of the putative rosy tetra clade (Weitzman & Palmer, 1997), plus anal- and pelvic-fin rays in *Nemathocharax venustus* (Weitzman *et al*., 1986), or still caudal-fin rays as *Nematobrycon* species (Weitzman & Fink, 1971). Other strictly derived sexually dimorphic features as the development of the caudal-fin ray pump are exclusive of males in Glandulocaudini (Weitzman & Menezes, 1998) or Glandulocaudinae *sensu* Weitzman *et al*. (2005). Burns & Weitzman (2005) briefly cited the elaborate derived anatomical secondary sexual characters that facilitate courtship and insemination in Glandulocaudinae and Stevardiinae *sensu* Weitzman *et al*. (2005), as the *Pterobrycon* males that have derived body scales on each body side dorsal to the pectoral fin.

Zanata & Vari (2005: fig. 36) illustrated a male of *Nannopetersius ansorgii* with similar notable elongation of fin rays of the dorsal, pectoral, pelvic and anal fin. The filamentous 1st-3rd pectoral-fin, and the 4th-8th branched anal-fin rays in males of this species are unique among the alestids examined by Zanata & Vari (2005), but in the dorsal, and pelvic-fins occurring in other representatives of the Alestidae.

Character 105 (CI = 0.50) - Adipose fin (Ch. 12, Malabarba, 1998; Ch. 17, Weitzman & Malabarba, 1999; Ch. 90, modified of Serra, 2003): (0) present; (1) absent.

The derived lack of adipose fin is apomorphic in *Spintherobolus* (except *Spintherobulus* n. sp.) among cheirodontines, and in *Priocharax*. This absence of adipose fin is a synapomorphy to *Hasemania* (Serra, 2003: Ch. 90), but with an inclusive Clade 4 defined by another state of the character not seen in cheirodontines, the occasional presence of the adipose.

Character 106 (CI = 0.14) - Number of pelvic-fin rays (Ch. 14, modified of Malabarba, 1998; Ch. 19 modified of Weitzman & Malabarba, 1999; Chs. 70, 74, modified of Benine, 2004; Ch. 138, modified of Zanata & Vari, 2005): (0) i7, rarely some individuals of a given species may present i6 or i6i; (1) i5i, i6, i6i, rarely some individuals of a given species may present i7; (2) i4, i4i, i5, rarely some individuals of a given species may present i5i, i6, i6i.

The outgroup taxa and most cheirodontines have i7 pelvic-fin rays, state 0. State 1 is coded for *Lobodeuterodon*, *Odontostilbe* n. sp. "b", *Odontostilbe* n. sp. "e", and *Odontostilbe* n. sp. "h" that usually have i6i, although some specimens present i7. State 1 is also coded for *Axelrodia lindeae*, *Cheirodon*, *Heterocheirodon*, *Nanocheirodon*, *Serrapinnus heterodon*, and New genus n. sp. C, with usually i6 or i6i pelvic-fin rays, being a new synapomorphy to the Cheirodontinae, modified to state 2 in the clade X with all *Spintherobolus* species. In *Serrapinnus micropterus* and only in *Serrapinnus microdon* of clade V, it is reversed to state 0. In the outgroup taxa, clade E1, *Priocharax* present a lower number of pelvic-fin rays, i5, by parsimony analogous to that of *Spintherobolus*, and *Aphyocharacidium* in the clade H has state 1, i6i pelvic-fin rays.

State 1 is also a synapomorphy to the clade A4 (*Odontostilbe* n. sp. "h" (*Lobodeuterodon euspilurus*, *Amblystilbe* + *Prodontocharax*)), but reversed to state 0 in *Amblystilbe*. In Odontostilbini, state 1 is still present independently in *Odontostilbe* n. sp. "b" and only in *Odontostilbe* n. sp. "e" of the clade A10.

The lower number of pelvic-fin rays described in state 2 was already proposed as a synapomorphy for the species of *Spintherobolus* (Ch. 14, Malabarba, 1998; Ch. 19 Weitzman

& Malabarba, 1999), but not as described here considering the last unbranched pelvic-fin ray in the count ranges, being state 0= i7 and state 1= i5-6.

Benine treated separately the total number of pelvic-fin rays (Ch. 70) and the presence or not of branches in the last pelvic-fin ray (Ch. 74). He found the last pelvic-fin ray unbranched as a synapomorphy for his Clade 7, including *Piabina*, *Creagrutus*, *Knodus*, *Moenkhausia crisnejas*, and *Bryconamericus*, and independently in *Ctenobrycon* and *Gymnocorymbus ternetzi*. He found the presence of seven pelvic-fin rays as derived, and considered as autapomorphies independently derived in *Poptella* and *G. ternetzi* (*versus* 8 pelvic-fin rays in most characids). Benine did not discuss intraspecific variation to these two characters, and did not discuss a possible correlation between them. The exam of cheirodontines revealed a remarked intraspecific variation in the presence of the last unbranched pelvic-fin ray, which causes some variation in the total number of pelvic-fin rays. Counting the last unbranched pelvic-fin ray together with the branched ones can disguise diagnostic patterns of these fin ray counts among species. Thus, the character states established herein are consistent with the intraspecific patterns of variation observed in each species, and are rather consistent in cheirodontines. For example, the two *Heterocheirodon* species, *Prodontocharax melanotus* are diagnosed by the occurrence of both counts, i6 or i6i pelvic-fin rays, or *Lobodeuterodon euspilurus* by i6i, i7. If treating the character as absolute i6 and i7, the *Heterocheirodon* would not fit in these states, and *Lobodeuterodon* would be in the same state of most *Odontostibe* species that have the true i7 count. Regarding the separate character related to the presence or absence of the last pelvic-fin ray, *Heterocheirodon* species and *Lobodeuterodon* would have to assume one of the states, when they equally manifest both states.

Character 107 (CI= 1.00) - Proximal radials of the anal-fin rays in males: (0) the first proximal radial with a conspicuous anteriorly extended lamina, and the 2nd to 5th or 6th proximal radials with a small flat expansions in the sagittal plane on the ventral portion; absence of laminar expansions in the coronal plane; (1) the first proximal radial with a conspicuous anteriorly extended lamina, and the 2nd to 5th, 6th proximal radials with developed flat expansions in the sagittal plane on the ventral portion; the 1st to 5th or 6th proximal radials with conspicuous laminar expansions in the coronal plane, more expanded in mid portion of the proximal radials.

State 1 is an autapomorphy of *Axelrodia lindeae*. We have seen this feature in no other characiforms. At least, this modification seems to be unique in Characidae, strictly different from any other modifications of the sustaining radials of the anal fin and associated to sexual dimorphism. In the characid *Attonitus*, mature males have modifications in the form of the anal-fin base and the proximate ventral portions of the body, the portion of the body along the anal-fin base is convexly expanded ventrally (Vari & Ortega, 2000). In the *incertae sedis* in Characidae "*Cheirodon*" *ortegai*, males have a distinct sigmoid anal-fin base with anterior portion convex and posterior region concave (Vari & Géry, 1980). The proximal radials of the anal-fin rays of *Attonitus* species and "*Cheirodon*" *ortegai* were not described. In Alestids, excepting *Chalceus*, Zanata & Vari (2005) report the fusion of medial and proximal anal-fin rays in males or both sexes.

Brycon, *Cynopotamus*, *Gnathocharax*, and *Spintherobolus* n. sp are coded as state 0, based on nearly related species information, the same applied in the next Ch. 111.

Character 108 (CI = 1.00) - The anteriormost proximal radial of the anal fin: (0) with a short anteriorly extended lamina, not entering abdominal cavity; (1) with an anteriorly extended lamina slightly entering abdominal cavity, between distal portions of the 12th-14th pleural ribs.

State 1 is an autapomorphy of *Spintherobolus* n. sp. Román-Valencia *et al.* (2003: fig. 3) diagnosed a *Grundulus cochae* by a slender anteriormost proximal radial of the anal fin in contrast to that of *G. bogotensis*. Close relationships of *Spintherobolus* and *Grundulus* were refuted by Weitzman & Malabarba (1999), recognized an *incertae sedis* genus in Characidae. Furthermore, the present expanded anteriormost proximal radial of the anal fin in *Spintherobolus* n. sp. seems to be wider than that illustrated to *G. bogotensis*.

Character 109 (CI = 0.66) - Anal-fin rays of males (Ch. 17, Malabarba, 1998; Ch. 10, Weitzman & Malabarba, 1999): (0) anal-fin rays usually circular in cross section and progressively reduced in diameter from the anteriormost element to the posteriormost one; (1) the anterior branched anal-fin rays 1 to 6-8 (usually those bearing hooks) slab shaped, more expanded in the sagittal plane than comparable rays in females; (2) the anterior branched anal-fin rays 1 to 4-5 (usually those bearing hooks) slab shaped, more expanded in the sagittal plane than comparable rays in females.

State 1 is an exclusive synapomorphy for the Clade B in Malabarba (1998: fig. 1) including *Heterocheirodon* + New genus n. sp. C + (*Serrapinnus* + (*Spintherobolus* + †*Megacheirodon*)), with a polytomy in the basal node. Here, state 1 is a unique synapomorphy to clade Q (*Heterocheirodon* + New genus n. sp. C (+ (*Serrapinnus* + (*Axelrodia lindeae* + (*Spintherobolus*)))), and then modified to state 2 only in New genus n.

sp. C. This topology corroborates the alternative topology B of the subclade B showed in fig. 10 by Malabarba (1998), but without †*Megacheirodon* and including *Axelrodia lindeae*.

Among the outgroup taxa *Aphyocharacidium* has about six somewhat expanded anal-fin rays in males, but not as the slab shaped anal-fin rays, and is coded as state 0. *Priocharax* is also coded as state 0, but the fully mature male of *P. pigmaeus* has the 1-3 anterior branched anal-fin rays partially slab shaped in the proximal portions, but not at the middistal portions with hooks.

Brycon, and *Cynopotamus* are coded as state 0 (same in the next Chs. 113-116) since the related species are reported to have anal-fin rays of males bearing hooks but not modified (Lima, 2001; Menezes, 1987). The presence of modified anal-fin rays or hooks is unknown in *Gnathocharax* (Böhlke, 1955), and it is assumed to have the state 0 in this and next Ch. 113-116.

Spintherobolus n. sp is uncoded for this character and the next 110-113, since no mature males are available. By parsimony, this species is assumed to present state 1.

Character 110 (CI = 1.00) - Anal-fin ray segments (Ch. 18, Malabarba, 1998; Ch. 11, Weitzman & Malabarba, 1999): (0) not fused; (1) ray segments of the expanded slab shaped rays progressively fused to each other as the males become fully mature.

The fused anal-fin ray segments is a unique synapomorphy to Subclade C (*Serrapinnus* + *Spintherobolus* + †*Megacheirodon*) in Malabarba (1998). Here, this clade is confirmed, though not including †*Megacheirodon*, and with the insertion of *Axelrodia lindeae* in clade T. Furthermore, the presence of fused anal-fin ray segments was found also in the outgroup *Aphyocharacidium*, not more being an exclusive feature of these cheirodontine genera. Malabarba (1998: 201) affirmed that *Aphyocharacidium* sp., of uncertain relationships in Characidae, did not share the Cheirodontinae synapomorphies, but greatly resembles Characinae taxa as *Phenacogaster*. Here the *Aphyocharacidium bolivianum* appear as basal in clade J, being a sister species of the clade K including exactly *Phenacogaster* + Cheirodontinae. Noteworthy, a clade formed by *Aphyocharacidium* + *Phenacogaster* is obtained in the weitghted and unweighted cladograms (Figs. 2, 3), reinforcing close relationships between them. Géry (1973: 102) when described *A. bolivianum* did not examined mature males, "no sexual hooklets observed".

Priocharax is coded as state 0, as *P. pigmaeus* do not have fused segments on the anal-fin rays.

Character 111 (CI = 0.66) - Proximal apex of the anal-fin rays of males (Ch. 19, Malabarba, 1998; Ch. 12, Weitzman & Malabarba, 1999): (0) lacking an anterior extension; (1) with lepidotrich bases extended anteriorly; (2) the lepidotrich bases extended anteriorly penetrating between the lepidotrichia base of nearest anterior fin ray.

State 1 is another unique synapomorphy to the Clade B of Malabarba (1998) including *Heterocheirodon* + New genus n. sp. C + (*Serrapinnus* + (*Spintherobolus* + †*Megacheirodon*)), with a polytomy in the basal node. Here state 1 corroborates this clade and agrees with topology B in fig. 10 of Malabarba (1998), but without the extinct genus in the analysis, and including *Axelrodia lindeae*.

State 2 was described by Malabarba (1994: Ch. 23, state 2) as a synapomorphy of *Serrapinnus kriegi* and of an undescribed species of *Serrapinnus* (both not examined here), also found in *Spintherobolus broccae*. Here, this condition is shared by *S. ankoseion* and *S. broccae*, being a unique synapomorphy to clade Z. The unique male available of *Spintherobolus papilliferus* in alcohol seems do not have the lepidotrichia bases extended anteriorly, and is coded as state 0.

Character 112 (CI = 0.27) - Anal-fin profile of males (Ch. 20, modified of Malabarba, 1998): (0) concave to almost straight; absence of sexual dimorphism; (1) anterior lobe pointed and distal profile concave; sexually dimorphic; the last unbranched anal-fin ray and first two branched anal-fin rays in males elongate, longer than in females; (2) almost straight profile to slight concave; sexually dimorphic; the last unbranched anal-fin ray and 1st to 10th branched anal-fin rays in males somewhat longer than in females; (3) concave, anterior lobe slightly convex; sexually dimorphic; the last unbranched anal-fin ray and 1st to 5th-6th branched anal-fin rays in males somewhat longer than in females.

The presence of sexual dimorphism in the anal-fin profile of the cheirodontines was evaluated only in *Nanocheirodon* by Malabarba (1998: Ch. 20), and corresponds to the present state 1. Here, we redefine the character to include two additional states found in the cheirodontines. The state 1 define *Nanocheirodon* as in Malabarba (1998). State 2 is independently derived in the Compsurini, in the Cheirodontini *Cheirodon interruptus*, and in the Odontostilbini in clade A3 (*Pseudocheirodon*), and clade A5 (*Lobodeuterodon* + (*Prodontocharax* + *Amblystilbe*). State 3 is uniquely derived in clade Q containing *Heterocheirodon* + (New genus n. sp. C + (*Serrapinnus* (*Axelrodia lindeae* + *Spintherobolus*). The state 3 seems to be related to the development of the slap shaped anal-fin rays.

Spintherobolus papilliferus has a modified rounded anal-fin profile only checked in the unique mature male available, probably an autapomorphy, uncoded here. It was not possible to code the character for *Amblystilbe* by the lack of fully mature males. Some outgroup taxa have not only males, but also females with the anal-fin profile nearly straight, as *Phenacogaster*.

A male and a female of *Acinocheirodon* are illustrated by Malabarba & Weitzman (1999: figs. 1-2), with the anal-fin profile not well-defined by the gray contrast. The anal-fin profiles of males and a female of *Kolpotocheirodon theloura* (Malabarba & Weitzman, 2000, figs. 1-3,) also show the almost straight to slightly concave profile in males. However, this is better seen in two males and one female of *K. figueiredoi* illustrated by Malabarba *et al*. (2004: figs. 5, 6, 7).

Character 113 (CI = 1.00) - Ligament between anal-fin rays of males (Ch. 21, Malabarba, 1998): (0) a small ligament uniting the basal segment of lepidotrichia of the anal-fin rays proximally; (1) presence of huge obliquely-aligned ligaments between enlarged anal-fin rays of males, connected approximately at midlength of posterior face of the basal segment of lepidotrichia to the proximal anterior face of the opposing basal segment of lepidotrichia; ligament diameter nearly equal to expanded anal-fin ray diameter.

This is an exclusive synapomorphy for the Clade B of Malabarba (1998) including *Heterocheirodon* + New genus n. sp. C + (*Serrapinnus* + (*Spintherobolus* + †*Megacheirodon*)), with a polytomy in the basal node. Here, as in the previous characters 109 and 111 the obtained clade Q confirms the topology B in fig. 10 of Malabarba (1998), but without the extinct genus in the analysis and including *Axelrodia lindeae*.

Character 114 (CI = 0.16) - Extent of the laterosensory canal of the lateral line onto caudal fin (Ch. 125, modified of Zanata, 2000; Ch. 163, modified of Zanata & Vari, 2005): (0) not extended between caudal-fin rays, reaching or not to the caudal-fin base; (1) relatively long, extending nearly half-length of the middle caudal-fin rays; (2) long, practically reaching to posterior tip of middle caudal-fin rays.

The laterosensory canal extending onto the caudal fin usually remains in c&s specimens, conspicuously between the 10th and 11th principal caudal-fin rays. Curiously, this feature was noticed by Hoedeman (1952) in *Gasteropelecus* species that proved to be an extension of the lateral line tube by filling it with a carmin-solution and tracking its path from the caudal fin to the opercle.

The Odontostilbini has a derived somewhat long laterosensory canal extending onto middle caudal-fin rays, state 1, a synapomorphy to them, but not as long as that of state 2 derived in *Brycon pesu* and *Cynopotamus*. This state 2 is an additional state to the character, not considered by Zanata (2000). She considered just two states in her Ch. 125 (state 0, lateral line reaching to caudal peduncle; state 1, extended lateral line onto median caudal-fin rays), finding the state 1 apomorphic to *Brycon*. Zanata (2000: 152) referred the "*Odontostilbe* aff. *paraguayensis*" as possessing an incomplete lateral line, and considered the Ch. 125 inapplicable to it. This an error because *O. paraguayensis* posses a complete lateral line. The "*O.* aff. *paraguayensis*" examined by Zanata, MZUSP 38055 from rio Taquari, Mato Grosso, Brazil, is probably a cheirodontine species with incomplete lateral line beloning to the genus *Serrapinnus*). Actually, most *Odontostilbe* species have a relatively long laterosensory canal onto the caudal fin, excepting *Odontostilbe* n. sp. "b" with incomplete lateral line, reversed to state 0.

New gen. n. sp. C. (Malabarba, 1998) was coded as state 0, but similarly to *Phenacogaster*, the laterosensory canal is slightly extending through end of caudal peduncle (posterior border of hypural fan), not as long as in other cheirodontines. On the other hand, *Saccoderma,* coded as state 1, shows a somewhat longer laterosensory canal reaching to the base of caudal-fin rays branches, not as long as that of *Brycon*. All the other Compsurini shares state 0, having an incomplete lateral line, which is a feature of most species of the Cheirodontini, *Aphyocheirodon hemigrammus* and *Pseudocheirodon arnoldi*.

Hemibrycon is among the species of Zanata (2000) that share the plesiomorphic state. The exam of *Hemibrycon surinamensis* (MZUSP 30529, same lot Zanata examined) revealed that it shares the relatively long laterosensory canal with most cheirodontines. The *Hemibrycon* sp. here examined, and the outgroup taxa *Astyanax*, and *Gnathocharax* have independently the relatively long laterosensory canal on the caudal fin.

Character 115 (CI = 1.00) - Hypural (Ch. 31, Malabarba, 1998): (0) autogenous or different from state 1; (1) hypural 1 fused to parhypural.

The state 1 is an autapomorphy of *Saccoderma hastata* as verified by Malabarba (1998). Remarkably, two specimens of *Carlana*, a male and a female, have hypurals 1, 2, 3 fused, being hypurals 1-2 fused along all the extension of the contact between the two bones, and 2-3 only fused on anterior portion. This was not described by Fink & Weitzman (1974), and is unknown to other Rhoadsinae (A. Cardoso, pers. comm.).

Character 116 (CI = 0.50) - Hemal spines and procurrent caudal-fin rays support (Ch. 32, Malabarba, 1998; Ch. 9, Weitzman & Malabarba, 1999): (0) hemal spines of posterior one, two, or sometimes three caudal vertebrae directly articulating with the ventral procurrent caudal-fin rays; (1) hemal spines of at least the four posterior caudal vertebrae, those anterior to the terminal "half centrum" and its processes, elongate and associated with the ventral procurrent caudal-fin rays support.

State 1 is a recognized unique synapomorphy for the Cheirodontini by Malabarba (1998), now including *Axelrodia lindeae*, and reversed to state 0 in *Spintherobolus* n. sp.

Character 117 (CI = 1.00) - Hemal spines (Ch. 33, Malabarba, 1998): (0) hemal spines of the posterior three caudal vertebrae elongate; (1) hemal spines of the four posterior caudal vertebrae of adult males, those anterior to the terminal "half centrum" (preural vertebrae) and its processes with slab shaped tips.

State 1 is a recognized unique synapomorphy to the Subclade C of Malabarba (1998) containing *Serrapinnus* + *Spintherobolus* + †*Megacheirodon*, now including *Axelrodia lindeae*. However, *Spintherobolus* n. sp. and *S. papilliferus* are uncoded to the character; the former by the lacking of mature males, and the latter by the lacking of mature males c&s. By parsimony they would share state 1.

Only two hemal spines of the posterior caudal vertebrae of adult males of *Serrapinnus micropterus* are slab shaped, but it is coded as state 1 considering their putative homology with remaining *Serrapinnus* species.

Brycon, *Cynopotamus*, and *Gnathocharax* are coded as state 0, based on the lack of this modification on nearly related species.

Character 118 (CI = 1.00) - Caudal-fin rays in males (Ch. 34, Malabarba, 1998): (0) not modified as described in states 1 or 2; (1) thirteenth and fourteenth caudal-fin rays curved, dorsally concave along their proximal half length, bearing ventrally expanded segments; (2) twelfth and thirteenth caudal-fin rays curved, dorsally concave along their proximal half length, bearing ventrally expanded segments.

State 1 is a unique synapomorphy to *Acinocheirodon* (Malabarba, 1998; Malabarba & Weitzman, 1999: figs. 4, 5) and state 2 a unique synapomorphy to *Kolpotocheirodon theloura* (Malabarba, 1998; Malabarba & Weitzman, 2000: fig. 4).

Spintherobolus n. sp. and the outgroup taxa *Brycon*, *Cynopotamus*, or *Gnathocharax* are coded as state 0 (same in next Chs. 122-138).

Character 119 (CI = 1.00) - Distance between caudal-fin rays in males (Ch. 35, modified of Malabarba, 1998): (0) regular, not differentiated between a given pair or group of caudal-fin rays; (1) the 13th through the 15th principal caudal-fin rays of males ventrally bowed, with larger spaces between 12th to 15th principal caudal-fin rays than found between other caudal-fin rays; (2) a large space between the 12th and 13th caudal-fin rays, filled with hypertrophied tissues.

The state 1 is an exclusive condition of *Acinocheirodon* (Malabarba, 1998; Malabarba & Weitzman, 1999: figs. 4, 5), and state 2 to *Macropsobrycon* (Malabarba, 1998). A distance between 15th and 17th caudal-fin rays increasing and filled with hypertrophied soft tissues is found in "*Odontostilbe*" *dialeptura* and not included in present study (Malabarba, 1998).

Character 120 (CI = 1.00) - Skin flaps along the caudal and dorsal-fin rays in males (Ch. 36, Malabarba, 1998): (0) smooth; (1) marginated with papillae.

The skin flaps along the caudal and dorsal-fin rays bearing hypertrophied papillae were described only in *Kolpotocheirodon theloura*, being more numerous and developed in males (Malabarba & Weitzman, 2000: fig. 5; Malabarba *et al.*, 2004: figs. 3, 9).

Character 121 (CI = 1.00) - “Pineapple” organs of the caudal fin of males: (0) absent; (1) present.

Kolpotocheirodon theloura and *K. figueiredoi* share modified tissues in the ventral lobe of the caudal fin of males, forming what was called a pineapple organs by Malabarba *et al.* (2004: figs.1-3), apparently derived of modified club cells.

Character 122 (CI = 1.00) - Skin flaps along the rays of the lower lobe of the caudal-fin in males (Ch. 37, Malabarba, 1998): (0) not excessively developed; (1) well-developed; roundish skin flaps along the dorsal margins of 15th to 19th caudal-fin rays.

These modified skin flaps are exclusive of *Compsura* and *Saccoderma* as noted by Malabarba (1998), here clade L.

Character 123 (CI = 1.00) - Skin flaps along the lower lobe of the caudal-fin rays in males (Ch. 38, Malabarba, 1998): (0) not excessively developed; if developed not associated with 14th caudal-fin ray; (1) the 14th and 15th principal caudal-fin rays of males with a large dorsally extending flap that overlaps the 14th ray along almost its entire length; there is a ventral, smaller flap, along the posterior half of this structure that does not overlap the 15th principal caudal-fin ray ventrally.

In *Acinocheirodon* the skin flaps along 14th and 15th principal caudal-fin rays of males are uniquely large, well-developed, among cheirodontines (Malabarba & Weitzman, 1999: fig. 6).

Character 124 (CI = 0.40) - Number of ventral procurrent caudal-fin rays of males (Ch. 42, Malabarba, 1998; Ch. 5, modified by Weitzman & Malabarba, 1999): (0) 5 to 13 ventral elements, a number nearly identical to or slightly smaller than dorsal series; (1) 11 to 16 ventral elements, a number nearly identical to or slightly smaller than dorsal series; (2) 16 to 30 ventral elements, a number always larger than and never overlapping number of dorsal procurrent caudal-fin rays.

Malabarba (1998) described state 0 as possessing 5 to 11 ventral procurrent caudal-fin rays. A review of several species of the genus *Odontostilbe* (partially in Bührnheim & Malabarba, 2006), revealed that a range reaching 12-13 elements is not unusual in species with a small number of ventral procurrent caudal-fin rays, and state 0 is changed to 5-13. *Heterocheirodon* species have an intraspecific range of 9-14 ventral procurrent caudal-fin rays (Malabarba & Bertaco, 1999), and so both states 0 and 1 can be assigned to its species. We follow Malabarba (1998) and (Malabarba & Bertaco, 1999) in assigning state 1 for *Heterocheirodon* species, a decision further supported by several homologies shared by that genus with other genera bearing 11 to 16 ventral procurrent caudal-fin rays (*Serrapinnus*, *Spintherobolus* and †*Megacheirodon*). The New genus n. sp. C, with a range of 16-19 ventral elements was coded as state 1 by Malabarba (1998), considering the distinct general morphology of these elements in comparison to that of *Nanocheirodon*, and *Cheirodon*. Here the same is applied. Thus, state 1 is a unique synapomorphy to the Cheirodontini, and uniquely modified to state 2 in the clade O, *Nanocheirodon* + *Cheirodon*, as in Malabarba (1998). None mature males of *Spintherobolus* n. sp. are available, and then it is conservatively uncoded for the character. However, the counts for this species observed in unsexed specimens are 7-9 ventral procurrent caudal-fin rays. In the remaining *Spintherobolus* species even females and immature specimens have higher number of ventral procurrent caudal-fin rays 11 to 16 (state 1).

Character 125 (CI = 1.00) - Sexual dimorphism in the number of ventral procurrent caudal-fin rays (Ch. 43, Malabarba, 1998): (0) absent; (1) larger number of ventral procurrent caudal-fin rays in males, not overlapping observed ranges in females.

State 1 is only known in *Nanocheirodon*, as in Malabarba (1998).

Character 126 (CI = 0.66) - Lepidotrichia of the ventral procurrent caudal-fin rays of females (Ch. 44, Malabarba, 1998; Ch. 7, Weitzman & Malabarba, 1999): (0) lepidotrichia forming a "V" shaped bone in frontal view with the two halves fused only distally; (1) anterior ventral procurrent caudal-fin rays of females with proximal portions of the ray-halves fused to each other, usually retaining an opening near their distal tips; giving a needle-like shape to these rays; (2) the 2, 3, or 4 anteriormost ventral procurrent rays laminar in both males and females, without opening near distal tip, or having a characteristic "V" shaped bone.

All the species of the tribe Cheirodontini have the ventral procurrent caudal-fin ray-halves fused proximally, retaining or not an opening near their distal tips and are coded as state 1 as in Malabarba (1998). *Spintherobolus. papilliferus* is coded as state 1, though the females of *S. papilliferus* are not c&s and the ventral procurrent caudal-fin rays are not totally visible.

Character 127 (CI = 1.00) - Lepidotrichia of the ventral procurrent caudal-fin rays of males (Ch. 45, modified of Malabarba, 1998; Ch. 6, Weitzman & Malabarba, 1999): (0) lepidotrichia forming a "V" shaped bone in frontal view with its two halves fused only distally; (1) lepidotrichia of each ventral procurrent caudal-fin ray of males fused along entire length and becoming progressively laminar with maturation; (2) lack of sexual dimorphism in procurrent caudal-fin rays, being identical to state 2 described for females in Ch. 128.

State 1 is a known synapomorphy for the Cheirodontini, excepting *Heterocheirodon* with state 2, as in Malabarba (1998). At present, *Axelrodia lindeae* also shares state 1.

Spintherobolus n. sp. is coded as state 1, even without available mature males, considering the overall homologies shared with the remaining genera of Cheirodontinae.

Character 128 (CI = 1.00) - Shape of the anterior ventral procurrent caudal-fin rays of males (Ch. 46, Malabarba, 1998): (0) lateral laminar bony extensions absent; (1) the anterior ventral procurrent caudal-fin rays of males with lateral laminar bony extensions between skin and muscles.

These laterally expanded anterior ventral procurrent caudal-fin rays are only known in *Cheirodon* and *Nanocheirodon* (Malabarba, 1998: fig. 11a, b).

Character 129 (CI = 0.50) - Distal tip of the anterior ventral procurrent caudal-fin rays of males (Ch. 47, Malabarba, 1998; Ch. 8, Weitzman & Malabarba, 1999): (0) the anterior ventral procurrent caudal-fin rays buried in muscles and skin and not visible along ventral surface of caudal peduncle; (1) the most of anterior ventral procurrent caudal-fin rays of males projecting far enough through muscles and skin to be seen along ventral margin of the caudal peduncle, and forming sort of keel.

The ventral keel on the caudal peduncle is a known synapomorphy for the Cheirodontini, only absent in *Heterocheirodon* (Malabarba, 1998: fig. 4; Malabarba & Bertaco, 1999: fig. 3).

Spintherobolus n. sp. is coded as state 1 here, considering all other *Spintherobolus* and Cheirodontini share the presence of the keel.

Character 130 (CI = 1.00) **-** Distal tip of the ventral procurrent caudal-fin rays of males (Ch. 48, Malabarba, 1998): (0) distal tip of all procurrent rays slender and posteriorly directed; (1) exposed tip of the ventral procurrent caudal-fin rays of males enlarged, with distal tip curved and oriented towards the anal-fin base.

This is a synapomorphy of *Cheirodon* and *Nanocheirodon*, the Clade A in Malabarba (1998), while its sister group Clade B with *Heterocheirodon*, New genus and sp. C, S*errapinnus*, *Spintherobolus* and †*Megacheirodon* shares a spatulate and usually rounded distal tip of the ventral procurrent caudal-fin rays (next Ch. 135).

Spintherobolus n. sp. is coded as state 0 here, considering all other *Spintherobolus* species and Cheirodontini share the presence of the keel.

Character 131 (CI =0.50) - Ventral procurrent caudal-fin rays position in males (Ch. 49, Malabarba, 1998): (0) procurrent caudal-fin rays angled relative to body axis and posteriorly directed; (1) main axis of the ventral procurrent caudal-fin rays not supported by the parhypural perpendicular to body axis, and main axis of the anteriormost ventral procurrent caudal-fin rays angled relative to body axis with their tips anteriorly directed.

The state 1 was found apomorphic to *Serrapinnus* and New genus n. sp. C in the Clade B of Cheirodontini by Malabarba (1998: fig. 13). *Axelrodia lindeae* also shares this condition, and this is here by parsimony interpreted as a unique synapomorphy of the present clade S, reversed to state 0 in *Spintherobolus* (clade X), supporting the alternative topology B in Malabarba (1998: fig. 10). *Spintherobolus* n. sp. is coded as state 0, considering all other *Spintherobolus* species share state 0 as a reversion.

Character 132 (CI = 1.00) - Fused ventral procurrent caudal-fin rays of males (Ch. 50, Malabarba, 1998): (0) lacking lateral laminar bony extensions; (1) with a large lateral laminar bony extensions between skin and muscles.

The lateral laminar extension on fused ventral procurrent caudal-fin rays is only present in males of *Spintherobolus* (character not listed in Weitzman & Malabarba, 1999: fig. 8). As this is not present in Cheirodontini, we conservatively uncoded that to *Spintherobolus* n. sp. that lacks a mature male (the same for the Ch. 133-134).

Character 133 (CI = 1.00) - Ventral procurrent caudal-fin rays of males (Ch. 51, Malabarba, 1998, Ch. 23, Weitzman & Malabarba, 1999): (0) the anterior ventral procurrent caudal-fin rays not reduced in proximal portions; (1) the anterior ventral procurrent caudal-fin rays of males with proximal portions reduced, not rising above area of fusion between rays, while posterior dorsal portions of these rays are fused into a flat compressed plate that inserts between the hemal spine of the antepenultimate vertebra and the hemal spines of the adjacent anterior vertebrae.

The reduction of the proximal portions of fused ventral procurrent caudal-fin rays is only present in males of *Spintherobolus* (Weitzman & Malabarba, 1999: fig. 8).

Character 134 (CI = 1.00) - Ventral procurrent caudal-fin rays of males (Ch. 52, Malabarba, 1998; Ch. 22, Weitzman & Malabarba, 1999; Ch. 22, Weitzman & Malabarba, 1999): (0) absence of fused elements; (1) all elements not articulating to the parhypural fused in mature males.

This is another modification of fused ventral procurrent caudal-fin rays only present in males of *Spintherobolus* (Weitzman & Malabarba, 1999: fig. 8).

Character 135 (CI = 1.00) - Distal tip of ventral procurrent caudal-fin rays of males (Ch. 53, Malabarba, 1998; Ch. 14, Weitzman & Malabarba, 1999): (0) distal tip of all procurrent rays slender; (1) adult males have distal tip of ventral procurrent caudal-fin rays spatulate and rounded in profile.

The state is present in *Heterocheirodon*, *Serrapinnus*, *Spintherobolus*, New genus n. sp. C, and † *Megacheirodon*, the Clade B of the Cheirodontini in Malabarba (1998: fig. 13a,b), here forming the clade Q also includingin *Axelrodia lindeae*. *Spintherobolus* n. sp. is coded as state 1 since mature males are nor available. Considering the overall presence of these ventral procurrent caudal-fin rays spatulate and rounded in the clade Q, the *Spintherobolus* n. sp. is coded as state 1.

Character 136 (CI = 1.00) - Penultimate and antepenultimate procurrent caudal-fin rays of males (Ch. 54, Malabarba, 1998): (0) not expanded; (1) with distal tips ventrally expanded, forming a small keel in the ventral profile of the caudal fin.

This is an autapomorphy of *Acinocheirodon melanogramma* (Malabarba & Weitzman, 1999: fig. 1, 3).

Fin hooks

Character 137 (CI = 0.08) - Hooks on the first unbranched pelvic-fin ray in males: (0) absent; (1) hooks on the mid portion of the first unbranched pelvic-fin ray.

In the Cheirodontini, the state 1 is a derived character to the clade P (*Cheirodon ibicuhiensis* + *C. interruptus*), to the clade V (*Serrapinnus heterodon* + *S. microdon*), and to the clade X (*Spintherobolus* species). In the Compsurini, state 1 is a synapomorphy to the clade N (*Acinocheirodon* + *Macropsobrycon*). Among Odontostilbini, hooks on the mid portion of the first unbranched pelvic-fin ray are present independently in *O. microcephala*, *O. pulchra*, *Lobodeuterodon*, *Pseudocheirodon arnoldi* and in clade A12 with *Holoshesthes* species (except *Holoshesthes* n. sp. "p and *H. hemigrammus*).

Among outgroup taxa, hooks are reported to the first unbranched pelvic-fin ray in *Phenacogaste*r and *Aphyocharacidium* (both composing a clade in the weitghted and unweigthed cladogram, Figs. 2, 3). In *Phenacogaster* this character has to be checked considering interspecific variation, as in Lucena (2003) *P. carteri* (unique male examined), *P. jancupa* (males probably not fully mature in Malabarba & Lucena (1995)), *Phenacogaster* n. sp. E, n. sp. I, and n. sp. G do not have these hooks, but otherwise *P. calverti*, *P. franciscoensis*, *Phenacogaster* n. sp. A, n. sp. C, n. sp. D, n. sp. F, n. sp H, and n. sp. J have the hooks on the firt unbranched pelvic-fin ray.

Pseudocheirodon arnoldi is coded as state 1 based on the reported presence of hooks on the unbranched pelvic-fin ray in Fink & Weitzman (1974), not seen in the present examined males. *Spintherobolus* n. sp. is uncoded for the character, even though most Cheirodontini, including the remaining *Spintherobolus* species have hooks on the first unbranched pelvic-fin ray in males, because there is a reversion to state 0 in the nearly related *Axelrodia lindeae*.

In *Cynopotamus tocantinensis*, hooks are present on the anal-fin rays, but not on the pelvic-fin rays (Menezes (1987). In *Brycon*, there are some species with pelvic-fin hooks as

Brycon coquenani, but most species have hook only on the anal-fin rays (Lima, 2001), and then it is uncoded in the present analysis. The character is considered inapplicable to *Gnathocharax*, with unknown hooks in males.

Character 138 (CI = 1.00) - Hooks on the fins of males: (0) distributed in pelvic- and anal-fin rays, or different from state 1; (1) distributed in dorsal-, pectoral-, pelvic-, anal-, and caudal-fin rays.

Noteworthy, the presence of hooks on all fins is a uniquely derived feature of the clade A16 formed by *Holoshesthes* n. sp. "b" and *Holoshesthes hemigrammus*. However, this was not regularly observed in *H. hemigrammus*, that has just one examined male 29.9 mm SL (NRM 17307) with vestigial (not well-developed) hooks on dorsal- and pectoral-fin rays, beyond those on the pelvic- and anal-fin rays. Another male 27.2 mm SL, same lot, has vestigial hooks pelvic- and anal-fin rays, and on distal portions of the 1st to 6th, and 15th to 19th principal caudal-fin rays, but none on dorsal- and pectoral-fin rays.

Astyanax species are reported to have hooks in all fins. However, *A. troya* do not have hooks on all dorsal-fin rays, neither all pectoral-fin rays (Azpelicueta *et al*., 2002), *A. ojiara* in the 1st to penultimate branched dorsal-fin rays (Azpelicueta *et al*., 2000). Another species remarked to have many fins with hooks is *A. leonidas*, but it does not have hooks on dorsal-fin (Azpelicueta *et al*., 2002), and *A. elachylepis* does not have on the caudal-fin rays (Bertaco & Lucinda, 2005). Casciotta & Almirón (2004) commented that presence of hooks on all fins could be a derived character of *A. chico*, *A. pynandi*, *A. ojiara*, *A. troya*, and *A. stenohalinus*. The *A. chico* and *A. pynandi* do not have hooks on all dorsal-fin rays (Casciotta *et al*., 2003; Casciotta & Almirón, 2004). Contrasting, the Cheirodontinae new genus n. sp. bul always have hooks on 2nd unbranched dorsal-fin rays, on all pectoral- and pelvic-fin rays. *Hyphessobrycon* species such *H. hamatus* have hooks on almost all fins, but again not all dorsal-, and pectoral-fin rays, and none hooks on the caudal-fin rays (Bertaco & Malabarba, 2005).

Brycon coquenani has hooks on dorsal-, pectoral-, pelvic-fin rays in males (Lima, 2001), but the genus is coded as state 0 for the character. Some *Phenacogaster* species as *P. carteri* bears hooks on pectoral-fin rays (Lucena, 2003).

Character 139 (CI = 1.00) - Hooks on the pelvic-fin rays of females (Ch. 16, Malabarba, 1998): (0) absent; (1) present.

The hooks on the pelvic-fin rays of females are exclusively present in females of *Cheirodon*. In *Brycon* n. sp. "Pardo", Lima (2001) found hooks on the anal-fin rays of one female, not in pelvic-fin rays. *Brycon*, *Cynopotamus*, *Gnathocharax*, and *Spintherobolus* n. sp. are coded as state 0, based on nearly related species without hooks on females. As this is present in some Cheirodontini, though only in *Cheirodon*, we conservatively uncoded that to *Spintherobolus* n. sp. that lacks a mature male.

Character 140 (CI = 0.33) - Number of hooks per bony ray segment on the anal fin of males (Ch. 22, modified of Malabarba, 1998): (0) 1-2 hooks, rarely 1-3, on posterior border of hook-bearing anal-fin ray segments; (1) 2-5 hooks, usually 2 or 3, on posterior border of hook-bearing anal-fin ray segments.

This is an exclusive synapomorphy for the Clade B of Malabarba (1998) including *Heterocheirodon* + New genus n. sp. C + (*Serrapinnus* + (*Spintherobolus* + †*Megacheirodon*)) in a polytomy in the basal node. Here, the obtained clade Q confirms the topology B in fig. 10 of Malabarba (1998), but without the extinct genus in the analysis and including *Axelrodia lindeae*. Malabarba (1998: 22) described state 1 range as 1-2 hooks, but we found intraspecific variation of 1-3 hooks in some species. State 1 is also independently present in the Cheirodontini *Cheirodon ibicuhiensis* as noted by Malabarba (1998).

Spintherobolus n. sp. with none fully mature males examined and *Spintherobolus papilliferus* lacking hooks on the anal-fin rays in only one male availiable are uncoded to the character considering not all Cheirodontinae present the condition in state 1. *Spintherobolus ankoseion* and *S. broccae* are coded as state 1 considering Weitzman & Malabarba (1999) report's of hooks to these species. *Spintherobolus* n. sp. is also uncoded for the character as mature males are lacking.

This character is considered inapplicable to *Carlana* (same in the next Chs. 141-150) because it does not have anal-fin hooks, but other structures named spinules by Fink & Weitzman (1974), commented in the next Ch. 151. *Gnathocharax* hooks are unknown, but coded as state 0 assuming no report of modification similar to state 1 in nearly related species (same in the next Chs. 141-150).

Character 141 (CI = 1.00) - Hooks on the first branched anal-fin ray of males (Ch. 23, Malabarba, 1998): (0) present; (1) absent.

The absence of hooks on the first branched anal-fin ray of males is exclusive in *Nanocheirodon*.

Spintherobolus n. sp. with none fully mature males examined and *S. papilliferus* with no hooks on anal-fin rays are coded as state 0, considering all Cheirodontinae have hooks on first branched anal-fin ray of males. *Brycon*, and *Cynopotamus*, with none fully mature males examined, are coded as state 0 based in Lima (2001), and Menezes (1987), respectively.

Character 142 (CI= 1.00) - Hooks distribution on anal-fin rays of males (Ch. 24, Malabarba, 1998): (0) distributed along variable number of anal-fin rays, and different from state 1; (1) hooks well-developed on slab shaped anal-fin rays only, along almost their entire lengths.

This character is a synapomorphy to the Clade B of Malabarba (1998) including *Heterocheirodon* + New genus n. sp. C + (*Serrapinnus* + (*Spintherobolus* + †*Megacheirodon*)) in a polytomy in the basal node. This clade is confirmed here, now including *Axelrodia lindeae* but without the fossil species in the analysis.

Among *Spintherobolus species*, *S. ankoseion* and *S. broccae* are reported to have 2-4 extremely reduced hooks per segment on 1st to 2nd branched anal-fin rays by Weitzman & Malabarba (1999). The *S. broccae* hooks were seen in only one male among 14 males of lot USNM 342064, and *S. ankoseion* hooks were found in three of six examined males, all not examined at the present work. However, *S. ankoseion* and *S. broccae* are coded as state 1 considering these reports of hooks by Weitzman & Malabarba (1999). *Spintherobolus* n. sp. is not coded by the unknown hooks, and *S. papilliferus* by the absence of them in the male available.

Character 143 (CI= 1.00) - Hooks distribution on anal-fin rays of males (Ch. 29, Malabarba, 1998): (0) distributed along variable number of anal-fin rays, and different from state 1; (1) hooks well-developed on anal-fin rays i4 only.

This was reported to be unique in *Saccoderma* by Malabarba (1998). At present, up to six branched anal-fin rays with hooks are observed in *Saccoderma hastata*, identified from the río Magdalena basin. We conservatively do not modify the present character waiting for the taxonomic revision of the Compsurini.

Character 144 (CI= 1.00) - Hooks distribution on anal-fin rays of males (Ch. 30, Malabarba, 1998): (0) distributed along variable number of anal-fin rays, and different from state 1; (2) hooks on anal-fin rays i5 only.

This was reported to be unique in *Kolpotocheirodon* by Malabarba (1998). The examined *K. theloura* revealed i6 well-developed anal-fin rays with hooks, reaching to i7 rays in one specimen. We conservatively do not modify the present character waiting for the taxonomic revision of the Compsurini.

Character 145 (CI= 100) - Distribution of hooks on the anal-fin ray of males (Ch. 25, Malabarba, 1998): (0) anal-fin hooks paired, bilaterally symmetrical; (1) anal-fin hooks bilaterally asymmetrical, with irregular arrangements, unpaired, and differing in number and position between contralateral segments of the lepidotrichia.

This is another exclusive synapomorphy for the Clade B of Malabarba (1998) including *Heterocheirodon* + New genus n. sp. C + (*Serrapinnus* + (*Spintherobolus* + †*Megacheirodon*)) in a polytomy in the basal node. Here, the obtained clade Q confirms the topology B in fig. 10 of Malabarba (1998), but without the extinct genus in the analysis and including *Axelrodia lindeae*.

Spintherobolus ankoseion, and *S. broccae* are coded as state 1 considering the report of hooks to these species by Weitzman & Malabarba (1999), as well the hooks described to †*Megacheirodon unicus* by Malabarba (1998: fig. 5). Conservatively, *Spintherobolus* n. sp. is not coded by the absence of males, and *S. papilliferus* by the absence of hooks in the unique male available, considering not all the Cheirodontini shares state 1.

One not fully mature male of *Amblystilbe* has one pair of symmetrical hooks on the segments of the 1st to 3rd branched anal-fin rays. *Aphyocharacidium* have somewhat expanded anal-fin rays, not slab shaped, and have bilateral symmetrical hooks. *Cynopotamus* is coded as state 0, assuming symmetrical hooks, because they are not described in detail by Menezes (1987), and not observed in the examined material.

Character 146 (CI = 1.00) - Arrangement of the anal-fin hooks of males (Ch. 26, Malabarba, 1998): (0) positioned along the posterolateral border of the anal-fin rays, with their distal tips dorsally curved and oriented towards the anal-fin base, retrorse hooks, or different from state 1; (1) positioned along the posterolateral border of the anal-fin rays, with distal tip curved over lateral surface of the anal-fin rays and directed to the anterior surface of the anal-fin ray.

This is a synapomorphy for the Compsurini recognized by Malabarba (1998). *E.g. Kolpotocheirodon theloura*, have this distal tip of anal-fin hooks curved over lateral surface of anal-fin rays (Malabarba & Weitzman, 2000: fig. 6).

For the taxa with unknown mature males, it is assumed the state 0, as there is not report for nearly related species with state 1, except *Carlana* considered inapplicable to the characters by the known absence of hooks on the anal-fin of mature males. The same for the next Chs. 147-152, relative to sexually dimorphic fin hooks or the spinelets (Ch. 151).

Character 147 (CI = 1.00) - Distribution of hooks on the anal-fin ray of males (Ch. 27, Malabarba, 1998): (0) more numerous and distributed along middle of length of the anal-fin rays, with reduced number on the most proximal and most distal portions; (1) anal-fin hooks more numerous and distributed along distal half or third portion of anal-fin rays.

The state 1 is a synapomorphy for the Compsurini conmprising *Acinocheirodon* (New genus n. sp. B), *Kolpotocheirodon* (New genus n. sp. A), *Macropsobrycon*, *Compsura*, and *Saccoderma*. In Malabarba (1998), *Kolpotocheirodon* (New genus n. sp. A) does not share state 1 with the remaining compsurins.

In *Diapoma* the anal-fin hooks are remarkably disposed distally on the anal-fin rays, but different from state 1 and coded as state 0. The character is coded as state 0 in four outgroup taxa considering there is no report of the pattern described in state 1 in the examined species. This is the case to *Brycon* (Lima, 2001), *Cynopotamus* (Menezes, 1976, 1987), *Gnathocharax* character is coded as state 0 to *Spintherobolus papilliferus* and *Spintherobolus* n. sp., both with unknown hooks on anal-fin rays, but considering the overall homologies of Cheirodontini (the same in the next Ch. 148, 149, 150, 152).

Character 148 (CI = 1.00) - Number of hooks on the anal-fin ray of males (Ch. 28, Malabarba, 1998): (0) number progressively reduced from the anterior to posterior anal-fin rays; (1) more numerous in both anterior and posterior portions of anal fin, reduced in the middle portion of anal fin.

The state 1 is present only in the examined *Compsura heterura*, but is known in other nearly related inseminating cheirodontines, *Compsura gorgonae*, "*Odontostilbe*" *mitoptera*, and "*Odontostilbe*", *dialeptura* in the Clade CO2 of Malabarba (1994), or in a wider clade including *Saccoderma melanostigma* of Malabarba (1998).

Character 149 (CI = 1.00) - Fin hooks general shape: (0) retrorse or somewhat retrorse hooks, distal tip curved; (1) straight or practically straight, distal tip perpendicular to anal-fin ray long axis.

The small straight hooks are an autapomorphy of the *Holoshesthes* n. sp. "b".

Character 150 (CI = 0.50) - Caudal-fin hooks position (Ch. 39, Malabarba, 1998): (0) absent or not as states 1 and 2; (1) dorsal, straight, angled toward caudal-fin base; (2) dorsal, retrorse, laterally and ventrally curved, oriented toward the caudal-fin base and ventral margin of caudal fin.

State 1 is a unique synapomorphy to the Compsurini, reversed in *Compsura*, state 0, independently modified to state 2 in *Saccoderma* and *Macropsobrycon* according Malabarba (1998).

Holoshesthes n. sp. "b", and *Holoshesthes hemigrammus* have hooks on the caudal-fin rays, but not as states 1 or 2, and they are described in Ch. 152. In *Holoshesthes* n. sp. "b" hooks of upper caudal fin lobe are positioned on lower border of fin rays, hooks of lower caudal-fin lobe on upper border of fin rays, and hooks of middle fin rays 10-11th on both fin ray borders. In *H. hemigrammus* the hooks are vestigial, not well-developed, positioned on the lateral and both upper and lower borders of 1st-6th and 15th-19th caudal-fin rays, at fin-ray tips.

Character 151 (CI = 1.00) - Small and flexible spinelets, or spinules (Fink & Weitzman, 1974), along the proximal portion on the principal caudal-fin rays of the ventral lobe (Ch. 40, Malabarba, 1998): (0) absent; (1) present.

The uniquely apomorphic spinelets of *Macropsobrycon uruguayanae*, among cheirodontines, occurs in other characids, but differently distributed on fins. In the present outgroup, *Carlana eigenmanni* have flexible spinules on the pelvic fin and anal fin of males, already reported by Fink & Weitzman (1974). The Stevardiinae *Hysteronotus myersi* have spinelets on the pelvic fin of males (Weitzman & Thomerson, 1970), and *the incertae sedis* in Characidae *Nematocharax venustus* on dorsal, pelvic, and anal fins (Weitzman *et al*., 1986).

Character 152 (CI = 0.50) - Caudal-fin hooks (Ch. 41, modified of Malabarba, 1998): (0) absent; (1) along distal portions of the principal caudal-fin rays 11 to 14; (2) on the caudal-fin rays 13-18; (3) on almost all caudal-fin rays, 2-18.

State 1 is present in *Acinocheirodon*, *Kolpotocheirodon*, and *Macropsobrycon*, and state 2 in *Saccoderma* following Malabarba (1998). The state 3 is unique in clade A16 formed by *Holoshesthes* n. sp. "b" and *H. hemigrammus*. *Holoshesthes* n. sp. "b" has hooks on 2nd to 18th principal caudal-fin rays, positioned on fin rays as described in Ch. 150. *H. hemigrammus* are coded as state 3, having not well-developed hooks on 1st-6th and 15th-19th caudal-fin rays, but this is observed in only one male examined.

Hooks on the caudal-fin rays 12-16 are found in the compsurin "*Odontostilbe*" *dialeptura*, and assigned to a different state in Malabarba (1998), not evaluated here.

Scales

Character 153 - Lateral line (CI = 0.16) (Ch. 60, Malabarba, 1998): (0) complete; (1) interrupted. Mean number of lateral line perforated scales more than 6.5; (2) reduced to 2-6 perforated scales.

The complete lateral line is plesiomorphic in the present analysis, modified to incomplete in clade J, state 1, and then reversed to the complete lateral line, state 0, in the Odontostilbini, a condition apomorphic to them. Among the Odontostilbini, only *Odontostilbe* n. sp "b" has a derived incomplete lateral line, with mean number of 8.7 lateral line scales in Malabarba (1988).

The interrupted lateral line, state 1, is also derived in the Compsurini, independently reversed to sate 0 in *Saccoderma* and *Acinocheirodon*. Among the Cheirodontini, the state 1 is again derived to the clade O (*Nanocheirodon* + *Cheirodon*), and to the clade T (reversed to state 0 in *Serrapinnus heterodon*), but modified to state 2 in clade X with the *Spintherobolus* species.

The complete lateral line was used to diagnose the genus *Odontostilbe* by Cope (1870), distinguishing it from *Cheirodon*. A character considered labile by Fink & Weitzman (1974) that put *Odontostilbe* in synonym of *Cheirodon*. Here, this character contributes to group a wide range of species beyond the *Odontostilbe* forming the Odontostilbini. However, complete lateral line appears in all the three main lineages of Cheirodontinae and is present in most outgroup taxa examined, excepting *Diapoma*, *Aphyocharax* and *Carlana* witht interrupted lateral line as state 1.

This character was considered non-informative by Malabarba (1998), reducing the tree consistency index, increasing the shortest tree length, and altering the topology of strict consensus tree (figs. 1, 20). However, it reduced the number of equally parcimonious trees from 72 to 48. Here, the exclusion or inclusion of the character in the analysis do not alter the topology of the of the strict consensus tree.

Acinocheirodon has an almost complete lateral line, usually not complete, averaging 34.9 lateral line scales in Malabarba & Weitzman (1999), and coded as state 0, following Malabarba (1998).

Charax stenopterus has 2-10 lateral line scales, with a mean of 5.9 scales in a range of 316 specimens examined by Lucena (1987), being coded as state 2. In the previous analysis of

Malabarba (1998) only *Spintherobolus* had the reduced 2-6 perforated scales. *Priocharax* is uncoded for the character, as it does not have lateral line scales (Weitzman & Vari, 1987).

Pseudocheirodon arnoldi is uncoded as in Malabarba (1998), because it has variable lateral line scales, from incomplete 7-11 scales to complete lateral line with as many as 33 scales remarked by López (1972) and Fink & Weitzman (1974). The same for *Odontostilbe* n. sp. "h", having 9 to 29 lateral line scales (Malabarba, 1988), or up to 36 in examined specimens.

Character 154 (CI = 1.00) - Posteriormost scale of the longitudinal series of scales just below the lateral line (Ch. 61, modified of Malabarba, 1998): (0) equal in shape to other caudal peduncle scales and not connected to skin flaps; (1) posterior margin of the scale free and concave, dorsally connected to skin flap originating between 12th - 13th principal caudal-fin rays and ventrally connected to the 19th principal caudal-fin ray;

In the clade L, *Saccoderma* and *Compsura* exclusively share the state 1 as in Malabarba (1998). Eigenmann (1915: fig. 19g) noticed "a lobe of large scales in the male extending along the base of the middle caudal rays" in the original diagnosis of *Compsura*. While "a dermal bag on the lower lobe of caudal fin with the opening posteriorly and partially covered by enlarged scales basally and dorsally" were cited by Schultz (1944: fig. 41c) in the original diagnosis of *Saccoderma*. This development of associated scales and skin flaps forms a caudal organ not homologous of those of the Stevardiinae *sensu* Weitzman *et al*. (1995) as discussed by Malabarba & Weitzman (1999, 2000). These caudal organs contain pheromone glands at the base of male's caudal fin, needing investigation in the Compsurini.

The posterior margin of the last scale free and concave, dorsally connected to skin flap originating from 14th principal caudal-fin rays and ventrally connected to the 19th principal caudal-fin ray, is known only in "*Odontostilbe*" *dialeptura* (Malabarba, 1998), not analyzed here.

Character 155 (CI = 1.00) - Caudal-fin scales (Ch. 62, Malabarba, 1998): (0) absence of scales with reduced size comparatively to body scales; (1) presence of reduced size and unusual shape scales, with free borders, distributed along proximal length of the middle caudal-fin rays.

This is only present in *Saccoderma*, and known in "*Odontostilbe*" *mitoptera* and "*Odontostilbe*" *dialeptura*, following Malabarba (1998).

Character 156 (CI = 1.00) - Caudal-fin scales (Ch. 63, Malabarba, 1998): (0) absence of elongate scales; (1) presence of one or two elongate scales posterior to the large modified scale of the longitudinal series of scales just below the lateral line.

State 1 is unique to *Saccorderma* as in Malabarba (1998).

Color pattern

Character 157 (CI = 0.50) - Humeral spot (Ch. 64, Malabarba, 1998): (0) present; (1) absent.

The lack of humeral spot is a recognized synapomorphy for the Cheirodontinae (Malabarba, 1998), but here also independently acquired in *Priocharax*.

Aphyocharacidium bolivianum was described by Géry (1973: fig. 12) as having a black humeral spot, but not all specimens examined show this spot. In two examined lots (MCP 37959, MCP 37960) the specimens lack the humeral spot or have a few chromatophores on that region. The species is coded as state 0.

Character 158 (CI = 0.33) - Distribution of scattered black chromatophores in the dorsal fin: (0) scattered black chromatophores on entire or almost entire dorsal-fin, or not as state 1; (1) scattered black chromatophores slightly darker and more numerous on middistal portion of the dorsal-fin, extending on the 2nd unbranched dorsal-fin ray and 1st to 5th, 6th branched fin ray; (2) black spot on dorsal fin, along distal midlength of 2nd unbranched and 1st to 6th-7th branched fin rays, usually not reaching tip of fin rays.

State 1 is a synapomorphy to the clade A11 formed by the Odontostilbe n. sp. "b" + *Holoshesthes* species, and to the clade A10 formed by *Odontostilbe* n. sp. "e" + *Odontostilbe* n. sp. "p". In the clade A11, *Odontostilbe* n. sp. "b" and *H. pequira* have a distinct derived dark spot, state 2, and *H. hemigrammus* a reversion to state 0. State 1 is also a synapormorphy to clade V with *Serrapinnus heterodon* + *S. microdon.* Eigenmann (1915: 84) in a key to *Holesthes* [sic] species, differed *H. pequira* of the *H. heterodon* (valid as *Serrapinnus heterodon*) by the dorsal-fin with a "black wedge extending from the upper part of the anterior ray toward the middle of the sixth ray" in the former, versus "tip of dorsal faintly dusky" in the latter. *S. microdon* has a somewhat marked dorsal-fin spot, not as distinct as the spot of the state 2, being coded as state 1.

Character 159 (CI = 0.50) - Dorsal-fin color pattern, pigmentation forming conspicuous small spot (Ch. 65, Malabarba, 1998): (0) none distinct spot, or with a different pattern from states 1 and 2; (1) small and distinct black spot approximately at distal tip of 1st unbranched dorsal-fin ray and midpoint of 2nd unbranched dorsal-fin ray.

This small black spot is a derived character to the clade N containing *Acinocheirodon* (Malabarba & Weitzman, 1999: figs. 1, 2) and *Macropsobrycon*, independently acquired in *Compsura*.

Character 160 (CI = 1.00) - Dorsal-fin color pattern, not forming conspicuous a spot (Ch. 66, modified of Malabarba, 1998): (0) none distinct spot, or with a different pattern from states 1 and 2; (1) dark black chromatophores along distal portion of 1st to 4th-5th branched dorsal-fin rays; (2) dark black chromatophores along mid-length of 2nd unbranched dorsal-fin ray and 1st to 5th branched dorsal-fin rays, with weakly pigments on distal portion of it.

State 1 is unique to *Compsura*, and state 2 to *Macropsobrycon*, according to Malabarba (1998). This pigmentation is different from the previous Ch. 158 (state 1), in which the distribution of chromatophores is fewer scattered dark chromatophores is on middistal portion of the dorsal-fin, instead of the distal portion of dorsal-fin ray in Compsura (this character, state 1). In *Macropsobrycon*, state 2, the pigmentation distribution is somewhat similar to that of previous Ch. 158 (state 1), more median, by the weakly pigments on distal portion of it.

Character 161 (CI = 1.00) - Dorsal-fin color pattern, pigmentation forming conspicuous spot (Ch. 67, modified of Malabarba, 1998): (0) none distinct spot, or with a different pattern from states 1 and 2; (1) black spot on dorsal fin, along midlength of 2nd unbranched and 1st to 6th branched fin rays.

State 1 is unique in *Prodontocharax.*

Character 162 (CI= 0.50) - Anal-fin color pattern (Ch. 68, Malabarba, 1998): (0) none distinct pigmentation, or with a different pattern from state 1; (1) more strongly pigmented along distal portion of branched anal-fin rays.

This is a unique synapomorphy of the Compsurini, *Compsura*, *Kolpotocheirodon*, *Macropsobrycon*, *Saccoderma*, reversed to state 0, none distinct pigmentation on anal fin, in *Acinocheirodon*, according to Malabarba (1998). The same anal-fin pigmentation was verified in other putative species related to Compsurini *Compstura gorgonae*, "*O. mitoptera*", and "*O. dialeptura*" (Malabarba , 1994). *Hemibrycon*, *Aphyocharax*, and *Gnathocharax* have pigmentation along distal portion of branched anal-fin rays, but different from the state 1.

Muscles

Character 163 (CI = 0.33) - Pseudotympanum between the first and second pleural ribs (Ch. 1, Malabarba, 1998; Ch. 52, Lucena, 1998; Ch. 2, Weitzman & Malabarba, 1999; Ch. 51, modified of Lucena, 1998): (0) absent; (1) a large, nearly triangular hiatus on muscles covering the anterior swimbladder, limited dorsally by the *lateralis superficialis* muscle, posteriorly by a naked anterior surface of the second pleural rib, anteroventrally by the *obliquus superioris* muscle, and posteroventrally by the *obliquus inferioris*; (2) a narrow hiatus on muscles covering the anterior swimbladder, limited dorsally by the *lateralis superficialis* muscle, posteriorly by a mid ventrally naked anterior surface of the second pleural rib, anterodorsally by the *obliquus superioris* muscle.

The large pseudotympanum is a recognized synapomorphy for the Cheirodontinae, confirmed here, but occurring independently in *Aphyocharacidium*, and in the characines *Charax* and *Phenacogaster*, also in *Roeboides* not examined here (Malabarba, 1998: figs. 2b, fig. 3a, b; Malabarba & Lucena, 1995). However, among the characines, *Priocharax* lacks this pseudotympanum (state 0), and *Cynopotamus* has a narrow hiatus (state 2).This narrow pseudotympanum, state 2, was found by Lucena (1998) to be a synapomorphy for his Clade 5, including *Galeocharax*, *Acestrocephalus* (though uncoded for the character), and *Cynopotamus*.

Character 164 (CI = 0.25) - Pseudotympanum anterior to the first pleural rib (Ch. 2, modified of Malabarba, 1998; Ch. 21, modified of Weitzman & Malabarba, 1999; Ch. 51, modified of Lucena, 1998): (0) absent; (1) presence of a pseudotympanum anterior to the first pleural rib, limited dorsally by the *lateralis superficialis* muscle, posteriorly by a naked anterior surface of the first pleural rib, and anteroventrally by the *obliquus superioris* muscle, slightly smaller or half of size of the posterior pseudotympanum; (2) presence of a small pseudotympanum anterior to the first pleural rib, partially filled by muscular tissue, and limited to the anterodorsal portion ahead of the first pleural rib, about less than 1/3 or less of the size of the posterior pseudotympanum.

The presence of a the pseudotympanum anterior to the first pleural rib is a recognized synapomorphy of *Spintherobolus* (Malabarba, 1998; Weitzman & Malabarba, 1999: figs. 4-6, 16-17), but here also found in *Priocharax*, *Gnathocharax*, *Charax*, and *Phenacogaster*, as already observed by Lucena (1998). The present character comprises an additional state 2, regarding the relative size of the anterior pseudotympanum to the posterior one equivalent to the Ch. 51, state 1 in Lucena (1998), not only the presence or absence of it as in Weitzman &

Malabarba (1998, 1999). *Spintherobolus papilliferus* has a small anterior pseudotympanum in adults coded as state 2, and already noticed as being smaller than those of the remaining *Spintherobolus* species by Weitzman & Malabarba (1999: fig. 17). Weitzman & Malabarba (1999) noticed the anterior pseudotympanum in juveniles of *S. papilliferus* was similar to that of all other *Spintherobolus* species. *Charax* has the anterior pseudotympanum covered or not by muscle, but the pseudotympanum when present is small, equivalent to that of *S. papilliferus,* being coded as state 2. In a juvenile of *C. stenopterus* the anterior pseudotympanum is an wider gap than in adults, similarly to that observed in *S. papilliferus*. *Phenacogaster* also has a small anterior pseudotympanum, state 2, but the two other Characinae *Priocharax* and *Gnathocharax* have wider anterior pseudotympanums coded as state 1.

In the Ch. 51-2 of Lucena (1998) the anterior pseudotympanum of *Priocharax* and *Gnathocharax* is considered large, "notably extended at ventral portion" , and the pseudotympanum of *Acanthocharax, Charax*, *Phenacogaster*, and *Roeboides* small, limited to the anterodorsal portion ahead the first pleural rib (his state 1). He found *Gnathocharax, Heterocharax, Hoplocharax*, and *Lonchogenys* (Clade 2), and the nearly related *Priocharax* at the basal position in a cladogram of Characinae genera, all sharing the large anterior pseudotympanum. Lucena's Ch. 51-1 (1998), smaller anterior pseudotympanum was present in his Clade 3, in the basal *Phenacogaster*, and in the terminal clade formed by *Charax*, *Acanthocharax*, and *Roeboides*, being reversed to the absence of it (his Ch. 51-0) in *Cynopotamus*, *Acestrocephalus* (though originally uncoded to the character), and *Galeocharax*.

Here, the large anterior pseudotympanum is a synapomorphy do clade X with most of the *Spintherobolus* species, excepting *S. pappiliferus* with the small anterior pseudotympanum, being independently acquired two times in *Charax*, and *Phenacogaster*; the two latter separate in different clades (respectively clades E and H).

Malabarba (1998) commented that *Atopomesus, Paracheirodon axelrodi*, and *Axelrodia* sp. (MZUSP 23684) have two small openings over the swimbladder, but apparently not homologous to those of *Spintherobolus*, as these species do not share the apomorphies of Cheirodontinae. The examination of *Axelrodia* sp. (MZUSP 23684) specimens revealed this is different from the present *Axelrodia lindeae*. Even though the taxonomic review of *Axelrodia lindae* is needed, the *Axelrodia* sp. (MZUSP 23684) does not have the strictly uniserial conical teeth or with two tiny, almost indistinct lateral cusps, the main diagnostic feature of *Axelrodia* following Géry (1965, 1977), instead have well-developed multicuspid dentition.

Character 165 (CI = 0.50) - Caudal peduncle of mature males (Ch. 3, Malabarba, 1998): (0) aligned with the main body axis; (1) deeply arched ventrally, the last vertebrae reaching a 45° position relative to the first caudal vertebrae.

This was assigned as a synapomorphy for the *Serrapinnus* species (Malabarba, 1998: fig. 4), but we found to be also present in *Axelrodia lindeae*, supporting clade W.

Other characters

Character 166 (CI =1.00) - Supraneurals (Ch. 13, 14, Malabarba, 1994): (0) autogenous; (1) 2nd-4th supraneurals fused.

This is an autapomorphy of *Odontostilbe paraguayensis* (Uj, 1987: fig. 19; Malabarba, 1988: fig. 96). The fused supraneurals can be noticed in the entire specimens, in which the dorsal profile anterior to dorsal-fin origin is somewhat straight right above supraneurals, and the anterodorsal portion of the piece with fused supraneurals is pointed like a spine.

Character 167 (CI = 1.00) - Neuromasts (Malabarba, 1998: Ch. 69; Weitzman & Malabarba, 1999: Ch. 16): (0) not as state 1; (1) a complex, patterned series of exposed neuromasts distributed on head and body.

In *Spintherobolus*, the pattern of neuromast distribution on head is described by Weitzman & Malabarba (1999: figs. 4, 10). Marked grooves nearly straight and parallel to each other, transversely crossing main longitudinal axis of the third infraorbital associated with neuromasts in rows is also known in *Phenacogaster* (Ch. 6, Malabarba & Lucena, 1995; Lucena, 2003: figs. 3-7). In some other Cheirodontinae species, as *e.g. Cheirodon ibicuhienis* and *C. interruptus* (Fig. 24a), *Holoshesthes hemigrammus*, and *Holoshesthes geayi* (Fig. 24b), neuromasts are distributed on head, mostly on infraorbitals, opercle, dentary lateral portion, and also anteroventral portion of head nearly symphysial joint of dentaries (*H. hemigrammus*), but not forming the pattern of *Spintherobolus*. The distribution of neuromasts in cheirodontines remains to be investigated by extensive electronic microscopy, not obtained here.

Character 168 (CI = 1.00) - Insemination (Ch. 70, Malabarba, 1998): (0) absent; (1) present.

Insemination was described for the cheirodontines by Burns *et al*. (1997), determined by the presence of sperm in ovary, and latter described as a synapomorphy for the tribe Compsurini of the Cheirodontinae (Malabarba, 1998), confirmed here. However, here mainly scanning electronic microscopy (SEM) were applied to investigate gonads of males of the Odontostilbini, verifying the shape of spermatozoa. Considering that all the Odontostilbini were found to have the spherical sperm nuclei (next character), and that it is usually found species without insemination, all the Odontostilbini are coded as state 0. Thus, indirectly by the shape of the spermatozoa, the insemination is deduced here. Exceptions are *Odontostilbe fugitiva*, and *Holoshesthes* n. sp. "b", in histological analysis of gonads of females confirmed not presenting insemination, and the already investigated species by Burns *et al*. (1997) and Burns & Weitzman (2005). In these studies, the genera of Cheirodontionae referred that do not have insemination are "*Aphyocheirodon*", *Pseudocheirodon*, *Cheirodon*, *Spintherobolus*, and *Odontosilbe*. In Burns *et al*. (1997), the *O. fugitiva* and *O. paraguayensis* were found not having insemination. Among the Odontostilbini, at present, only *Amblystilbe* and the two species of *Pseudocheirodon*, did not have gonads of males examined under SEM.

The insemination had been already reported to the Glandulocaudinae (Burns *et al.*, 1995 – now the Glandulocaudinae + Stevardiinae), but it was not considered to be homologous to that of the Cheirodontinae (Malabarba, 1998). The glandulocaudines and stevardiines have the sperm stored in a specific wide posterior portion of the testis (Burns *et al.*, 1995: fig. 2b-e, 4c-g), differently in cheirodontines that have spermatocysts throughout most of the testis (Burns *et al*., 1997).

Character 169 (CI = 0.50) - Sperm nuclei (Ch. 71, modified Malabarba, 1998): (0) spherical (Fig. 25a-c); (1) elongate (Fig. 25d).

The elongate sperm nucleus is a synapomorphy for the Compsurini, reversed in *Kolpotocheirodon* (Malabarba, 1998; Malabarba & Weitzman, 2000; Malabarba *et al*., 2004) and confirmed here. The elongate sperm nuclei were first described by Burns *et al*. (1997: fig. 2b) to the cheirodontines, and found present in most species in which the females were found inseminated. Therefore, it is somewhat linked to internal fertilization, excepting in the inseminating species of *Kolpotocheirodon*, which have the spherical sperm nuclei (Burns *et al*. (1997: fig. 2a for *Serrapinnus kriegi*), forming the aquasperm of most externally fertilizing teleosts. All the *Odontostilbe* species were checked in SEM, having spherical sperm nuclei, the aquasperm (Fig. 25a-c), also *Prodontocharax*, *Lobodeuterodon* and the Cheirodontini New genus n. sp. C and *Nanocheirodon*.

In Characidae, the elongate sperm nucleus has been described for the Glandulocaudinae (Burns *et al*., 1995), the Glandulocaudinae and Stevardiinae *sensu* Weitzman *et al*. (2005), but it does not seem to be homologous to that of the Cheirodontinae, since it presents a series of ultrastructural modifications not found in the sperm cells of the compsurins (Burns & Weitzman, 2005).

Unused characters

The low number of branched anal-fin rays 9-16, a reduced number among most Characids and a synapomorphy to *Spintherobolus* (Ch. 20, Weitzman & Malabarba, 1999) is not included in the present matrix. This is because those authors commented that similar low number of branched anal-fin rays is known in the Chilean species of *Cheirodon*, not examined here. Furthermore, in Odontostilbini the number of anal-fin rays is higher, usually more than 18 anal-fin rays, up to 26 (except in 11-16 anal-fin rays in *Prodontocharax*). Two other unique characters sustaining the monophyletic *Spintherobolus* treated in Weitzman & Malabarba (1999), the relatively small eyes and short pectoral fin among cheirodontines were not checked here considering the need of an extent morphometric analysis to do that. Furthermore, pectoral-fin length varies between females and males in some *Odontostilbe* species, *e.g. Odontostilbe nareuda* (Bührnheim & Malabarba, 2006).

Another character not included in our analysis is the light black pigmentation on midlenght of the last unbranched anal-fin ray extending through 1st to 5th branched anal-fin rays of males, indicated as a possible synapomorphy of *Holoshesthes pequira* and *Odontostilbe* n. sp. "b" by Malabarba (1999). This character is not used considering interspecific variation, low occurrence in alcohol examined males, and the detected presence of it in females (Bührnheim & Malabarba, in manuscript). However, it would reinforce the near relationships of *H. pequira* and *Odontostilbe* n. sp. "b" found in the weighted tree (Fig. 3).

Number of branchiostegals rays, extensively used in phylogenies including Characidae representatives (Lucena, 1993; Buckup, 1998; Lucena & Menezes, 1998; Zanata, 2000), were considered uninformative to the Cheirodontinae. This is because all Cheirodontinae have four branchiostegals rays, and only one of four specimens examined of *Cheirodon ibicuhiensis* has five rays in both sides. The same was found in the outgroup taxa, mostly of them with four branchiostegals rays, and only *Diapoma* with five rays at one side of one specimen examined. In *Carlana*, from two specimens examined, one had five rays in both sides. McAllister (1968) defined the branchiostegals of Characidae as spathiforms varying from three to five. Actually, a number of four branchiostegal rays appear in most characiforms (Roberts, 1969; Zanata & Vari, 2005). Five branchiostegal rays has been hypothesized as a synapomorphy for the Cynodontinae (Lucena & Menezes, 1998), or putatively primitive to *Thoracocharax* in Gasteropelecidae (Weitzman, 1960). Three branchiostegal rays support a clade formed by

Pyrrhulina + *Nannostomus* (Buckup, 1998; the Pyrrhulininae *sensu* Weitzman & Cobb, 1975).

The shape of the metapterygoid-quadrate fenestra was also considered uninformative to the Cheirodontinae phylogeny, though widely employed in phylogenetic analysis including characids (Lucena, 1993; Lucena & Menezes, 1998; Zanata, 2000; Benine, 2004). This is because all Cheirodontinae have a horizontally elongate fenestra, the plesiomorphic condition in Characiformes (Vari, 1979, Lucena & Menezes, 1998, Zanata, 2000). However, the shape of the metapterygoid-quadrate fenestra grouped *Hemibrycon* to a clade formed by *Priocharax*, *Gnathocharax*, *Charax*, and *Cynopotamus*. These genera share a derived spherical fenestra, excepting *Priocharax*. The derived spherical condition independently evolved in some african alestids, in a clade formed by *Triportheus, Lignobrycon,* and also in *Hemiodus* (Zanata, 2000), or in Cynodontinae, and *Cynopotamus* (Lucena & Menezes, 1998).

The number of supraneurals (state 0: 6 or more, usually 7; state 1: 4-6, usually 5; state 2: 3-5, usually 4) was tentatively polarized to the Cheirodontinae, but was removed from the analysis. The use of this character resulted in a different topology to the clade formed by the *Holoshesthes* species and *Acinocheirodon*, though did not change the topology of the Cheirodontinae clade in the weighted tree without the use of it. This character had CI of 0.11 and IR of 0.53, grouping in the unweighted tree the *Holoshesthes* clade with three species of *Odontostilbe* at the basal position, the *Odontostilbe microcephala* + (*Odontostilbe* n. sp. "p" + (*Odontostilbe* n. sp. "e" + (*Acinocheirodon* + *Holoshesthes* species). Most cheirodontines have 3-5, usually 4, supraneurals, excepting: the Cheirodontini, *Cheirodon*, *Heterocheirodon*, and *Serrapinnus microdon* with, 6 or more, usually 7 supraneurals; the Compsurini *Acinocheirodon* and *Macropsobrycon*, and the Odontostilbini *Prodontocharax*, *Holoshesthes* (excepting *H. geayi*, state 2), *Odontostilbe* n. sp. "h", *Odontostilbe microcephala*, and *Odontostilbe* n. sp. "e", all with 4-6, usually 5 supraneurals. However, *Holoshesthes* n. sp. "p" has a nearly equal occurrence of 4-5 supraneurals being uncoded for the character, and to *Odontostilbe* n. sp. "e" the state 1 is assumed based on two specimens with 5 supraneurals against one specimen with 6 supraneurals. Comparing the number of steps among the weighted and unweighted trees admitting or not the number of supraneurals, the number of steps increased from 843 to 857 in the unweighted tree and from 802 to 821 in the weighted tree. The number of trees obtained without the implicit weighting increased from 300 to 390 trees. These results lead to a reevaluation of the applicability of this character, mainly regarding its interspecific variation and the overlapping in the delimited ranges of states. The number of supraneurals seems to need more sampling, which means a higher number of c&s

specimens than examined here. Serra (2003: Ch. 95, CI= 0.28) found the number of 5-6 supraneurals as a synapomorphy of the characid *Hasemania*, but independently acquired in *Alestes*, *Rhinobrycon*, *Knodus moenkhausii*, *Creagrutus britskii*, and *Brycon* sp. (rio Teles Pires, rio Tapajós basin). She did not mention the number of c&s specimens used in the study. Benine (2004: Ch. 61) delimited the number of supraneurals in absolute numbers, state 0= 5, state 1= 4, and state 3= 2, finding it highly homoplastic in his analysis of *Moenkhausia*. His samplings varied from 1 to 2 or rarely 3 specimens examined of each species. Here the number of the c&s specimens examined varied from 1 to 14 (Appendix I).

Phylogenetic reconstruction. The phylogenetic hypothesis of the relationships of Cheirodontinae taxa is presented in the weighted cladogram (Fig. 3), but jointly considering a more conservative hypothesis in the unweighted cladogram (Fig. 2). These hypotheses review the Cheirodontinae cladogram obtained by Malabarba (1998) (Fig. 1, reproduced). A new tribe is proposed based on 13 synapomorphies. Synapomorphies and autapomorphies are commented below to each monophyletic clade, and more inclusive taxa. The diagnostic characters found to the internal clades of the tribes Cheirodontini and Compsurini are only listed by their codeds below respective clades, since it was not the objective of this paper the extensive review of these tribes.

Taxonomic Account. The present phylogeny resulted in rearrangements in the subfamily Cheirodontinae as diagnosed by Malabarba (1998), mainly regarding the *incertae sedis* genera and the proposition of a new tribe. The new classification proposed is presented in Table 1.

Subfamily Cheirodontinae

Aphiocharacinae Eigenmann, 1909: 254 [in part; diagnosed in key]. - Eigenmann, 1910 [in part; diagnosis; list of genera and species].

Aphyocharacinae. - Eigenmann, 1912: [in part; emended].

Cheirodontinae Eigenmann, 1915 [in part; Aphyocharacinae *auctorum*].

Diagnosis. Cheirodontines share the following synapomorphies: (1) anteromedial process of the mesethmoid forming a short projection, wide at its base and narrower at its tip, with slightly sinusoidal lateral borders, similar to brackets contour [2*-1]; (2) first infraorbital subrectangular with anteroventral portion extended.[14*-1]; (3) long, preopercular canal reaching the anterodorsal corner of opercle [27-0]; (4) laminas of the medial border of the premaxilla in articulation with the mesethmoid slightly pronounced, forming a V-shaped bifurcation, the posteromedial lamina oblique to anteromedial lamina [34-1]; (5) posterior edentulous portion of the maxilla approximately of equal size of the anterior tooth bearing portion of maxilla [50*-1]; (6) ventral margin of posterior portion of maxilla extended ventrally beyond maxillary teeth tips [51-1]; (7) usually two or three maxillary teeth [54*-2]; (8) all tooth bearing portion of dentary nearly straight and forming an angle of approximate 120° relative to the posterior dorsal border of dentary, in lateral view [56-2]; (9) short lateral ridge with a somewhat straight surface of the upper portion of angulo-articular, on posterolateral portion of lower jaw, near the posterior portion of maxilla, observed in dorsal view [57-1]; (10) approximately the third anterior portion of dentary longitudinal axis with teeth [62-1]; (11) anteriormost portion of dentary, at the symphyseal joint, narrow, 4-5 times in the height of middle portion of dentary; (2) narrow, 7 times or more the height of middle portion of dentary, in lateral view [64-1]; (12) posteroventral border of the coracoid nearly forming an angle of 90° or slight extended, forming a small point or a truncate corner [100-1]; (13) anal-fin profile of males with the anterior lobe pointed and distal profile concave; sexually dimorphic; the last unbranched anal-fin ray and first two branched anal-fin rays in males elongate, longer than in females [112-1]; (14) absence of humeral spot [157-1]; (15) a large pseudotympanum between the first and second pleural ribs, nearly triangular hiatus on muscles covering the anterior swimbladder, limited dorsally by the *lateralis superficialis* muscle, posteriorly by a naked anterior surface of the second pleural rib, anteroventrally by the *obliquus superioris* muscle, and posteroventrally by the *obliquus inferioris* [163-1].

Remarks. Fifteen synapomorphies support the monophyly of Cheirodontinae, only two of them corresponding to the synapomorphies found in Malabarba (1998), the lack of humeral spot and the presence of the large triangular pseudotympanum between the first and second pleural ribs. The two other characters of the phylogenetic analysis of Malabarba (1998), the pedunculated teeth and the single tooth row with teeth perfectly aligned and similar in shape and cusp number in the premaxilla were found here to define a broader clade with the cheirodontines plus *Carlana*. Notably, five new unique synapomorphies are found to the Cheirodontinae: the anteromedial process of the mesethmoid in a brackets contour shape; the first infraorbital subrectangular with anteroventral portion extended; the posterior edentulous portion of the maxilla approximately of equal size of the anterior tooth bearing portion of maxilla; the sexually dimorphic anal-fin profile of males with the anterior lobe pointed and distal profile concave; and the presence of usually two or three maxillary teeth.

Tribe Cheirodontini Eigenmann, 1915

Diagnosis. The following seven synapomorphies diagnose the cheirodontins: (1) posterior border of all branchiostegals rays or at least the two posteriormost branchiostegals rays markedly crenulated [78-1]; (2) pelvic-fin rays i5i, i6, i6i, rarely some individuals of a given species may present i7 [106-1]; (3) hemal spines of at least the four posterior caudal vertebrae, those anterior to the terminal "half centrum" and its processes, elongate and associated with the ventral procurrent caudal-fin rays support [116*-1]; (4) 11 to 16 ventral procurrent caudal-fin rays in males, a number nearly identical to or slightly smaller than dorsal series [124-1]; (5) anterior ventral procurrent caudal-fin rays of females with proximal portions of the ray-halves fused to each other, usually retaining an opening near their distal tips; giving a needle-like shape to these rays [126*-1]; (6) lepidotrichia of each ventral procurrent caudal-fin ray of males fused along entire length and becoming progressively laminar with maturation [127*-1]; (7); the most of anterior ventral procurrent caudal-fin rays of males projecting far enough through muscles and skin to be seen along ventral margin of the caudal peduncle, and forming sort of keel [129*-1].

Nanocheirodon + Cheirodon

[Clade O]

[27-1], [124-2], [128*-1] [130*-1].

Nanocheirodon

[43-0], [45-0], [57-2], [58-1], [125*-1], [141*-1].

Cheirodon ibicuhiensis + Cheirodon interruptus

[Clade P]

[17-1], [19-1], [20-0], [40-2], [50-2], [137-1], [139-1]

Cheirodon ibicuhiensis

[18-1], [112-0], [140-1]

Cheirodon interruptus

[10-0], [12-1], [54-3], [89-0], [90-0], [112-2]

***Heterocheirodon* +**

New genus n. sp. C + (*Serrapinnus* + (*Axelrodia lindeae* + *Spintherobolus*))

[Clade Q]

[41*-2], [109*-1], [111*-1], [112*-3], [113*-1], [135*-1], [140-1], [142*1], [145*-1], [153-0]

Heterocheirodon jacuiensis* + *Heterocheirodon yatai

[Clade R]

[2-0], [4*-1], [10-0], [17-1], [18-1], [30-2], [44-2], [57-0], [60-0], [61-0]. [77-1], [85-1], [86-1], [89-0], [90-2], [96-1], [124-2], [126*-2], [127*-2], [129-0]

Heterocheirodon jacuiensis

none unique characters found

Heterocheirodon yatai

[50-2]

New genus n. sp. C + (*Serrapinnus* + (*Axelrodia lindeae* + *Spintherobolus*))

[Clade S]

[11-0], [15-0], [22-1], [57-2], [131*-1]

New genus n. sp. C

[21-0], [41-3], [57-3], [78-0], [109*-2]

***Serrapinnus* + (*Axelrodia lindeae* + *Spintherobolus*))**

[Clade T]

[40-2], [41-1], [43-0], [110*-1], [117*-1], [153-1], [165*-1]

***Serrapinnus micropterus* + (*S. heterodon* + *S. microdon*)**

[Clade U]

[17-1], [18-1], [22-2], [57-3], [106-0]

Serrapinnus micropterus

[39-2], [40-3], [41-3], [45-0]

Serrapinnus. heterodon + *S. microdon*

[Clade V]

[46-1], [50-2], [56-1], [58-1], [59-0], [60-0], [65-1], [72*-1], [73-1], [76-1], [86-1], [90-0], 137[0-1], 158[0-1]

Serrapinnus. heterodon

[1-0], [57-1], [72-2], [81-0], [82-0], [83-1], [85-1], [106-1], [153-0]

Serrapinnus microdon

[27-1], [40-1], [42-1], [78-0]

Axelrodia lindeae + *Spintherobolus*

[Clade W]

[11-1], [14-0], [19-2], [22-0], [25-2], [27-1], [30-1], [40-0], [51-0], [54-1], [55-2], [57-0], [70*-1], [74-1], [79-0], [83-1], [89-2], [93-1], [99-1]

Axelrodia lindeae Géry, 1973

[30-2], [41-0], [44-2], [63-0], [70-0], [74-2], [82-0], [107*-1], [126-0]

Remarks. The genus *Axelrodia* was erected by Géry, 1965 with *Axelrodia fowleri*, later recognized as a junior synonym of *Hyphessobrycon stigmatias* by Géry (1966) when he described *Axelrodia riesei*. Thus, the type species of the genus is valid as *Axelrodia stigmatias*. Later, Géry described *A. lindeae*, remarking its distinct black line extending from mouth through pseudotympanum area. All of the type material these species did not included mature males and there is no report of hooks on fins. The genus was diagnosed mostly by having teeth unicuspid. The examined material of *A. lindeae* contains mature males with hooks on fins and modified ventral procurrent caudal-fin rays, sharing the derived characters of the Cheirodontini. The genus needs taxonomical revision.

Spintherobolus n. sp. + (*S. papilliferus* + (*S. ankoseion* + *S. broccae*))

[Clade X]

[2-0], [3*-1], [6-1], [7-1], [8-1], [9-1], [10-0], [11-2], [12-2], [13-1], [16-1], [25-3], [26-1], [27-2], [31*-1], [68-1], [69*-2], [81-0], [84-0], [85-1], [88-0], [91*-1], [92*-1], [97-1], [100-0], [101*-1], [106-2], [131-0], [132*-1], [133*-1], [134*-1], [137-1], [153-2], [164-1], [165-0], [167*-1]

***Spintherobolus* n. sp.**

[30-2], [70-2], [78-0], [108*-1], [116-0], [124-0]

***Spintherobolus papilliferus* + (*S. ankoseion* + *S. broccae*)**

[Clade Y]

[30-0], [80*-1], [89-1], [95-1], [105-1]

Spintherobolus papilliferus

[7-0], [10*-2], [25-1], [61-0], [109-0], [111-0], [164-2]

Spintherobolus ankoseion* + *S. broccae

[Clade Z]

[94*-1], [111*-2]

Spintherobolus ankoseion

[30-1]

Spintherobolus broccae

[89-2]

Tribe Compsurini Malabarba, Weitzman & Burns in Malabarba, 1998

Diagnosis. The following derived characters diagnose the compsurins: (1) anal-fin profile of males almost straight profile to slight concave; sexually dimorphic; the last unbranched anal-fin ray and 1st to 10th branched anal-fin rays in males somewhat longer than in females [112-2]; (2) hooks on the anal-fin ray of males more numerous in both anterior and posterior portions of anal fin, reduced in the middle portion of anal fin [146*-1]; (3) anal-fin hooks more numerous and distributed along distal half or third portion of anal-fin rays [147*-1]; (4) caudal-fin hooks dorsal, straight and angled toward caudal-fin base [150*-1]; (5) caudal-fin hooks along distal portions of the principal caudal-fin rays 11 to 14 [152-1], (6) anal-fin more strongly pigmented along distal portion of branched anal-fin rays [162*-1]; (7) insemination present [168*-1]; (8) sperm nuclei elongate [169*-1].

Compsura* + *Saccoderma

[Clade L]

[15-0], [57-2], [122*-1], [154*-1]

Compsura heterura

[22-1], [77-1], [148*-1], [150-0], [152-0], [159-1], [160*-1]

***Saccoderma hastata* Eigenmann**

[18-1], [45-0], [57-3], [71*-1], [90-0], [114-1], [115*-1], [143*-1], [150-2], [152*-2], [153-0], [155*-1], [156*-1]

***Kolpotocheirodon* + (*Acinocheirodon* + *Macropsobrycon*)**

[Clade M]

[6-1], [10-0], [12-1], [17-1], [21-0], [27-1], [30-1], [60-0], [118*-1]

Kolpotocheirodon theloura

[24-0], [30-2], [39-2], [77*-2], [118*-2], [120*-1], [121*-1], [144*-1], [169-0]

Acinocheirodon* + *Macropsobrycon

[Clade N]

[18-1], [20-0], [22-1], [39-0], [40-2], [41-1], [50-2], [76-1], [86-1], [119*-1], [137-1], [139-1]

Acinocheirodon

[1-0], [10-1], [11-0], [12-0], [15-0], [22-2], [27-0], [29-1], [30-0], [46-1], [59-0], [64-0], [72-2], [73-1], [90-0], [123*-1], [136*-1], [153-0], [162-0]

Macropsobrycon

[2-0], [5*-1], [21-1], [25-2], [30-2], [40-0], [42-1], [43-0], [44-2], [54-4], [58-1], [74-2], [90-2], [96-1], [98-0], [118-0], [119*-2], [150-2], [151*-1], [160*-2]

Odontostilbini, new tribe

Diagnosis. The following thirteen derived characters diagnose the odontostilbins: (1) longitudinal branch of the laterosensory canal of parietal posteriorly contiguous to the transverse laterosensory canal of parietal, and anteriorly contiguous to the laterosensory canal of frontal [11-0]; (2) laterosensory canal along almost the entire length of the longest axis of the first infraorbital or reaching to about half length of the longest axis [15-0]; (3) anterodorsal border of the second infraorbital with a small to well-developed pointed projection, underneath the posterodorsal portion of the first infraorbital [18-1]; (4) anterior border of the sixth infraorbital with the anterior lamella expanded in a lingual-like shape [22-2]; (5) palatine regular rectangular, well developed [30-1]; (6) present of the flange on anterodorsal portion of the maxilla, posterior to rod-like ascending process of the maxilla [45-0]; (7) laminar ridge with a straight surface of the upper portion of the angulo-articular, on posterolateral portion of the lower jaw, near the posterior portion of the maxilla, well-marked in dorsal view [57-3]; (8) lower branch of the angulo-articular on lateral surface of dentary short, not extended anteriorly or slightly extended, anterior border forming a slight convexity, 4-5 times in the longitudinal length of the dentary [61-0]; (9) ventral border of the posteriormost branchiostegal ray in males slightly concave on the anterior to median length of the ventral border [77-1]; (10) unbranched pelvic-fin ray elongate [103*-1]; (11) anal-fin profile of males concave to almost straight; absence of sexual dimorphism ([112-0]; (12) laterosensory canal of the lateral line relatively long, extending nearly half-length of the middle caudal-fin rays [114-1]; (13) lateral line complete [153-0].

Remarks. The new tribe Odontostilbini is supported by twelve derived characters and one uniquely derived character. This unique synapomorphy, the unbranched pelvic-fin ray elongate, was before proposed as a synapomorphy to the genus *Odontostilbe* by Malabarba (1998). Noteworthy, the regular rectangular palatine is practically only found in odontostilbins, but also observed in the cheirodontin *Spintherobolus ankoseion*.

The complete lateral line was another diagnostic character to *Odontostilbe* proposed in its original description by Cope (1870). Malabarba (1998) finished to consider the lateral line character non-informative in his analysis, not changing the tree topology but reducing the tree consistency index and increasing the tree length. Here, if removed from the analysis, the character did not change the tree topology, consistency index, or length, or still the number of most parcimonious trees obtained.

In the unweighted tree (Fig. 2), the tribe is not sustained, and all of its components are in a wide polytomy in the Cheirodontinae. Despite of that, the tribe obtained in the weighed tree (Fig. 3) is considered consistent, and herein proposed. Notable, the two other tribes of the Cheirodontinae, Cheirodontini and Compsurini are present in the unweighted tree (Fig. 2), denoting the remaining taxa do not share its synapomorphies. The importance of the homoplastic characters in the recovery of the historical evolution of the Characidae is further discussed. Interrelationships of the Odontostilbini components are unclear in a polytomy comprising *Odontostilbe nareuda*, *O. parecis*, *O. pulchra*, and the clades A1 and A7. These taxa and clades are further presented.

***Odontostilbe* Cope, 1870**

Odontostilbe Cope, 1870: 566 (type species *Odontostilbe fugitiva* Cope, 1870: 566 by original description).

Diagnosis. *Odontostilbe* species are diagnosed by the synapomorphies of the tribe and absence of the diagnostic characters of *Pseudocheirodon*, *Lobodeuterodon*, *Prodontocharax*, *Amblystilbe,* and *Holoshesthes*.

Remarks. The genus *Odontostilbe* is not monophyletic in the present hypothesis, but conservatively fifteen species are retained in the genus considering the results obtained in the two strict consensus trees obtained, the weighted and unweighted trees (Figs. 2, 3). Considering the weighted tree, twelve of the fifteen species are grouped in three distinct clades, while *O. nareuda*, *O. parecis*, and *O. pulchra* remain in unresolved positions (Fig. 3). Especially, most of the species of *Odontostilbe* are grouped in the clade A8, being eight species including the type species *O. fugitiva*. In the clade A1 jointly with the two species of *Pseudocheirodon,* at basal position stay *O. splendida* and *O. pao*. In the clade A11, *Odontostilbe* n. sp. "b" also at basal position grouped with the six species of *Holoshesthes*. However, in the unweighted tree (Fig. 2) the fifteen species of *Odontostilbe* that grouped in the weighted tree are found in polytomy with the clades of the subfamilies Cheirodontini, Compsurini, and with the distinct clades formed by *Pseudocheirodon*, *Prodontocharax* + *Amblystilbe*, *Acinocheirodon* + *Holoshesthes,* and *Lobodeuterodon* not grouped. Considering the clades retained in the more conservative unweighted analysis, the genus is maintained valid though polyphyletic, and only the clades supported by both hypotheses are admitted monophyletic. The clades formed by *Acinocheirodon* + *Holoshesthes,* and *Prodontocharax* + *Amblystilbe,* and the *Lobodeuterodon* are shortly discussed below, and will be treated in subsequent papers. The monophyletic clade A8 in the weighed tree is sustained by only one synapomorphy, unreversed and unique, listed below.

***Odontostilbe nareuda* Bührnheim & Malabarba, 2006**

Diagnosis. One derived character is found in this species: absence of a flange on anterodorsal portion of the maxilla, posterior to rod-like ascending process of the maxilla [45-1]

Odontostilbe parecis Bührnheim & Malabarba, 2006

Diagnosis. Four derived characters are found in this species: (1) ventral border of the second infraorbital with a slight concavity near its half length, close to the posterior tip of the maxilla [17-1]; (2) ascending process of the premaxilla absent or with small point on dorsal border of the premaxilla [32-1]; (3) upper branch of the angulo-articular short, not extended anteriorly or slightly extended, anterior border pointed or slightly pointed, 4-5 times in the longitudinal length of the dentary [60-0]; (4) unbranched pelvic-fin ray of males not elongate [103-0].

Odontostilbe pulchra Gill (1858)

Diagnosis. Three derived characters are found in this species: (1) absence of the flange on anterodorsal portion of the maxilla, posterior to rod-like ascending process of the maxilla [45-1]; (2) lower branch of the angulo-articular on lateral surface of dentary elongate, extended anteriorly, anterior border pointed or slightly pointed, 2-3 times in the longitudinal length of the dentary [61-1]; (3)) presence of hooks on the mid portion of the first unbranched pelvic-fin ray in males [137-1].

Odontostilbe splendida + (*O. pao* + *Pseudocheirodon*) + (*O.* n. sp. "h" + (*Lobodeuterodon* + (*Prodontocharax* + *Amblystilbe*)))

[Clade A1]

Diagnosis. This clade is supported by the uniquely derived posteroventral portion of the posterior edentulous lamina of the maxilla turned medially, being settled in a different plane regarding anterior portion of the maxilla [52*-1].

Odontostilbe splendida Bührnheim & Malabarba, in manuscript

None unique characters found.

Odontostilbe pao + *Pseudocheirodon*

[Clade A2]

Diagnosis. The following synapomorphies are found to support this clade: (1) absence of the flange on anterodorsal portion of the maxilla, posterior to rod-like ascending process of the maxilla [45-1]; (2) posterior portion of the somewhat triangular, short, median portion deeper and gradually narrowing to the posterior tip [48*-1]; (3) presence of the flange in the dorsolateral border of the dentary, forming a concavity in the dorsolateral surface of the dentary, at vertical after the posteriormost teeth of the dentary [66*-1].

Remarks. Although this clade is supported by two unique synapomorphies, it is not sustained in the unweighted tree (Fig. 1). *Odontostilbe pao* does not share sixteen synapomorphies with the species of the genus *Pseudocheirodon*. Considering that, the polytomy found in the clade A1 only sustained by one synapomorphy, and the overall unsolved relationships of the species of the *Odontostilbe*, *O. pao* is not admitted in the genus *Pseudocheirodon*. The Ch. 48 is a redescription of the Ch. 6 proposed by Malabarba (1998), which was an exclusive synapomorphy to *Pseudocheirodon*.

Odontostilbe pao **Bührnheim & Malabarba, in manuscript**

Diagnosis. Two derived characters are found in this species: (1) slightly subterminal mouth, mouth slit at horizontal below the middle of eye [75-1]; second unbranched dorsal-fin ray elongate and surpassing the first unbranched dorsal-fin ray, forming a short to long filament in males [102-1].

Pseudocheirodon arnoldi + P. terrabae

[Clade A3]

Diagnosis. Sixteen synapomorphies support this clade: (1) anteromedial process of the mesethmoid pointed [2-0]; (2) lateral wings of the mesethmoid almost indistinct or absent [6-1]; (3) fifth infraorbital broad with expanded lateral laminas from the laterosensory canal [21-0]; (4) palatine spherical [30*-3]; (5) ascending process of the premaxilla ascending process absent or with small point on dorsal border of the premaxilla [32-1]; (6) slightly pronounced laminas of the medial border of the premaxilla that articulate with the mesethmoid, the posteromedial lamina at the coronal plane and perpendicular to the anteromedial lamina [34*-2]; (7) all cusps similar in form and size in the single tooth row of the premaxilla [39-2]; (8) presence of a protruding spine-like projection on the ventral border of the maxilla, just ahead anteriormost teeth [47*-1]; (9) maxilla curved, with tooth-bearing portion continuous with premaxillary tooth-bearing portion and angled relative to edentulous portion of the maxilla [49*-1]; (10) posterior edentulous portion of the maxilla short, smaller than the anterior tooth bearing portion of the maxilla [50-0]; (11) lower branch of the angulo-articular elongate extended anteriorly on lateral surface of dentary, anterior border pointed or slightly pointed, 2-3 times in the longitudinal length of the dentary [61-1]; (12) symphyseal dentary joint articulates through rounded bony surfaces joined by tough ligamentous tissue [68-1]; (13) each tooth of the anterior large dentary teeth with 8-9 cusps, being 6-7 central cusps larger, similar in size, and in a row forming a sharp cutting edge [71*-2]; (14) ventral border nearly straight of the posteriormost branchiostegal ray in males [77-0]; (15) unbranched pelvic-fin ray of males not elongate [103-0]; (16) anal-fin profile of males almost straight profile to slight concave; sexually dimorphic; the last unbranched anal-fin ray and 1st to 10th branched anal-fin rays in males somewhat longer than in females [112-2].

Remarks. *Pseudocheirodon* was proposed by Meek & Hildebrand (1916), with *P. affinis*. Subsequently, Bussing (1967) described *P. terrabae*, and later *Cheirodon arnoldi* Boulenger, 1909 was found to be the senior synonym of *P. affinis* by Fink & Miller (1985). Previously *Pseudocheirodon* was considered a synonym of *Cheirodon* by Fink & Weitzman (1974), and later the genus was considered valid by Malabarba (1998) and diagnosed by three derived characters. Sixteen synapomorphies sustain the genus, Malabarba (1998) already referred the Ch. 68, the round symphyseal dentary joint to diagnose *Pseudocheirodon*. Character 49 was also a synapomorphy to *Pseudocheirodon* in Malabarba (1998: Ch. 7), but found in *Prodontocharax* with *Amblystilbe* in synonym, and here considered exclusive to *Pseudocheirodon*. The narrow posterior tip of maxilla of Malabarba (1998: Ch. 6), another synapomorphy to *Pseudocheirodon* is redescribed here and also shared by *Odontostilbe pao*.

Pseudocheirodon arnoldi Boulenger (1909)

Diagnosis. The following derived characters are found in this species: (1) tooth bearing portion of the dentary in lateral view in two sections with teeth, the horizontal anterior section with 5-6 large teeth, and an oblique and ascending posterior section with smaller teeth. Teeth of the posterior section sometimes disposed in an almost perpendicular axis in relation to the longer axis of teeth of anterior section [56-3]; (2) laterosensory canal of the lateral line not extended between caudal-fin rays, reaching or not to the caudal-fin base [114-0]; (3) presence of hooks on the mid portion of the first unbranched pelvic-fin ray in males [137-1].

Pseudocheirodon terrabae Bussing, 1967

Diagnosis. The following derived characters are found in this species: (1) anterodorsal border of the second infraorbital without pointed projection or not as state 1 [18-0]; (2) usually five or six maxillary teeth [54-1].

Odontostilbe n. sp. “h” + (*Lobodeuterodon* + (*Prodontocharax* + *Amblystilbe*))

[Clade A4]

Diagnosis. Four synapomorphies support this clade: (1) anterodorsal border of the second infraorbital without pointed projection [18-0]; (2) thick lateral ridge with a slightly convex surface of the upper portion of the angulo-articular, on posterolateral portion of the lower jaw, near the posterior portion of the maxilla, well-marked in dorsal view and discernible in not dissected specimens [57-2]; (3) mouth subterminal, mouth slit at horizontal with the lower edge of eye [75-2]; (4) pelvic-fin rays i5i, i6, i6i, rarely some individuals of a given species may present i7 [106-1].

Odontostilbe n. sp. “h

Diagnosis. Nine synapomorphies support this clade: (1) posteroventral process of the orbitosphenoid absent, or presence of a tiny posteroventral process associated to a small posterior concavity in the orbitosphenoid [10-0]; (2) laterosensory canal of the first infraorbital absent or nearly absent at the posterior portion of the first infraorbital, never reaching to about half length of the longest axis [15-1]; (3) fourth infraorbital squarish, similar in width and height, or reduced [20-0]; (4) anterior border of the sixth infraorbital with the anterior lamella small, reduced, once in laterosensory tube width, in a somewhat small lingual-like shape [22-1]; (5) dorsal border of opercle ascendant, posterior portion elevated, protruded [25-2]; (6) upper branch of the angulo-articular short, not extended anteriorly or slightly extended, anterior border pointed or slightly pointed, 4-5 times in the longitudinal length of the dentary [60-0]; (7) posterior border of all branchiostegals rays or at least the two posteriormost branchiostegals rays markedly crenulated [78-1]; (8) basibranchial 1 elongate, located between and somewhat separating the paired hypobranchial 1 elements [81-0]; (9) gill rakers in the ceratobranchial 1 in two rows, one row along the lateral border of the ceratobranchial 1, and one row along the medial border of the ceratobranchial 1[85-1].

Lobodeuterodon + (*Prodontocharax* + *Amblystilbe*)

[Clade A5]

Diagnosis. Four synapomorphies support this clade: (1) fifth infraorbital broad, with expanded lateral laminas from the laterosensory canal [21-0]; (2) ascending process of the premaxilla absent or with small point on dorsal border of the premaxilla [32-1]; (3) tooth bearing portion of the dentary in lateral view in two sections with teeth, the horizontal anterior section with 5-6 large teeth, and an oblique and ascending posterior section with smaller teeth

[56-3]; (4) anal-fin profile of males almost straight to slight concave; sexually dimorphic; the last unbranched anal-fin ray and 1st to 10th branched anal-fin rays in males somewhat longer than in females [112-2].

***Lobodeuterodon euspilurus* Fowler, 1945**

Diagnosis. The following derived character are found in this species: (1) longitudinal branch of the laterosensory canal of parietal posteriorly not contiguous to the transverse laterosensory canal of the parietal, divided by a gap, and anteriorly contiguous to the laterosensory canal of frontal [11-1]; (2) anterodorsal border of the second infraorbital with a small to well-developed pointed projection, underneath the posterodorsal portion of the first infraorbital[18-1]; (3) presence of hooks on the mid portion of the first unbranched pelvic-fin ray in males [137-1].

Remarks. The genus *Lobodeuterodon* was proposed as a subgenus of *Deuterodon* by Fowler (1945), having an anal-fin with convex border. Malabarba (2003) left its type species *Deuterodon* (*Lobodeuterodon*) *euspilurus* in synonym of *Odontostilbe fugitiva*, then admitting the synonym in the generic level too. This probable synonym was previously reported in Lucena & Lucena (2002), which reviewed the genus *Deuterodon*. In the redescription of the type species *Odontostilbe fugitiva* by Bührnheim & Malabarba (1996), *L. euspilurus* is treated as "*O. euspilura*" not found as synonym of *O. fugitiva*, instead treated as a valid senior synonym of *Odontostilbe roloffi* Géry, 1972. Here, the genus *Lobodeuterodon* is considered valid, diagnosed by three derived characters, and found nearly related to *Odontostilbe* n. sp. “h", *Prodontocharax* and *Amblystilbe* in clade A4. Notably, this clade is not sustained in the more conservative unweighted tree (Fig. 2). However the relationships in the clade A5, including *Lobodeuterodon* + (*Prodontocharax* + *Amblystilbe*) seems to be stronger, having a bootstrap value of 59, considered significant here (higher than the value of 41 obtained to the well supported subfamily Cheirodontinae). These relationships will be treated in a future paper, in which the redescription of *Lobodeuterodon euspilurus* will be provided.

Prodontocharax* + *Amblystilbe

[Clade A6]

Diagnosis. Eleven synapomorphies support this clade: (1) palatine squarish or ovoid [30-4]; (2) premaxilla cap-like shape, with an well-arched rounded dorsal border [33*-1]; (3) the first to third medial teeth with 3-6 cusps, usually 3-5 [40-1]; (4) usually 6-8 in the premaxilla [41-

1]; (5) premaxillary teeth spaced, space between teeth nearly equal to one tooth [42-1]; (6) absence of overlapping tooth cusps in the premaxillary teeth [43-0]; (7) absence of the flange on anterodorsal portion of the maxilla, posterior to rod-like ascending process of the maxilla [45-1]; (8) usually five or six maxillary teeth [54-1]; (9) anterior maxillary teeth tricuspid [55-1]; (10) larger anterior dentary teeth tricuspid [74-1]; (11) usually 17 or more gill rakers in the upper branch of the first gill arch [90*-2].

Prodontocharax melanotus Eigenmann & Pearson, 1924

Diagnosis. Three derived characters are found in this species: (1) posterior edentulous portion of the maxilla short, smaller than the anterior tooth bearing portion of the maxilla [50-0]; (2) gill rakers in the ceratobranchial 1 in two rows, one row along the lateral border of the ceratobranchial 1, and one row along the medial border of the ceratobranchial 1 [85-1]; (2) black spot on dorsal fin, along midlenght of 2nd unbranched and 1st to 6th branched fin rays [161*-1].

Remarks. *Prodontocharax* with the type species *P. melanotus* was diagnosed by Eigenmann & Pearson (1924) mainly by the presence of tricuspid teeth and the short anal-fin. Böhlke (1953) reviewed the genus, designating a lectotype and paralectotypes to *P. melanotus*, and remarking the diagnostic mouth distinctly inferior to the genus. This strictly inferior mouth here is redescribed as subterminal mouth and it is a synapomorphy to the previous clade A4. In his work of 1953, Böhlke also described *P. alleni*; next species diagnostic and considered valid in the genus *Amblystilbe*. Böhlke (1954) treated *Prodontocharax* and *Amblystilbe* as nearly related, proposing a tribe Prodontocharacini, though he did not examined specimens of *Amblystilbe*. This family group name , howver, was used only in the unpublished doctoral dissertation of Böhlke, being not available for nomenclatural purposes (ICZN, 1999: article 9, 9.7 paragraph) and which is stated by Böhlke (1953: 111). Géry (1977) considered *Prodontocharax* with *Amblystilbe* in synonym. This is because both species have tricuspid teeth and subterminal mouth. The tricuspid teeth here is treated in characters 40, 55, 74, being synapomorphies to the clade A6, confirming *Prodontocharax* and *Amblystilbe* as sister taxa. Malabarba (1998), as Géry (1977) considered *Prodontocharax* with *Amblystilbe* in synonym, but proposed four synapomorphies to his *Prodontocharax*. From these, only the dorsal-fin with a black spot is maintained here. The Ch. 53 corresponding to the Ch. 8 of Malabarba (1998), regarding a short maxilla as a synapomorphy to *Prodontocharax* is discussed under Ch. 53, and not admitted here. However, the notion of smaller size of maxilla in

Prodontocharax melanotus is somewhat related to the "posterior edentulous portion of the maxilla short" [Ch. 50-0], here a new derived character proposed to it.

***Amblystilbe alleni* (Böhlke, 1953)**

Diagnosis. Nine derived characters are found in this species: (1) posteroventral process of the orbitosphenoid absent, or presence of a tiny posteroventral process associated to a small posterior concavity in the orbitosphenoid [10-0]; (2) fourth infraorbital squarish, similar in width and height, or reduced [20-0]; (3) posterior edentulous lamina of the maxilla flat and plane [52-0]; (4) lateral laminar ridge with a straight surface in the upper portion of the angulo-articular, on posterolateral portion of the lower jaw, near the posterior portion of the maxilla, observed in dorsal view [57-3]; (5) narrow anteriormost portion of dentary at the symphyseal joint, in lateral view, 7 times or more the height of the middle portion of dentary [64*-2]; (6) posterior border of all branchiostegals rays or at least the two posteriormost branchiostegals rays markedly crenulated [78-1]; (7) gill rakers of similar length in the upper and lower branches [87*-1]; (8) 10 or more gill rakers in the upper branch of the first gill arch [89-0]; (9) pelvic-fin rays i7, rarely some individuals of a given species may present i6 or i6i [106-0].

Remarks. *Amblystilbe* is a monotypic genus proposed by Fowler (1940) (type species *A. howesi*) based on the inferior mouth and tricuspid teeth, but Fowler did not compare it to the possible related genus *Prodontocharax* of Eigenmann & Pearson (1924). Böhlke (1953), when described *Prodontocharax alleni*, differed it from *Prodontocharax melanotus* and remarked *Amblystilbe* as different of *Prodontocharax*. Soon later in an unpublished review of the Cheirodontinae, Böhlke (1954) suggested a tribe Prodontocharacini, referring *Prodontocharax* and *Amblystilbe* as nearly related, though he did not examined specimens of *Amblystilbe*. Finally, Géry (1977) considered *Amblystilbe* as synonym of *Prodontocharax,* a synonym also admitted by Malabarba (1998, 2003). Here *Amblystilbe* is considered valid, removed from the synonym of *Prodontocharax,* having nine derived characters (two of them uniquely derived).

***Odontostilbe dierythrura* + *O. paraguayensis* + Clade A8 + Clade A11**
[Clade A7]

Diagnosis. The following synapomorphies sustain this clade: (1) elongate, extended anteriorly lower branch of the angulo-articular on lateral surface of dentary, anterior border pointed or slightly pointed, 2-3 times in the longitudinal length of the dentary [61-1]; (2) second unbranched dorsal-fin ray elongate and surpassing the first unbranched dorsal-fin ray, forming a short to long filament in males [102-1].

Remarks. The elongation of the second unbranched dorsal-fin ray was a diagnostic character to the *Odontostilbe* sensu Malabarba (1998).

Odontostilbe dierythrura **Fowler, 1940**

Diagnosis. This species has a conspicuous slightly subterminal mouth, the mouth slit is at horizontal below the middle of eye [75-1].

Odontostilbe paraguayensis **Eigenmann & Kennedy, 1903**

Diagnosis. This species has the derived ventral border of the second infraorbital with a slight concavity near its half length, close to the posterior tip of the maxilla [17-1], and the autapomorphic 2nd-4th supraneurals fused [166*-1].

Odontostilbe ecuadorensis **+** ***O. fugitiva*** **+** ***Odontostilbe*** **n. sp. “ m” + Clade A9 [Clade A8]**

Diagnosis. The uniquely derived laterosensory canal of the sixth infraorbital branched with anterior branch extended along the expanded lingual-like shape anterior lamella of the sixth infraorbital [23*-1] supports this clade.

Odontostilbe ecuadorensis **Bührnheim & Malabarba, 2006**

None unique characters found.

Odontostilbe fugitiva **Cope, 1870**

None unique characters found.

Odontostilbe **n. sp. “ m”**

Diagnosis. This species has the mouth slightly subterminal with mouth slit at horizontal below the middle of eye [75-1].

Odontostilbe microcephala + (*Odontostilbe* n. sp. “e” + *Odontostilbe* n. sp. “ p”)
[Clade A9]

Diagnosis. Four synapomorphies support this clade: (1) posteroventral process of the orbitosphenoid absent, or presence of a tiny posteroventral process associated to a small posterior concavity in the orbitosphenoid [10-0]; (2) absence of the flange on anterodorsal portion of the maxilla, posterior to rod-like ascending process of the maxilla [45-1]; (3) upper branch of the angulo-articular short, not extended anteriorly or slightly extended, anterior border pointed or slightly pointed, 4-5 times in the longitudinal length of the dentary [60-0]; (4) basibranchial 1 elongate, located between and somewhat separating the paired hypobranchial 1 elements [81-0].

Odontostilbe microcephala Eigenmann, 1903

Diagnosis. Nine derived characters are found in this species: (1) posteroventral border of the third infraorbital ventrally contacting the laterosensory canal of preopercle, but leaving a posterior naked area between border of the third infraorbital and the laterosensory canal of preopercle [19-1]; (2) fifth infraorbital broad, with expanded lateral laminas from the laterosensory canal [21-0]; (3) tooth bearing portion of the dentary in lateral view in two sections with teeth, the horizontal anterior section with 5-6 large teeth, and an oblique and ascending posterior section with smaller teeth [56-3]; (4) lateral short ridge with a somewhat straight surface of the upper portion of the angulo-articular, on posterolateral portion of the lower jaw, near the posterior portion of the maxilla, observed in dorsal view [57-1]; (5) more than half length of the dorsal border of the dentary with teeth [62-0]; (6) mouth subterminal, mouth slit at horizontal with the lower edge of eye [75-2]; (7) gill rakers in the ceratobranchial 1 in two rows, one row along the lateral border of the ceratobranchial 1, and one row along the medial border of the ceratobranchial 1 [85-1]; (8) 10 or more gill rakers in the upper branch of the first gill arch [89-0]; (9) presence of hooks on the mid portion of the first unbranched pelvic-fin ray in males [137-1].

Odontostilbe n. sp. “e” + *Odontostilbe* n. sp. “ p”
[Clade A10]

Diagnosis. Two derived characters define this clade: (1) mesopterygoid teeth present, teeth grouped on median portion of the mesopterygoid [29-1]; (2) scattered black chromatophores slightly darker and more numerous on middistal portion of the dorsal-fin, extending on the 2nd unbranched dorsal-fin ray and 1st to 5th, 6th branched fin ray [158-1].

Odontostilbe n. sp. "e"

Diagnosis. Five derived characters are found in this species: (1) anteromedial process of the mesethmoid well-developed, extending between premaxillae and reaching anterior tooth bearing border of the premaxillae [1-0]; (2) fourth infraorbital squarish, similar in width and height, or reduced [20-0]; (3) palatine nearly rectangular, irregular, posterior portion somewhat narrow [30-0]; (4) basibranchial 1 short, located anteriorly between paired hypohyals; partially extending posteriorly between the paired hypobranchial 1 elements, but not totally separating them that are placed posteriorly [81-1]; (5) pelvic-fin rays i5i, i6, i6i, rarely some individuals of a given species may present i7 [106-1].

Odontostilbe n. sp. " p"

Diagnosis. The number of 5-7 cusps, usually 5-6, of the first to third medial teeth in the single tooth row of the premaxilla is derived to this species [40-2].

Odontostilbe n. sp. "b" + (*Holoshesthes pequira* + (*Holoshesthes* n. sp. " p" + (*Holoshesthes* n. sp. "k" + (*H. geayi* + (*H. hemigrammus* + *Holoshesthes* n. sp. " b"))))) [Clade A11]

Diagnosis. Four synapomorphies support this clade: (1) mesopterygoid teeth grouped on median portion of the mesopterygoid [29-1]; (2) 5-7 cusps, usually 5-6 cusps in the first to third medial teeth of the premaxilla [40-2]; (3) absence of overlapping tooth cusps between premaxillary teeth [43-0]; (4) scattered black chromatophores slightly darker and more numerous on middistal portion of the dorsal-fin, extending on the 2nd unbranched dorsal-fin ray and 1st to 5th, 6th branched fin ray [158-1].

Odontostilbe n. sp. "b"

Diagnosis. Thirteen derived characters are present in this species: (1) absence of posteroventral process of the orbitosphenoid or presence of a tiny posteroventral process associated to a small posterior concavity in the orbitosphenoid [10-0]; (2) longitudinal branch of the laterosensory canal of parietal posteriorly not contiguous to the transverse laterosensory canal of the parietal, divided by a gap, and anteriorly contiguous to the laterosensory canal of frontal [11-1]; (3) laterosensory canal absent or nearly absent at the posterior portion of the first infraorbital, never reaching to about half length of the longest axis [15-1]; (4) anterodorsal border of the second infraorbital without pointed projection [18-0]; (5) anterior border of the sixth infraorbital with the anterior lamella small, reduced, once in laterosensory tube width, in a somewhat small lingual-like shape [22-1]; (6) preopercular sensory short, preopercular canal reaching the posterior condylar articular surface of hyomandybular [27-1]; (7) mesopterygoid teeth present, conical teeth in two separate groups on median portion of the mesopterygoid [29*-2]; (8) lower branch of the angulo-articular on lateral surface of dentary short, not extended anteriorly or slightly extended, anterior border forming a slight convexity, 4-5 times in the longitudinal length of the [61-0]; (9) basibranchial 1 elongate, located between and somewhat separating the paired hypobranchial 1 elements [81-0]; (10) pelvic-fin rays i5i, i6, i6i, rarely some individuals of a given species may present i7 [106-1]; (11) laterosensory canal of the lateral line not extended between caudal-fin rays, not reaching to the caudal-fin base [114-0]; (12) lateral line reduced to 2-6 perforated scales [153-1]; (13) black spot on dorsal fin, along distal midlength of 2nd unbranched and 1st to 6th-7th branched fin rays, usually not reaching tip of fin rays [158-2].

Holoshesthes pequira **+ (***Holoshesthes* **n. sp. " p" + (*****Holoshesthes*** **n. sp. "k" + (*****H. geayi*** **+ (*****H. hemigrammus*** **+** ***Holoshesthes*** **n. sp. " b"))))**

[Clade A12]

Diagnosis. Twenty synapomorphies support this clade: (1) anteromedial process of the mesethmoid well-developed, extending between premaxillae and reaching anterior tooth bearing border of the premaxillae [1-0]; (2) ventral border of the second infraorbital with a slight concavity near its half length, close to the posterior tip of the maxilla [17-1]; (3) palatine nearly rectangular, irregular, posterior portion somewhat narrow [30-0]; (4) usually 6-8 premaxillary teeth [41-1]; (5) absence of the flange on anterodorsal portion of the maxilla, posterior to rod-like ascending process of the maxilla [45-1]; (6) presence of a longitudinal groove just below dorsolateral border of the maxilla [46-1]; (7) posterior edentulous portion of the maxilla extended, longer than the anterior tooth bearing portion of the maxilla [50-2]; (8) the posterior tooth bearing portion of dentary, with smaller teeth, elevated, forming a marked convexity [56-1]; (9) lateral short ridge with a somewhat straight surface of the upper portion of the angulo-articular, on posterolateral portion of the lower jaw, near the posterior portion of the maxilla, observed in dorsal view [57-1]; (10) longer axis of the anteriormost teeth of the dentary perpendicular to the longer axis of the [59-0]; (11) upper branch of the angulo-articular short, not extended anteriorly or slightly extended, anterior border pointed or slightly pointed, 4-5 times in the longitudinal length of the dentary [60-0]; (12) more than half length of the dorsal border of the dentary with teeth [62-0]; (13) anteriormost portion of dentary, at the symphyseal joint, in lateral view deep, 2-3 times in the height of the middle portion of dentary [64-0]; (14) presence of posterior small unicuspid teeth of the dentary, lingually turned [65-1]; (15) anterior larger dentary teeth with 3 central cusps larger, nearly equal in size, compressed and aligned at their distal tips in a row forming a sharp cutting edge; cusp tips distal [72-2]; (16) 3-4 anteriormost dentary teeth larger and following teeth decreasing in size posteriorly [73-1]; (17) lower jaw profile slightly projected on head profile [76-1]; (18) elongate gill rakers of the first gill, proportionally occupying more than half or half of the branchial cavity between the cranium base and the gill branches [86-1]; (19) 13-16 gill rakers, rarely 12 in the lower branch of the first gill arch [90-0]; (20) presence of hooks on the mid portion of the first unbranched pelvic-fin ray in males [137-1].

Remarks. The clade A12 comprises six species at present considered valid in the genus *Holoshesthes*. This genus was proposed by Eigenmann (1903) to reallocate *Chirodon pequira* of Steindachner (1882, 1883), its type species. Eigenmann (1915) described another species in this genus, *H. heterodon*, further removed to *Serrapinnus* by Malabarba (1998). Furthermore, Malabarba (1998) left *Holoshesthes* as synonym of *Odontostilbe* based on the finding of *H. pequira* as the sister species of *Odontostilbe fugitiva*. Herein, *Holoshesthes* is revalidated including three new species, and two monotypic genera as its synonyms, *Aphyocheirodon* with *A. hemigrammus* of Eigenmann (1915) and *Cheirodontops* with *C. geayi* of Schultz (1944). All of these species share the above twenty synapomorphies forming a concise monophyletic clade obtained in the weighted and unweighted trees (Figs. 2, 3). From these twenty synapomorphies, Ch. 72 (state 2) and Ch. 73 (state 1) correspond to synapomorphies found to the genus *Cheirodontops* in Malabarba (1998). The revalidation of *Holoshesthes* with the description of the new species, and redescription of the reallocated *H. hemigrammus* and *H. geayi* is the subject of a subsequent paper (Bührnheim & Malabarba, in manuscript).

Holoshesthes pequira (Steindachner, 1882)

Diagnosis. Three derived characters are found in this species: (1) premaxillary teeth with 1-4 tooth cusps overlapping between adjacent teeth, usually between posteriormost teeth or in all of teeth [43-1]; (2) the unique ontogenetic change in the shape and tooth cusp number between juveniles and adults in which the teeth of juveniles usually have 7 cusps, central cusp longer and slightly larger with lateral cusps decreasing in size, while the teeth of adults have 3 central cusps larger, compressed and in row forming a sharp cutting edge [67*-1]; (3) black spot on dorsal fin, along distal midlength of 2nd unbranched and 1st to 6th-7th branched fin rays, usually not reaching tip of fin rays [158-2].

Holoshesthes **n. sp. " p" + (*Holoshesthes* n. sp. "k" + (*H. geayi* + (*H. hemigrammus* + *Holoshesthes* n. sp. " b")))**

[Clade A13]

Diagnosis. Five synapomorphies support this clade: (1) mesopterygoid teeth absent [29-0]; (2) medial premaxillary tooth markedly larger than the following posterior teeth [36*-1]; (2) main cusps of the posteriormost teeth of the premaxilla slightly oblique to the ventral border of the premaxilla, curved posteriorly [38*-1]; (3) central cusp of premaxillary teeth notably larger than lateral cusps [39-0]; (3) lower border of the dentary slightly convex [58-1].

Holoshesthes **n. sp. " p"**

Diagnosis. This species has the autapomorphic elongate unbranched dorsal-, pectoral-, pelvic- and anal-fin rays in mature females [104*-1], and the derived presence of hooks on the mid portion of the first unbranched pelvic-fin ray in males [137-0].

Holoshesthes **n. sp. "k" + (*H. geayi* + (*H. hemigrammus* + *Holoshesthes* n. sp. " b"))**

[Clade A14]

Diagnosis. This clade is supported by two derived characters: (1) 3-6 cusps, usually 3-5, in the first to third medial premaxillary teeth [40-1], and usually one or none teeth in the maxilla [54-3].

Holoshesthes **n. sp. "k"**

None unique characters found.

H. geayi **+ (*H. hemigrammus* + *Holoshesthes* n. sp. " b")**

[Clade A15]

Diagnosis. Four derived characters support this clade: (1) anteromedial process of the mesethmoid short, not extending or partially extending between premaxillae, not reaching anterior tooth bearing border of the premaxillae [1-1]; (2) premaxillary teeth spaced, space between teeth nearly equal to one tooth [42-1]; (3) very short anterodorsal ascending rod-like process of the maxilla, articulated to the premaxilla, more than 6 times in the total length of the maxilla [44-2]; (4) long maxilla, almost reaching the posterior border of lower jaw, contacting the posteroventral portion of the angulo-articular, below anterodorsal extension of the angulo-articular, and beyond vertical through the mid-distal portion of the infraorbital 2 [53-0].

Holoshesthes geayi (Schultz, 1944)

Diagnosis. This species has one autapomorphy, the 1-3 posteriormost premaxillary teeth larger than the preceding teeth [37*-1].

H. hemigrammus + *Holoshesthes* n. sp. “ b”

[Clade A16]

Diagnosis. Five synapomorphies support this clade: (1) anterior maxillary teeth tricuspid [55-1]; (2) absence of the elongation of the second unbranched dorsal-fin ray in males [102-0]; (3) unbranched pelvic-fin ray of males not elongate [103-0]; (4) hooks on the fins of males distributed in dorsal-, pectoral-, pelvic-, anal-, and caudal-fin rays [138*-1]; (5) males with caudal-fin hooks along distal portions of the principal caudal-fin rays 11 to 14 [152-1].

Holoshesthes hemigrammus (Eigenmann, 1915)

Diagnosis. Twenty four derived characters are present in this species: (1) lateral wings of the mesethmoid almost indistinct or absent [6-1]; (2) posteroventral process of the orbitosphenoid absent, or presence of a tiny posteroventral process associated to a small posterior concavity in the orbitosphenoid[10-0]; (3) longitudinal branch of the laterosensory canal of parietal posteriorly not contiguous to the transverse laterosensory canal of the parietal, divided by a gap, and anteriorly contiguous to the laterosensory canal of frontal [11-1]; (4) laterosensory canal of frontal posteroventral branch of the laterosensory canal of frontal interrupted, or absent, not contiguous to the laterosensory canal of pterotic [12-1]; (5) laterosensory canal of the first infraorbital absent or nearly absent at the posterior portion of the first infraorbital, never reaching to about half length of the longest axis [15-1]; (6) anterodorsal border of the second infraorbital without pointed projection or not as state 1 [18-0]; (7) posteroventral border of the third infraorbital not contacting the laterosensory canal of preopercle, leaving a naked area between the posterolateral border of the third infraorbital and the laterosensory canal of preopercle [19-2]; (8) fourth infraorbital reduced [20-0]; (9) anterior border of the sixth infraorbital with the anterior lamella small, reduced, once in laterosensory tube width, in a somewhat small lingual-like shape [22-1]; (10) dorsal border of opercle ascendant, posterior portion elevated, protruded [25-2]; (11) preopercular sensory canal short, preopercular canal reaching the posterior condylar articular surface of hyomandybular [27-1]; (12) ectopterygoid teeth present [28*-1]; (13) more than 8 premaxillary teeth, usually more than 10 [41-0]; (14) premaxillary teeth juxtaposed, practically without space between teeth [42-0]; (15) absence of the longitudinal groove just below dorsolateral border of the maxilla [46-0]; (16) usually five or six maxillary teeth [54-1]; (17) lateral ridge absent or almost absent of the upper portion of the angulo-articular, on posterolateral portion of the lower jaw, near the posterior portion of the maxilla, observed in dorsal view [57-0]; (18) lower border of the dentary approximately straight [58-0]; (19) anterior larger dentary teeth with 3 central cusps larger, nearly equal in size, compressed and aligned at their distal tips in a row forming a sharp cutting edge; cusp tips of lateral cusps lateral [72*-3]; (20) 8 to 10 anteriormost dentary teeth larger and following teeth decreasing in size posteriorly [73*-2]; (21) less than 12 gill rakers in the lower branch of the first gill arch [90-1]; (22) laterosensory canal of the lateral line not extended between caudal-fin rays, not reaching to the caudal-fin base [114-0]; (23) absence of hooks on the first unbranched pelvic-fin ray in males [137-0]; (24) scattered black chromatophores on entire or almost entire dorsal-fin [158-0].

Holoshesthes n. sp. “ b”

Diagnosis. Seven derived characters are present in this species: (1) palatine regular rectangular, well developed [30-1]; (2) main cusps of the posteriormost teeth almost perpendicular to the ventral border of premaxilla [38-0]; (3) first to third medial premaxillary teeth usually conical tooth or conical tooth with a small lateral cusp [40-0]; (4) maxilla short, terminating at mid portion of lower jaw, contacting the anterodorsal extension of the angulo-articular or at mid portion of the angulo-articular, and reaching beyond the vertical through the contact area between the infraorbitals 1 and 2 or up to the mid portion of the infraorbital 2. [53-1]; (5) anterior maxillary teeth unicuspid [55-2]; (6) fin hooks straight or practically straight, distal tip perpendicular to anal-fin ray long axis. [149*-1]; (7) caudal-fin hooks on almost all caudal-fin rays, 2-18 [152*-3].

Discussion

Osteological studies on characids with phylogenetic purposes have been traditionally problematic. This is usually related to the high occurrence of homoplasies, that can be found between species of different lineages in all levels of the Characidae (Lucena, 1993), as subfamilies or genera (*e.g. Brycon*, Zanata, 2000; *Moenkhausia*, Benine, 2004), or even in the nearly related characiform families (*e.g.* Alestidae, Zanata & Vari, 2005). This is clearly exemplified along the character description and discussion in this work, where several characters that are variable and potentially informative to reconstruct cheirodontine phylogeny are found in equivalent states in other recognized monophyletic lineages of the

Characidae. The skeletal system of the Characidae seems to represent a very successful and conservative organization, from which selective pressures demand similar responses in different lineages. In contrast, characters other than skull morphology seem to be very informative, allowing the construction of well-corroborated hypothesis of relationships in some characid groups. The phylogenies of the Cheirodontini and Compsurini tribes of the Cheirodontinae, and of the subfamilies Stevardiinae and Glandulocaudinae based on primary and secondary sexual systems are examples of that, with well-supported hypothesis of relationships even at species level (*e.g.* Weitzman & Fink, 1985; Weitzman & Menezes, 1998; Weitzman *et al*., 2005). Unfortunately, such an alternative is the exception and not the rule.

The present paper deals with the phylogenetic study of a group of characid fishes that includes both examples of derived and basal taxa. The cheirodontines include the Cheirodontini, whose monophyly and relationships of included species are easily accessed through the analysis of a series of secondary sexually dimorphic modifications of the anal and caudal fins of males. It also includes the Compsurini, whose monophyly and relationships of included species are supported by primary sexual characters, as the elongation of the sperm cells, the presence of insemination, and secondary sexually dimorphic modifications of the caudal fin of males (different from those of the Cheirodontini). On the other hand, Cheirodontinae includes several basal species that are the main subject of this study, that lack the derived and unusual features described for the Cheirodontini and Compsurini and present a somewhat conservative skeletal organization. A large portion of the characters analyzed by Malabarba (1998) to propose the two tribes were related to primary and secondary sexual characters, and those basal taxa were left in *incertae sedis* genera in his review of the subfamily (Malabarba, 1998). In order to solve the phylogeny of these *incertae sedis* basal species, the present analysis included a larger number of characters based on a deep skull morphology study. The results, however, revealed most skull characters to be highly homoplastic, similar to that observed in phylogenetic studies of other characid taxa. Noteworthy homoplastic are those characters related to the upper and lower jaws, infraorbital series, suspensorium, hyoid arch and latero-sensory channel.

In order to test the influence of homoplastic characters in the final hypothesis, the analysis was performed both with unweighted and weighted characters. A better resolution in the cladogram was obtained in the weighted analysis that reduced the relative weight of homoplastic characters in the final hypothesis. The resulting hypothesis allowed the inclusion of all *incertae sedis* genera in a single monophyletic tribe, the Odontostilbini.

The three hypothetic monophyletic clades of the new tribe (the genus *Holoshesthes,* the genus *Pseudocheirodon*, and the clade containing *Lobodeuterodon*, *Prodontocharax* and *Amblystilbe*) were mostly supported by characters related to feeding mechanisms, a potentially informative morphological category for the Characidae recommended by Weitzman & Malabarba (1998), and used by Vari & Harold (1998, 2001) in supporting *Creagrutus* monophyly. However, the feeding mechanisms features defining *Holoshesthes* are repeatedly present in representatives of other lineages of the Cheirodontinae, in the cheirodontins *Serrapinnus heterodon* and *S. microdon,* and in the compsurin *Acinocheirodon melanogramma*. When unweighted, these characters grouped the compsurin *A. melanogramma* with *Holoshesthes*.

Finally, none of the treatments gave a satisfactory resolution to the most basal species of the Odontostilbini. These species form a basal polytomy in the tribe and are all herein referred in the genus *Odontostilbe,* containing mostly species lacking derived characters to solve their interrelationships. New character systems must be evaluated to solve the relationships of these basal taxa, and this is probably the same situation for several species of other characid lineages containing unspecialized fishes.

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Table 1. New classification proposed for the Cheirodontinae, and the position of the taxa in the classification of Malabarba (1998)

New Classification	Position in Classification of Malabarba (1998)
Cheirodontinae	Cheirodontinae
Cheirodontini	Cheirodontini
Cheirodon	*Cheirodon*
Spintherobolus	*Spintherobolus*
†*Megacheirodon* (not analysed)	†*Megacheirodon*
Nanocheirodon	*Nanocheirodon*
Heterocheirodon	*Heterocheirodon*
New genus and new species C	New genus and new species C
Serrapinnus	*Serrapinnus*
Axelrodia lindeae	not recognized
Compsurini	Compsurini
Compsura	*Compsura*
Saccoderma	*Saccoderma*
Macropsobrycon	*Macropsobrycon*
Odontostilbini, new tribe	*Incertae Sedis* genera
Odontostilbe	*Odontostilbe,* in part
Holoshesthes	*synonym of Odontostilbe*
Pseudocheirodon	*Pseudocheirodon*
Lobodeuterodon	not recognized
Prodontocharax	*Prodontocharax*
Amblystilbe	synonym of *Prodontocharax*
synonym of *Holoshesthes*	*Cheirodontops*
synonym of *Holoshesthes*	*Aphyocheirodon*

Appendix I

Characidae: *Aphyocharax nattereri*. MCP 34718, 2 c&s (1 male, 1 female) of 13, Brazil, Pará, Almeirim, rio Amazonas basin, Comunidade de São Raimundo, Pesqueiro. *Aphyocharacidium bolivianum*. MCP 14930, 12, Brazil, Pará, North, igarapé Apeú. MCP 37959, 28, Brazil, Acre, rio Purus basin, igarapé Marizinho, BR 364, drainage rio Antimari. MCP 37960, 3 c&s (1 male, 1 female, 1 unsexed) of 12, Brazil, Acre, Sena Madureira, rio Purus basin, igarapé Taquari between rio Atimani and Sena Madureira, BR 364. MCP 39961, 28, Brazil, Amazonas, Humaitá, rio Madeira basin, igarapé do Vinte e Dois, Recanto do Sanari, *ca*. 20 Km west Humaitá. *Astyanax* aff. *fasciatus*. MCP 18685, 7, Brazil, Rio Grande do Sul, Jacuí, rio Jacuí basin, left margin of the river, near bridge on road (BR 290) to Cachoeira do Sul. MCP 33402, 3 unsexed c&s, Brazil, Rio Grande do Sul, Guaíba, lago Guaíba, near Usina do Gasômetro. *Axelrodia lindeae*. MCP 37317, 7, Brazil, Rondônia, rio Madeira, creek on road 364 between Ariquemes and Candeias do Jamari, rio Candeias affluent. *Axelrodia lindeae*. MCP 37314, 4 c&s (1 male, 3 female) of 166, Brazil, Acre, rio Purus basin, igarapé Marizinho, BR 364, rio Antimari drainage. *Brycon pesu*. MCP 23299, 2 c&s of 3, Brazil, Pará, rio Amazonas basin, south rio Capim and marginal pool, near ferryboat between Paragominas and Tomé Açu, *ca*. 56 km W Paragominas. *Bryconops caudomaculatus*. MCP 22960, 3 males c&s of 34, Brazil, Pará, Puraquequara, rio Amazonas basin, igarapé Puraquequara, on the road between São Miguel do Guamá and Ourém. *Carlana eigemanni*. LACMNH 9181-8, 12, Costa Rica, Heredita, río Puerto Viejo, isolated pool. LACMNH 9230-20, 2 c&s of 12, Costa Rica, Heredita, río Puerto Viejo, 6 km upstream from Finca La Selva, pool above river level, CR 172. *Charax stenopterus*. MCP 9038, 2 c&s, Brazil, Rio Grande do Sul, rio Uruguay basin, rio Santa Maria, BR 293 km 246 between Dom Pedrito/Santana do Livramento. MCP 9063, 1 c&s, Brazil, Rio Grande do Sul, rio Tramandaí basin, Lagoa dos Quadros, Estação de Piscicultura da Secretaria da Agricultura. MCP 9042, 1 c&s, Brazil, Rio Grande do Sul, rio Uruguay basin, rio Negro, at bridge of the road (BR 293) from Bagé/Aceguá. MCP 10377, 2, Uruguay, Artigas, rio Uruguay basin, stream Catalan Grande. MCP 35258, 1, Brazil, Rio Grande do Sul, Bagé, rio Uruguay basin, creek affluent of the rio Piraizinho, affluent of the rio Negro, near villa San Martin, BR 293. *Cynopotamus kincaidi*. MCP 15701, 2, Brazil, Mato Grosso, Cáceres, rio Paraguay basin, rio Paraguai. MCP 17121, 1 c&s, Brazil, Mato Grosso, rio Paraguay basin, mouth of the rio Aricá in the rio Cuiabá. MCP 39034, 1, Brazil, Rondônia, Jaci-Paraná, rio Madeira basin, rio Jaci-Paraná, BR 364 between Porto Velho and Jaci-Paraná. *Diapoma speculiferum*. MCP 19498, 3 c&s (2 males, 1 female) of 23, Brazil, Rio Grande do Sul, Cruzeiro do Sul, rio Jacuí basin, rio Taquari. *Gnathocharax steindachneri*. MCP 37340, 2 females c&s of 5, Brazil, Amazonas, Humaitá, rio Purus basin, creek affluent rio Pixuna, ca. 96 km S Humaitá, BR 319. *Hemibrycon* sp. MCP 35022, 5 c&s (3 male, 2 female) of 18, Bolivia, Cochabamba, rio Madeira basin, rio Chipiriri, affluent rio Secure *Phenacogaster franciscoensis*. MCP 33950, 10, Brazil, Minas Gerais, rio São Francisco basin, rio Peruaçu, boundary Januária and Itacarambi, district Fabião I - Barragem. SAS 9320B, not catalogued., 2 c&s. Brazil, Minas Gerais, rio São Francisco basin. *Priocharax ariel*. Paratypes. MCP 9953, 2 c&s of 23, Venezuela, Amazonas, rio Casiquiare basin, caño Manu tributary of rio Casiquiare aproximately 250 m upstream from Solano. *Priocharax pygmaeus*. MCP 37470, 2 (1 male, 1 unsexed), Peru, Loreto Jenaro, Herrera, rio Ucayali basin, Quebrada Chiupiaí.
Cheirodontinae: *Acinocheirodon melanogramma*. MCP 19238, 1 male c&s, Brazil, Minas Gerais, east of rio Jequitinhonha below mouth of rio Aracuaí. MCP 40701, 1 c&s, Brazil, Minas Gerais, Itira, rio Jequitinhonha. MZUSP 5132, 1 male c&S, Brazil, Itaobin, rio Jequitinhonha. *Amblystilbe alleni*. MZUSP 12407, 6c&s (1 male, 5 unsexed) of 46, Brazil, Amazonas, Fonte Boa, río Solimões basin. USNM 280541, 3 c&s of 11, Peru, Ucayali, rio Ucayali. *Cheirodon ibicuhiensis*. MCP 13663, 52, Brazil, Rio Grande do Sul, rio Tramandaí

basin, pools near canal of João Pedro between Lagoa dos Quadros and Lagoa Pinguela. MCP 11910, 2 c&s, Brazil, Rio Grande do Sul, rio Uruguay basin, rio Ibicuí, at the bridge between São Rafael and Cacequi. MCP 39676, 2 c&s, Brazil, Rio Grande do Sul, Jacuí, rio Jacuí, Saco da Alemoa, near BR 116. *Cheirodon interruptus*. MCP 22813, 4 c&s (3 males, 1 female) of 190, Brazil, Rio Grande do Sul, rio Tramandaí basin, canal between lagoa Emboaba e Emboabinha. MCP 35234, 47, Brazil, Rio Grande do Sul, Quaraí, rio Uruguay basin, creek affluent of the rio Quaraí, on the road from Quaraí to Estação Férrea Baltazar Brum. *Compsura heterura*. MCP 17093, 3 c&s (1 male, 2 females) of 197, Brazil, Minas Gerais, rio São Francisco basin, rio Verde Pequeno, on road estrada Urandi/Espinosa, boundary of Minas Gerais and Bahia. *Heterocheirodon yatai*. MCP 11287, 4 c&s of 15, Brazil, Rio Grande do Sul, rio Uruguay basin, rio Santa Maria, BR 293, km 246, Dom Pedrito/Santana do Livramento. MCP 14283, 7 of 86 (4 males, 3 females), Brazil, Rio Grande do Sul, rio Uruguay basin, rio Ibicuí da Armada near the Campo Seco. MCP 15475, 1 c&s, Brazil, Rio Grande do Sul, rio Uruguay base, rio Santa Maria, BR 293, km 246, Dom Pedrito/Santana do Livramento. *Heterocheirodon jacuiensis*. MCP 11282, 4 c&s, Brazil, Rio Grande do Sul, rio Jacuí basin, stream Fão. MCP 21672, 2 males c&s of 190, Brazil, Rio Grande do Sul, rio Jacuí basin, marginal pools of the rio das Antas, locality Nossa Senhora da Glória. *Holoshesthes* n. sp. “b”. Paratypes, ANSP 173724, 3 c&s (2 males, 1 female) of 30, Colombia, Meta, río Meta basin, lake Mozambique (Mozambique ranch), N side. Paratypes, ANSP 156876, 2 c&s (1 male, 1 unsexed) of 46, Venezuela, lagoon Flores Moradas; 80 km S Calabozo. Paratypes, MCNG 55590, 1 male c&s of 6 males, Venezuela, Barinas, Puerto Nutrias, flooded zone. Paratypes. USNM 327302, 3 males, Venezuela, [Portuguesa], caño Falcón, [affluent of río Portuguesa]. *Holoshesthes geayi*. CAS 64344, 1 female c&s of 66, Venezuela, Portuguesa, río Maria basin, at bridge on Guanare-Acarigua highway. MCP 14954, 2 c&s of 3, Colombia, Meta, río Meta basin, laguna El Batin, *ca*. 4 km SW upstream of lake Mozambique, S side of río Metica. USNM 349409, 2 c&s (1 male, 1 female) of 12, Venezuela, Portuguesa, Quebrada Seca, río Portuguesa basin, río Las Marias, aproximately 45 min. upstream by car from highway, 5.22 km NNW Guanare. *Holoshesthes hemigrammus*. MNRJ 19470, 1 female c&s of 9, Brazil, São Paulo, Botucatu, rio Tietê basin. MZUSP 18588, 1 c&s, Brazil, São Paulo, Marimbondo, rio Grande. NRM 17307, 1 male c&s of 15, rio Paraná basin, rio Tietê, BR 153 below Usina de Promissão, isolated pool between road left bank of rio Tietê. NRM 23393, 1, Brazil, São Paulo, rio Paraná basin, rio Tietê, Usina de Promissão. *Holoshesthes* n. sp. “k”. Paratypes, MCP 38418, 2 females c&s, Ecuador, Napo, laguna Manduro Cocha, ca. 4.5 Km NE of Coca, drains via quebrada into río Coca 3.4 Km upstream from mouth. Paratype, KU 13508, 1 female c&s of 40, Ecuador, Sucumbíos, rio Napo basin, rio Aguarico at Santa Cecilia. Paratypes, KU 13509, 1 female c&s of 61, Ecuador, Napo, río Aguarico at Santa Cecília. Paratypes, KU 13508, 1 male c&s of 40, Ecuador, Napo, río Aguarico at Santa Cecília. NRM 50320, 1 immature c&s, río Tigre drainage, San Jacinto, quebrada at km 45.5. *Holoshesthes* n. sp. “p”. FMNH 101038, 1 female c&s of 62, Peru, rio Amazonas basin, río Pachitea of upper Ucayali, across from Porto Inca Hotel, town of Porto Inca. FMNH 113499, 1 c&s, of 30, Peru, Loreto, laguna Rimachi [or lago Rimachi or Rimachuima, río Pastaza, middle río Marañon basin]. MPEG 6789, 1 c&s of 30, Brazil, Acre, Tarauacá, upper rio Juruá basin, rio Tarauacá. Paratypes, MZUSP 26150, 2 c&s (1 male, 1 female) of 14. Peru, Ucayali, Coronel Portillo, Bagazán, [Nuevo Bagazán, río Ucayali basin]. MZUSP 30364, 1 female c&s of 106, Brazil, Acre, Tarauacá, upper rio Juruá basin, rio Tarauacá. Paratypes. *Holoshesthes pequira*. FMNH 107877, 2 c&s of 20, Paraguay, Alto Paraguay, upper Paraguay, río Paraguay in front of Fuerte Olympo. MCP 12001, 5 c&s, Brazil, Rio Grande do Sul. rio Uruguay basin, rio Ibicui, at bridge between São Rafael and Cacequi. MCP 12220, 1 c&s, Brazil, Rio Grande do Sul, rio Uruguay basin, rio Ibicuí-Mirim, mouth of rio Toropi. MCP 12221, 2 c&s, Brazil, Rio Grande do Sul, rio Uruguay basin, mouth of rio Uruguay. MCP 12540, 2 c&s, Brazil, Rio Grande do Sul, rio Uruguay basin, mouth of rio Ijuí-Mirim, affluent of rio Ijuí. MCP 13041, 39, Brazil, Rio Grande do Sul, rio Uruguay basin, mouth of the rio Ijuí, affluent rio Uruguay. MCP 33240, 1 female c&s of 61, Brazil, Mato Grosso, Jauquara, rio Paraguay basin, rio Jauquara, affluent rio dos Pássaros. MZUSP 21067, 1 male, 1 unsexed c&s of 53, Brazil, Paraná, rio Paraná below Sete Quedas, CETESB. NRM 44511, 45, Paraguay, San Pedro, río Paraguay basin, left side sand playa. *Kolpotocheirodon theloura*. MCP 11161, 1 c&s, Brazil, Goiás, rio Paranaíba basin, Ribeirão da Gama, above mouth of rio Taquara. *Kolpotocheirodon theloura*. Paratypes. MCP 12204, 3 c&s, Brazil, Distrito Federal, stream Margem de Trás. *Kolpotocheirodon theloura*. MNRJ 18081, 2 c&s (1 male, 1 female) of 133, Brazil, Minas Gerais, Palmital, rio São Francisco basin, lagoa Perta-Pé (right margin of rio Bezerra, left margin rio Preto, left margin rio Paracatu). *Lobodeuterodon euspilurus*. ANSP 143702, 2 c&s (1 male, 1 female) of 8, Peru, Cuzco/Madre de Dios, mouth of río Carbon, below Atalaya on N/S road; above and below ford. MEPN 1518, 2 c&s (1 male, 1 female) of 5, Ecuador, Provincia Napo, río Yanayacu, at Biological Reserve Jatun Sacha - Pto. Napo. MEPN 1519, 1 female c&s of 4, Ecuador, Provincia Orellana, río Tiguino, no. 3, waters 200m downstream below bridge, via Coca-Cononaco. MCP 38420, 2 males c&s, Ecuador, Napo, río Napo basin, distributary of río Payamino, few Km upstream from San Jose de Payamino. *Macropsobrycon uruguayanae*. MCP 37579, 2, Brazil, Rio Grande do Sul, Taim, lagoa do Nicola. MCP 11936, 3 c&s of 10, Uruguay, Cerro Largo, Arreria, río Uruguay basin, pool 10 m from the río Negro. Not catalogued, 1 male c&s. *Nanocheirodon insignis*. USNM 121511, 6 c&s of 352, Venezuela, río Maracaibo basin, río Machango, at Bridge S of Lagunillas. USNM 121513, 4 c&s (2 males, 2 females) of 114,Venezuela, río Maracaibo basin, río San Juan at bridge south of Mene Grande, trib. of río Motatan. USNM 121518, 4 c&s (2 males, 2 females) of 134, Venezuela, río Maracaibo basin, río Negro below mouth of río Yasa, 75 Km S. Rosario. USNM 121518, 4 c&s of 134, Venezuela, río Maracaibo basin, río Negro below mouth of río Yasa, 75 Km S. Rosario. New genus n. sp. C (in Malbarba, 1998). Paratypes. MZUSP 40535, 7 c&s. Brazil, Goiás, Ribeirão Macambira, near the bridge of road GO 112, Iaciara. *Odontostilbe* n. sp. "b". Paratypes, MCP 12111, 6, Brazil, São Paulo, rio Tietê basin, marginal pools of rio Corumbataí. *Odontostilbe* n. sp. "b". Paratypes. MCP 12110, 6 c&s, Brazil, São Paulo, rio Tietê basin, marginal pools of the rio Corumbataí. *Odontostilbe dierythrura*. Paratype. ANSP 69198, 1 c&s, Bolivia, Todos Santos, río Chapare. MCP 38624, 2 c&s (1 male, 1 female) of 7, Bolívia, Cochabamba, río Madeira, río Ichilo basin, río Samusabety, system Isiboro-Mamoré-Madeira. *Odontostilbe hasemani* (syn. *dierythrura*). CPULRA 400, 23, Bolivia, Cochabamba, Villa Tunari, Chapare, río Ichilo basin. CPULRA 401, 5, Bolivia, Cochabamba,río Chipiriri, río Ichilo basin. Paratype. ANSP 69125, 1 c&s, Bolivia, Boca Chapare, río Chimore. *Odontostilbe ecuadorensis*. ANSP 130574, 1 female c&s of 12, Ecuador, Napo, backwater of río Aguarico at Santa Cecilia. Paratypes, MEPN 1517, 1 female c&s of 2, Ecuador, Subumbíos, río Duguno, 2 km on south of indian group Cofán del Duguno, Aguarico [drainage]. Paratypes, KU 13524, 2 c&s (1 male, 1 female) of 32, Ecuador, Sucumbíos, rio Napo basin, isolated pool of rio Aguarico at Santa Cecilia. Paratypes, KU 13524, 1 c&s of 32, Ecuador, Napo, isolated pool of río Aguarico at Santa Cecilia. Paratypes, FMNH 113514, 1 male c&s of 5, Ecuador, Napo, quebrada Capihuara, distributary of río Payamino, [río Coca, río Napo drainage]. *Odontostilbe* n. sp. "e". MCP 12101, 1, Brazil, Mato Grosso do Sul, upper rio Paraná, marginal pools in front of Jupiá. Paratype. MCP 12102, 1 c&s, Brazil, Mato Grosso do Sul, upper rio Paraná, marginal pools of the rio Paraná basin, in front of Jupiá. Paratype. MCP 12104, 1 c&s, Brazil, São Paulo, upper rio Paraná, Ilha Solteira, rio Paraná basin. MCP 26004, 1 female c&s, Brazil, São Paulo, rio Paranapanema, reservoir Jurumirim. MCP 26002, 1, Brazil, Goiás, rio Paranaíba basin, mouth of rio do Peixe, affluent of rio Corumbá (upper rio Paraná system). MNRJ 19718, 1, Brazil, Goiás, Davinópolis, rio Paranaíba basin, rio São Bento, affluent of the left margin rio São Marcos, downstream the future barrier of the AHE. *Odontostilbe fugitiva*.

ANSP 178908, 2 c&s (1 female, 1 male) of 12, Peru, Loreto, Maynas, [lower río Itaya] at bridge on Iquitos-Nauta highway, approximately 25 miles SSW of Iquitos. INPA 18506, 3 c&s (1 male, 1 female, 1 unsexed) of 50. Brazil, Amazonas, Paraná do Xiborena. INPA 18512, 1 male c&s, Brazil, Amazonas, lago Pirapora, Catalão. INPA 18465, 4 c&s (2 males, 2 females) of 73, Brazil, Amazonas, Ilha da Marchantaria. MZUSP 87746, 2 females c&s of 11, Ecuador, Pastaza, dead arm of río Pastaza. *Odontostilbe madeirae*. Paratype. ANSP 39207, 1 female c&s, Brazil, tributary of rio Madeira, near Porto Velho. *Odontostilbe* n. sp. “h”. MCP 11136, 1 c&s, Brazil, Rio Grande do Sul, rio Uruguay basin, rio Piratini, Fazenda dos Hinz, district of Coimbra.MCP 12975, 4, Brazil, Santa Catarina, Volta Grande, rio Uruguay basin, rio do Peixe, affluent of rio Uruguai. MCP 13307, 1 c&s, alc. 25, Brazil, Santa Catarina, rio Uruguay basin, rio do Peixe at Volta Grande. MCP 13312, 4 c&s, Brazil, Rio Grande do Sul, rio Uruguay basin, rio Ligeiro, on road Marcelino Ramos/Maximiliano de Almeida. MCP 33482, 31, Brazil, Santa Catarina, Volta Grande, rio Uruguay basin, rio do Peixe. Holotype. MZUSP 37840, 1, Brazil, Rio Grande do Sul, Santo Ângelo, Coimbra district, rio Piratini. Paratypes. MZUSP 37841, 2, Brazil, Rio Grande do Sul, Santo Ângelo, Coimbra, rio Piratini, Fazenda dos Hinz. Paratypes. USNM s/n, 2, Brazil, Rio Grande do Sul, Santo Ângelo, Coimbra district, rio Piratini, Fazenda dos Hinz. *Odontostilbe nareuda*. Paratypes, FMNH 106433, 1 male c&s of 30, Bolivia, Pando, rio Madeira basin, creek at right margin of río Nareuda, ca. 3-4 km upstream of the mouth of río Tahuamanu. Paratypes, MCP 38417, 1 unsexed c&s of 20, Brazil, Rondônia, [Calama], poço da Angélica, rio Madeira. *Odontostilbe* n. sp. “m”. Paratypes, ROM 63983, 1 male c&s of 34, Peru, Madre de Dios, rios Amazonas, Madeira and Madre de Dios basin, Manu National Park, Pakitza, Manu River tributary, Fortaleza stream. Paratypes, ROM 63986, 2 c&s (1 male, 1 female), Peru, PNM - Pakitza, Manu river, beach near mouth of Pachija. Paratypes, *Odontostilbe* n .sp. “m”. MCP 14948, 2 female c&s of 10, Peru, Cuzco, Asuncion, near Patria, 2nd stream W of end of dirt track off km 44 on Huacarpay-Shintuya Rd. *Odontostilbe microcephala*. MZUSP 21068, 30, Brazil, Paraná, rio Paraná basin, downriver from Sete Quedas. MCP 38310, 4, Argentina, Salta, Rosario de la Frontera, lower rio Paraná basin, rio Horcones. MCP 38311, 4, Argentina, Salta, Rosario de la Frontera, lower rio Paraná basin, rio Horcones. MCP 38312, 2 males c&s, Argentina, Salta, Rosario de la Frontera, upper Paraná, río Uruena. MCP 38313, 2 c&s, Argentina, Salta, Rosario de la Frontera, upper Paraná, río Horcones. USNM 319279, 4 c&s of 200, Bolivia, Dept. Santa Cruz, río Parapeti at Rr Bridge a San Antonio, 40 Air Km E Camiri. USNM 321173, 3 c&s of 49, Bolivia, Dept. Chuquisaca, río Camatindi, 8 Km N border Dept. Tarija, 40 Km N Villamontes. USNM 321173, 2 c&s (1 female, 1 male) of 49, Bolivia, Chuquisaca, rio Camatindi, 8 Km N Border Dept. Tarija, 40 Km N Villamontes. *Odontostilbe pao*. Paratypes. MCNG 54107, 1 male c&s of 6, Venezuela, Cojedes, río Pao at el Caserio, El Pueblito. *Odontostilbe paraguayensis*. MCP 12031, 3 c&s, Paraguay, Concepción, río Paraguay basin, rio Apa, Estância Estrellas. MCP 35618, 2 females c&s, Brazil, Mato Grosso, Jauquara, rio Paraguay basin, rio Jauquara, affuent rio dos Pássaros. UMMZ 66390, 1 male c&s of 10, Bolivia, El Beni, río Amazonas basin, Huachi, at junction of río Bopi and río Cochabamba. *Odontostilbe* n. sp. “p”. Paratypes. MCP 12106, 4 c&s, Brazil, Mato Grosso do Sul, upper rio Paraná, in front of Jupiá. MCP 20337, 2 males c&s, alc. 48, Brazil, Goiás, upper rio Paraná, rio Corumbá, affluent of rio Paranaíba. UMMZ 206409, 46, Paraguay, Canendiyu, río Paraná basin, small pool along cascading stream into rio Paraná at Salto del Guaíra on border between Paraguay and Brazil. USNM 302520, 4 males, Brazil, São Paulo, rio Pardo basin, rio Pardo, near Santa Rosa de Viterbo, dam Itaipava, Usina Amália, main channel of river. *Odontostilbe parecis*. Paratypes. MCP 37319, 2 c&s (1 male, 1 female), Brazil, Mato Grosso, Pontes e Lacerda, rio Madeira basin, creek, affluent of rio Galera, *ca.* 71 Km ao N of rio Guaporé, BR 174. *Odontostilbe pulchra.* MCP 38863, 2 c&s (1 male, 1 female) of 49, Colômbia, Meta, río Meta basin, río Negrito at bridge at La Balsa, system of the río Orinoco. INHS 40081, 1 c&s of 4, Trinidad, Quare River, 1km E Valencia on road to Arima. INHS 40101, 2 c&s (1 male, 1 female) of 20m. Trinidad, Cumuto River, 5 km S Brazil on the road to Talparo. ROM 44764, 1 female c&s of 20, Trinidad and Tobago, Trinidad, near bamboo grove on Churchill and Roosevelt highway, St. Joseph River. *Odontostilbe splendida*. Paratypes, ANSP 181041, 2 c&s (1 male, 1 female) of 30. Colombia, Meta, río Negrito at bridge at La Balsa, Meta drainage. ANSP 139450, 2 c&s (1 male, 1 female) of 23, Colombia, Meta, río Meta basin, laguna 'Doctor Sanchez', a cut-off oxbow, entrance ca 5 km SW from inlet to lake Mozambique, N of río Metica. Paratypes, MCP 38862, 1 male c&s of 27, Colômbia, Meta, río Meta basin, río Negrito at bridge at La Balsa, system of the río Orinoco. *Pseudocheirodon arnoldi*. MCP 11990, 3 c&s, Panamá, Cocle, Pacific drainage, río Churube basin, at bridge on Inter-American highway, 13 mi E of Nata. MCP 16134, 2 c&s (1 male, 1 female), Panamá, Pacific drainage, río Bayano basin, creek about 5 mi. W of EL Llano on road. USNM 208515, 2 males c&s of 6, Panamá, Cocle province, rio Grande basin, swampy creek on Interamerican highway aAbout 2 Mi E of Nata. USNM 208520, 2 c&s (1 male, 1 female) of 21, Panamá, río Bayano basin, creek about 5 mi W of El Llano on road. *Pseudocheirodon terrabae*. UMMZ 194214, 4 c&s of 33, Costa Rica, Puntarenas, Pacific drainage, overflow pool of Rio Grande de Terraba, Palmar Norte (N bank about 100 m below Interamerican highway bridge). *Prodontocharax melanotus*. ANSP 143528, 2 c&s of 78, Peru, Madre de Dios, at Shintuya, upper Madre de Dios. ANSP 143534, 2 c&s (1 male, 1 female) of 12, Peru, Cuzco/Madre de Dios, mouth of rio Carbon, below Atalaya on N/S road; above and below ford. USNM 326941, 3, Peru, Madre de Dios, Manu National Park, Pakitza, Radial 3, Trail, Estaca 22, Quebrada Picaflor. *Saccoderma hastata*. ANSP 139487, 3 c&s (1 male, 2 females) of 100, Colombia, Caldas, oxbow of río Miel at Hacienda Sonadora, ca. 8 km downstream from San Miguel. Paratypes. FMNH 56300, 9, Colombia, Bernal creek. ICNMHN 1464, 2 c&s (1 male, 1 female) of 9, Colombia, Caldas, Samaná, Norcasia, Quebrada La Liberdad, rio La Miel, vertiente del Magdalena. *Spintherobolus ankoseion*. Paratypes, MCP 19253, 4, Brazil, Santa Catarina, Barra do Saí, stream in the forest, between Barra do Saí and Itapema, northern Santa Catarina. MCP 19260, 7, Brazil, Paraná, Paranaguá, rio Colônia Pereira under bridge on the road Alexandre Matinhos. MCP 38625, 2 c&s (1 male & 1 female) of 6, Brazil, Santa Catarina, Ilha de São Francisco, Ribeirão Grande stream. *Spintherobolus broccae*, MCP 19196, 1 male c&s of 5, Brazil, Rio de Janeiro, Cachoeira de Macacu, rio Macacu near town of Cachoeira de Macacu, small tributary about 1-2 km from town, highway bridge over stream. *Spintherobolus papilliferus*, MZUSP 49408, 1 female c&S of 4, Brazil, São Paulo, Paranapiacaba, rio Tietê basin, last creek on road to Paranapiacaba. MZUSP 51021, 1, Brazil, São Paulo, rio Ipiranga, rio Tietê basin. MZUSP 51022, 1 c&s of 16, Brazil, São Paulo, Paranapiacaba and Campo Grande, rio Tietê basin. *Serrapinnus microdon*. MCP 15077, 5 c&s of the 30, Brazil, Mato Grosso, rio Paraguay basin, creek at km 18 road Cuiabá/Chapada dos Guimarães, on the road to Coxipó do Ouro. MZUSP 4452, 125, Brazil, Mato Grosso, Santo Antônio de Leverger, dam. *Serrapinnus micropterus*. MCP 37316, 3 c&s (2 males, 1 female), Brazil, Amazonas, Manaus, rio Amazonas basin, lago Camaleão, island Marchantaria. *Serrapinnus heterodon*. MZUSP 16740, 38, Brazil, São Paulo, Corumbataí, rio Corumbataí. MCP 26896, 4 c&s (2 males, 2 females), Brazil, Bahia, east rio Utinga, affuent rio Paraguaçu. **Examined material not included in matrix analysis:** *Acestrorhynchus lacustris*. MCP 34623, 1, Brazil, Minas Gerais, Iguatama, rio São Francisco basin, stream Desterro. *Aphyocharax anisitsi*. MCP 26808, 9, Brazil, Rio Grande do Sul, Cacequi, rio Uruguai basin, rio Ibicuí between São Vicente do Sul and Cacequi. *Cynopotamus amazonus*. MCP 37979, Brazil, 1 c&s, alc. 2, Rondônia, Ji-Paraná, rio Madeira basin, rio Machado, up bridge at Ji-Paraná. *Compsura dialeptura*. MCP 11992, 5 c&s, Panamá, Herrera, Pacific drainage, creek about 4 mi up Pese Road from junction with Chitre-Divisa road. *Coptobrycon bilineatus* or *Hasemania bilineata*. MCP 39051, 2 c&s (1 male, 1 female) of 8, Brazil, São Paulo, southeast rio Itatinga, under bridge, 2 Km from visitor center, Parque das Neblinas. *Kolpotocheirodon* sp. MCP 23455, 5, Brazil, Bahia, east rio Pratinha at Fazenda Pratinha. *Paracheirodon axelrodi*. MCP 11994, 2 c&s, aquarium material. *Phenacogaster jancupa*. Paratypes. MCP 16129, 2 c&s, Brazil, Mato Grosso, rio Paraguay basin, stream Espinheiro, rio Cuiabá drainage, crossing BR 364 (Cuiabá/Jangada), 21 km south of Jangada. *Hyphessobrycon elachys*. MCP 10737, 22, Brazil, Mato Grosso, rio Paraguay basin, pool on side of the road, 36 km from Cuiabá to Campo Grande. *Saccoderma melanostigma*. Paratypes. SU 18145, 6, Venezuela, rio Maracaibo basin, río Negro, below mouth of río Yasa. USNM 228325, 7, Venezuela, río Yasa, Mcpo. Libertad Edo. Zulia. *Serrapinnus* aff, *microdon*. MCP 14955, 6, Brazil, Pará, rio Amazonas basin, paraná Mirim, lagoa Grande into rio Amazonas at Centro Comercial, east of Óbidos). *Serrapinnus* n. sp. MCP 37311, 3 c&s (2 males, 1 female), Brazil, Amazonas, Manaus, rio Amazonas basin, lago Camaleão, island Marchantaria.

Appendix II. Character matrix for 58 taxa and 169 characters. Nummeration according text.

	Characters								
	1	1 1 1 1 1 1 1 1 1 2	2 2 2 2 2 2 2 2 2 3	3 3 3 3 3 3 3 3 3 4	4 4 4 4 4 4 4 4 4 5	5 5 5 5 5 5 5 5 5 6	6 6 6 6 6 6 6 6 6 7	7 7 7 7 7 7 7 7 7 8	8 8 8 8
Taxa	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4
Characidae *incertae sedis*									
Brycon pesu	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 ? ? ? ? ?	? ? ? 0 0 0 0 0 0 0	0 0 0 0 1 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 ? 0 0 0	0 0 0 0
Bryconops caudomaculatus	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 1	0 0 0 1 0 0 0 0 0 2	0 0 0 0 0 ? ? ? ? ?	? ? ? 1 1 0 0 0 0 ?	0 0 0 4 ? 0 0 0 0 0	1 0 1 0 1 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0
Astyanax aff. *fasciatus*	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1 1	0 2 0 1 0 0 1 0 0 0	0 0 0 0 0 ? ? ? ? ?	? ? ? 1 1 1 0 0 0 2	1 0 0 3 1 0 0 0 0 1	1 1 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1 0	1 1 0 0
Aphyocharacidium bolivianum	0 0 0 0 0 0 0 0 0 1	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 0 0	0 0 0 0 1 0 0 0 1 1	0 0 0 1 1 1 0 0 0 2	1 0 1 0 1 2 0 1 0 1	1 1 1 1 0 0 0 0 0 0	0 0 0 1 0 1 0 0 0 0	1 1 0 0
Hemibrycon sp.	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 4	0 0 0 0 0 ? ? ? ? ?	? ? ? 1 1 1 0 0 0 0	0 0 0 0 1 0 0 1 0 1	1 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 1 0 0
Stevardiinae									
Diapoma speculiferum	0 0 0 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 ? 0 0 0 0 0 4	0 0 0 0 0 ? ? ? ? ?	? ? ? 0 1 1 0 0 0 2	0 0 0 1 1 0 0 1 0 0	1 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 1 0 0	0 1 0 0
Aphyocharacinae									
Aphyocharax nattereri	0 0 0 0 0 1 0 1 1 0	1 1 0 0 0 0 0 0 0 1	1 0 0 1 0 0 1 0 0 4	0 0 0 0 1 0 0 0 ? 1	0 0 0 0 1 0 0 0 0 0	0 0 0 0 1 0 0 1 0 0	1 0 1 0 0 0 0 0 0 0	0 0 0 1 0 1 0 1 1 0	0 1 0 0
Characinae									
Charax stenopterus	0 0 0 0 0 ? 1 0 0 0	1 1 0 0 1 0 0 0 2 1	1 0 0 1 0 0 1 0 0 0	0 0 0 1 0 ? ? ? ? ?	? ? ? 2 0 0 0 0 0 0	0 0 0 0 2 0 0 0 0 0	0 0 1 1 0 0 0 0 0 0	0 0 0 2 0 0 0 0 0 0	1 0 0 0
Cynopotamus kincaidi	0 0 0 0 0 ? 1 1 1 0	0 0 0 0 0 0 0 0 1 0	0 0 0 0 0 0 3 0 0 0	0 0 0 0 0 ? ? ? ? ?	? ? ? 0 0 0 0 0 0 0	0 0 0 0 2 0 0 1 0 1	1 0 0 1 0 0 0 0 0 0	0 0 0 2 0 0 0 0 0 0	1 0 0 0
Gnathocharax steindachneri	0 0 0 0 0 0 0 0 0 3	1 0 1 0 0 0 0 0 0 1	1 0 0 1 1 0 1 0 0 2	0 0 0 0 0 0 0 0 ? ?	? ? ? 2 0 0 0 0 0 0	0 0 0 0 2 0 0 0 0 0	1 0 1 0 1 0 0 0 0 0	0 0 0 2 0 1 0 0 0 0	0 0 1 1
Phenacogaster franciscoensis	1 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 2 0	0 1 0 1 2 0 3 0 0 0	0 0 0 1 0 ? ? ? ? ?	? ? ? 2 1 1 0 0 0 0	0 0 1 0 2 2 1 0 1 1	1 1 1 1 0 0 0 0 1 0	0 0 0 1 0 0 0 1 0 0	1 1 0 0
Priocharax ariel	0 0 0 0 0 ? 1 1 1 0	2 2 1 0 ? 1 0 0 2 ?	? 0 0 1 3 1 2 0 0 0	0 0 0 ? 1 0 0 0 ? 0	0 0 0 2 0 0 0 0 0 0	0 0 0 0 2 0 0 0 0 0	1 0 1 1 0 0 0 0 1 0	0 0 0 2 0 0 0 0 0 0	0 0 1 0
Rhoadsiinae									
Carlana eigenmanni	1 0 0 0 0 ? 0 0 0 1	1 0 0 0 1 0 0 0 0 1	0 0 0 1 1 0 1 0 0 0	0 0 0 0 1 0 0 0 1 3	3 0 1 0 1 0 0 0 0 0	0 0 0 0 0 0 0 0 1 1	1 0 1 0 0 0 0 0 0 2	0 0 0 0 0 0 0 0 1 0	1 1 0 0
Cheirodontinae									
Cheirodontini									
Axelrodia lindeae	1 1 0 0 0 0 0 0 0 1	1 0 0 0 0 0 0 0 2 ?	1 0 0 1 2 0 1 0 0 2	0 0 0 1 1 0 0 0 ? 0	0 0 0 2 1 0 0 0 0 1	0 0 1 1 2 2 0 0 1 1	1 1 0 1 0 0 0 0 0 0	0 0 0 2 0 0 0 1 0 0	1 0 1 0
Cheirodon ibicuhiensis	1 1 0 0 0 0 0 0 0 1	1 0 0 1 1 0 1 1 1 0	1 0 0 1 1 0 1 0 0 0	0 0 0 1 1 0 0 0 1 2	3 0 1 0 1 0 0 0 0 2	1 0 1 2 0 2 1 0 1 1	1 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 0 1 1 0	1 1 0 0
Cheirodon interruptus	1 1 0 0 0 0 0 0 0 0	1 1 0 1 1 0 1 0 1 0	1 0 0 1 1 0 1 0 0 0	0 0 0 1 1 0 0 0 1 2	3 0 1 0 1 0 0 0 0 2	1 0 1 3 0 2 1 0 1 1	1 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 0 1 1 0	1 1 0 0
Heterocheirodon jacuiensis	1 0 0 1 0 0 0 0 0 0	1 0 0 1 1 0 1 1 0 1	1 0 0 1 1 0 0 0 0 2	0 0 0 1 1 0 0 0 1 3	2 0 1 2 1 0 0 0 0 1	1 0 1 2 0 2 0 0 1 0	0 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 1 1 1 0	1 1 0 0
Heterocheirodon yatai	1 0 0 1 0 0 0 0 0 0	1 0 0 1 1 0 1 1 0 1	1 0 0 1 1 0 0 0 0 2	0 0 0 1 1 0 0 0 1 3	2 0 1 2 1 0 0 0 0 2	1 0 1 2 0 2 0 0 1 0	0 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 1 1 1 0	1 1 0 0
Nanocheirodon insignis	1 1 0 0 0 0 0 0 0 1	1 0 0 1 1 0 0 0 0 1	1 0 0 1 1 0 1 0 0 0	0 0 0 1 1 0 0 0 1 3	3 0 0 0 0 0 0 0 0 1	1 0 1 2 0 2 2 1 1 1	1 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 0 1 1 0	1 1 0 0
Serrapinnus micropterus	1 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 1 1 0 1	1 2 0 1 1 0 0 0 0 0	0 0 0 1 1 0 0 0 2 3	3 0 0 0 0 0 0 0 0 1	1 0 1 2 0 2 3 0 1 1	1 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 0 1 1 0	1 1 0 0
Serrapinnus heterodon	0 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 1 1 0 1	1 2 0 1 1 0 0 0 0 0	0 0 0 1 1 0 0 0 1 2	1 0 0 0 1 1 0 0 0 2	1 0 1 2 0 1 1 1 0 0	1 1 1 1 1 0 0 0 0 2	0 2 1 0 0 1 0 0 1 0	1 1 0 0
Serrapinnus microdon	1 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 1 1 0 1	1 2 0 1 1 0 1 0 0 0	0 0 0 1 1 0 0 0 1 1	1 1 0 0 1 1 0 0 0 2	1 0 1 2 0 1 3 1 0 0	1 1 1 1 1 0 0 0 0 2	0 1 1 0 0 1 0 0 1 0	1 1 0 0
Spintherobolus ankoseion	1 0 1 0 0 1 1 1 1 0	2 2 1 0 ? 1 0 0 2 ?	? 0 0 1 3 1 2 0 0 1	1 0 0 ? 1 0 0 0 ? 0	1 0 0 0 1 0 0 0 0 1	0 0 1 1 2 2 0 0 1 1	1 1 1 1 0 0 0 1 2 1	0 0 0 1 0 0 0 1 0 1	0 1 1 1
Spintherobolus broccae	1 0 1 0 0 1 1 1 1 0	2 2 1 0 ? 1 0 0 2 ?	? 0 0 1 3 1 2 0 0 0	1 0 0 ? 1 0 0 0 ? 0	1 0 0 0 1 0 0 0 0 1	0 0 1 1 2 2 0 0 1 1	1 1 1 1 0 0 0 1 2 1	0 0 0 1 0 0 0 1 0 1	? ? 1 1
Spintherobolus papilliferus	1 0 1 0 0 1 0 1 1 2	2 2 1 0 ? 1 0 0 2 ?	? 0 0 1 1 1 2 0 0 0	1 0 0 ? 1 0 0 0 ? 0	1 0 0 0 1 0 0 0 0 1	0 0 1 1 2 2 0 0 1 1	0 1 1 1 0 0 0 1 2 1	0 0 0 1 0 0 0 1 0 1	0 1 1 1
Spintherobolus n. sp.	1 0 1 0 0 1 1 1 1 0	2 2 1 0 ? 1 0 0 2 ?	? 0 0 1 3 1 2 0 0 2	1 0 0 ? 1 0 0 0 ? 0	1 0 0 0 1 0 0 0 0 1	0 0 1 1 2 2 0 0 1 1	1 1 1 1 0 0 0 1 2 2	0 0 0 1 0 0 ? 0 0 0	0 1 1 1
New genus n. sp. C	1 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 0 0 0 1	0 1 0 1 1 0 0 0 0 0	0 0 0 1 1 0 0 0 1 3	3 0 1 0 1 0 0 0 0 1	1 0 1 2 0 2 3 0 1 1	1 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 0 0 1 0	1 1 0 0

	Characters								
	1	1 1 1 1 1 1 1 1 1 2	2 2 2 2 2 2 2 2 2 3	3 3 3 3 3 3 3 3 3 4	4 4 4 4 4 4 4 4 4 5	5 5 5 5 5 5 5 5 5 6	6 6 6 6 6 6 6 6 6 7	7 7 7 7 7 7 7 7 7 8	8 8 8 8 8
Taxa	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5
Compsurini									
Acinocheirodon melanogramma	0 1 0 0 0 1 0 0 0 1	0 0 0 1 0 0 1 1 0 0	0 2 0 1 1 0 0 0 1 0	0 0 0 1 1 0 0 0 0 2	1 0 1 0 1 1 0 0 0 2	1 0 1 2 0 2 1 0 0 0	1 1 1 0 0 0 0 0 0 2	0 2 1 0 0 1 0 0 1 0	1 1 0 0 0
Compsura heterura	1 1 0 0 0 0 0 0 0 1	1 0 0 1 0 0 0 0 0 1	1 1 0 1 1 0 0 0 0 0	0 0 0 1 1 0 0 0 1 3	3 0 1 0 1 0 0 0 0 1	1 0 1 2 0 2 2 0 1 1	1 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 1 0 1 0	1 1 0 0 0
Kolpotocheirodon theloura	1 1 0 0 0 1 0 0 0 0	1 1 0 1 1 0 1 0 0 1	0 0 0 0 1 0 1 0 0 2	0 0 0 1 1 0 0 0 2 3	3 0 1 0 1 0 0 0 0 1	1 0 1 2 0 2 1 0 1 0	1 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 2 0 1 0	1 1 0 0 0
Macropsobrycon uruguayanae	1 0 0 0 1 ? 0 0 0 0	1 1 0 1 1 0 1 1 0 0	1 1 0 1 2 0 1 0 0 2	0 0 0 ? 1 0 0 0 ? 0	1 1 0 2 1 0 0 0 0 ?	1 0 1 4 ? 2 1 1 1 0	1 1 1 1 0 0 0 0 0 2	0 0 0 2 0 1 0 0 1 0	1 1 0 0 0
Saccoderma hastata	1 1 0 0 0 0 0 0 0 1	1 0 0 1 0 0 0 1 0 1	1 0 0 1 1 0 0 0 0 0	0 0 0 1 1 0 0 0 1 3	3 0 1 0 0 0 0 0 0 1	1 0 1 2 0 2 3 0 1 1	1 1 1 1 0 0 0 0 0 2	1 0 0 0 0 0 0 0 1 0	1 1 0 0 0
Odontostilbini									
Amblystilbe alleni	1 1 0 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 2 0 1 1 0 0 0 0 4	0 1 1 1 1 0 0 0 1 1	1 1 0 0 1 0 0 0 0 1	1 0 1 1 1 3 3 0 1 1	0 1 1 2 0 0 0 0 0 2	0 0 0 1 2 0 ? 1 1 0	1 1 0 0 0
Holoshesthes n. sp. "b"	1 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 1 1 0 1	1 2 0 1 1 0 0 0 0 1	0 0 0 1 1 1 0 0 0 0	1 1 0 2 1 1 0 0 0 2	1 0 1 3 2 1 1 1 0 0	1 0 1 0 1 0 0 0 0 2	0 2 1 0 0 1 1 0 1 0	1 1 0 0 0
Holoshesthes geayi	1 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 1 1 0 1	1 2 0 1 1 0 0 0 0 0	0 0 0 1 1 1 1 1 0 1	1 1 0 2 1 1 0 0 0 2	1 0 0 3 0 1 1 1 0 0	1 0 1 0 1 0 0 0 0 2	0 2 1 0 0 1 1 0 1 0	1 1 0 0 0
Holoshesthes hemigrammus	1 1 0 0 0 1 0 0 0 0	1 1 0 1 1 0 1 0 2 0	1 1 0 1 2 0 1 1 0 0	0 0 0 1 1 1 0 1 0 1	0 0 0 2 1 0 0 0 0 2	1 0 0 1 1 1 0 0 0 0	1 0 1 0 1 0 0 0 0 2	0 3 2 0 0 1 1 0 1 0	1 1 0 0 0
Holoshesthes n. sp. "k"	0 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 1 1 0 1	1 2 0 1 1 0 0 0 0 0	0 0 0 1 1 1 0 1 0 1	1 0 0 0 1 1 0 0 0 2	1 0 1 3 0 1 1 1 0 0	1 0 1 0 1 0 0 0 0 2	0 2 1 0 0 1 1 0 1 0	1 1 0 0 0
Holoshesthes n. sp. "p"	0 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 1 1 0 1	1 2 0 1 1 0 0 0 0 0	0 0 0 1 1 1 0 1 0 2	1 0 0 0 1 1 0 0 0 2	1 0 1 2 0 1 1 1 0 0	1 0 1 0 1 0 0 0 0 2	0 2 1 0 0 1 1 0 1 0	1 1 0 0 0
Holoshethes pequira	0 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 1 1 0 1	1 2 0 1 1 0 0 0 1 0	0 0 0 1 1 0 0 0 1 2	1 0 1 0 1 1 0 0 0 2	1 0 1 2 0 1 1 0 0 0	1 0 1 0 1 0 1 0 0 2	0 2 1 0 0 1 1 0 1 0	1 1 0 0 0
Lobodeuterodon euspilurus	1 1 0 0 0 0 0 0 0 1	1 0 0 1 0 0 0 1 0 1	0 2 0 1 1 0 0 0 0 1	0 1 0 1 1 0 0 0 1 3	3 0 1 0 0 0 0 0 0 1	1 1 1 2 0 3 2 0 1 1	0 1 1 1 0 0 0 0 0 2	0 0 0 0 2 0 1 0 1 0	1 1 0 0 0
Odontostilbe n. sp. "b"	1 1 0 0 0 0 0 0 0 0	1 0 0 1 1 0 0 0 0 1	1 1 0 1 1 0 1 0 2 1	0 0 0 1 1 0 0 0 1 2	3 0 0 0 0 0 0 0 0 1	1 0 1 2 0 2 3 0 1 1	0 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 1 0 1 0	0 1 0 0 0
Odontostilbe dierythrura	1 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 0 1 0 1	1 2 0 1 1 0 0 0 0 1	0 0 0 1 1 0 0 0 1 3	3 0 1 0 0 0 0 0 0 1	1 0 1 2 0 2 3 0 1 1	1 1 1 1 0 0 0 0 0 2	0 0 0 0 1 0 1 0 1 0	1 1 0 0 0
Odontostilbe n. sp. "e"	0 1 0 0 0 0 0 0 0 0	0 0 0 1 0 0 0 1 0 0	1 2 1 1 1 0 0 0 1 0	0 0 0 1 1 0 0 0 1 3	3 0 1 0 1 0 0 0 0 1	1 0 1 2 0 2 3 0 1 0	1 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 1 0 1 0	1 1 0 0 0
Odontostilbe ecuadorensis	1 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 0 1 0 1	1 2 1 1 1 0 0 0 0 1	0 0 0 1 1 0 0 0 1 3	3 0 1 0 0 0 0 0 0 1	1 0 1 2 0 2 3 0 1 1	1 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 1 0 1 0	1 1 0 0 0
Odontostilbe fugitiva	1 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 0 1 0 1	1 2 1 1 1 0 0 0 0 1	0 0 0 1 1 0 0 0 1 3	3 0 1 0 0 0 0 0 0 1	1 0 1 2 0 2 3 0 1 1	1 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 1 0 1 0	1 1 0 0 0
Odontostilbe n. sp. "h"	1 1 0 0 0 0 0 0 0 0	0 0 0 1 1 0 0 0 0 0	1 1 0 1 2 0 0 0 0 1	0 0 0 1 1 0 0 0 1 3	3 0 1 0 0 0 0 0 0 1	1 1 1 2 0 2 2 0 1 0	0 1 1 1 0 0 0 0 0 2	0 0 0 0 2 0 1 1 1 0	0 1 0 0 1
Odontostilbe n. sp. "m"	1 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 0 1 0 1	1 2 1 1 1 0 0 0 0 1	0 0 0 1 1 0 0 0 1 3	3 0 1 0 0 0 0 0 0 1	1 0 1 2 0 2 3 0 1 1	1 1 1 1 0 0 0 0 0 2	0 0 0 0 1 0 1 0 1 0	1 1 0 0 0
Odontostilbe microcephala	1 1 0 0 0 0 0 0 0 0	0 0 0 1 0 0 0 1 1 1	0 2 1 1 1 0 0 0 0 1	0 0 0 1 1 0 0 0 1 3	3 0 1 0 1 0 0 0 0 1	1 0 1 2 0 3 1 0 1 0	1 0 1 1 0 0 0 0 0 2	0 0 0 0 2 0 1 0 1 0	0 1 0 0 1
Odontostilbe nareuda	1 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 0 1 0 1	1 2 0 1 1 0 0 0 0 1	0 0 0 1 1 0 0 0 1 3	3 0 1 0 1 0 0 0 0 1	1 0 1 2 0 2 3 0 1 1	0 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 1 0 1 0	1 1 0 0 0
Odontostilbe n. sp. "p"	1 1 0 0 0 0 0 0 0 0	0 0 0 1 0 0 0 1 0 1	1 2 1 1 1 0 0 0 1 1	0 0 0 1 1 0 0 0 1 2	3 0 1 0 1 0 0 0 0 1	1 0 1 2 0 2 3 0 1 0	1 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 1 0 1 0	0 1 0 0 0
Odontostilbe n. sp. pao	1 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 0 1 0 1	1 2 0 1 1 0 0 0 0 1	0 0 0 1 1 0 0 0 1 3	3 0 1 0 1 0 0 1 0 1	1 1 1 2 0 2 3 0 1 1	0 1 1 1 0 1 0 0 0 2	0 0 0 0 1 0 1 0 1 0	1 1 0 0 0
Odontostilbe paraguayensis	1 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 1 1 0 1	1 2 0 1 1 0 0 0 0 1	0 0 0 1 1 0 0 0 1 3	3 0 1 0 0 0 0 0 0 1	1 0 1 2 0 2 3 0 1 1	1 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 1 0 1 0	1 1 0 0 0
Odontostilbe parecis	1 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 1 1 0 1	1 2 0 1 1 0 0 0 0 1	0 1 0 1 1 0 0 0 1 3	3 0 1 0 0 0 0 0 0 1	1 0 1 2 0 2 3 0 1 0	0 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 1 0 1 0	1 1 0 0 0
Odontostilbe pulchra	1 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 0 1 0 1	1 2 0 1 1 0 0 0 0 1	0 0 0 1 1 0 0 0 1 3	3 0 1 0 1 0 0 0 0 1	1 0 1 2 0 2 3 0 1 1	1 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 1 0 1 0	1 1 0 0 0
Odontostilbe splendida	1 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 0 1 0 1	1 2 0 1 1 0 0 0 0 1	0 0 0 1 1 0 0 0 1 3	3 0 1 0 0 0 0 0 0 1	1 1 1 2 0 2 3 0 1 1	0 1 1 1 0 0 0 0 0 2	0 0 0 0 0 0 1 0 1 0	1 1 0 0 0
Prodontocharax melanotus	1 1 0 0 0 0 0 0 0 1	0 0 0 1 0 0 0 0 0 1	0 2 0 1 1 0 0 0 0 4	0 1 1 1 1 0 0 0 1 1	1 1 0 0 1 0 0 0 0 0	1 1 1 1 1 3 2 0 1 1	0 1 1 1 0 0 0 0 0 2	0 0 0 1 2 0 1 0 1 0	1 1 0 0 1
Pseudocheirodon arnoldi	1 0 0 0 0 1 0 0 0 1	0 0 0 1 0 0 0 1 0 1	0 2 0 1 1 0 0 0 0 3	0 1 0 2 1 0 0 0 2 3	3 0 1 0 1 0 1 1 1 0	1 1 1 2 0 3 3 0 1 1	1 1 1 1 0 1 0 1 0 2	2 0 0 0 0 0 0 0 1 0	1 1 0 0 0
Pseudocheirodon terrabae	1 0 0 0 0 1 0 0 0 1	0 0 0 1 0 0 0 0 0 1	0 2 0 1 1 0 0 0 0 3	0 1 0 2 1 0 0 0 2 3	3 0 1 0 1 0 1 1 1 0	1 1 1 1 0 2 3 0 1 1	1 1 1 1 0 1 0 1 0 2	2 0 0 0 0 0 0 0 1 0	1 1 0 0 0

Appendix II. Continued.

	Characters								
		1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1
	8 8 8 8 9	9 9 9 9 9 9 9 9 9 0	0 0 0 0 0 0 0 0 0 1	1 1 1 1 1 1 1 1 1 2	2 2 2 2 2 2 2 2 2 3	3 3 3 3 3 3 3 3 3 4	4 4 4 4 4 4 4 4 4 5	5 5 5 5 5 5 5 5 5 6	6 6 6 6 6 6 6 6 6
Taxa	6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9
Characidae *incertae sedis*									
Brycon pesu	0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 2 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0
Bryconops caudomaculatus	0 0 0 1 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0
Astyanax aff. *fasciatus*	0 0 1 1 1	0 0 0 0 0 0 0 1 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0
Aphyocharacidium bolivianum	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 1 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0
Hemibrycon sp.	0 0 0 1 1	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 1 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0
Stevardiinae									
Diapoma speculiferum	0 0 1 1 0	0 0 0 0 0 ? 0 0 0 1	0 0 0 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0
Aphyocharacinae									
Aphyocharax nattereri	1 0 1 1 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0
Characinae									
Charax stenopterus	0 0 1 1 1	0 0 0 2 0 0 0 1 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 2 0 0 0 0 0 0 0	0 0 1 2 0 0 0 0 0
Cynopotamus kincaidi	0 0 1 1 1	0 0 0 2 0 0 0 1 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 2 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 2 0 0 0 0 0 0
Gnathocharax steindachneri	1 0 0 1 1	0 0 0 0 0 ? 1 ? 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 1 0 0 0 0 0
Phenacogaster franciscoensis	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 2 0 0 0 0 0
Priocharax ariel	1 0 1 1 1	0 0 1 2 1 ? 1 ? 1 0	0 0 0 0 1 2 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 ? 0 0 0 1 0 0 0	0 0 0 1 0 0 0 0 0
Rhoadsiinae									
Carlana eigenmanni	0 0 1 1 1	0 0 0 0 0 0 0 1 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 ?	? ? ? ? ? ? ? ? ? ?	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0
Cheirodontinae									
Cheirodontini									
Axelrodia lindeae	0 0 1 2 1	0 0 1 0 0 0 0 1 1 1	0 0 0 0 0 1 1 0 1 1	1 3 1 0 0 1 1 0 0 0	0 0 0 1 0 0 1 0 1 0	1 0 0 0 1 0 0 0 0 1	0 1 0 0 1 0 0 0 0 0	0 0 1 0 0 0 1 0 0 0	0 0 1 0 1 0 0 0 0
Cheirodon ibicuhiensis	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 1 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 2 0 1 1 1 1 1	0 0 0 0 0 0 1 0 1 1	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Cheirodon interruptus	0 0 1 0 0	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 1 0 0 0 0	0 2 0 0 0 1 0 0 0 0	0 0 0 2 0 1 1 1 1 1	0 0 0 0 0 0 1 0 1 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Heterocheirodon jacuiensis	1 0 1 0 2	0 0 0 0 0 1 0 1 0 1	0 0 0 0 0 1 0 0 1 0	1 3 1 0 0 1 0 0 0 0	0 0 0 2 0 2 2 0 0 0	0 0 0 0 1 0 0 0 0 1	0 1 0 0 1 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Heterocheirodon yatai	1 0 1 0 2	0 0 0 0 0 1 0 1 0 1	0 0 0 0 0 1 0 0 1 0	1 3 1 0 0 1 0 0 0 0	0 0 0 2 0 2 2 0 0 0	0 0 0 0 1 0 0 0 0 1	0 1 0 0 1 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Nanocheirodon insignis	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 1 0 0 0 0	0 1 0 0 0 1 0 0 0 0	0 0 0 2 1 1 1 1 1 1	0 0 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Serrapinnus micropterus	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 0 0 0 1 1	1 3 1 0 0 1 1 0 0 0	0 0 0 1 0 1 1 0 1 0	1 0 0 0 1 0 0 0 0 1	0 1 0 0 1 0 0 0 0 0	0 0 1 0 0 0 1 0 0 0	0 0 1 0 1 0 0 0 0
Serrapinnus heterodon	1 0 1 1 0	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 1 0 0 1 1	1 3 1 0 0 1 1 0 0 0	0 0 0 1 0 1 1 0 1 0	1 0 0 0 1 0 1 0 0 1	0 1 0 0 1 0 0 0 0 0	0 0 0 0 0 0 1 1 0 0	0 0 1 0 1 0 0 0 0
Serrapinnus microdon	1 0 1 1 0	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 0 0 0 1 1	1 3 1 0 0 1 1 0 0 0	0 0 0 1 0 1 1 0 1 0	1 0 0 0 1 0 1 0 0 1	0 1 0 0 1 0 0 0 0 0	0 0 1 0 0 0 1 1 0 0	0 0 1 0 1 0 0 0 0
Spintherobolus ankoseion	0 0 0 1 ?	1 1 1 1 1 0 1 ? 1 0	1 0 0 0 1 2 0 0 1 1	2 3 1 0 0 1 1 0 0 0	0 0 0 1 0 1 1 0 1 0	0 1 1 1 1 0 1 0 0 1	0 1 0 0 1 0 0 0 0 0	0 0 2 0 0 0 1 0 0 0	0 0 1 1 0 0 1 0 0
Spintherobolus broccae	0 0 0 2 ?	1 1 1 1 1 0 1 ? 1 0	1 0 0 0 1 2 0 0 1 1	2 3 1 0 0 1 1 0 0 0	0 0 0 1 0 1 1 0 1 0	0 1 1 1 1 0 1 0 0 1	0 1 0 0 1 0 0 0 0 0	0 0 2 0 0 0 1 0 0 0	0 0 1 1 0 0 1 0 0
Spintherobolus papilliferus	0 0 0 1 ?	1 1 1 0 1 0 1 ? 1 0	1 0 0 0 1 2 0 0 0 1	0 ? 1 0 0 1 ? 0 0 0	0 0 0 1 0 1 1 0 1 0	0 1 1 1 1 0 1 0 0 ?	0 1 0 0 ? 0 0 0 0 0	0 0 2 0 0 0 1 0 0 0	0 0 1 2 0 0 1 0 0
Spintherobolus n. sp.	0 0 0 2 ?	1 1 1 0 0 0 1 ? 1 0	1 0 0 0 0 2 0 1 ? ?	? ? ? 0 0 0 ? 0 0 0	0 0 0 0 ? 1 1 0 1 0	0 ? ? ? 1 0 ? 0 0 ?	0 1 0 0 ? 0 0 0 0 0	0 0 2 0 0 0 1 0 0 0	0 0 1 1 0 0 1 0 0
New genus n. sp. C	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 1 0 0 2 0	1 3 1 0 0 1 0 0 0 0	0 0 0 1 0 1 1 0 1 0	1 0 0 0 1 0 0 0 0 1	0 1 0 0 1 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0

	Characters								
		1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1
	8 8 8 8 9	9 9 9 9 9 9 9 9 9 0	0 0 0 0 0 0 0 0 0 1	1 1 1 1 1 1 1 1 1 2	2 2 2 2 2 2 2 2 2 3	3 3 3 3 3 3 3 3 3 4	4 4 4 4 4 4 4 4 4 5	5 5 5 5 5 5 5 5 5 6	6 6 6 6 6 6 6 6 6
Taxa	6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9
Compsurini									
Acinocheirodon melanogramma	1 0 1 1 0	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 0 0 0 0 0	0 2 0 0 0 0 0 1 1 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 1 1 0 0 0	0 0 0 0 0 1 1 0 0 1	0 1 0 0 0 0 1 0 1 0	0 0 1 0 0 0 0 1 1
Compsura heterura	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 0 0 0 0 0	0 2 0 0 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 1 1 0 0	0 0 1 1 0 0 1 0 1 1	0 1 1 0 0 0 0 1 1
Kolpotocheirodon theloura	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 0 0 0 0 0	0 2 0 0 0 0 0 2 0 1	1 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 1 0 1 1 0 0 1	0 1 1 0 0 0 1 0 0 0	0 1 1 0 0 0 0 1 0
Macropsobrycon uruguayanae	1 0 1 1 2	0 0 0 0 0 1 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 2 0 0 0 0 0 0 2 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 0 0 0 1 1 0 0 2	1 1 1 0 0 0 1 0 1 2	0 1 1 0 0 0 0 1 1
Saccoderma hastata	0 0 1 1 0	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 0 0 0 0 0	0 2 0 1 1 0 0 0 0 0	0 1 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 1 1 0 0 2	0 2 0 1 1 1 1 0 0 0	0 1 1 0 0 0 0 1 1
Odontostilbini									
Amblystilbe alleni	0 1 1 0 2	0 0 0 0 0 0 0 1 0 1	0 ? ? 0 0 0 0 0 0 0	0 ? 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Holoshesthes n. sp. "b"	1 0 1 1 0	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 1 0 0	0 0 0 0 0 0 0 0 1 0	0 3 0 0 0 0 1 1 0 0	0 0 1 0 0 0 0 0 0
Holoshesthes geayi	1 0 1 1 0	0 0 0 0 0 0 0 1 0 1	0 1 1 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 1 0 0	0 0 1 0 0 0 0 0 0
Holoshesthes hemigrammus	1 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 1 0 0	0 0 0 0 0 0 0 0 0 0	0 ? 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Holoshesthes n. sp. "k"	1 0 1 1 0	0 0 0 0 0 0 0 1 0 1	0 1 1 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 1 0 0	0 0 1 0 0 0 0 0 0
Holoshesthes n. sp. "p"	1 0 1 1 0	0 0 0 0 0 0 0 1 0 1	0 1 1 1 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 1 0 0	0 0 1 0 0 0 0 0 0
Holoshethes pequira	1 0 1 1 0	0 0 0 0 0 0 0 1 0 1	0 1 1 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	2 0 1 0 0 0 0 0 0
Lobodeuterodon euspilurus	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 0 1 0 0 1 0 0 0 0	0 2 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Odontostilbe n. sp. "b"	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 1 1 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 1 0 0 0	2 0 1 0 0 0 0 0 0
Odontostilbe dierythrura	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 1 1 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Odontostilbe n. sp. "e"	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 ? ? 0 0 1 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 1 0 0	0 0 1 0 0 0 0 0 0
Odontostilbe ecuadorensis	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 1 1 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Odontostilbe fugitiva	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 1 1 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Odontostilbe n. sp. "h"	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 0 1 0 0 1 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 ? 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Odontostilbe n. sp. "m"	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 1 1 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Odontostilbe microcephala	0 0 1 0 1	0 0 0 0 0 0 0 1 0 1	0 1 1 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Odontostilbe nareuda	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 ? ? 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Odontostilbe n. sp. "p"	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 ? ? 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 1 0 0	0 0 1 0 0 0 0 0 0
Odontostilbe n. sp. pao	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 1 1 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Odontostilbe paraguayensis	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 1 1 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 1 0 0 0
Odontostilbe parecis	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Odontostilbe pulchra	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 0 1 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Odontostilbe splendida	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 1 1 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Prodontocharax melanotus	0 1 1 0 2	0 0 0 0 0 0 0 1 0 1	0 0 1 0 0 1 0 0 0 0	0 2 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	1 0 1 0 0 0 0 0 0
Pseudocheirodon arnoldi	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 0 0 0 0 0	0 2 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 ? 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0
Pseudocheirodon terrabae	0 0 1 1 1	0 0 0 0 0 0 0 1 0 1	0 0 0 0 0 0 0 0 0 0	0 2 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0

	WEIGHTED TREE			UNWEIGHTED TREE		
	STEPS	CI	RI	STEPS	CI	RI
1	7	0.14	0.62	6	0.16	0.68
2	5	0.20	0.8	5	0.20	0.80
3	1	1.00	1	1	1.00	1.00
4	1	1.00	1	1	1.00	1.00
5	autapomorphy					
6	5	0.20	0.55	6	0.16	0.44
7	3	0.33	0.60	4	0.25	0.4
8	3	0.33	0.66	4	0.25	0.5
9	3	0.33	0.66	4	0.25	0.5
10	18	0.16	0.34	19	0.15	0.3
11	13	0.15	0.45	12	0.16	0.5
12	10	0.20	0.11	9	0.22	0.22
13	3	0.33	0.60	2	0.5	0.8
14	2	0.50	0.94	2	0.5	0.94
15	9	0.11	0.27	8	0.12	0.36
16	2	0.50	0.75	2	0.5	0.75
17	8	0.12	0.61	8	0.12	0.61
18	12	0.08	0.59	13	0.07	0.55
19	12	0.16	0.23	11	0.18	0.3
20	9	0.11	0.38	11	0.09	0.23
21	10	0.10	0.47	10	0.1	0.47
22	14	0.14	0.57	15	0.13	0.53
23	1	1.00	1.00	6	0.16	0
24	3	0.33	0.00	3	0.33	0
25	14	0.21	0.26	13	0.23	0.33
26	2	0.50	0.75	2	0.5	0.75
27	17	0.17	0.22	16	0.18	0.27
28	autapomorphy					
29	5	0.40	0.00	6	0.33	0.33
30	30	0.13	0.07	27	0.14	0.17
31	1	1.00	1.00	1	1.00	1.00
32	3	0.33	0.60	4	0.25	0.40
33	1	1.00	1.00	1	1.00	1.00
34	4	0.50	0.80	4	0.50	0.80
35	3	0.33	0.75	4	0.25	0.62
36	1	1.00	1.00	1	1.00	1.00
37	autapomorphy					
38	2	0.50	0.66	2	0.50	0.66
39	5	0.40	0.62	5	0.40	0.62
40	18	0.16	0.28	19	0.15	0.23
41	16	0.18	0.31	16	0.18	0.31
42	5	0.20	0.20	5	0.20	0.20
43	7	0.14	0.70	7	0.14	0.70
44	16	0.12	0.41	14	0.14	0.07
45	12	0.08	0.35	15	0.06	0.17
46	6	0.16	0.58	5	0.20	0.66
47	1	1.00	1.00	1	1.00	1.00
48	1	1.00	1.00	2	0.50	0.50
49	1	1.00	1.00	1	1.00	1.00
50	14	0.14	0.52	13	0.15	0.56
51	4	0.25	0.80	4	0.25	0.80
52	2	0.50	0.83	6	0.16	0.16
53	4	0.25	0.75	4	0.25	0.75
54	19	0.21	0.34	19	0.21	0.34
55	9	0.22	0.61	8	0.25	0.66
56	9	0.33	0.71	10	0.30	0.66
57	22	0.13	0.45	25	0.12	0.37
58	9	0.11	0.33	8	0.12	0.41
59	5	0.20	0.78	4	0.25	0.84
60	11	0.09	0.58	12	0.08	0.54
61	9	0.11	0.38	12	0.08	0.15
62	5	0.20	0.75	4	0.25	0.81
63	3	0.33	0.00	3	0.33	0.00
64	6	0.33	0.71	6	0.33	0.71
65	3	0.33	0.77	4	0.25	0.66
66	1	1.00	1.00	2	0.50	0.50
67	autapomorphy					
68	2	0.50	0.80	2	0.50	0.80
69	4	0.50	0.50	4	0.50	0.50
70	5	0.40	0.78	5	0.40	0.78
71	3	0.66	0.00	3	0.66	0.00
72	7	0.42	0.33	5	0.60	0.66
73	4	0.50	0.71	3	0.66	0.85
74	11	0.18	0.30	9	0.22	0.46
75	7	0.28	0.16	11	0.18	0.18
76	6	0.16	0.58	6	0.16	0.58
77	7	0.28	0.80	9	0.22	0.73
78	9	0.11	0.46	9	0.11	0.46
79	2	0.50	0.92	4	0.25	0.78
80	1	1.00	1.00	1	1.00	1.00
81	10	0.10	0.35	8	0.12	0.50

Appendix III. Continued.

82	3	0.33	0.71	4	0.25	0.57
83	5	0.25	0.57	3	0.33	0.71
84	2	0.50	0.75	2	0.5	0.75
85	7	0.12	0.36	7	0.12	0.36
86	7	0.14	0.57	7	0.14	0.6
87			autapomorphy			
88	3	0.33	0.71	4	0.25	0.57
89	8	0.25	0.14	8	0.25	0.14
90	12	0.18	0.40	11	0.2	0.46
91	1	1.00	1.00	3	1.00	1.00
92	1	1.00	1.00	1	1.00	1.00
93	2	0.50	0.80	2	0.5	0.8
94	3	0.66	0.66	6	0.33	0.33
95	2	0.50	0.66	2	0.5	0.66
96	3	0.33	0.33	3	0.33	0.33
97	3	0.33	0.60	2	0.5	0.8
98	4	0.25	0.25	3	0.33	0.5
99	2	0.50	0.80	2	0.5	0.8
100	4	0.25	0.76	4	0.25	0.76
101	1	1.00	1.00	1	1	1
102	3	0.33	0.81	10	0.1	0.18
103	4	0.25	0.81	7	0.14	0.62
104			autapomorphy			
105	2	0.50	0.66	2	0.5	0.66
106	14	0.14	0.42	13	0.15	0.47
107			autapomorphy			
108			autapomorphy			
109	3	0.66	0.85	3	0.66	0.85
110	1	1.00	1.00	1	1.00	1.00
111	3	0.66	0.85	4	0.50	0.71
112	11	0.27	0.52	15	0.20	0.29
113	1	1.00	1.00	1	1.00	1.00
114	12	0.16	0.62	15	0.13	0.51
115			autapomorphy			
116	2	0.50	0.91	2	0.50	0.91
117	1	1.00	1.00	1	1.00	1.00
118			autapomorphy			
119			autapomorphy			
120			autapomorphy			
121			autapomorphy			
122	1	1.00	1.00	1	1.00	1.00
123			autapomorphy			
124	5	0.40	0.75	5	0.40	0.75
125			autapomorphy			
126	3	0.66	0.90	3	0.66	0.90
127	2	1.00	1.00	2	1.00	1.00
128	1	1.00	1.00	1	1.00	1.00
129	2	0.50	0.90	2	0.50	0.90
130	1	1.00	1.00	1	1.00	1.00
131	2	0.50	0.75	2	0.50	0.75
132	1	1.00	1.00	1	1.00	1.00
133	1	1.00	1.00	1	1.00	1.00
134	1	1.00	1.00	1	1.00	1.00
135	1	1.00	1.00	1	1.00	1.00
136			autapomorphy			
137	12	0.08	0.38	12	0.08	0.38
138	1	1.00	1.00	1	1.00	1.00
139	1	1.00	1.00	1	1.00	1.00
140	3	0.33	0.80	3	0.33	0.80
141			autapomorphy			
142	1	1.00	1.00	1	1.00	1.00
143			autapomorphy			
144			autapomorphy			
145	1	1.00	1.00	1	1.00	1.00
146	1	1.00	1.00	2	0.50	0.75
147	1	1.00	1.00	2	0.50	0.75
148			autapomorphy			
149			autapomorphy			
150	4	0.50	0.00	5	0.40	0.25
151			autapomorphy			
152	6	0.50	0.80	7	0.42	0.20
153	12	0.16	0.37	12	0.16	0.37
154	1	1.00	1.00	1	1.00	1.00
155			autapomorphy			
156			autapomorphy			
157	2	0.50	0.90	2	0.50	0.90
158	6	0.33	0.50	8	0.25	0.25
159	2	0.50	0.50	3	0.33	0.00
160			autapomorphy			
161			autapomorphy			
162	2	0.50	0.66	1	1.00	1.00
163	6	0.33	0.42	5	0.40	0.57
164	8	0.25	0.00	6	0.33	0.33
165	2	0.50	0.66	2	0.50	0.66
166			autapomorphy			
167	1	1.00	1.00	1	1.00	1.00
168	1	1.00	1.00	2	0.50	0.75
169	2	0.50	0.66	3	0.33	0.33

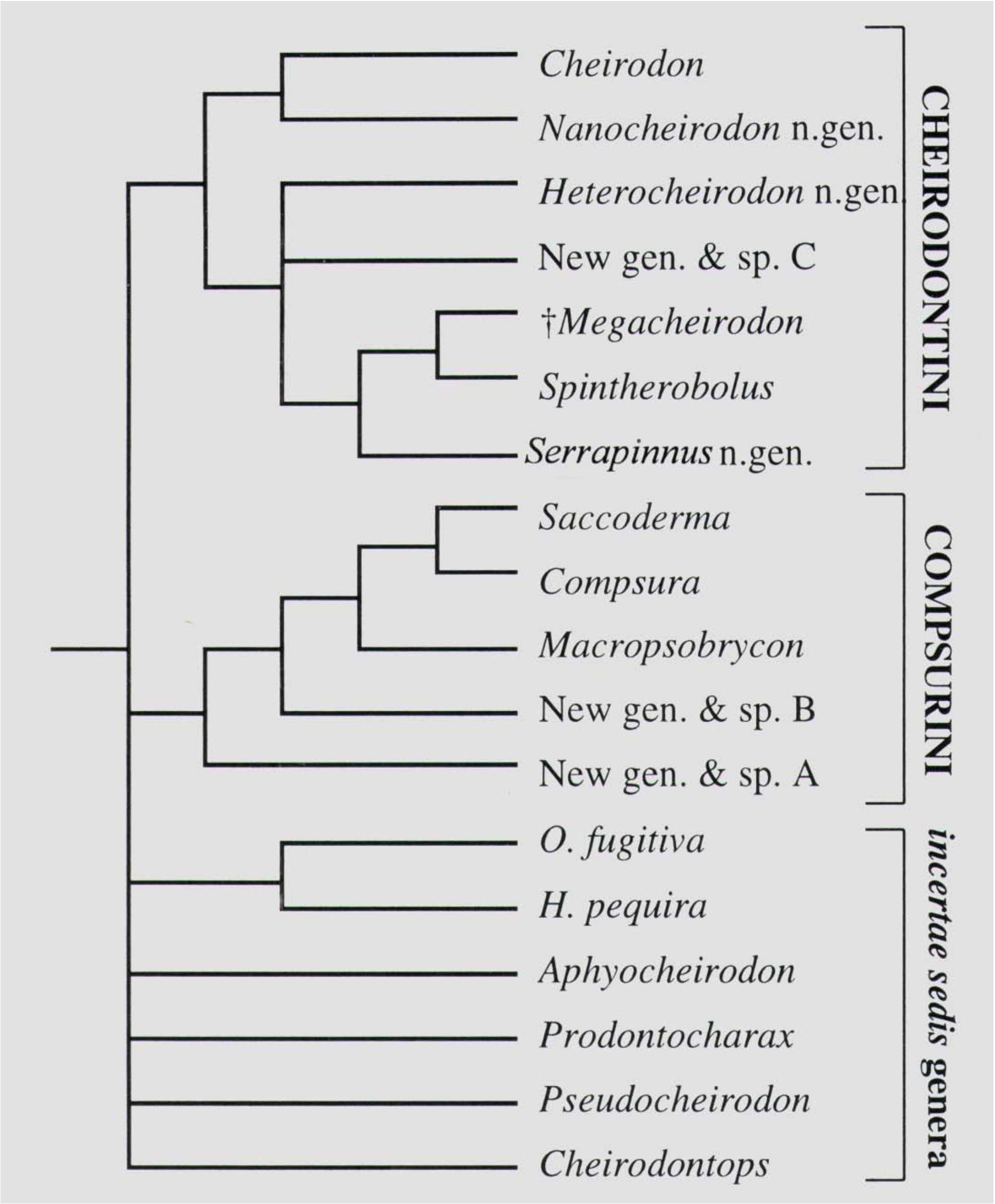

Fig. 1. Cladrogram obtained by Malabarba (1998). New gen. & sp. B is *Acinocheirodon* Malabarba & Weitzman (1999) and New gen. & sp. A is *Kolpotocheirodon* Malabarba & Weitzman (2000).

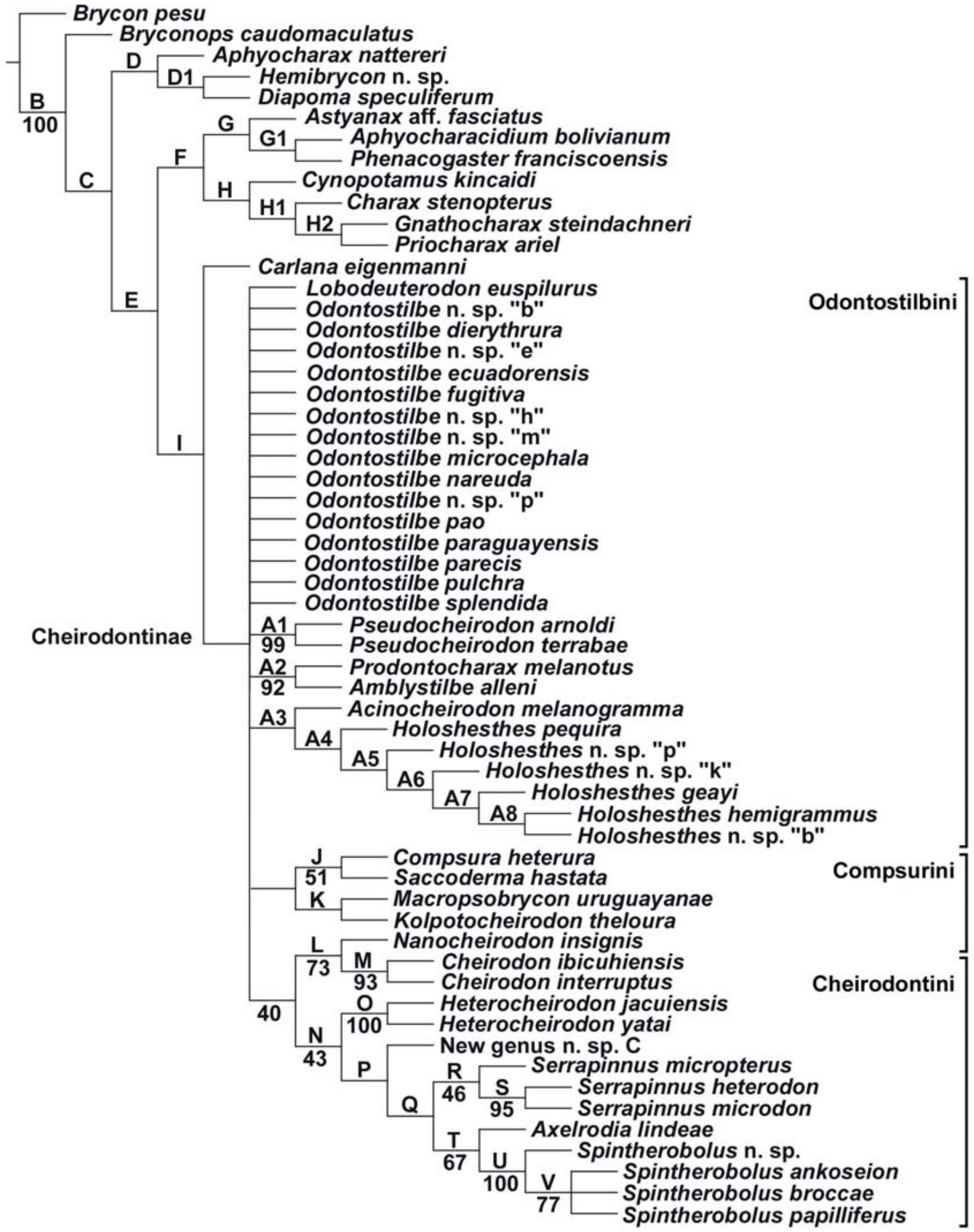

Fig. 2. Strict consensus unweighted cladogram (811 steps, CI= 25, IR= 55) of 300 equally parsimonious shortest trees (minimun length 743 steps). Bootstrap values below the node.

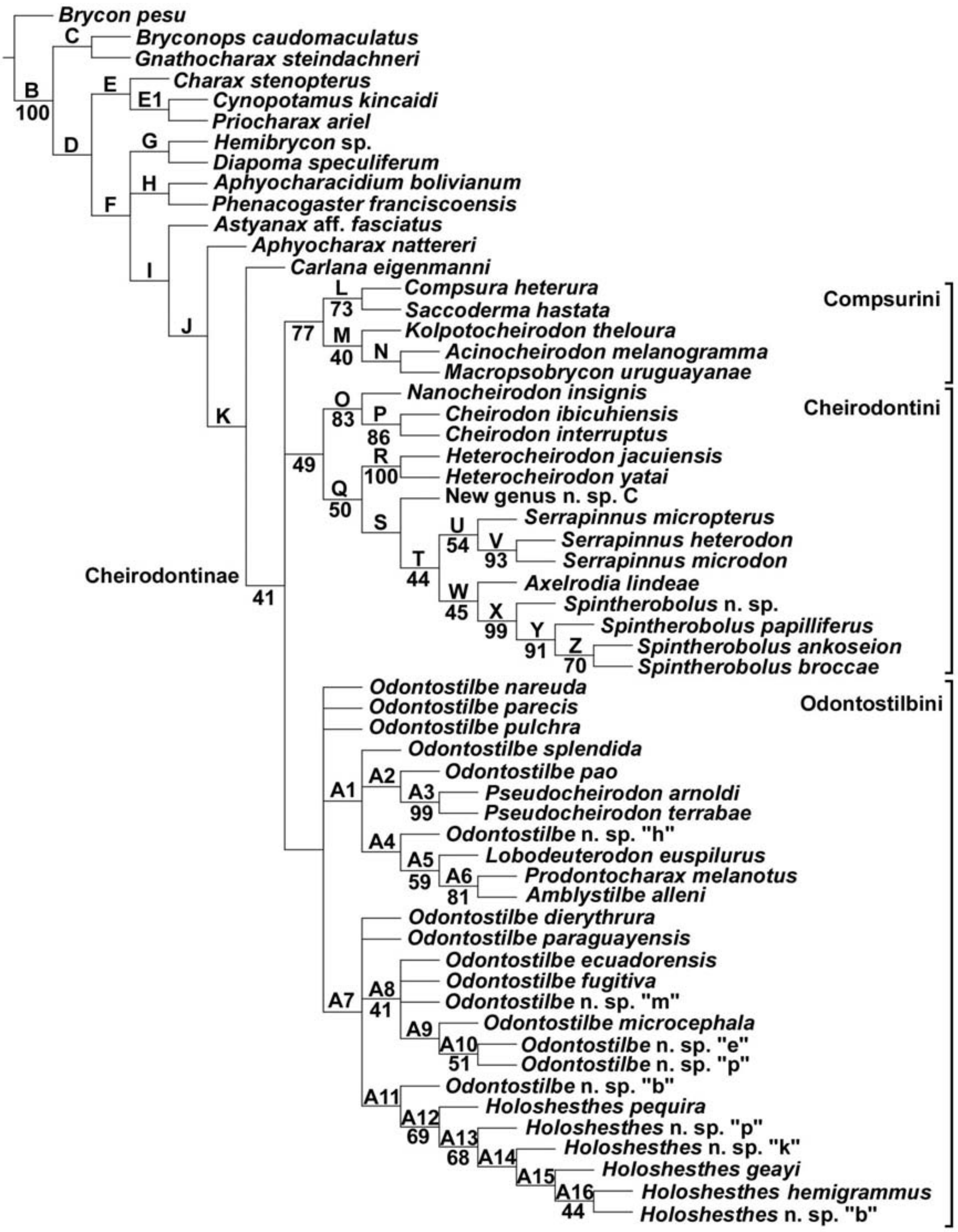

Fig. 3. Strict consensus weighted cladogram (771 steps, CI= 26, RI= 58) of 10 equally parsimonious shortest trees (minimun length 768). Bootstrap values below the node.

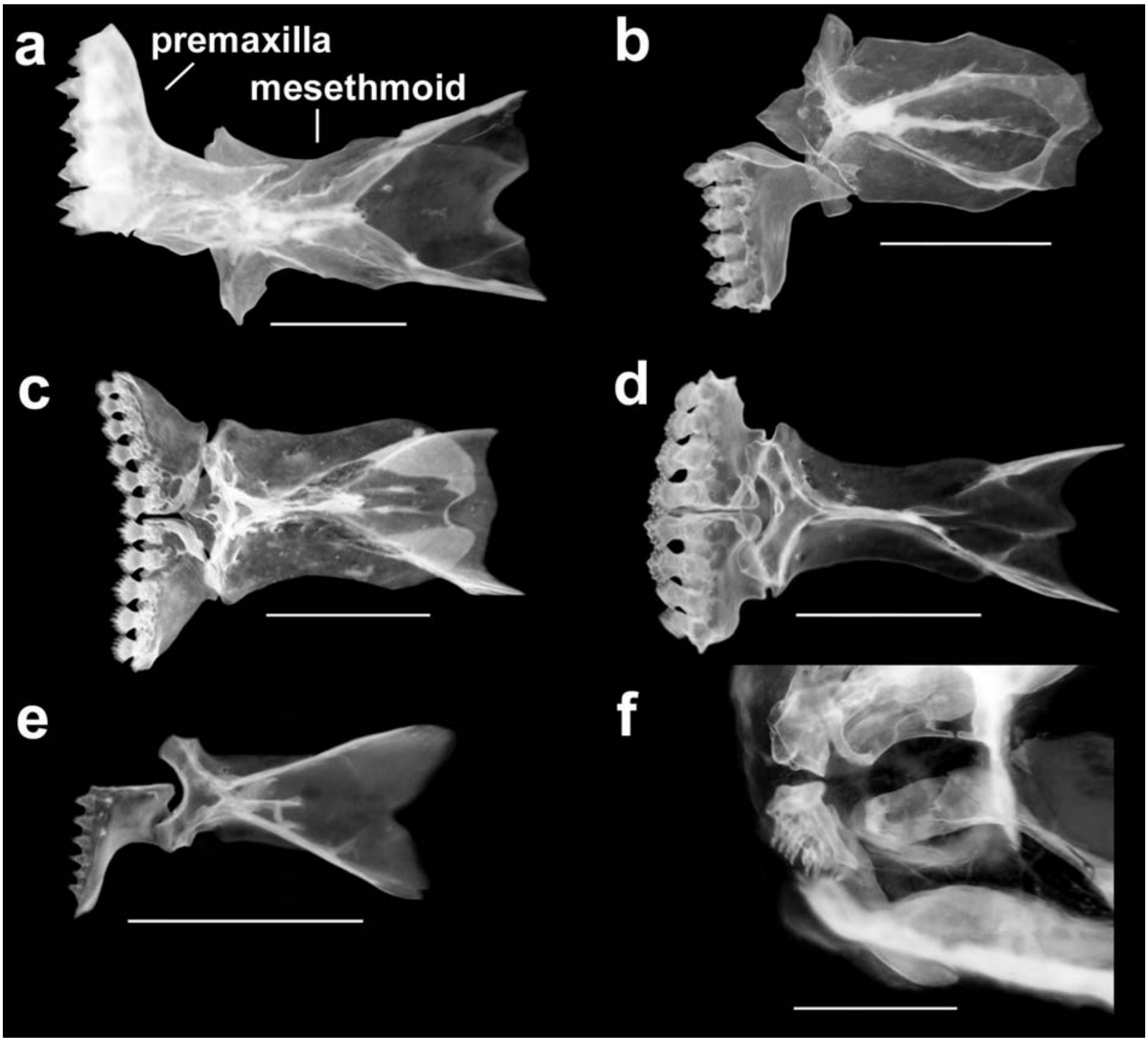

Fig. 4. Premaxillae and mesethmoids, ventral views: a- *Hemibrycon* sp. (MCP 35022); b- *Holoshesthes* n. sp. “k” (KU 13508); c- *Odontostilbe fugitiva* (INPA 18465); d- *Heterocheirodon jacuiensis* (MCP 21672); e- *Macropsobryconn uruguayanae* (MCP 11936); f- *Spintherobolus ankoseion* (MPC 12561). Bars, 1 mm.

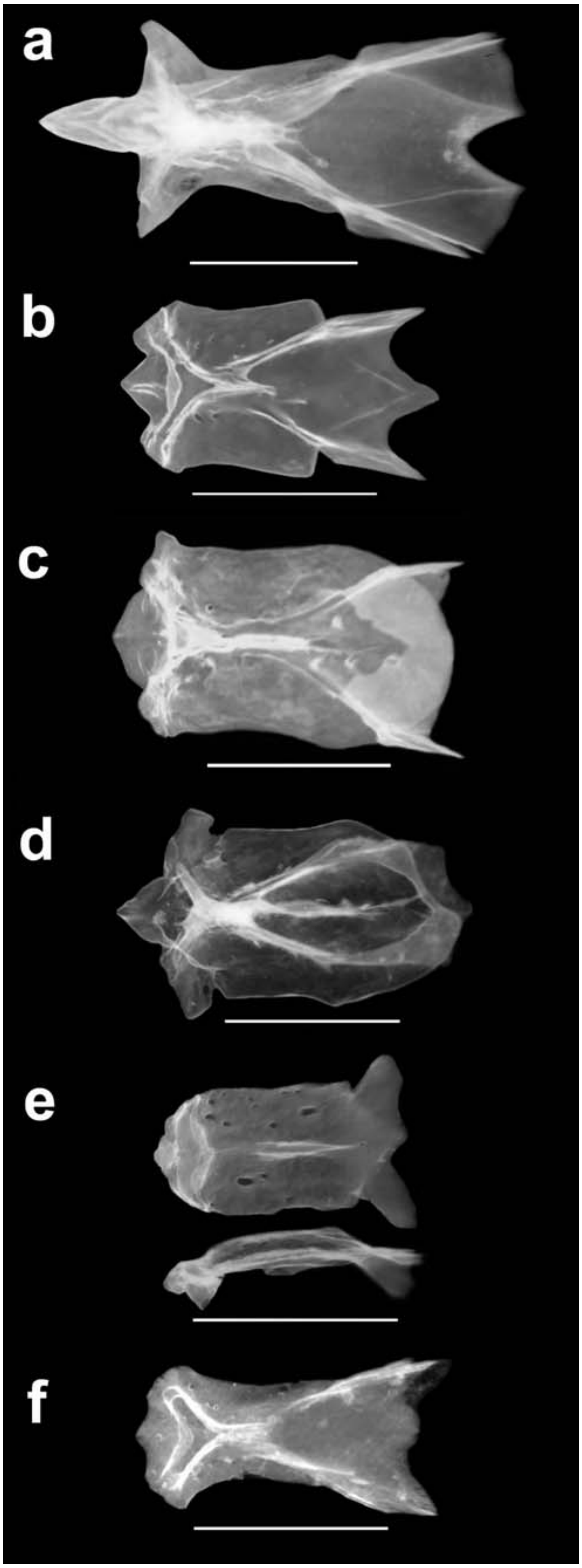

Fig. 5. Mesethmoids, dorsal views: a- *Hemibrycon* sp. (MCP 35022); b- *Pseudocheirodon arnoldi* (MCP 16134); c- *Odontostilbe fugitiva* (INPA 18465); d- *Holoshesthes* n. sp. “k” (KU 13508); e- *Spintherobolus ankoseion* (MPC 12561), lateral view below; f- *Heterocheirodon jacuiensis* (MCP 21672). Bars, 1 mm.

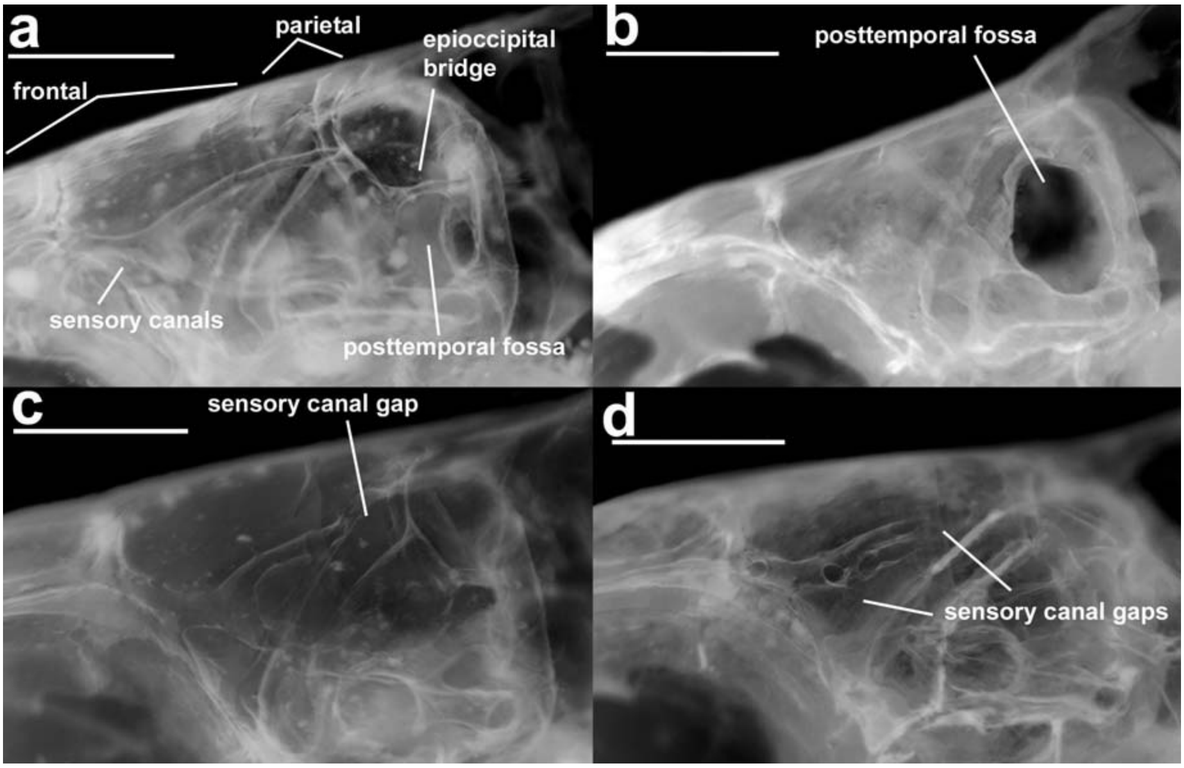

Fig. 6. Head, dorsolateral view, laterosensory canals on frontal and parietal and posttemporal fossa in detail: a- *Odontostilbe fugitiva* (ANSP 178908); b- *Spintherobolus ankoseion* (MPC 12561); c- *Heterocheirodon yatai* (MCP 11287), sensory canal gap in the parietal; d- *Holoshesthes hemigrammus* (NRM 17307), sensory canal gaps in the frontal and parietal. Bars, 1 mm.

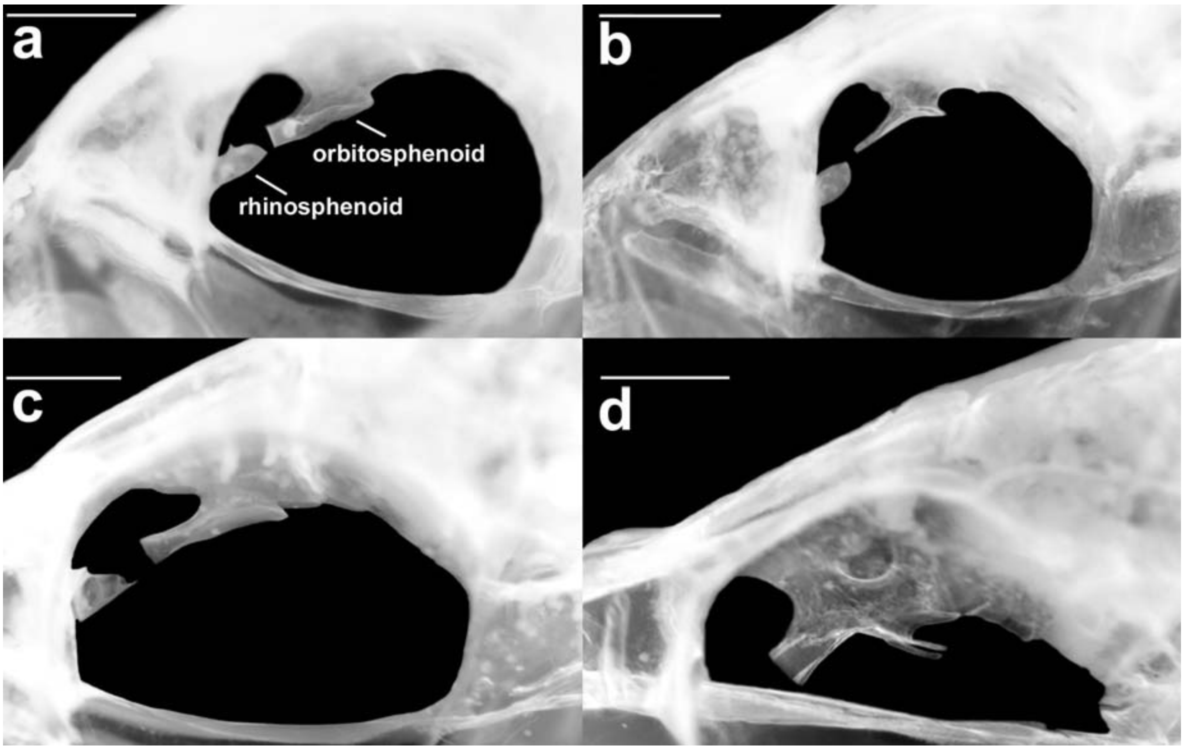

Fig. 7. Eye orbit, lateral view of the head, orbitosphenoid and rhinosphenoid in detail: a- *Cheirodon interruptus* (MCP 22813); b- *Odontostilbe fugitiva* (ANSP 178908); c- *Odontostilbe* n. sp. “e” (MCP 26004); d- *Spintherobolus papilliferus* (MZUSP 49408). Bars, 1 mm.

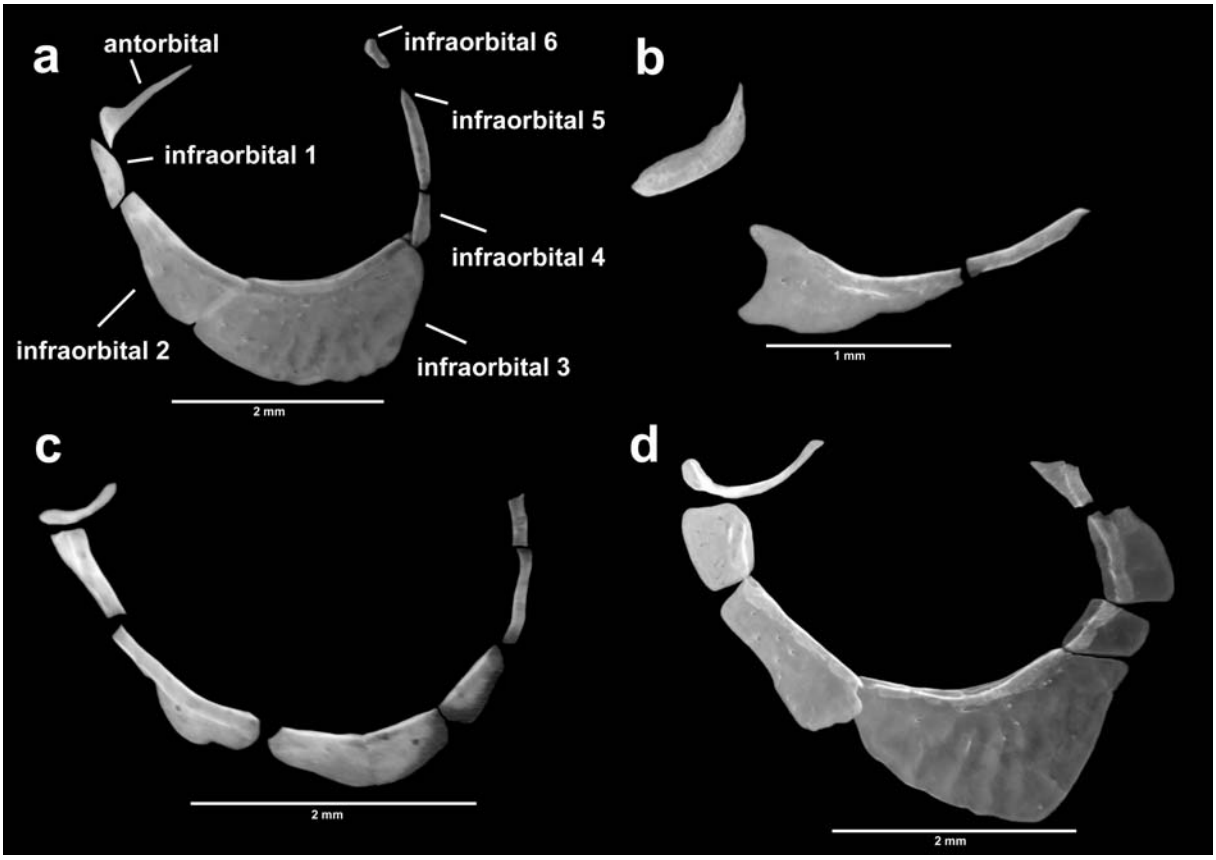

Fig. 8. Circumorbitals: a- *Cheirodon interruptus* (MCP 22813); b- *Spintherobolus ankoseion* (MCP 12561); c- *Axelrodia lindeae* (MCP 37314); d- *Phenacogaster franciscoensis* (not catalogued).

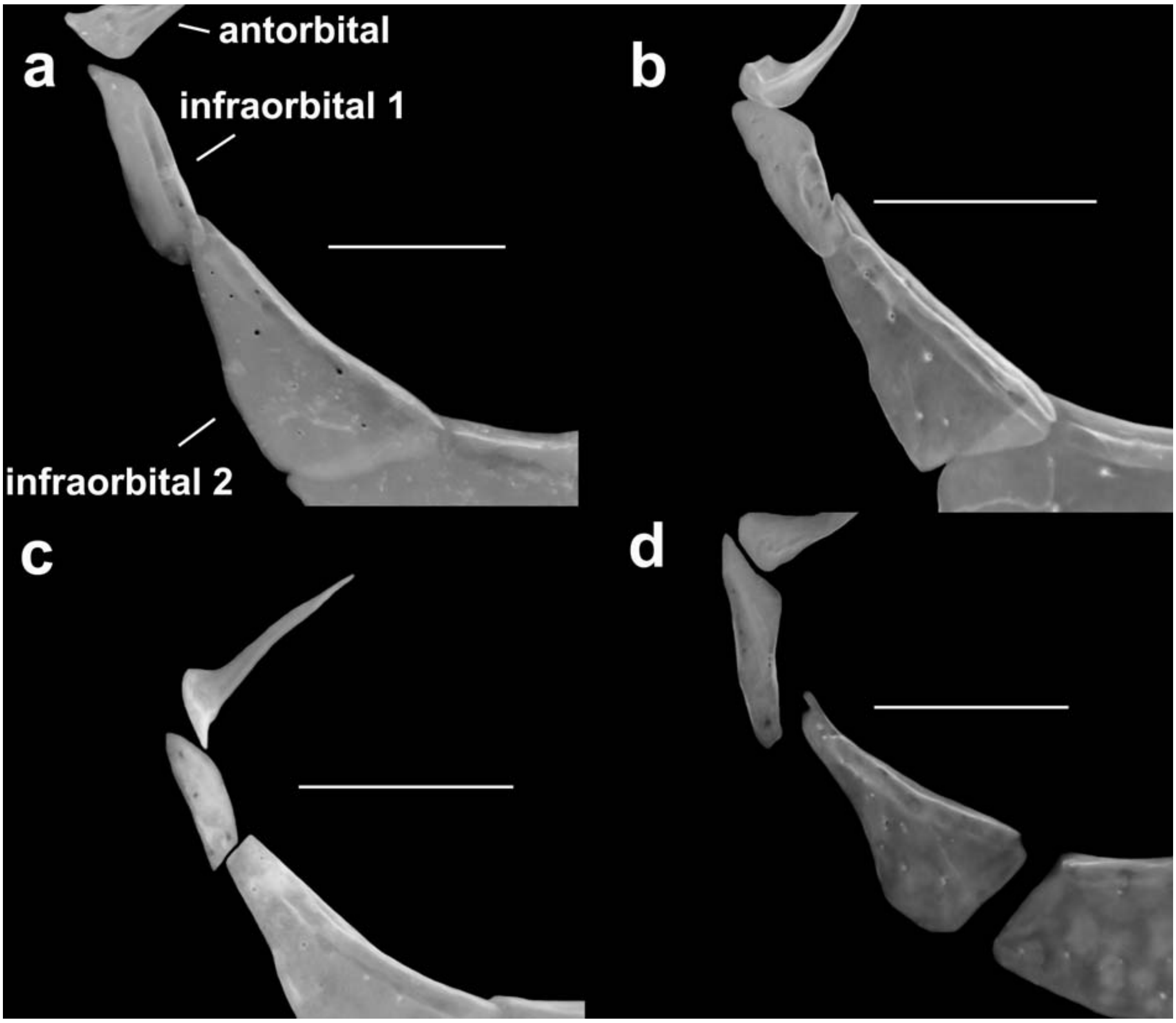

Fig. 9. Infraorbitals 1 and 2 in detail: a- *Odontostilbe* n. sp. “e” (MCP 26004); b- *Odontostilbe pulchra* (INHS 40101); c- *Cheirodon interruptus* (MCP 22813); d- (MCP 37314); d- *Macropsobryconn uruguayanae* (MCP 11936). Bars, 1 mm.

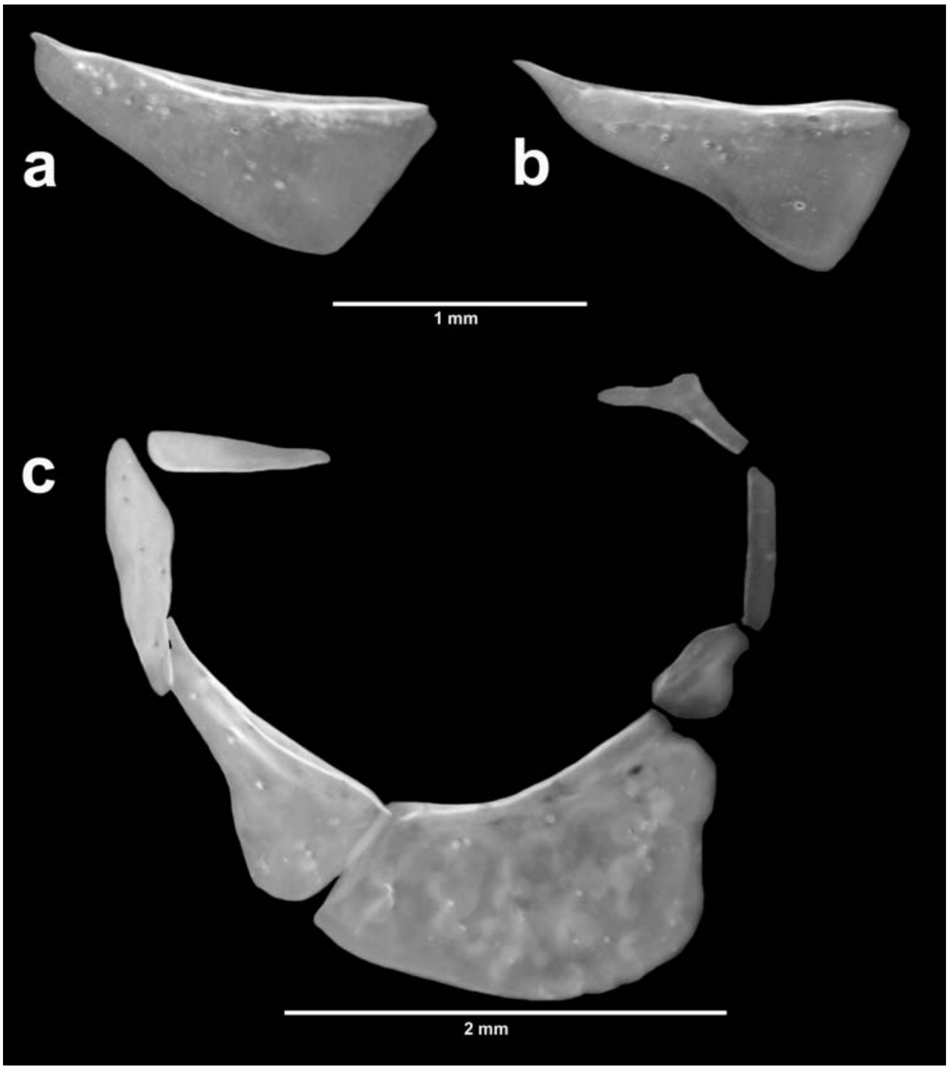

Fig. 10. Infraorbital 2 (above) and circumorbital series (below): a- *Odontostilbe fugitiva* (INPA 18465); b- *Holoshesthes pequira* (MCP 33240); c- *Macropsobrycon uruguayanae* (MCP 11936).

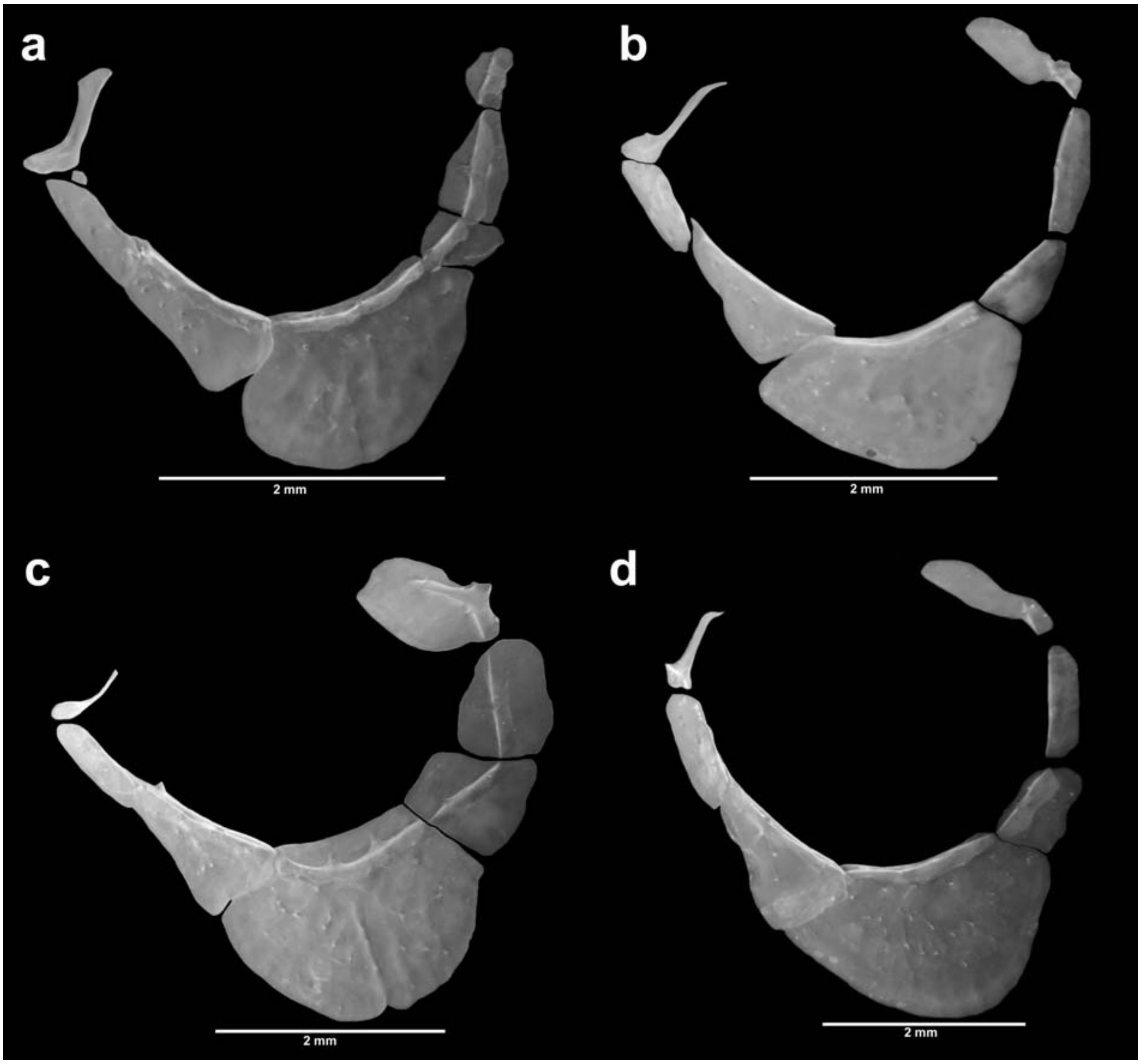

Fig. 11. Circumorbitals: a- *Holoshesthes hemigrammus* (NRM 17307); b- *Odontostilbe paraguayensis* (MCP 35618); c- *Odontostilbe microcephala* (USNM 321173); d- *Holoshesthes* n. sp. “k” (KU 13508).

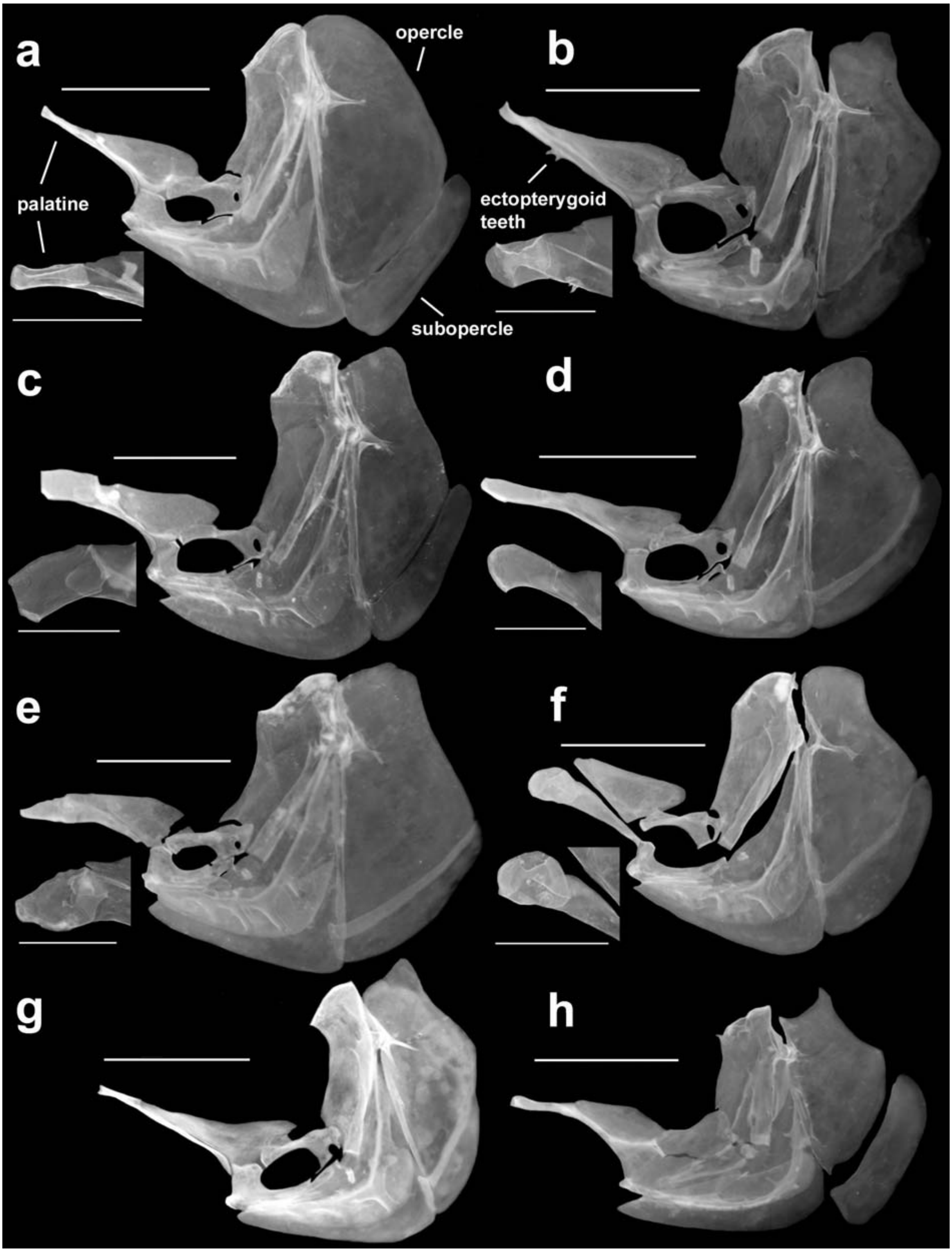

Fig. 12. Suspensory apparatus, palatine in detail: a- *Kolpotocheirodon theloura* (MNRJ 18051); b- *Holoshesthes hemigrammus* (MNRJ 19470); c- *Odontostilbe pulchra* (INHS 40101); d- *Holoshesthes pequira* (MZUSP 21067); e- *Amblystilbe alleni* (MZUSP 12407); f- *Pseudocheirodon arnoldi* (MCP 16134); g- *Macropsobrycon uruguayanae* (MCP 11936); h- *Spintherobolus ankoseion* (MCP 12561). Bars, 2 mm above suspensories and 1 mm below palatines.

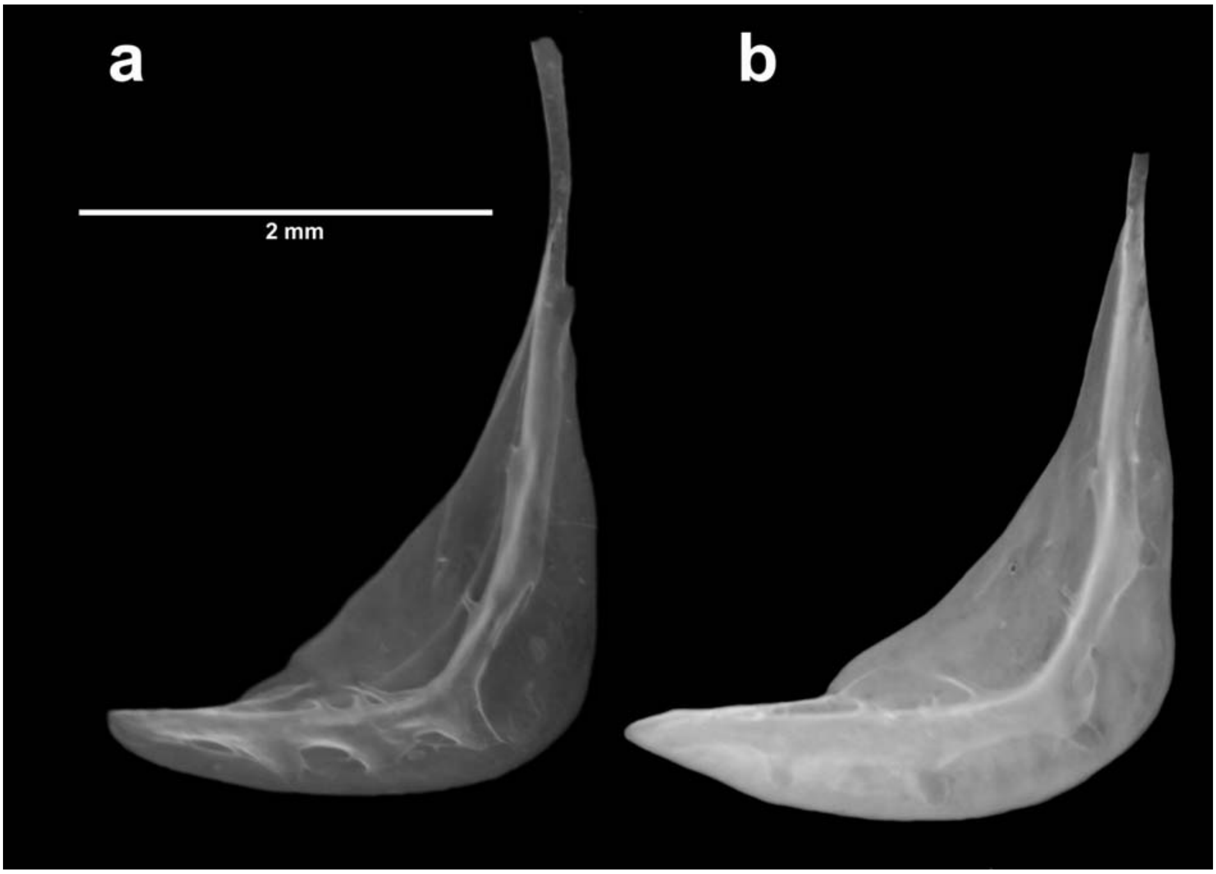

Fig. 13. Preopercles: a- *Lobodeuterodon euspilurus* (MEPN 1518); b- *Cheirodon interruptus* (MCP 22813).

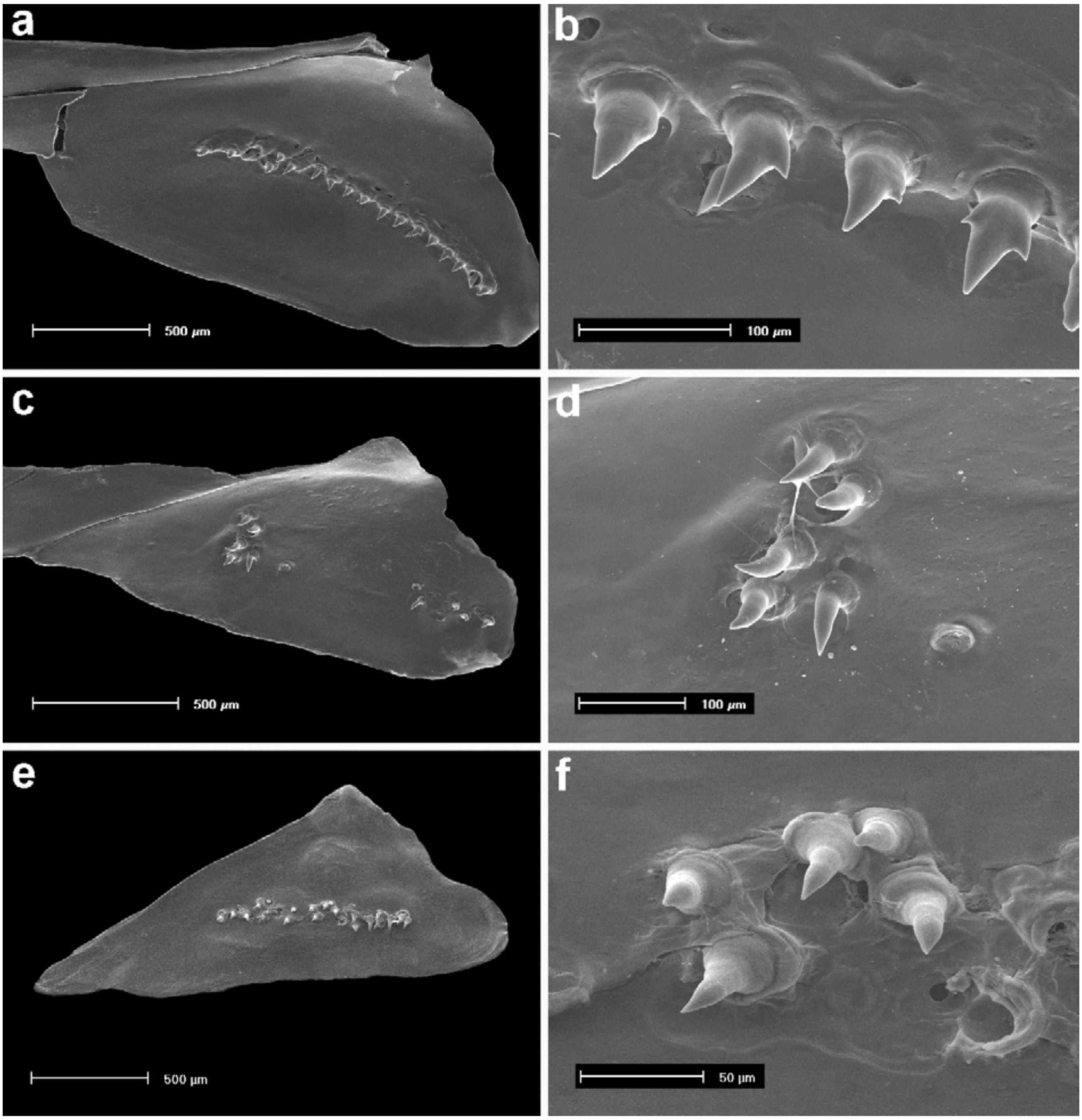

Fig. 14. Mesopterygoids with teeth: a-b- *Odontostilbe* n. sp. “p” (MCP 20337); c-d- *Odontostilbe* n. sp. “b” (MCP 12110); e-f- *Holoshesthes pequira* (MZUSP 21067). Scanning electron micrographs (SEM).

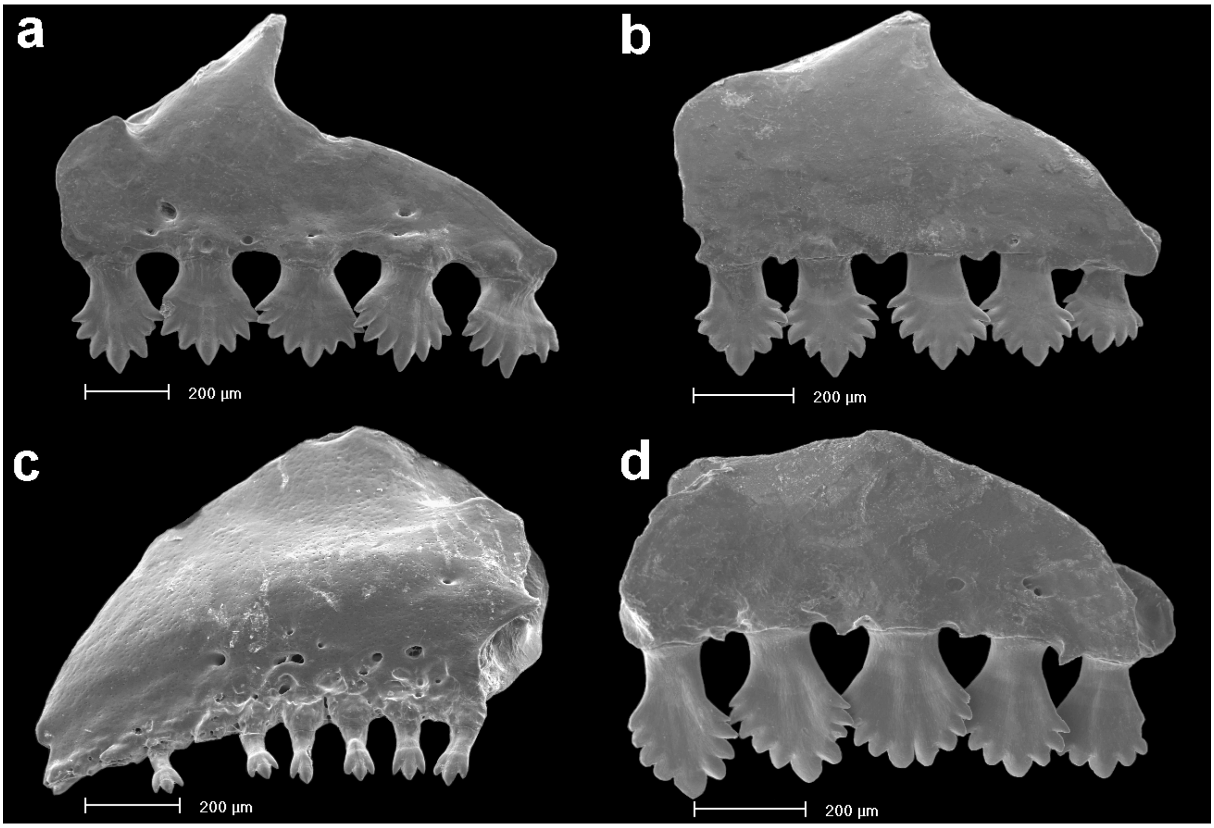

Fig. 15. Premaxillae, left side (a-b, d) and right side (c): a- *Odontostilbe microcephala* (USNM 32473); b- *Odontostilbe paraguayensis*, (MCP 35618); c- *Amblystilbe alleni* (USNM 280541); d- *Lobodeuterodon euspilurus* (FMNH 113517). Scanning electron micrographs (SEM).

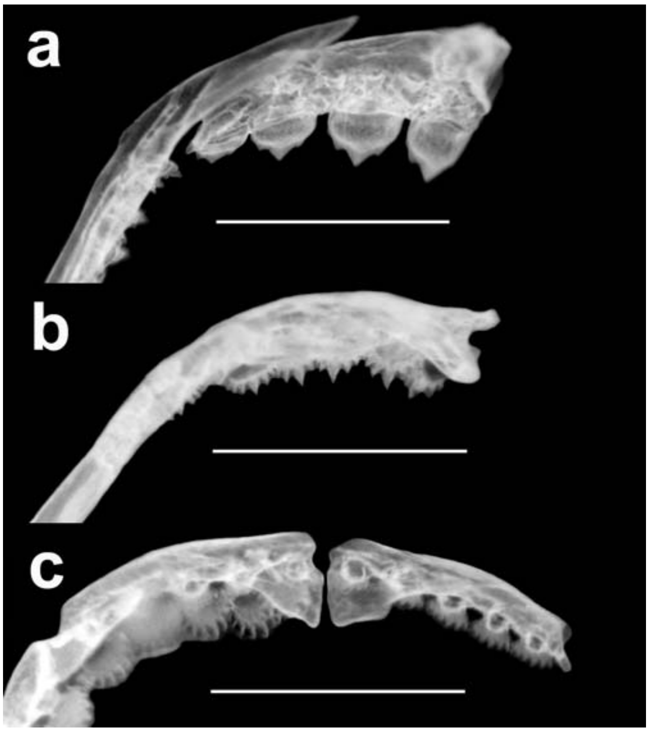

Fig. 16. Premaxillae articulated with the maxilla on the left, dorsal view: a- *Hemibrycon* sp. (MCP 35022); b-; *Odontostilbe ecuadorensis* (FMNH 113514); c- *Pseudocheirodon terrabae* (UMMZ 194214), left and rigth premaxillae. Bars, 1 mm.

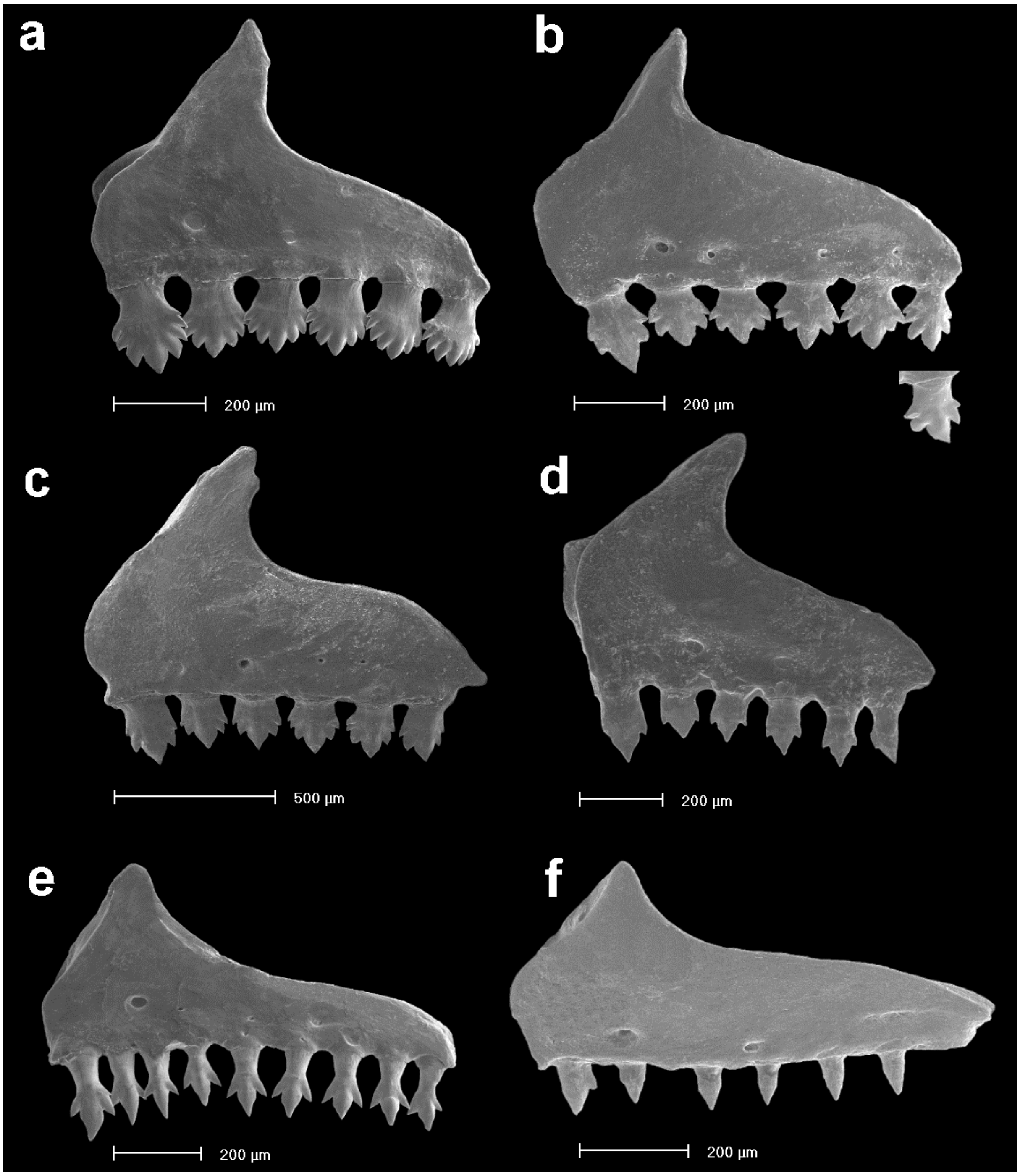

Fig. 17. Premaxillae, left side: a- *Holoshesthes pequira* (MZUSP 21067); b- *Holoshesthes* n. sp. “p” (FMNH 113499) (separate posteriormost tooth, FMNH 101038) ; c- *Holoshesthes* n. sp. “k” (KU 13509); d- *Holoshesthes geayi,* (CAS 64344); e- *Holoshesthes hemigrammus* (NRM 17307); f- *Holoshesthes* n. sp. “ b” (ASNP 156876). Scanning electron micrographs (SEM).

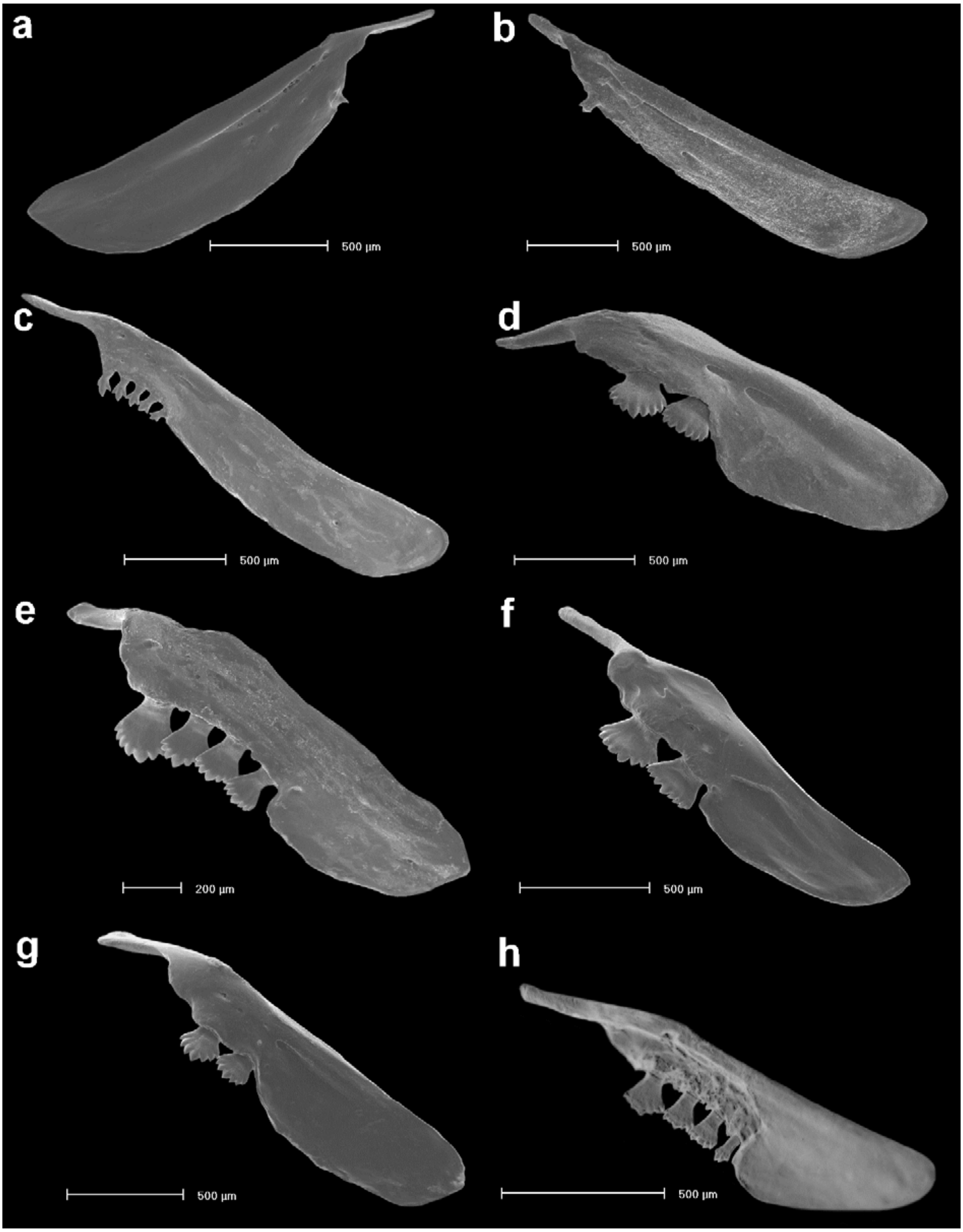

Fig. 18. Maxillae, left side: a- *Holoshesthes* n. sp. “ b” (ASNP 156876); b- *Holoshesthes geayi* (CAS 64344); c- *Holoshesthes hemigrammus* (NRM 17307); d- *Odontostilbe fugitiva* (ANSP 178908); e- *Lobodeuterodon euspilurus* (FMNH 113517); f- *Odontostilbe parecis* (MCP 37319); g- *Odontostilbe pulchra* (INHS 40101); h- *Odontostilbe pao* (MCNG 54107). Scanning electron micrographs (SEM).

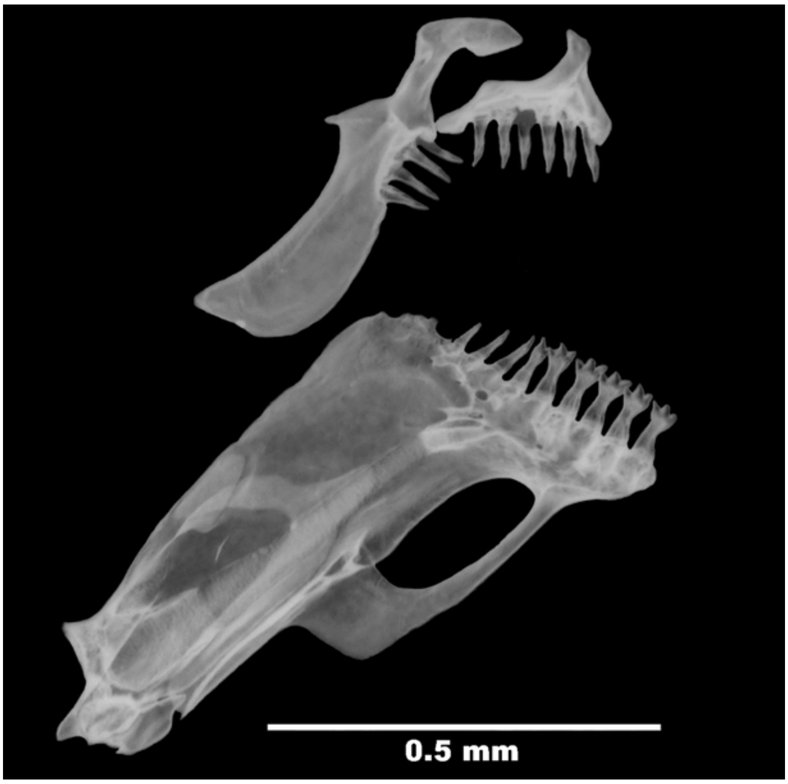

Fig. 19. Dentition of *Spintherobolus* n. sp. (MCP 37572). Left side premaxilla, maxilla (top) and lower jaw (bottom).

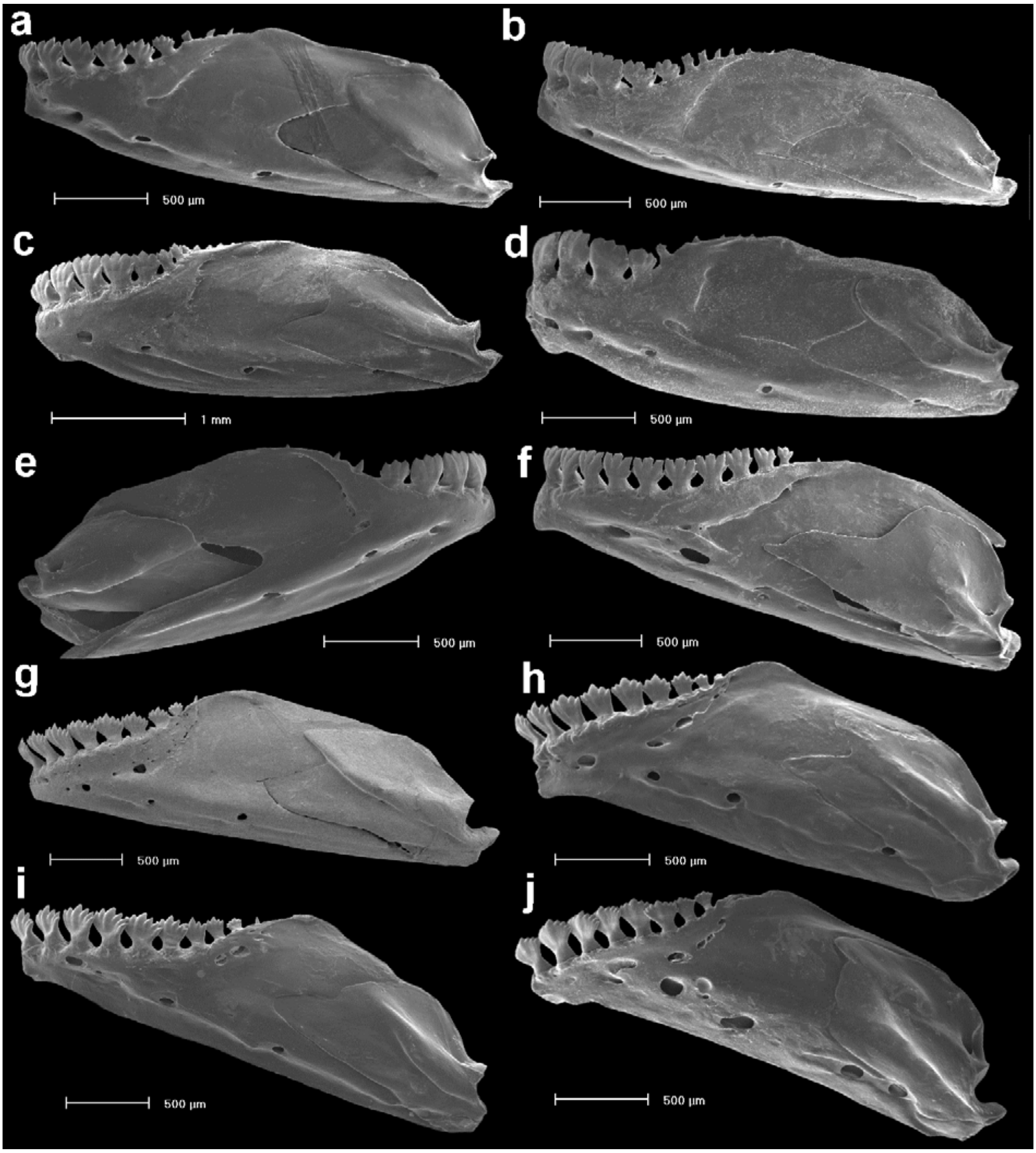

Fig. 20. Lower jaws: a- *Holoshesthes pequira* (MZUSP 21067); b- *Holoshesthes* n. sp. "p" (FMNH 113499); c- *Holoshesthes* n. sp. "k" (KU 13509); d- *Holoshesthes geayi* (CAS 64344); e- *Holoshesthes* n. sp. " b" (ASNP 156876); f- *Holoshesthes hemigrammus,* (NRM 17307); g- *Odontostilbe fugitiva* (ANSP 178908); h- *Odontostilbe pulchra* (INHS 40101); i- *Odontostilbe microcephala* (USNM 32473); j- *Lobodeuterodon euspilurus* (FMNH 113517). Scanning electron micrographs (SEM).

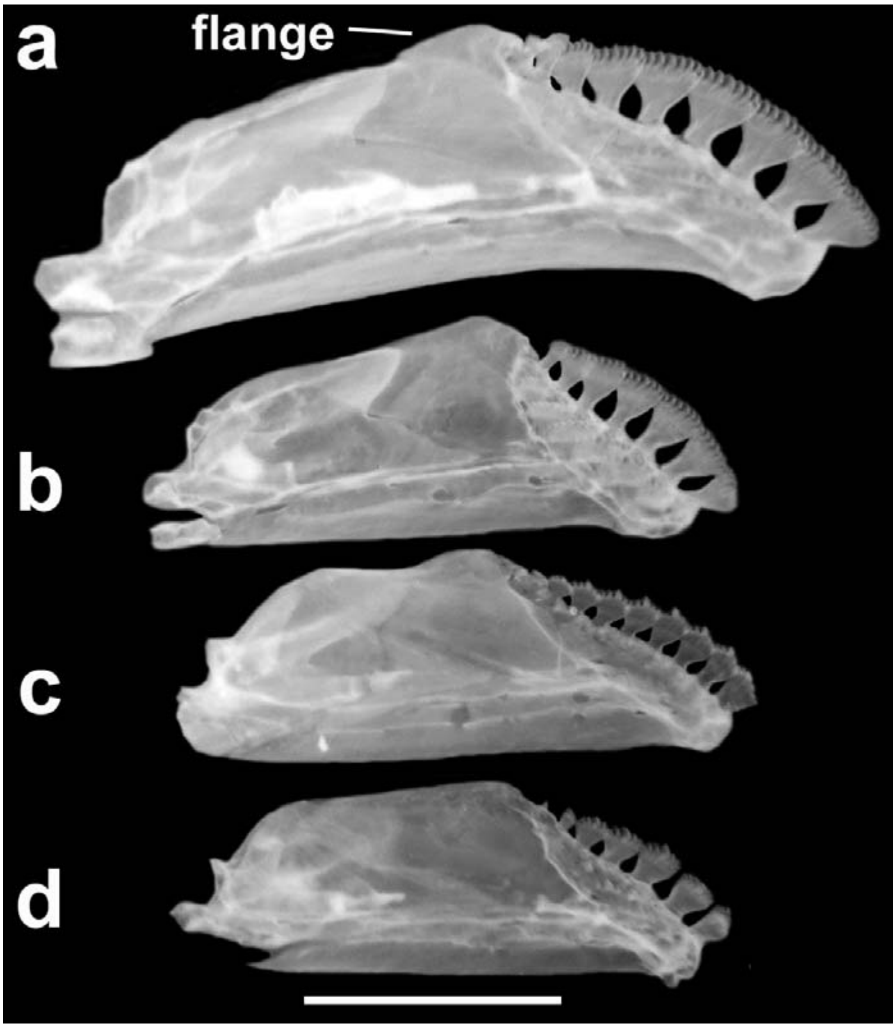

Fig. 21. Lower jaws, left side: a- *Pseudocheirodon terrabae* (UMMZ 194214); b- *Pseudocheirodon arnoldi* (MCP 16134); c- *Odontostilbe pao* (MCNG 54107), d- *Odontostilbe splendida* (MCP 38862). Bars, 1 mm.

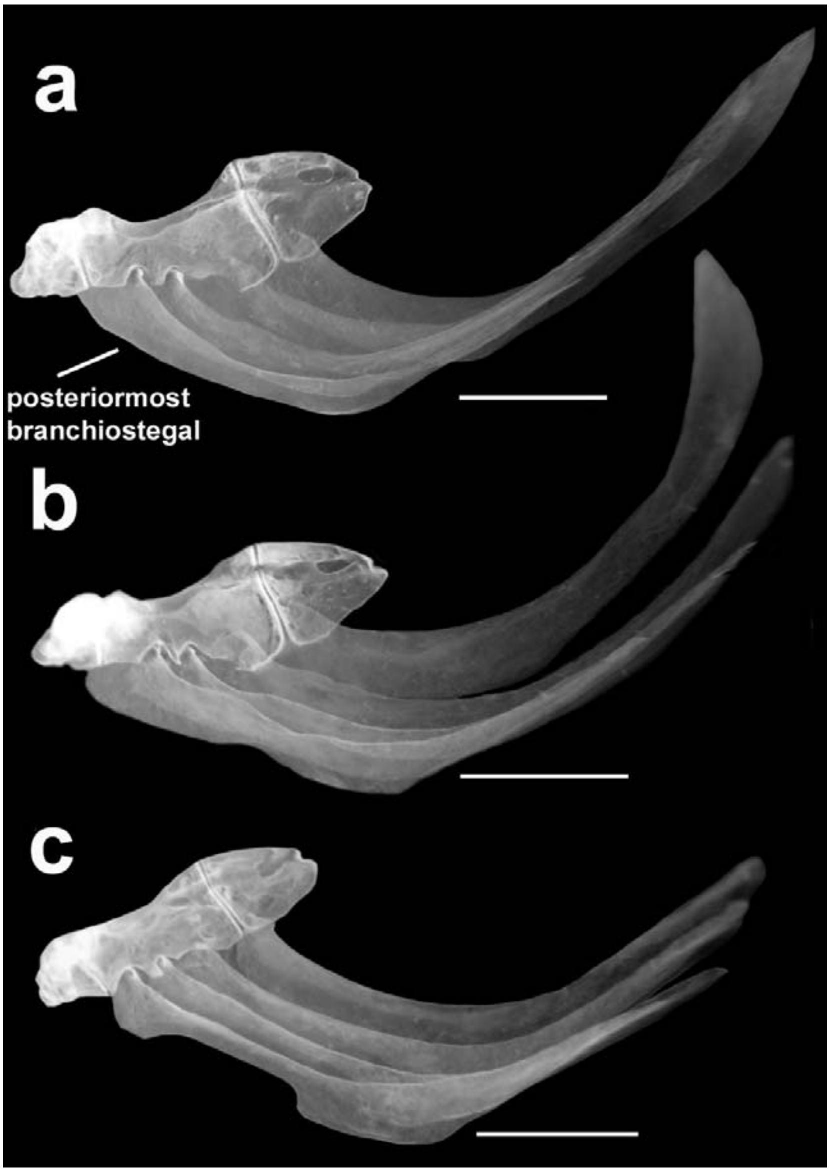

Fig. 22. Brachiostegals, inner view of the right side: a- *Odontostilbe fugitiva*, female (MZUSP 87746) and b- male (INPA 18512); c- *Kolpotocheirodon theloura*, male (MNRJ 18081). Bars, 1 mm.

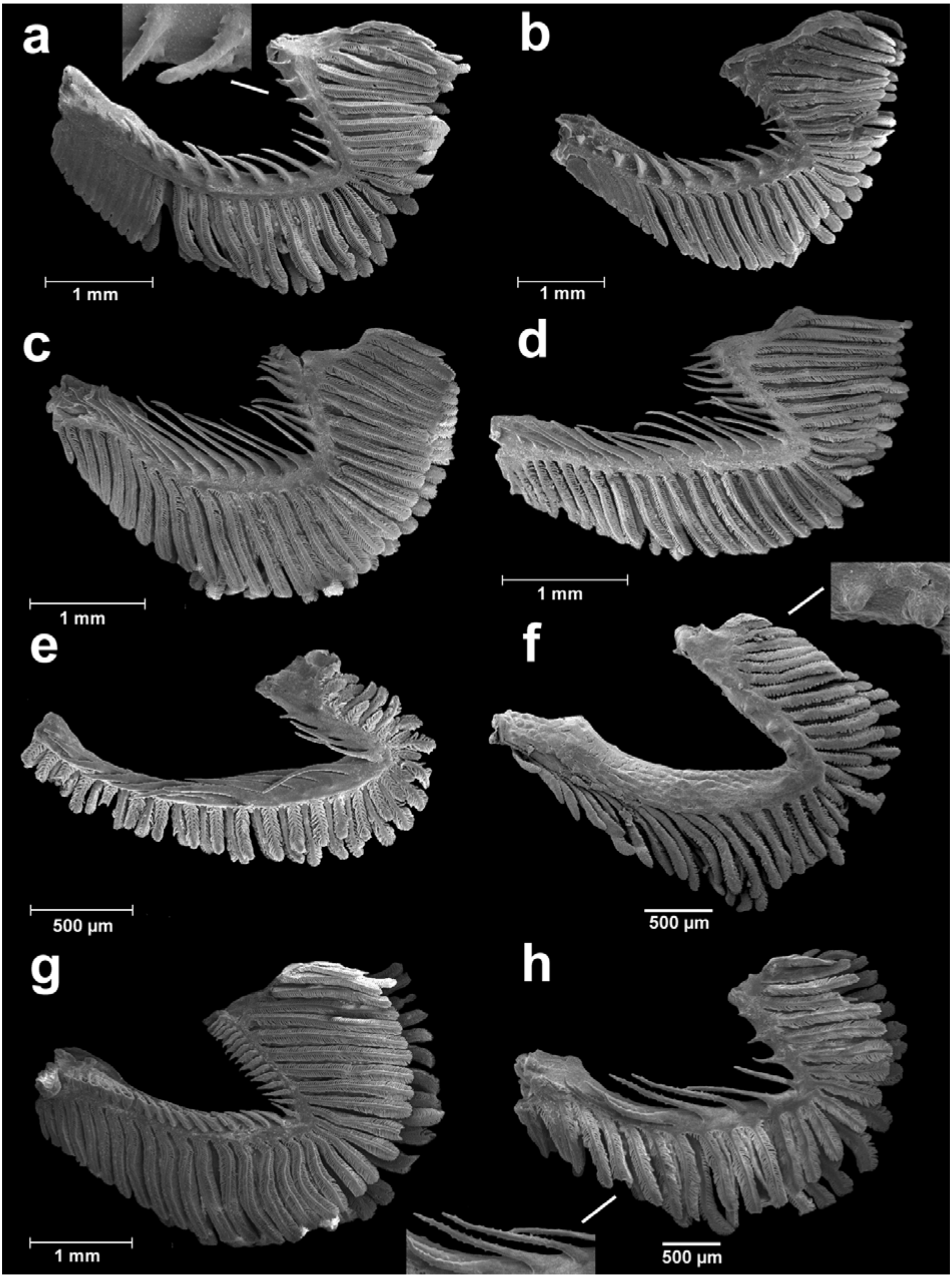

Fig. 23. First gill arches: a- *Odontostilbe dierythrura* (CPULRA 400); b-*Odontostilbe paraguayensis* (MCP 12032); c- *Macropsobrycon uruguayanae* (MCP 20900); d- *Holoshesthes* n. sp. “b” (ANSP 156876); e- *Priocharax arie*l (MCP 9953); f- *Spintherobolus ankoseion* (MCP 38625); *Aphyocharax nattereri* (MCP 34718).

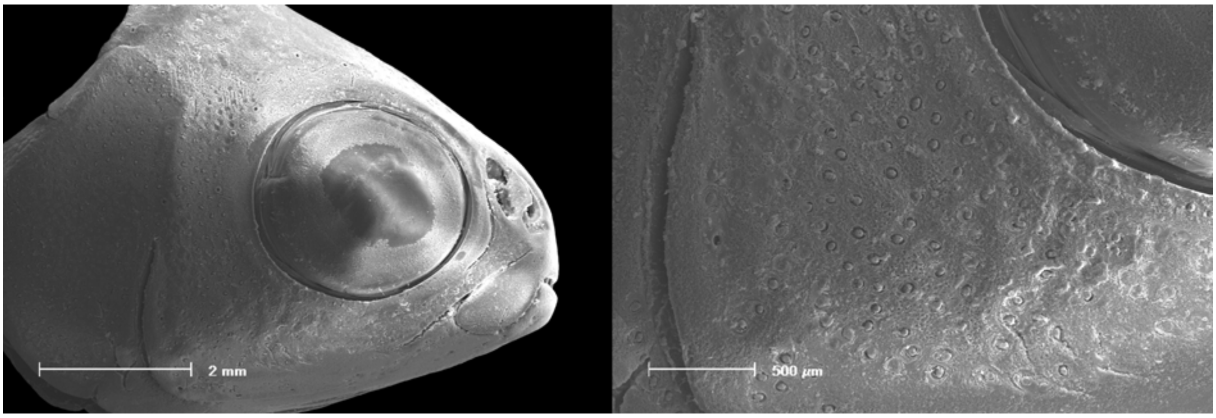

Fig. 24. Neuromasts on head of *Cheirodon interruptus* (in detail, third infraorbital) (MCP 37.9 mm SL. Scanning electron micrographs (SEM).

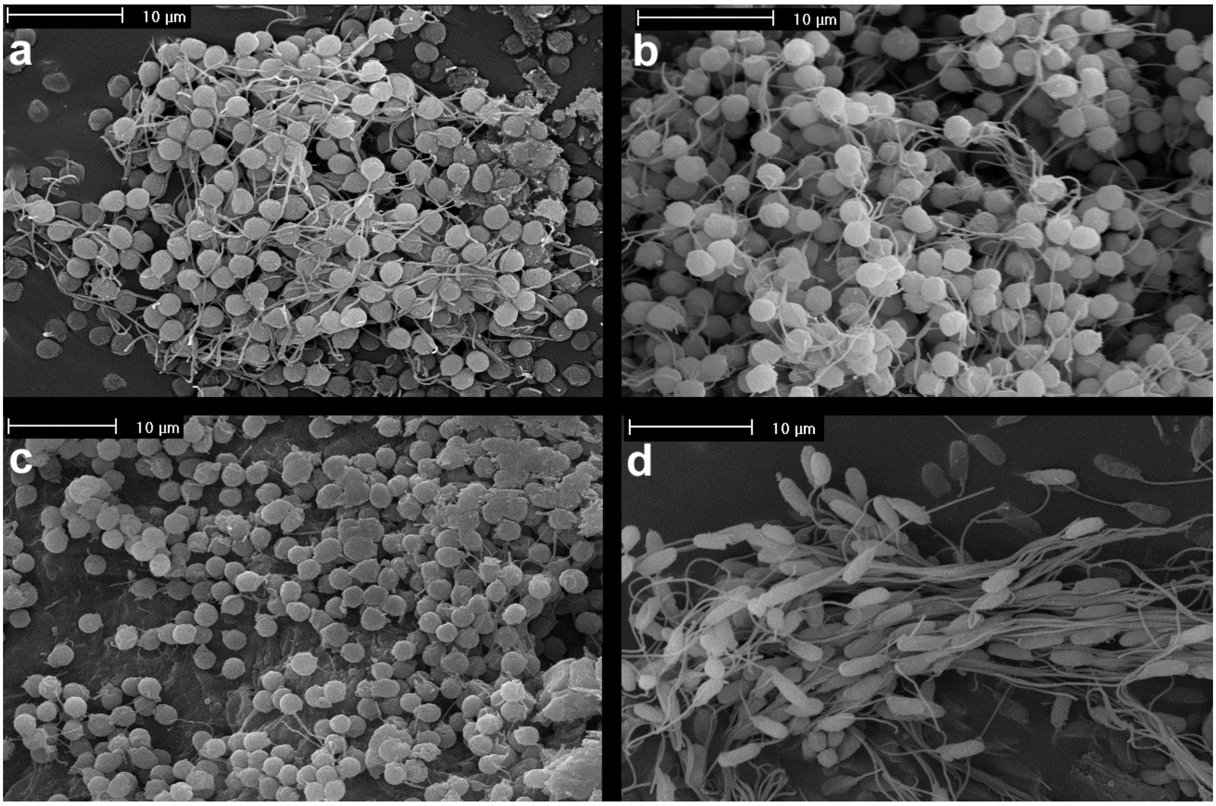

Fig. 25. Spermatozoa: a- *Odontostilbe pulchra* (INHS 40101); b- *Odontostilbe microcephala* (USNM 321173); c- *Holoshesthes* n. sp. “ k” (KU 13508) ; d- *Acinocheirodon melanogramma* (MCP 19238). Scanning electron micrographs (SEM).

CAPÍTULO II

Revision and revalidation of the genus *Holoshesthes* Eigenmann, 1903, with the description of three new species and proposition of two new synonyms (Teleostei: Cheirodontinae: Odontostilbini)

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Abstract

Holoshesthes Eigenmann, 1903 is revalidated and recognized as monophyletic, comprising six species and diagnosed by 21 characters. The genus before previously confined to the La Plata basin (rio Paraná, rio Paraguay and rio Uruguay), is now recognized to be widely distributed in the rio Amazonas and río Orinoco basins. The type species *Holoshesthes pequira* is redescribed. The monotypic genera *Cheirodontops* Schultz, 1944, and *Aphyocheirodon* Eigenmann, 1915, are considered junior synonyms, and their type species are redescribed. Three new species, two from the upper rio Amazonas drainage, and one from the río Orinoco drainage are described. A lectotype is designated to *H. pequira*.

Key words: Neotropical, Systematics, *Aphyocheirodon*, *Cheirodontops*, Phylogeny.

Introduction

The genus *Holoshesthes* was initially proposed by Eigenmann (1903: 144) based on a very short diagnosis: “Premaxillaries and mandible with a single series of many-pointed incisors; maxillaries with teeth along its entire edge. Lateral line complete.” The initial diagnosis, however, is based on a misinterpretation of the original description in German, of its type species, *Cheirodon pequira* Steindachner, 1882. According to Steindachner (1883:

38), the maxilla of *Cheirodon pequira* has very small teeth along all **anterior** [our quote] border ("Oberkiefer am ganzen **vorderen** Rande sehr fein gezähnt"), and not along its entire length, as translated by Ulrey (1895), or along its entire edge, as translated by Eigenmann (1903). The differences between the interpretation of the original description and data in the observed specimens were discovered by Eigenmann (1915: 84-85) and erroneously attributed to Steindachner (1883) due to the possible lack of microscopic preparations. Curiously, the etymology of the name proposed by Eigenmann (1903: 145), *Holoshesthes*, is an allusion to a complete dentition of the maxilla that actually is absent in the type species.

The genus was completely redefined by Eigenmann (1915:83-84) in the proposition of the new subfamily Cheirodontinae, mostly based on characters of dentition. In the new diagnosis, the maxillary is described as possessing few teeth, and the most noteworthy character in diagnosing "*Holesthes*" (invalid emendation of Eigenmann, 1915) was the "mandibulary teeth much expanded at the tip, with a basal notch on each side and three median points of about the same size" [Eigenmann's notch and points mean cusp]. Two species were recognized for the genus, the type species *H. pequira*, and a new species, *H. heterodon* Eigenmann, 1915.

In a phylogenetic study of all cheirodontines (Malabarba, 1998), the main character in diagnosing *Holoshesthes* ("dentary teeth with at least five cusps, with the three central cusps larger, compressed and in a row forming a sharp cutting edge"; character 58, state 1 in Malabarba, 1998: 228) was found to be homoplastic and independently acquired in the two species of the genus, *H. pequira* and *H. heterodon*, and at least in two other cheirodontine lineages (*Acinocheirodon* and *Cheirodontops*). The lack of unambiguous synapomorphies grouping the two species of *Holoshesthes*, the hypothesis that *H. pequira* was more closely related to *Odontostilbe fugitiva*, and the hypothesis that *H. heterodon* was more closely related to the species of *Serrapinnus*, lead Malabarba (1998) to propose *Holoshesthes* as a junior synonym of *Odontostilbe*, and to transfer *H. heterodon* to the genus *Serrapinnus*.

Aphyocheirodon is a monotypic genus described along with its type species, *A. hemigrammus*, by Eigenmann (1915), and *Cheirodontops* a monotypic genus described along with its type species, *C. geayi*, by Schultz, 1944. *Cheirodontops* was considered a junior synonym of *Holoshesthes* in an unpublished Ph.D. dissertation by Böhlke (1954), but both genera were considered valid and defined by their own autapomorphies in Malabarba (1998).

At present, following an extensive systematic and taxonomic revision of the *incertae sedis* cheirodontine genera *Odontostilbe* (including *Holoshesthes*), *Aphyocheirodon*, *Cheirodontops*, *Prodontocharax*, and *Amblystilbe* by Bührnheim & Malabarba (in manuscript), *Holoshesthes* is revalidated with 21 diagnostic characters, forming a clade with six species, and different of that proposed by Eigenmann (1915). This Clade comprises three new species along with the type species of *Holoshesthes* (*H. pequira*), and the type species of the monotypic genera *Aphyocheirodon* (*A. hemigrammus* Eigenmann, 1915) and *Cheirodontops* (*C. geayi* Schultz, 1944). The terminal position of the type species of *Aphyocheirodon* and *Cheirodontops* in the proposed phylogeny turns it obligatory to consider both genera as junior synonyms in order to keep *Holoshesthes* monophyletic.

Material and Methods

Counts and measurements were taken as Fink & Weitzman (1974), primarily on the left side of the specimen. Head length is the distance between the tip of the snout and the posterior end of subopercle, which is slight posterior to margin of opercle. Total vertebrae number includes the four vertebrae of the Webberian apparatus, and the terminal "half centrum" as Malabarba & Weitzman (1999). The gill raker at the junction of the ceratobranchial and the epibranchial is referred as the posteriormost gill raker of the lower branch of the arch, and counted jointly to the gill rakers on this lower branch as in Bührnheim & Malabarba (2006). Specimens were cleared and stained according Taylor & Van Dyke (1985), and/or radiographs were used for counting vertebrae, teeth, and gill rakers. Scanning electron micrographs (SEM) were obtained from teeth and denticulation of gill rakers. Values of the holotypes, or when the holotype was not examined, corresponding to type material examined, are marked in bold along descriptions. Males and females are recognized only when dissected, or when showing sexual dimorphism in specimens of similar size in the same collecting lot, otherwise they were termed as unsexed (Bührnheim & Malabarba, 2006).

The following institutions provided material for the study: ANSP - Academy of Natural Sciences, Philadelphia, USA; CAS - California Academy of Sciences, San Francisco, USA; FMNH - Field Museum of Natural History, Chicago, USA; IAvHP – Instituto Alexander van Humboldt, Boyacá, Colombia; INHS - Illinois Natural History survey, Illinois, USA; ICNMNH - Universidad Nacional de Colombia, Museu de Historia Natural, Bogotá, Colombia; KU - University Kansas, Kansas, USA; MCP - Museu de Ciências e Tecnologia, Porto Alegre, Brazil; MCNG - Museo de Ciencias Naturales de Guanare, Guanare, Venezuela; MEPN - Museo de la Escuela Politécnica Nacional, Quito, Ecuador; MHNG - Muséum d'histoire naturelle, Geneva, Switzerland, MNHN - Muséum d'historie naturelle, Paris, French; MNRJ - Museu Nacional, Rio de Janeiro, Brazil; MPEG - Museu Paranaense Emílio Goeldi, Belém, Brazil; MUSM - Museo de Historia Natural de la Universidad Nacional Mayor de San Marcus, Lima, Peru; MZUSP - Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; NRM - (Naturhistoriska Riksmuseet) Swedish Museum of Natural History, Stockholm, Sweden; NMW - Natuurhistorisches Museum Wien, Wien, Austria; UF - Florida Museum of Natural History, Gainsville, USA; UMMZ - University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA; USNM - National Museum of Natural History, Washington D.C., USA. Abbreviatures given along with the number of specimens are the following: m- morphometrics and meristics taken; c- only meristics taken; x- meristics taken from x-rays; c&s- cleared and stained specimens. The synonym given for each species does not intend to be exhaustive. It is mostly directed to papers that imply taxonomic decisions of that discuss and/or illustrate characters and relationships.

Phylogenetic reconstruction. The phylogenetic hypothesis used in this paper is that obtained by Bührnheim & Malabarba (in manuscript). We herein summarize the characters in the presented diagnoses. The synapormorphies, respectively the character number and state number, are enumerated as Bührnheim & Malabarba (in manuscript). Uniquely derived and unreversed characters are indicated by one asterisk.

Statistical analyses. Principal component analysis (PCA) was used to check overall variation among samples, looking for differences in morphometrics among species or between sexes, being an input to multiple regressions (Johnson & Wichern, 1998). PCA on covariances of logarithmically transformed measurements were obtained using Past version 1.28 2004, and Sigma Plot version 6.10 2000. The first principal component was partitioned out, considering it mostly accounts for size variation (Strauss, 1985). Multiple linear regressions were applied to describe morphometric differences among species or between sexes.

Results

Holoshesthes Eigenmann, 1903

Holoshesthes Eigenmann 1903: 144 [Type species by original designation and monotypy *Chirodon pequira* Steindachner, 1882]. -Malabarba, 1998: 219 [phylogeny; synonym of *Odontostilbe*, Cope 19870]. - Malabarba, 2003: 217 [synonym of *Odontostilbe*, Cope 1870].
Holesthes. -Eigenmann 1915: 83 [unjustified emendation].
Holoesthes. -Eigenmann 1917: 35 [mispelling].
Holoshestes. -Géry, 1977: 546, 551 [mispelling, in key].
Aphyocheirodon Eigenmann 1915: 58 [Type by original designation and monotypy: *Aphyocheirodon hemigrammus* Eigenmann, 1915]. - Malabarba, 1998: 220 [phylogeny; diagnosis]. - Malabarba, 2003: 215 [valid].
Cheirodontops Schultz 1944: 319 [Type by original designation and monotypy: *Cheirodontops geayi* Schultz, 1944]. -Böhlke, 1954 [synonym of *Holoshesthes*]. - Malabarba, 1998: 220 [phylogeny; diagnosis]. - Malabarba, 2003: 216 [valid].

Type species: by original designation and monotypy *Chirodon pequira* Steindachner, 1882.

Diagnosis. Twenty one derived characters define the monophyletic *Holoshesthes* containing six species (Fig. 1), as follows: (1) anteromedial process of the mesethmoid well-developed, extending between premaxillae and reaching anterior tooth bearing border of the premaxillae [1-0] ; (2) ventral border of the second infraorbital with a slight concavity near its half length, close to the posterior tip of maxilla [17-1]; (3) palatine nearly rectangular, irregular, posterior portion somewhat narrow [30-0]; (4) tooth cusp number of the first to third medial teeth in the single tooth row of the premaxilla 5-7 cusps, usually 5-6 [40-2] (Fig. 2); (5) number of teeth in the single tooth row of the premaxilla usually 6-8 teeth [41-1] (Fig. 2); (6) absence of the flange on anterodorsal portion of the maxilla, posterior to rod-like ascending process of the maxilla [45-1] (Fig. 2); (7) presence of a longitudinal groove just below dorsolateral border of maxilla [46-1] (Fig. 2); (8) posterior edentulous portion of the maxilla extended, longer than the anterior tooth bearing portion of maxilla [50-2] (Fig. 2); (9) dorsal border of the posterior tooth bearing portion of dentary, with smaller teeth, elevated, forming a marked convexity, in lateral view [56-1] (Fig. 2); (10) lateral short ridge with a somewhat straight surface of the upper portion of the angulo-articular, on posterolateral portion of the lower jaw, near the posterior portion of the maxilla, observed in dorsal view [57-1]; (11) longer axis of anteriormost teeth perpendicular to longer axis of dentary [59-0]; (12) upper branch of angulo-articular short, not extended anteriorly or slightly extended, anterior border pointed or slightly pointed, 4-5 times in the longitudinal length of dentary [60-0]; (13) more than half length of the dorsal border of the dentary with teeth [62-0] (Fig. 2); (14) deep anteriormost portion of dentary at the symphyseal joint, 2-3 times in the height of middle portion of dentary [64-0] (Fig. 2); (15) presence of posterior small unicuspid teeth of dentary lingually turned [65-1] (Fig. 2); (16) anterior larger dentary teeth with 3 central cusps larger, nearly equal in size, compressed and aligned at their distal tips in a row forming a sharp cutting edge, cusp tips distal [72-2] (Fig. 2); (17) 3-4 large anterior dentary teeth and following teeth decreasing in size posteriorly [73-1] (Fig. 2); (18) lower jaw profile slightly projected on head profile [76-1] (Fig. 3); (19) elongate gill rakers of the first gill arch relative to branchial cavity below cranium base, proportionally occupying more than half or half of gill cavity between cranium base and the gill branches [87-1] (Fig. 4); (20) 13-16 gill rakers, rarely 12 gill rakers on lower branch of first gill arch [91-0] (Fig. 4); (21) presence of few hooks on mid portion of the first unbranched pelvic-fin ray in males [137-1].

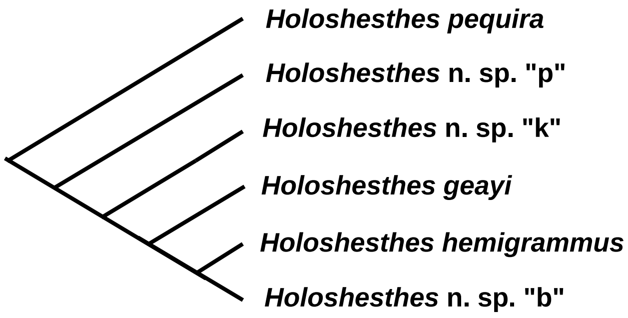

Fig. 1. Phylogeny of *Holoshesthes* obtained by Bührnheim & Malabarba (in manuscript).

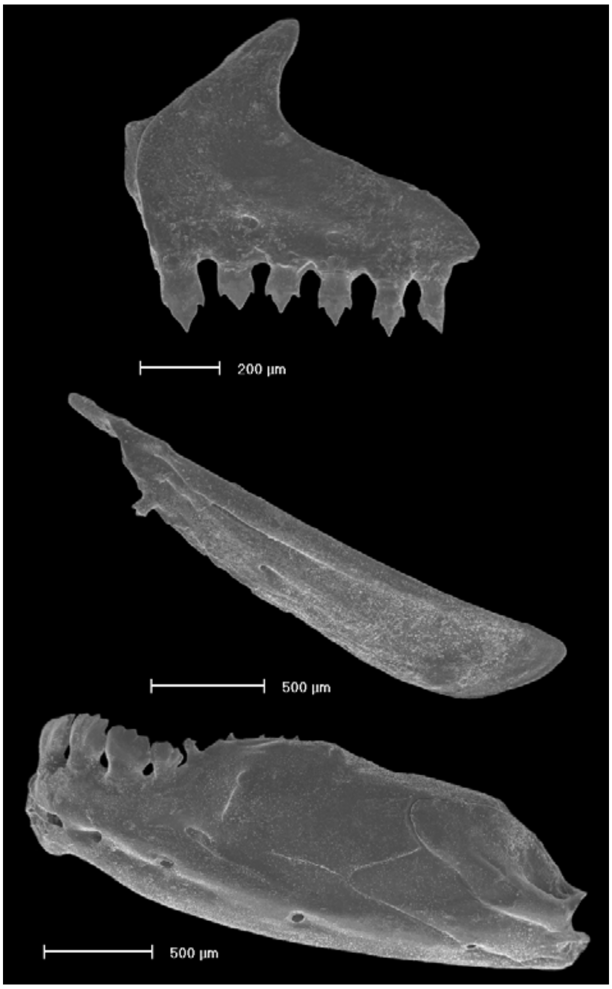

Fig. 2. Dentition of *Holoshesthes geayi*, CAS 64344, female 30.0 mm SL: left side premaxilla (top), maxilla (middle), and dentary (bottom). Scanning electron micrographs (SEM).

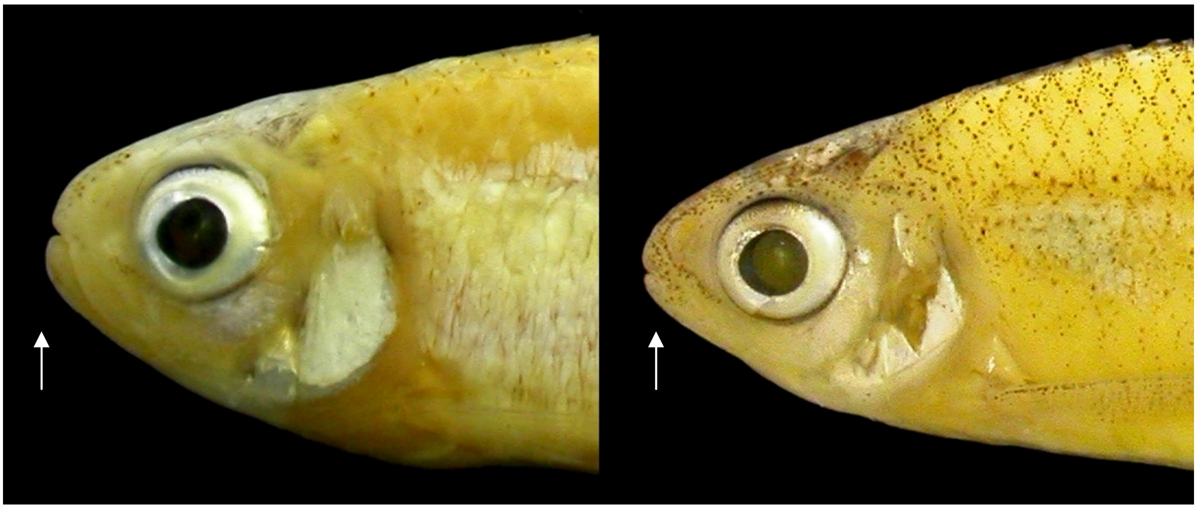

Fig. 3. Detail of head profile of *Holoshesthes geayi*, CAS 64344, male 34.3 mm SL and *Odontostilbe fugitiva*, neotype MUSM 27501, male 34.6 mm SL.

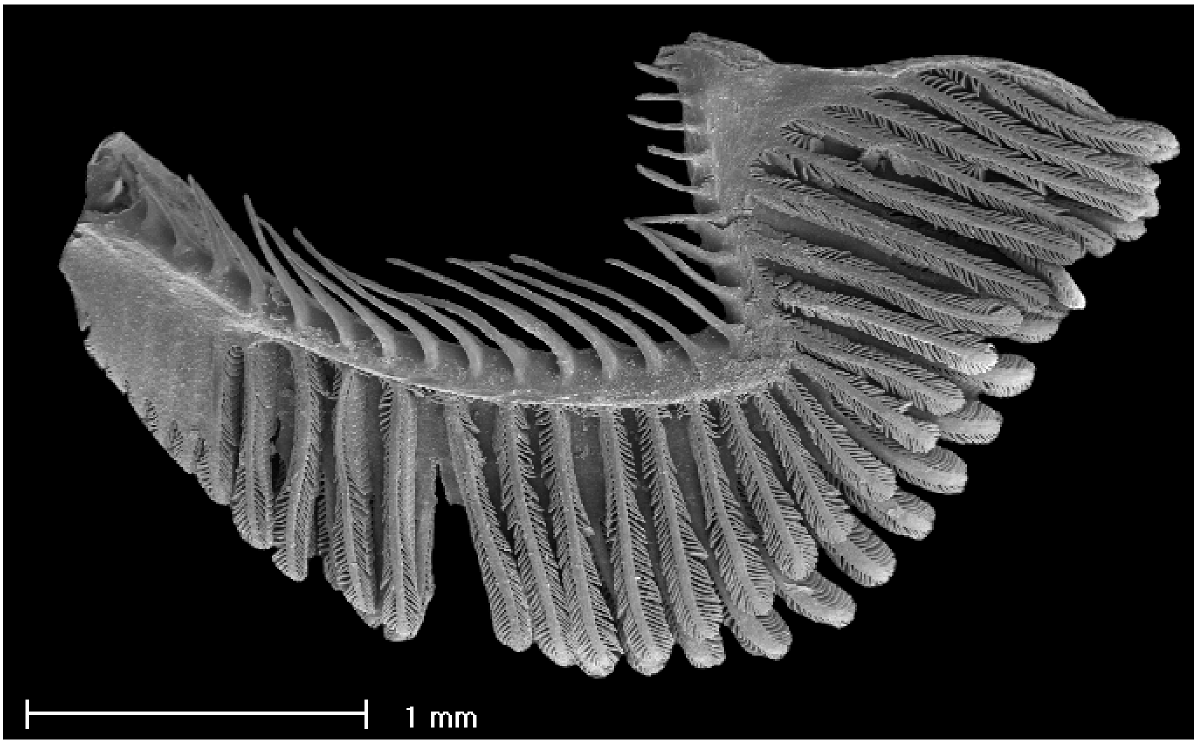

Fig. 4. First left side gill arch of *Holoshesthes geayi*, CAS (SU) 50332, male 27.1 mm SL, showing 8 elongate gill rakers on upper branch and 15 on lower branch. Scanning electron micrograph (SEM).

Monophyly of *Holoshesthes*. As remarked by Bührnheim & Malabarba (in manuscript), though the 21 synapomorphies supporting the *Holoshesthes* clade are homoplastic, they identify a rather concise lineage of cheirodontines with profound modifications linked to feeding mechanisms, including dentition, gill rakers, and associated bones as the second infraorbital, and mesethmoid. Most of these characters appear independently in *Serrapinnus heterodon*, *Serrapinnus microdon*, and *Acinocheirodon melanogramma*. However, these species do not share with *Holoshesthes* the 14 synapomorphies of the Odontostibini, otherwise having respectively the synapormorphies of the tribes Cheirodontini (*Serrapinnus* species), and Compsurini (*A. melanogramma*) (Bührnheim & Malabarba, in manuscript). Remarkably, the peculiar anterior larger dentary teeth with 3 central cusps larger, nearly equal in size, compressed and aligned at their distal tips in a row forming a sharp cutting edge, cusp tips distal [72-2] do not have equivalent form among Characidae (Bührnheim & Malabarba, in manuscript).

Noteworthy, only one of the 21 synapomorphies is related to sexual dimorphism, the occurrence of a few hooks on mid portion of the first unbranched pelvic-fin ray in males. This character is highly homoplastic, most parcimoniously hypothesized to be lost in *Holoshesthes*

n. sp. "p", and independently acquired in other lineages of cheirodontinae, the *Cheirodon* (*C. interruptus* + *C. ibicuhiensis*), *Serrapinnus* (*S. heterodon* + *S. microdon*), *Acinocheirodon*, *Macropsobrycon*, *Lobodeuterodon* (*L. euspilurus*), and *Odontostilbe microcephala* and *Odontostilbe pulchra* (Bührnheim & Malabarba, in manuscript). Thus, the importance of modifications in the feeding mechanisms in *Holoshesthes* evolution is exceptional, not having an equivalent in the currently recognized main lineages of the Cheirodontinae, that are especially linked to sexual system differentiation, the Cheirodontini and Compsurini (Malabarba, 1998; Bührnheim & Malabarba, in manuscript).

Holoshesthes pequira **(Steindachner, 1882)**

Figs. 5-7

Salmo pequira Natterer in Steindachner 1882:39 [not available, Natterer identification name mentioned under *Chirodon pequira* Steindachner, 1882].

Chirodon pequira Steindachner, 1882: 180 [diagnosis, erroneous type locality: Guapore] - Steindachner, 1883: 38-39 [detailed description, type locality: Cuiabá, Mato Grosso, Brazil, reference to a type series of numerous specimens, see remarks below].

Cheirodon pequira. -Eigenmann & Eigenmann, 1892: 54 [listed]. -Ulrey, 1895: 288-290 [listed, in key]. -Eigenmann & Kennedy, 1903: 513 [comparison with *Odontostilbe trementinae*]. -Eigenmann & Ogle, 1907: 10 [comparison with *Odontostilbe microcephalus*].

Holoshesthes pequira. -Eigenmann, 1903: 144 [type species of *Holoshesthes* by original designation, monotypic].- Uj, 1987: 132, 133-136, 152-153, 160, [in key, refers to the type locality as Vila Bela, Brazil, description, distribution, osteology; photo 1, specimen; fig. 11, dentition].

Odontostilbe trementinae Eigenmann & Kennedy, 1903: 513-514 [description, type locality: Arroyo Trementina, Paraguay, holotype IUM 9987a, now CAS 58787, 9 paratypes: IUM 9987, now 3 CAS 59788, 2 FMNH, same data as the holotype]. -Eigenmann, 1915 [Synonym of *Odontostilbe pequira*]. -Malabarba in Reis et al., 2003:218 [Synonym of *Odontostilbe pequira*].

Holesthes pequira. -Eigenmann, 1915: 84 [in key, unjustified emendation of the spelling of the generic name].

Holoshetes pequira. -Pearson, 1937: 108 [mispelling, listed to rio Mamoré and río Paraguay basins].

Holoshestes pequira. -Géry, 1977: 551, 558 [mispelling, rio Mamoré and río Paraguay basins diagnosis, specimen illustration reproduced from Eigenmann, 1915, comparison with *Saccoderma*].

Odontostilbe pequira. -Malabarba, 1998 [phylogeny, transferred to *Odontostilbe*].

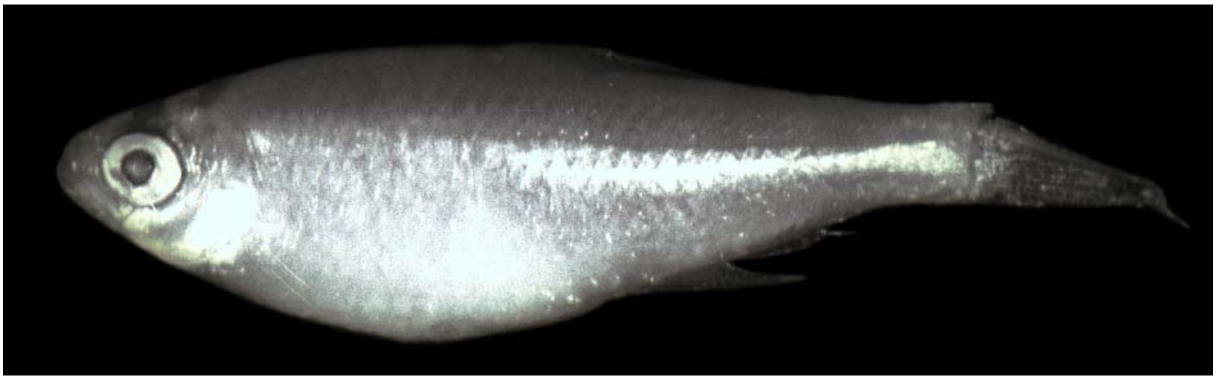

Fig. 5. Lectotype of *Holoshesthes pequira*, NMW 57160:1, unsexed 29.8 mm SL .

Fig. 6. *Holoshesthes pequira*, MCP 19873, female 35.5 mm SL, showing the dark dorsal-fin spot, and anal-fin with dark chromatophores concentrated on anterior middistal portion of last unbranched anal-fin ray and 1st-3rd branched anal-fin rays, forming a conspicuous dark mark.

Fig. 7. *Holoshesthes pequira*, MCP 13041, male 40.4 mm SL (top) with elongate dorsal- and pelvic-fin rays, and female 45.3 mm SL (bottom).

Type material examined. ***Chirodon pequira*.** Lectotype [by present designation], NMW 57160:1, 29.8 mm SL, Brazil, Mato Grosso, Cuiabá; 1824; Natterer. Paralectotypes, NMW 57160:2, 28.7 mm SL, same locality as the Lectotype. NMW 62633:1, 2, 28.6-30.4 mm SL (actually 2 specimens of *Odontostilbe paraguayensis*, see remarks above), same locality as the Lectotype. ***Odontostilbe trementinae*.** Holotype CAS 59787 (unsexed), 37.4 mm SL, Paraguay, [near Concepción], arroyo Trementina, tributary of the río Aquido Canigi; 1 Jan-31 Dec 1900; J. D. Anisits. Paratypes: CAS 59788, 3, unsexed, 32.1, 33.9, and 36.5 mm SL), same data as holotype.

Rio Paraná basin, ARGENTINA, BUENOS AIRES: MCP 16386, 10 (1 male 34.6 mm SL, 9 unsexed 26.8-38.2 mm SL), Buenos Aires, lower río Paraná, arroio Itacuá, delta. MISIONES: MNHN 1982-0786, 1 unsexed 38.2 mm SL, Monte Carlo, río Parana. BRAZIL, PARANÁ: MZUSP 21067, 33 of 53 (m16, 10 males, 26.9-33.0 mm SL, 1 male 31.0 mm SL c&s, 2 females 34.6-35.5 mm SL, 2 unsexed 21.2-23.5 mm SL, 1 unsexed 21.7 mm SL c&s), rio Paraná below Sete Quedas, CETESB. PARAGUAY: NRM 42170, 10 of 172 (2 males 28.3 mm SL & 31.0 mm SL, 8 unsexed 26.3-33.2 mm SL), Misiones, Ayolas, arroyo Alenquy. NRM 42961, 20 of 98 (11 males 25.3-28.8 mm SL, 9 unsexed 17.8-35.1 mm SL), Itapúa, arroyo Tacuary, at Ruta 1 bridge. **Río Paraguay basin,** BRAZIL, MATO GROSSO: MCP 12000, 1 (unsexed 30.9 mm SL), Poconé, rio Bento Gomes, southwest Poconé. MCP 33238, 1 (unsexed 28.7 mm SL), Barra do Bugres, arroio crossing road Barra do Bugres/Cáceres, 51 km south of Barra do Bugres, affuent of the río Paraguay, 15°47'S, 57°30'W. MCP 33239, 41 (unsexed 26.5-32.4 mm SL), Barra do Bugres, rio Bugres in Barra do Bugres, affuent of the río Paraguay, 15°05'S, 57°10'W. MCP 33240, 61 (10m, 2 males 31,2 mm SL & 32.2 mm SL, 1 female 31.7 mm SL c&s, 7 unsexed 25.1-33.4 mm SL), Barra do Bugres, rio Jauquara at Jauquara, affluent of rio dos Pássaros. MCP 33241, 234 (10m unsexed 29.1-37.7 mm SL), Jangada, stream Espinheiro crossing road BR 364 (Cuiabá/Jangada), 21 km south of Jangada, rio Cuiabá drainage. MCP 33399, 1m (unsexed 23.7 mm SL), Barra do Bugres, stream in Porto Estrada on the road Barra do Bugres / Cáceres 35 km south of Barra do Bugres, affluent of rio Paraguai. MCP 34576, 23 (2 males 30.7 mm SL & 33.3 mm SL, 21 unsexed 30.3-40.8 mm SL), Cáceres, Ribeirão das Flechas on the road Cuiabá/Cáceres, 69 km east of Cáceres, río Paraguay affluent, 16°03’S 57°15’W. MCP 39807, 2 (unsexed 22.9-28.2 mm SL), Barra do Bugres, stream crossing road Tangará da Serra/Barra do Bugres, 13 km south of Nova Olímpia, affluent of the rio Paraguay, 14°50'00"S, 57°13'00"W. MCP 39827, 5 (unsexed 24.2-28.2 mm SL), Barra do Bugres, rio Sangradouro on road Cuiabá/Cáceres, 93 km east of Cáceres, affluent of the río Paraguay), 15°57'S, 57°06'W. MNRJ 12826, 1m (male 35.5 mm SL), Estação Ecológica – SEMA, Serra das Araras, [west of Cuiabá]. MZUSP 19091, 30 (11m unsexed, 23.8-32.6 mm SL), Cáceres, Ilha de Taiamã (Sema), río Paraguay. MZUSP 28552, 6 (1 male 28.4 mm SL, 5 unsexed 27.5-35.8 mm SL), Taquari, rio Taquari, near city Coxim. MATO GROSSO DO SUL: FMNH 108441, 7 (unsexed 34.4-39.8 mm SL), Bonito, rio da Prata, at “Recanto Rio da Prata”. FMNH 108442, 14 (6 males 30.8-36.0 mm SL, 8 unsexed 28.7-36.6 mm SL), Bodoquena, rio Salobrinha, *ca*. 2 km from the bridge crossing rio Salobra. *ca*. 18 km on road Bonito to Bodoquena. PARAGUAY, ALTO PARAGUAY: FMNH 107868, 20 of 54 (20 unsexed 30.1-34.7 mm SL), río Paraguay in front of the second company post at the border with Brazil, [near Fuerte Olympo]. FMNH 107877, 20 of 43 (unsexed 19.1-22.9 mm SL), upper Paraguay, río Paraguay in front of Fuerte Olympo. NRM 43814, 25 (4 males 24.5-26.8 mm SL, 21 unsexed 16.6-27.9mm SL), Riacho Mosquito at right side Estancia near mouth. CAAGUAZÚ: NRM 45018, 20 of 109 (14 males 29.7-33.4 mm SL, 6 females 30.7-35.9 mm SL), río Tebicuary [río Tebicuari Mi], where crossing road Cnel. Oviedo - Villarica. CANINDEYÚ: NRM 22695, 26 (13 males 25.0-31.5 mm SL, 6 females 32.3-35.7 mm SL, 7 unsexed 28.6-31.2 mm SL), [Jejuí-Guazú drainage], *ca.* 12 km on road Curuguaty - Mbutuy, small stream. CENTRAL: NRM 41950, 66 (56 unsexed 12.0-33.9 mm SL, 10 males 23.9-33.2 mm SL), creek + ditch west of Lago Ypacarai, 1 km north of Iglesia Espiritu Santo Yukyry-Aregua in Aregua. NRM 45286, 26 (10m, 4 males 28.2-31.3 mm SL, 1 male 27.6 mm SL c&s, 4 females 32.0-33.8 mm SL, 1 female 33.5 mm SL c&s), arroyo Yaguaresau where crossing road Ypacaraí, Caacupé (fork to San Bernardino). CONCEPCIÓN: FMNH 107882, 20 of 120 (1 male 29.7 mm SL, 19 unsexed 24.5-32.6 mm SL), río Apa, left margin, above San Carlos. NRM 23646, 64 (48 unsexed 26.8-31.4 mm SL, 16 males 25.0-28.7 mm SL), Paso Barreto, Estancia Laguna Negra, Laguna Negra, [río Aquidabán drainage], *ca*. 1.5 km from estancia buildings. NRM 43653, 37 (15 males 22.4-30.7 mm SL, 8 females 25.5-37.8 mm SL, 14 unsexed 17.3-30.4 mm SL), río Paraguay, left side shore some km upstream of Foncier. NRM 43701, 41 (2 males 26.2 mm SL & 26.4 mm SL, 39 unsexed 17.8-29.4 mm SL), río Apa at midriver sandbank. CORDILLERA: NRM 42310, 20 of 90 (4 males 25.6-27.6 mm SL, 16 unsexed 21.8-33.9 mm SL), arroyo Yhaguy where crossing Ruta 2 at about km 83. GUAIRÁ: NRM 42712, 13m (9 males 28.8-32.7 mm SL, 4 females 32.6-36.2 mm SL), río Tebicuary [río Tebicuary Mi] where crossing road Mauricio J Troche – Independencia. MISIONES: NRM 33083, 20 of 202 (6 males 25.1-28.0 mm SL, 14 unsexed 18.0-31.9 mm SL), Villa Florida, río Tebicuary at Centu-Cué. ÑEEMBUCU: NRM 45246, 10 unsexed 17.7-25.8 mm SL, río Paraguay, right shore about 25 km upstream of Alberdi, at Estancia Agatapé. PARAGUARÍ: NRM 22710, 20 of 208 (6m, 1 male 26.5 mm SL, 5 females 30.9-37.6 mm SL), Lago Ypoá, Estancia Ypoá. PRESIDENTE HAYES: NRM 22444, 31 (24 unsexed 28.7-39.4 mm SL, 7 males 27.4-34.3 mm SL), río Confuso, Estancia La Rural, tajamar *ca.* 2.5 km from the main building. SAN PEDRO: NRM

15907, 63 (11 males 25.9-32.3 mm SL, 52 unsexed 22.6-28.9 mm SL), río Aguaray Guazú in village Lima. NRM 33363, 20 of 264, (10m, 5 males 25.4-29.7 mm SL, 5 females 27.6-34.8 mm SL), río Jejuí-Guazú, about 3 km from San Pedro. NRM 44511, 10m of 45 (5 males 24.2-26.0 mm SL, 5 females 27.4-31.1 mm SL), río Paraguay, left side sand playa, 23°39'39"S, 57°23'40"W. **Río Uruguay basin,** ARGENTINA, MISIONES: MCP 13324, 2 (males 37.7-38.3 mm SL), arroyo Chimiray, 5 km from Azara, at the boundary of Misiones and Corrientes, affluent of the rio Uruguay, 28°05'S, 55°42'W. MCP 13448, 7 (unsexed 10.4-23.5 mm SL), arroyo Guerreiro, affluent of the río Uruguay, 27°50'S, 55°08'W. BRAZIL, SANTA CATARINA: MCP 20794, 1 (unsexed 45.8 mm SL), Riqueza, rio Iracema and affluent in Riqueza, 27°08'S, 53°20'W. RIO GRANDE DO SUL: MCP 6922, 10 unsexed 26.3-37.5 mm SL, Uruguaiana, rio Touro Passo, 29°38'S, 56°56' W. MCP 9894, 7 (2 males 33.4-37.5 mm SL, 5 unsexed 36.0-38.7 mm SL), São Francisco de Assis, arroio Jaguari-Mirim, 29°36'S, 55°05'W. MCP 11999, 2 (unsexed 19.5-20.3 mm SL), Cacequi, rio Santa Maria, road to vila São Simão, 29°57'S, 54°55'W. MCP 12001, 52 (10 males 33.3-37.7 mm SL, 36 unsexed 17.6-41.6 mm SL, 6 c&s), Cacequi, rio Ibicuí, at the bridge between São Rafael and Cacequi, 29°49'S, 54°41'W. MCP 12002, 48 (19 males 31.8-36.6 mm SL, 29 unsexed 32.5-39.1 mm SL), same locality as MCP 11999. MCP 12003, 1 (unsexed 40.0 mm SL), Uruguaiana, arroio at the campus of Faculdade de Zootecnia de Uruguaiana, 29°46'S, 57°06'W. MCP 12004, 2 (unsexed 32.4-40.2 mm SL), Cacequi, rio Saicã, 29°53'S, 55°02'W. MCP 12006, 10 (3 males 31.3-33.3 mm SL, 7 unsexed 29.0-33.9 mm SL), Uruguaiana, arroio Quaraí-Chico in mouth of the rio Quarai, 30°13'S, 57°31'W. MCP 12007, 5 (2 males 33.0-37.0 mm SL, 3 unsexed 36.4-39.6 mm SL), Itaqui, rio Ibicuí near mouth, 29°25'S, 56°45'W. MCP 12008, 19 (7 males 24.6-39.3 mm SL, 6 females 33.8-45.4 mm SL, 6 unsexed 30.1-36.8 mm SL), río Uruguay, 29°46'S, 57°06'W. MCP 12540, 6 (males 37.8-39.9 mm SL, 2 c&s), Pirapó, mouth of the rio Ijuí-Mirim, affluent of rio Ijuí, 28°03'S, 55°11'W. MCP 12625, 57 (15 males 30.6-36.0 mm SL, 42 unsexed 30.2-41.0 mm SL), São Borja, rio Uruguai at Rancho da Amizade, 28°38'S, 56°02'W. MCP 12691, 7 (4 males 39.5-41.1 mm SL, 1 female 49.2 mm SL, 2 unsexed 39.5-41.7 mm SL), São Nicolau, rio Uruguai at Porto de Santo Izidro, 28°03'00"S, 55°24'00"W. MCP 12695, 1 (unsexed 43.8 mm SL), Porto Lucena, rio Comandaí, road Porto Lucena/Porto Xavier, 27°53'S, 55°03'W. MCP 13041, 39 (10 males 33.4-40.4 mm SL, 19 females 35.4-48.7 mm SL, 10 unsexed 31.1-37.2 mm SL), Roque Gonzales, mouth of rio Ijuí, 27°57'S, 55°20'W. MCP 13047, 45 (14m, 7 males 33.5-37.4 mm SL, 7 females 38.3-44.1 mm SL), same locality as MCP 12691. MCP 13157, 2 (males 36.8-40.8 mm SL), same locality as MCP 12540. MCP 13165, 17 (7 males 36.2-40.9 mm SL, 3 females 41.8-48.3 mm SL, 7 unsexed 35.7-39.5 mm SL), same locality as MCP 12691. MCP 13243, 1 (unsexed 40.0 mm SL), same locality as MCP 12695. MCP 13247, 6 (2 males 41.4-43.7 mm SL, 4 unsexed 40.8-46.3 mm SL), same locality as MCP 13041. MCP 13325, 7 (male 38.0 mm SL & 6 unsexed 19.4-39.1 mm SL), São Borja, arroio do Barreiro, locality Barreiro, 28°40'S, 56°01'W. MCP 13558, 35 (11 males 31.2-39.9 mm SL, 24 unsexed 20.1-47.0 mm SL), same locality as MCP 13041. MCP 13565, 42 (13 males 35.3-41.3 mm SL, 5 females 44.8-47.5 mm SL, same locality as MCP 12695. MCP 16375, 41 (13 males 29.9-37.5 mm SL, females 35.1-37.6 mm SL, 17 unsexed 29.2-37.6 mm SL), Rosário do Sul, rio Santa Maria at Rosário do Sul, 30°15'01"S, 54°55'14"W. MCP 16401, 38 (1 male 32.1 mm SL, 14 females 36.6-39.5 mm SL, 23 unsexed 18.8-36.9 mm SL), Uruguaiana, marginal lake at the Formosa beach, São Marcos, 29°30'15"S, 56°50'37"W. MCP 16408, 2 (1 males 30.9 mm SL, 36.8 mm SL). same locality as MCP 16375. MCP 18347, 55 (8 males 31.4-35.7 mm SL, 24 females 35.8-44.2 mm SL, 23 unsexed 17.8-38.4 mm), same locality as MCP 16401. MCP 19873, 4 (unsexed 30.3-35.8 mm SL), Uruguaiana, arroio do Salso, 29°46'S, 57°07'W. MCP 20308, 13 (2 males 32.2-33.0 mm SL, 11 unsexed 28.2-36.9 mm SL), Uruguaiana, arroio Imbaá, 29°46'S, 57°05'W. MCP 20327, 45 (7 males 32.7-35.6 mm SL, 38 unsexed 23.4-40.0 mm SL), same locality as MCP 19873. MCP 23126, 46 (25 males 29.8-39.2 mm SL, 21 unsexed 27.9-42.4 mm SL), São

Francisco de Assis, rio Jaguari, on the road São Vicente do Sul/São Francisco de Assis, 29°40'45"S, 54°56'44"W. MCP 23150, 7 (2 males 27.4-36.0 mm SL, 5 unsexed 30.0-40.6 mm SL), São Francisco de Assis, rio Inhacunda in São Francisco de Assis to Manuel Viana, 29°32'51"S, 55°08'11"W. MCP 25200, 10 (5 males 34.2-38.0 mm SL, 5 unsexed 36.9-40.2 mm SL), São Francisco de Assis, arroio Taquari *ca.* 10 km south of Vila Kramer, 29°23'46"S, 55°08'52"W. MCP 25211, 14 (6 males 27.6-33.5 mm SL, 8 unsexed 30.1-40.2 mm SL), same locality as MCP 23150. MCP 26796, 14 (1 male 34.6, 13 females 34.2-39.9 mm SL), São Pedro do Sul, rio Toropi at boundary São Pedro do Sul and São Vicente do Sul, 29°39'56"S, 54°28'12"W. MCP 27627, 4 (unsexed 35.4-39.6 mm SL), Jaguari, arroio Caracol, on road BR 453/ Jarí, affluent of the rio Jaguari-rio Ibicuí, 29°25'00"S, 54°35'15"W. MCP 28620, 62 (29 males 31.3-44.4 mm SL, 33 unsexed 34.1-47.7 mm SL), Derrubadas, río Uruguay, small islands about 3500 m from beginning of Salto do Yucumã, Parque Estadual do Turvo, 27°08'13"S, 53°51'35"W. URUGUAY, SORIANO: MZUSP 45855, 7 (3 males 27.2-29.2 mm SL, 4 unsexed 27.3-34.1 mm SL), boca del arroyo Gutierrez, La Agraciada. MZUSP 45872, 4 (unsexed 24.7-35.4 mm SL), río Negro, Villa Soriano.

Diagnosis. *Holoshesthes pequira* differs from all other *Holoshesthes* species by four derived characters: (1) presence of mesopterygoid teeth [29-1] (Fig. 8); (2) premaxillary teeth with 1-4 tooth cusps overlapping between adjacent teeth, usually between posteriormost teeth or in all of teeth [43-1]; (3) the unique ontogenetic change in the shape and tooth cusp number between juveniles and adults in which the teeth of juveniles usually have 7 cusps, central cusp longer and slightly larger with lateral cusps decreasing in size, while the teeth of adults have 3 central cusps larger, compressed and in row forming a sharp cutting edge [67*-1] (Fig. 9); (4) black spot on dorsal fin, along distal midlength of 2nd unbranched and 1st to 6th-7th branched fin rays, usually not reaching tip of fin rays [158-2] (Fig. 6)..

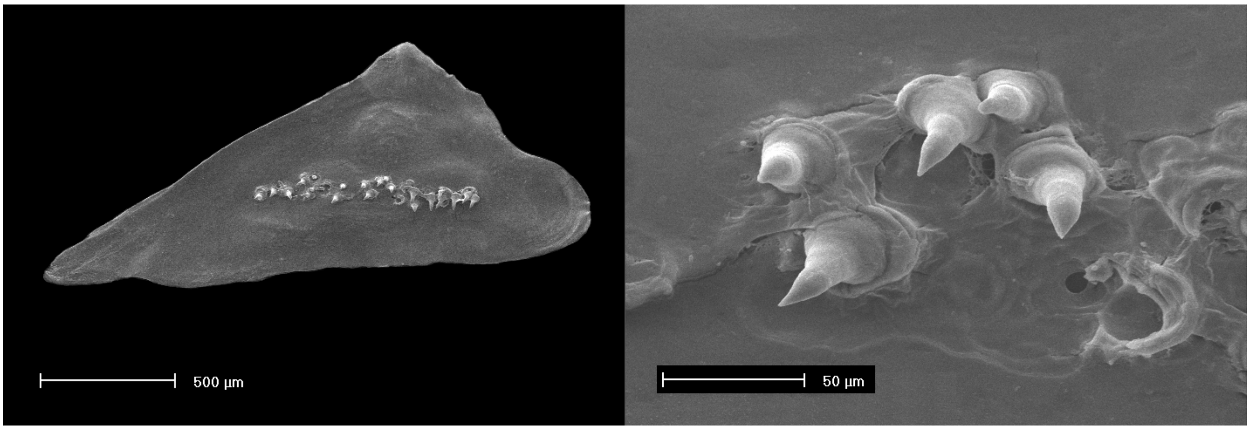

Fig. 8. Metapterygoid teeth in *Holoshesthes pequira*, unsexed specimen 21.7 mm SL, MZUSP 21067. Scanning electron micrographs (SEM).

Additionally, the small number of branched anal-fin rays, 18-22 (mostly 20) distinguishes *H. pequira* from all other *Holoshesthes* species (usually 21-24 branched anal-fin rays) (Fig. 10). Some specimens of *H. pequira*, males or females, have dark chromatophores concentrated on anterior middistal portion of last unbranched anal-fin ray and 1st-3rd branched anal-fin rays, forming a conspicuous dark mark, not seen in any other *Holoshesthes* species. The elongate 2nd unbranched dorsal-fin ray and the elongate unbranched pelvic-fin ray in mature males differ *H. pequira* from *H. hemigramus* and *Holoshesthes* n. sp. “b”, that lack these elongate fin rays, a synapormorphy to them. Addittionally, *H. pequira* mostly have 7-8 upper gill rakers, *vs*. 5-6 lower gill rakers in *H. hemigrammus*, 6-8 (mostly 6-7) in *Holoshesthes* n. sp. “k”, and 8-9 in *Holoshesthes* n. sp. “b”, and 13-14 gill rakers on lower branch *vs*. mostly 14-15 in *Holoshesthes* n. sp. “p”, and *Holoshesthes* n. sp. “b”, mostly 15-16 in *H. geayi*, and 10-11 in *H. hemigrammus* (Fig. 11).

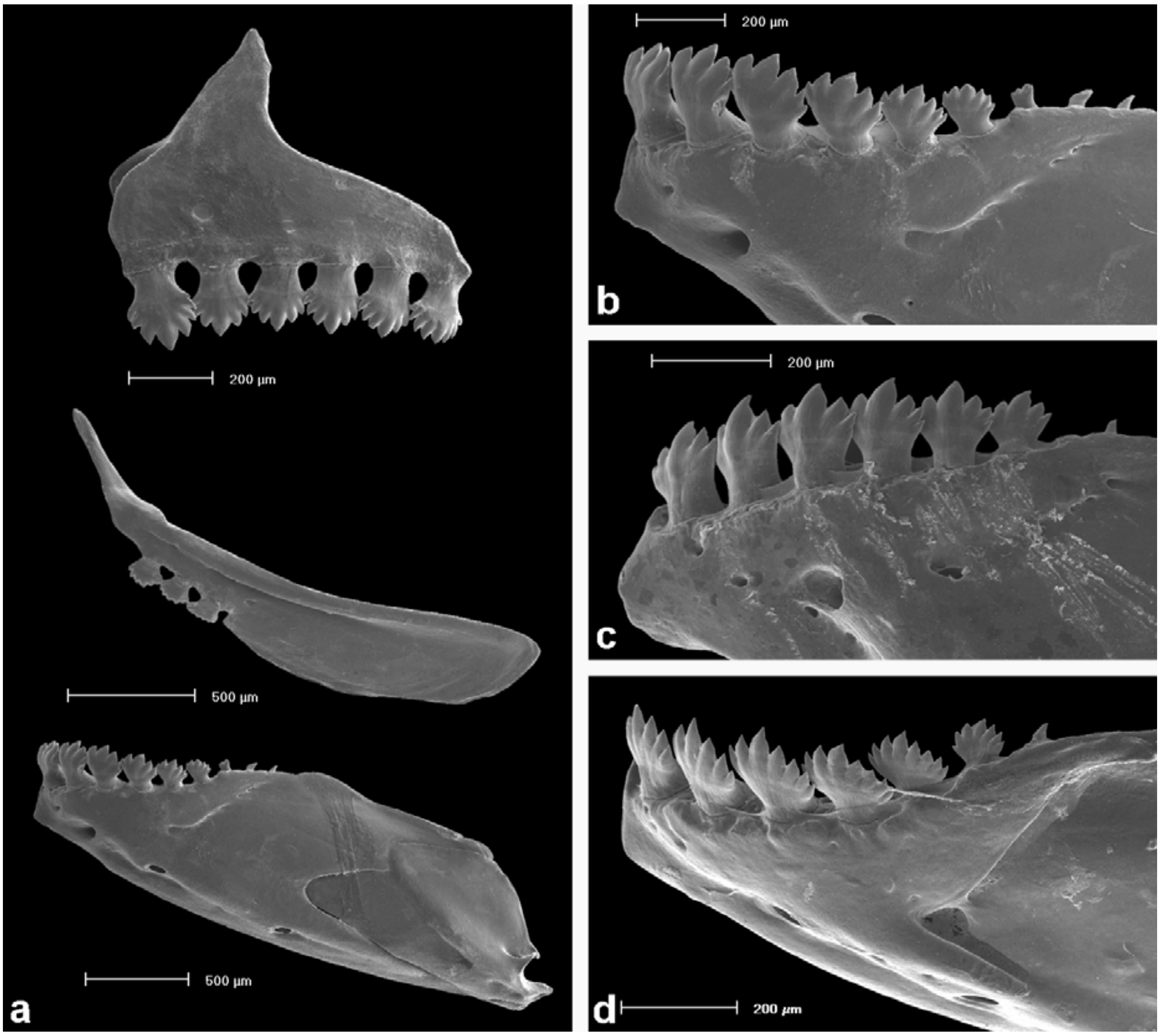

Fig. 9. Dentition of *Holoshesthes pequira*: (a) dentition of male 31.0 mm SL, MZUSP 21067, left side premaxilla (top), maxilla (middle), and dentary (bottom). In detail, ontogenetic changes in the lower jaw dentition of *Holoshesthes pequira*: (b) adult dentition, dentary teeth of male 31.0 mm SL, MZUSP 21067; (c) intermediate state of dentary teeth formation of unsexed specimen 21.7 mm SL, MZUSP 21067; (d) juvenile multicuspid dentary teeth of unsexed specimen 20.5 mm SL, MCP 12001. Scanning electron micrographs (SEM).

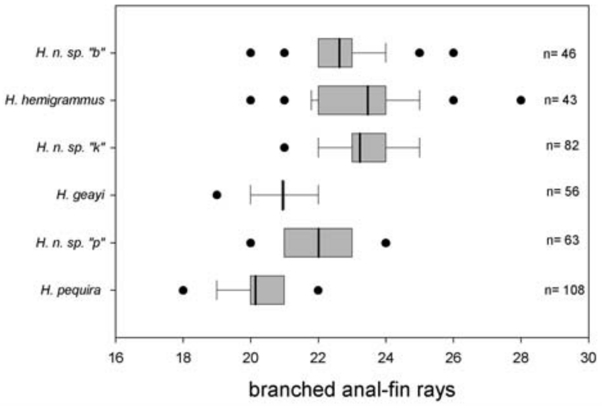

Fig. 10. Anal-fin rays counts of the *Holoshesthes* species.

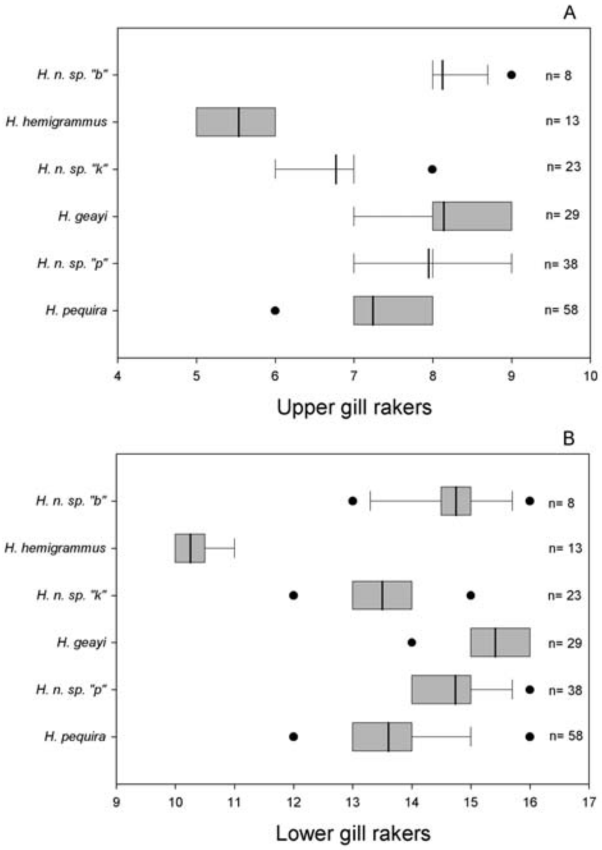

Fig. 11. Upper and lower gill rakers counts of the *Holoshesthes* species.

Description. Morphometric data given in Table 1. Largest male 43.7 mm SL, largest female 49.2 mm SL. Body elongate and compressed. Males with more compressed and elongated bodies. Greatest body depth at dorsal-fin origin. Snout pointed. Head profile almost straight from snout to posterior tip of supraoccipital bone. Predorsal profile slightly convex to nearly straight between posterior tip of supraoccipital bone and dorsal-fin origin, then straight to caudal peduncle. Ventral profile convex from mouth to anal-fin origin. Anal-fin base straight. Caudal peduncle longer than deeper.

Head relatively small. Posterior margin of opercle sinusoidal, upper posterior margin concave and lower posterior margin convex. Mouth terminal. Lower jaw profile slight projected on head profile. Maxilla obliquous; posterior tip at vertical crossing anterior border of eye or slightly posterior, and at horizontal below ventral border of eye. Premaxillary teeth 5-7 bearing 5-8 cusps; central cusp longest (Fig. 6a). Maxilla with 2 or 3 teeth bearing 5, 7 or 8 cusps, decreasing cusp number to posterior teeth. Dentary teeth 8-13 bearing 1-6 cusps. In specimens larger than 20 mm SL, anterior 3-4 teeth largest with 3 large compressed central cusps and 2-3 lateral small cusps; 6-8 posterior teeth gradually decreasing in size and cusp number, 6 cusps to conic (1-3 conic teeth). Anterior 3-4 largest dentary teeth with large compressed central cusps oriented distally. Smaller lateral cusps of anteriormost dentary teeth overlapping lateral cusps of adjacent tooth. Dentary teeth of specimens up to nearly 20 mm SL with all cusps of similar shape and size (Fig. 6b-d). One juvenile 21.7 mm SL (MZUSP 21067, c&s) with 25 small conical teeth on mesopterygoid (Fig. 5).

Dorsal-fin rays **ii, 9** (108). Dorsal-fin origin behind middle SL, slightly posterior to pelvic-fin origin. Second unbranched dorsal-fin ray elongate in mature males, extending beyond dorsal-fin distal profile. Anal-fin rays **iii**(2), iv(13), v(85), or vi(7), 18(1), 19(24), **20**(46), 21(32), or 22 (5). Anal-fin distal border concave, anterior 6-7 branched rays longest. Pectoral-fin rays i(102), 10(13), **11**(71), 12 (23), or 13(1). Pectoral-fin reaching pelvic-fin origin, passing pelvic-fin origin in some males. Pelvic-fin rays **i**(108), 6(10), **7**(96), 8(2). Unbranched pelvic-fin ray elongate in mature males**,** extending beyond anal-fin origin. Lateral border of unbranched pectoral-fin ray and unbranched pelvic-fin ray thickened in mature males, bearing thin laterodorsal projection of hard tissue covered with soft tissue. Principal caudal-fin rays **19**(107). Dorsal procurrent caudal-fin rays 8(1), 9(1), **10**(7), 11(13), 12(50), 13(29), or 14(6), ventral procurrent caudal-fin rays 7(1), 8(2), 9(25), **10**(49), 11(24), 12(5), or 13(1). Caudal-fin ray with skin flaps ventrally on 4th-8th rays of upper lobe, and dorsally on 12th-16th (mostly 13th-15th) rays of lower lobe. Adipose-fin at vertical through last anal-fin ray insertion.

Males with acute, elongate, retrorse hooks on posterior border of pelvic- and anal-fin rays. Last unbranched anal-fin ray, and 1st-9th (mostly 5th-7th) anal-fin branched rays with 1-3 paired and unpaired hooks per segment of lepidotrichia, positioned at distal half length. One to 3 unpaired, very slender hooks per segment of lepidotrichia along midlenght portion of 1st branched pelvic-fin ray and almost entire length of 1st-7th branched pelvic-fin rays. Rarely 1-2 unpaired and paired hooks per segment of lepidotrichia on anterior border of some branches of pelvic- and anal-fin rays.

Scales cycloid: lateral line complete 35(3), **36**(37), 37(42), or 38(1); predorsal row 10(11), 11(59), 12(31), or 13(1); scale rows between lateral line and dorsal-fin origin 5(2), **6**(99), or 7(6); scale rows between lateral line and anal-fin origin **4**(107); scales rows around peduncle 14(101). Triangular modified scale on pelvic-fin base extended posteriorly covering 2-3 scales. Scales on anal-fin base 6-7 (missing or partially missing in types).

Cleared and stained specimens (3): supraneurals 4(1), or 5(2); precaudal vertebrae, 15(1), 16(2); caudal vertebrae 19. Gill rakers (55 specimens, 3 c&s), upper 6(2), **7**(40), or 8(16), lower 12(3), **13**(28), 14(17), 15(9), or 16(1) (2 or 3 on hypobranchial) (in bold gill raker counts of *O. trementinae* holotype). Upper gill rakers with none or 1-4 recurved denticles on anterolateral border, and anteriormost upper gill rakers with none or 1-2 similar denticles on posterolateral border; lower gill rakers with none or 1-7 recurved denticles on anterolateral border, and none or 1 denticle on posterolateral surface; and posteriormost lower gill raker with none or 1-7 denticles on anterolateral border, and none on posterolateral border (Fig. 12). Denticulation mainly on basal portion of gill rakers. Gill arch of a juvenile (MCP 16401. 19.0 mm SL) with shorter filaments, and lacking gill rakers on upper branch (Fig. 12b, d, f).

Color in alcohol. General ground body color pale yellow or beige. Darker pigmentation on dorsum from head to caudal peduncle, dark chromatophores mostly on border of scales. Dorsal-fin spot at distal half length of 2nd unbranched dorsal-fin ray and 1st-6th (mostly 4-5th) branched dorsal-fin rays, usually not reaching tip of fin rays. Dorsal-fin base with few dark chromatophores. Pectoral fins with few chromatophores on 1st unbranched fin ray and 1st-5th branched fin rays or almost hyaline. Pelvic fins hyaline or with scarce chromatophores on 1st unbranched fin ray and 1st-3rd branched fin rays. Adipose fin hyaline. Some specimens, males or females, with dark chromatophores concentrated on anterior middistal portion of last unbranched anal-fin ray and 1st-3rd branched anal-fin rays, forming conspicuous dark mark. Both caudal fin lobes with scattered chromatophores along fin rays, but absent on mid-central portion of fin in front of caudal fin blotch. Rounded black or brown caudal spot on base of caudal fin and caudal peduncle, anteriorly continuous with longitudinal stripe and posteriorly on proximal base of middle caudal-fin rays, reaching upper and lower borders of caudal peduncle, but fainter borders in older preserved specimens.

Numerous dark chromatophores on snout, upper and lower lips, anteriormost portion of maxilla, anteriormost portion of dentary, and antorbital. Some dark chromatophores on upper portion of opercle in fresh specimens. Top of head with dark chromatophores on frontals and parietals, deep-lying over brain membrane below frontals and parietals, covering epidermis of fontanel, but clearer in interorbital portion. Recently preserved specimens with snout and parietal area almost black. Pigmented scales extends laterally on body, mostly on 1 to 3 longitudinal scales series, or up to lateral line in fresher specimens. Pseudotympanum area with scattered dark chromatophores. Dark and/or silver midlateral stripe beginning behind pseudotympanum, at vertical through dorsal-fin origin and reaching caudal spot. Guanine on eye iris, laterally on dentary under posterior portion of maxilla, opercle, preopercle, subopercle and interopercle, 2nd-4th infraorbitals, isthmus, laterally exposed portion of cleithrum, and on belly between pectoral and pelvic fins. Below lateral line, belly faint without pigmentation surrounding pectoral and pelvic fins. Scarce dark chromatophores above anal-fin base, not forming chevron shaped markings, or forming 8-10 chevron -shaped markings in freshly preserved specimens.

Sexual dimorphism. Males with hooks on anal- and pelvic-fin rays, and elongate dorsal- and pelvic-fin rays (Fig. 7), in contrast to the absence of these features in females. The gill gland, as described in Bührnheim & Malabarba (2006) to *Odontostilbe* species, is present in mature males on first gill arch, covering about 7-10 anterior branchial filaments (Fig. 12a). Oliveira (2003) described the gill gland to *Odontostilbe* sp., actually *H. pequira* populations from río Uruguay, covering up to 10 anterior branchial filaments. Snout length longer in males, depth at dorsal-fin larger in females (Table 1).

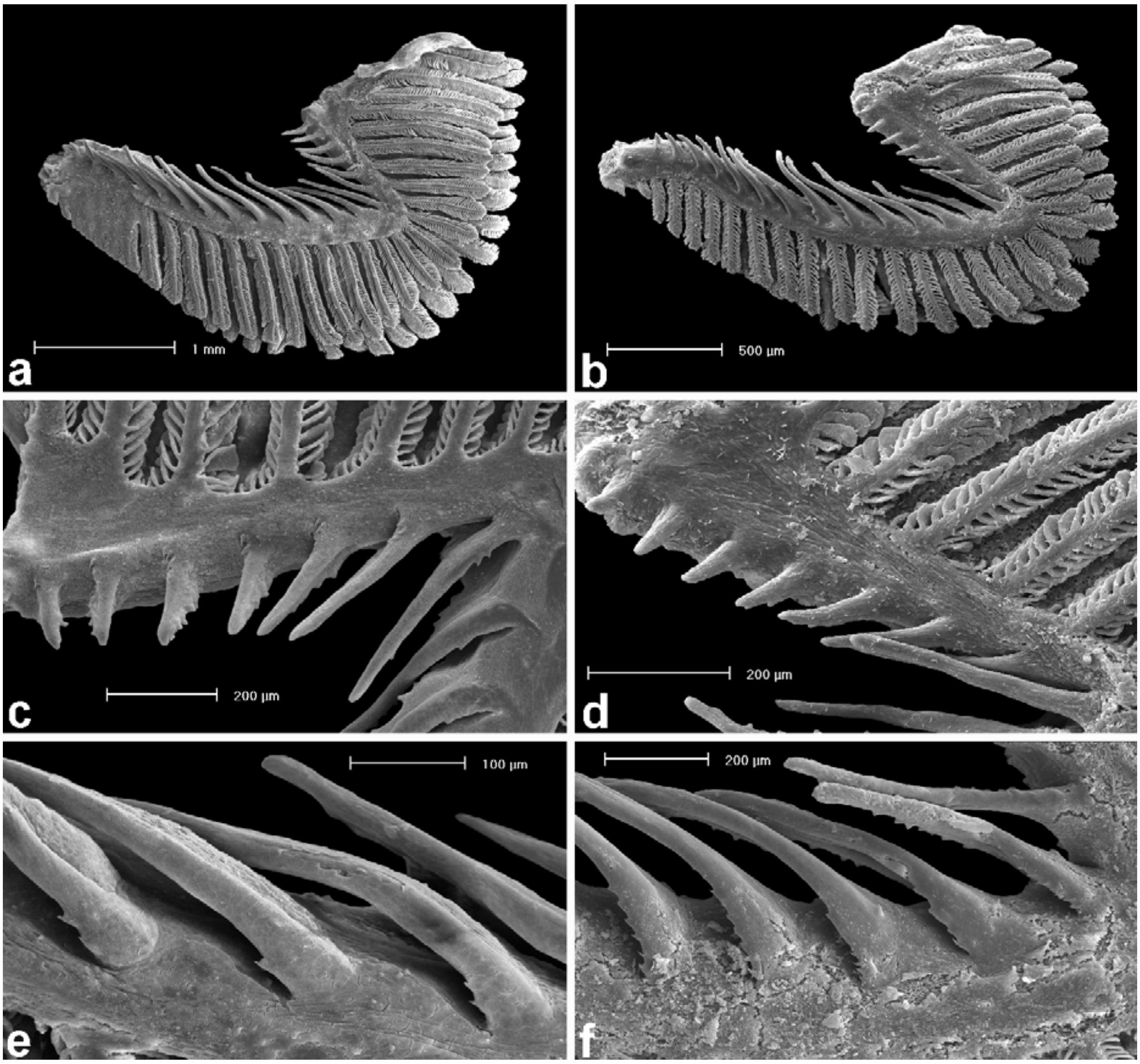

Fig. 12. First left side gill arches of *Holoshesthes pequira*, lateral views: (a) showing gill gland, male MCP 16401, 32.1 mm SL; (b) short gill filaments, juvenile MCP 16401, 19.0 mm SL; (c) gill rakers on upper branchial branch, male MCP 45286, 28.5 mm SL; (d) gill rakers absent on upper branchial branch, juvenile MCP 16401, 19.0 mm SL; (e) on lower branchial branch, male MCP 45286, 28.5 mm SL; (f) gill rakers on lower branchial branch, juvenile MCP 16401, 19.0 mm SL. Scanning electron micrographs (SEM).

Remarks on the type locality of *Holoshesthes pequira*. *Chirodon pequira* Steindachner, 1882, was first published in the “Anzeiger der Kaiserlichen Akademie der Wissenschaften”, that included short descriptions of several freshwater fish species from South American. In this abstract of the Imperial Academy of Natural Sciences of Vienna, *Chirodon pequira* was shortly described, and the type locality referred as Guaporé. This statement about the type locality was repeated by Eigenmann (1915: 84) and Malabarba (2003). Uj (1987) erroneously listed the type locality as Vila Bela, Brazil, repeated in Eschmeyer (1998). However, in a detailed description of *C. pequira* published shortly after the first description in 1882b, Steindachner referred the specimens used in the original description as originated from “Cuyaba” [Cuiabá, Mato Grosso, Brazil – “Zahlreiche Exemplare bis zu 38Mm. Länge, von J. Natterer im Jahre 1824 … im Cuyaba gesammelt, und *Salmo pequira* genannt”]. Indeed, in the NMW fish collection, there are only three lots referred as syntypes of *Chirodon pequira* (NMW 57160, NMW 62633, and NMW 77978), all collected in Cuiabá, Mato Grosso, Brazil, actually the correct type locality of the species.

Remarks on the syntypes of *Holoshesthes pequira*, with lectotype designation. The type material of *Chirodon pequira* listed in the NMW holdings includes NMW 57160 (6 specimens), NMW 62633 (4 specimens), and NMW 77978 (4 specimens). The type series was partially examined by one of us (LRM) and identity of non-examined type specimens checked by Barbara Herzig at NMW. Two of the 6 specimens of NMW 57160 (NMW 57160:1 and NMW 57160:2) were examined and identified as *H. pequira*, being one selected as the lectotype (NMW 57160:1).

Two of the 4 specimens of NMW 62633 (NMW 62633:1 and NMW 62633:2) were examined and identified as *O. paraguayensis*, a sympatric species usually collected jointly with *H. pequira*, and so, besides they are referred in the labels as syntypes of *C. pequira*, they are clearly distinct and can not be considered part of the type series. The remaining specimens of this lot (NMW 62633:3 and NMW 62633:4) were examined by Barbara Herzig and identified as *H. pequira*.

The third lot of specimens labeled as syntypes NMW 77978 corresponds to 4 specimens collected by Natterer in 1832. According to Steindachner (1883), however, the description was based in specimens collected by J. Natterer in January 1824, and so these specimens are not included in the type series. Thus, the type series recognized herein comprises a designated lectotype NMW 57160:1, and 7 paralectotypes, NMW 57160:2,3,4,5,6, and NMW 62633:3,4.

Remarks on type material of *Odontostilbe trementinae*. The holotype CAS 59787 and paratypes CAS 59788 are damaged, and dark colored (Fig. 13). The holotype probably was dried out, all anal-fin rays are broken, and some lateral line scales are missing, but it retains a fade dorsal-fin spot and the dark longitudinal stripe. Dentition of the holotype is mostly preserved, but the cusps of the teeth of the right side of dentary are broken. Among the three paratypes, the specimen with 32.1 mm SL lacks premaxillae, maxillae, and lower jaw bones, all pectoral-fin rays are broken, and the dorsal-fin is partially broken (the SL was tentatively estimated). The paratype of 36.5 mm SL lacks the lower jaws, and have all pelvic-fin rays broken. The best preserved is the specimen with 33.9 mm SL (Fig. 13, bottom), but the second unbranched and 1st-2nd branched dorsal-fin rays, the unbranched pectoral-fin rays (both sides), and all caudal-fin rays are broken. The gill rakers are intact in all type material of *O. trementinae,* with 7 on upper branch, and 13 (3), and 14 (paratype) on lower branch of the first gill arch.

We were unable to find the arroyo Trementina as a tributary of the río Aquido Canigi, Paraguay, as listed in the type locality. We have found only the arroyo Trementina as a tributary of the río Aquidabán, Paraguay, as referred by Géry *et al*. (1987:360).

Fig. 13. Holotype of *Odontostilbe trementinae*, CAS 59788, 37. 4 mm SL (top), and paratype CAS 59788, unsexed 33.9 mm SL (bottom).

Distribution. *Holoshesthes pequira* is widespread in the río La Plata basin, río Paraguay, río Uruguay, and rio Paraná down to Itaipu dam, that innundated Sete Quedas Falls (Fig. 14).

Fig. 14. Distribution of four *Holoshesthes* species in South America: *Holoshesthes pequira* in the La Plata basin (rio Paraná, rio Paraguay and rio Uruguay) (circles), and respective type localities (open circles), *Chirodon pequira* on top, and *Odontostilbe trementinae* on bottom; *Holoshesthes* n. sp. "p" (squares) in the upper Amazon basin, mostly río Ucayali, type locality (open square); *Holoshesthes* n. sp. "k" (triangles) in the upper Amazon basin, mostly río Napo, type locality (open triangle); and *Holoshesthes geayi* (lozenges) in the río Orinoco basin, type locality (open lozenge). Some symbols represent more than one lot, and more than one locality.

Table 1. Morphometrics of *Holoshesthes pequira*. Lectotype of *Chirodon pequira* NMW 57160:1, and paralectotype NMW 57160:2. Holotype of *Odontostilbe trementinae*, CAS 59788, and paratypes CAS 59788. Other specimens: rio Paraná (10 of MZUSP 21067), río Paraguay (10 of MCP 33240, 10 of 33241, 1 of MNRJ 12826, 9 of MZUSP 19091, 10 of NRM 44511, 13 of NRM 42712, 5 of NRM 22710, 10 of NRM 33363, 10 of NRM 45286), and río Uruguay (14 of MCP13047).

	C. pequira		*O. trementinae*				Males				Females				Unsexed			
	Lectotype	Paralectotype	Holotype	Paratypes			n	Low	High	Mean	n	Low	High	Mean	n	Low	High	Mean
standard length	29.8	28.7	37.4	33.9	32.1	36.5	42	24.2	37.4	30.3	31	27.4	44.1	33.7	29	25.1	37.7	31.7
Percentages of standard length																		
head length	24.2	23.7	24.3	24.5	24.3	24.4	42	23.9	27.3	25.0	31	22.5	26.1	24.3	29	23.3	28.5	25.2
snout-anal fin origin	63.8	60.6	67.6	66.1	69.8	64.7	42	60.7	63.9	62.5	31	48.5	66.6	64.1	29	61.3	65.4	63.5
snout-dorsal fin origin	48.0	46.3	53.2	51.6	51.4	49.9	42	47.5	51.7	49.3	31	48.2	52.7	50.7	29	48.1	52.5	50.3
snout-pelvic fin origin	45.3	43.9	46.0	47.5	50.8	46.0	42	43.5	47.9	45.6	31	44.8	48.8	46.9	29	44.8	48.3	46.4
dorsal-fin base	12.8	13.2	13.6	13.6	14.6	13.4	42	12.4	14.4	13.8	31	12.3	14.5	13.7	29	12.7	14.8	13.9
anal-fin base	24.8	23.7	26.2	23.6	28.3	26.8	42	22.5	28.9	26.7	31	24.6	28.4	27.0	29	25.5	28.8	27.3
caudal peduncle length	14.4	13.6	15.5	13.9	12.5	14.2	42	12.7	15.6	14.0	31	11.9	14.9	13.3	29	11.7	14.1	13.0
caudal peduncle depth	10.4	10.8	11.2	11.5	11.5	10.7	42	9.0	11.6	10.6	31	9.0	11.6	10.7	29	9.5	11.7	10.7
depth at dorsal-fin origin	30.5	31.4	34.8	35.4	34.3	34.8	42	25.0	30.7	28.4	31	28.7	35.6	32.4	29	27.8	34.9	31.6
dorsal-fin length	26.5	24.4	-	-	31.2	27.1	42	24.1	40.0	31.3	31	25.7	29.6	27.3	29	25.9	30.6	27.7
pelvic-fin length	16.8	16.7	17.9	14.7	16.8	-	42	16.3	24.6	20.5	31	15.8	18.1	16.8	27	16.1	19.1	17.4
pectoral-fin length	21.1	20.9	20.3	-	-	20.8	42	18.2	24.2	21.3	31	19.0	22.1	20.6	29	19.7	22.6	21.2
snout-pectoral-fin origin	22.5	22.6	23.8	23.0	23.7	24.4	42	23.0	27.3	24.6	31	22.4	26.1	24.0	29	23.1	28.8	24.9
Percentages of head length																		
snout length	23.6	25.0	22.0	21.7	23.1	20.2	42	20.5	25.6	23.5	31	20.3	23.8	22.2	29	18.5	23.5	21.7
upper jaw length	36.1	33.8	36.3	34.9	-	34.8	42	30.5	36.5	33.9	31	32.9	38.7	35.0	29	30.9	36.6	33.8
horizontal eye diameter	37.5	39.7	37.4	38.6	41.0	40.4	42	33.3	40.3	37.9	31	36.0	44.3	38.8	29	35.8	41.5	38.2
least interorbital width	30.6	30.9	30.8	31.3	32.1	30.3	42	28.4	34.3	31.1	31	28.3	39.2	30.8	29	29.3	34.6	32.0

Clade *Holoshesthes* n. sp. "p" + (*Holoshesthes* n. sp. "k" + (*Holoshesthes geayi* + (*Holoshesthes hemigrammus* + *Holoshesthes* n. sp. "b")))

Diagnosis. Five synapomorphies support this clade: (1) absence of mesopterygoid teeth [29-0]; (2) medial premaxillary tooth markedly larger than the following posterior teeth [36*-1] (Fig. 15); (3) main cusps of the posteriormost teeth of the premaxilla slightly oblique to the ventral border of the premaxilla, curved posteriorly [38*-1] (Fig. 15); (4) central cusp of premaxillary teeth notably larger than lateral cusps [39-0] (Fig. 15); (5) lower border of the dentary slightly convex [58-1](Fig. 15). An additional distinguishing character to this clade is the scattered black chromatophores slightly darker and more numerous on middistal portion of dorsal-fin, extending on the 2nd unbranched dorsal-fin ray and 1st to 5th, 6th branched fin rays is (Fig. 16), only not present in *Holoshesthes hemigrammus*.

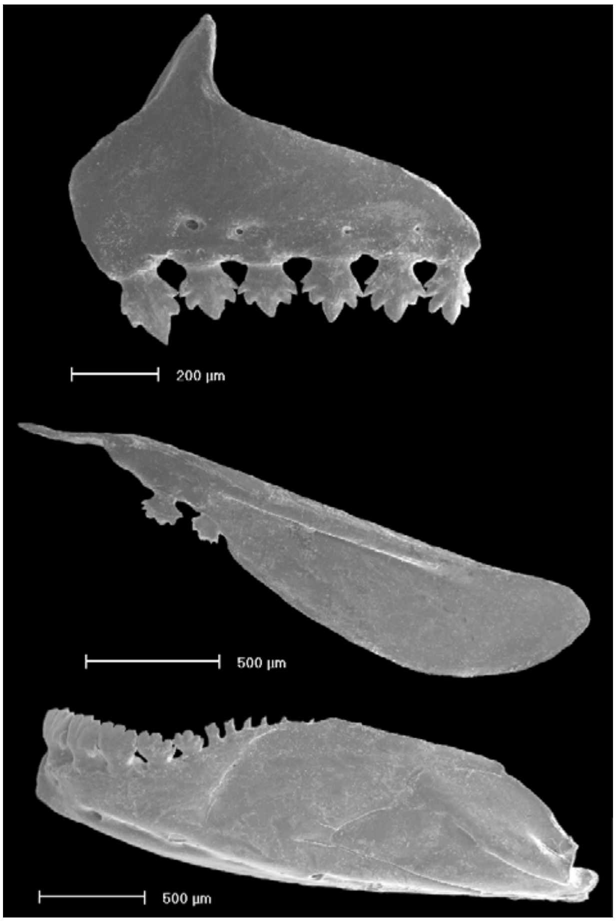

Fig. 15. Dentition of *Holoshesthes* n. sp. "p", FMNH 113499, unsexed 30.7 mm SL: left side premaxilla (top), maxilla (middle), and dentary (bottom). Scanning electron micrographs (SEM).

Fig. 16. Dorsal-fin in detail of *Holoshesthes* n. sp. "p", paratype USNM 359005, male 32.1 mm SL, showing conspicuous dark chromatophores slightly darker and more numerous on middistal portion of dorsal-fin, extending on the 2nd unbranched dorsal-fin ray and 1st to 5th branched fin rays.

Holoshesthes n. sp. "p", new species

Fig. 17

Holotype. MZUSP 87763, 1 (female 38.0 mm SL), Peru, Ucayali, Coronel Portillo, Bagazán, [Nuevo Bagazán, río Ucayali basin], H. Ortega, 25 Nov 1979.
Paratypes. PERU, UCAYALI: MZUSP 26150, 14m (2 males 35.8-37.7 mm SL, 1 male 35.4 mm SL c&s, 10 females 35.3-38.8 mm SL, 1 female 37.9 mm SL c&s, 1 unsexed 30.6 mm SL), same as holotype. MZUSP 41087, 4m (1 male 36.4 mm SL, 3 females 37.0-38.1 mm SL), Pucallpa, río Ucayali, H. Ortega, 17 Nov 1979. MUSM 28002, 5m (2 males 31.8-32.1 mm SL, 1 female 34.4 mm SL, 2 unsexed 30.6- 30.9 mm SL), Atalaya, Sepahua, quebrada Shamboyacu, H. Ortega et al., 3 Nov 1998. USNM 359005, 55 (5m, 3 males 33.3 mm SL & 36.3 mm SL, 2 females 32.3-32.5 mm) (27 males 26.7-30.0 mm SL, 23 unsexed 24.8-30.8 mm SL), same as MUSM 28002. USNM 362042, 1m (female 38.4 mm SL), Atalaya, Sepahua, rio Urubamba, quebrada Shambuyacu, H. Ortega *et a*l., 3 Nov 1998. CUSCO: MCP 35569, 12 (6 males 30.3-36.7 mm SL, 5 females 32.5-35.3 mm SL, 1 unsexed 28.3 mm SL), Echarate, río Urubamba, quebrada Pakiria, formerly USNM 359007. MUSM 28001, 2m (1 male 31.8 mm SL, 1 female 37.3 mm SL), Echarate, Peruanita, cocha Konkariari, M. Hidalgo, 19 Oct 1997. USNM 358988, 17 (3m, 1 male 35.2 mm SL, 2 females 36.9-47.6 mm SL) (11 unsexed 28.2-36.1 mm SL), same data as MUSM 28001. USNM 358990, 1m (female 37.4 mm SL), Echarate, Segakiato, quebrada Natianiroato, M. Hidalgo, 29 Sep 1997. HUÁNUCU: FMNH 101038, 62 unsexed 22.0-30.2 mm SL (m5, 1 female 28.8mm SL c&s, 1 unsexed 26.3mm c&s, 3 unsexed 26.2-30.1mm), río Pachitea, upper Ucayali, across from Porto Inca Hotel, town of Porto Inca.

Non-type material. Río Yanayacu basin, PERU, LORETO: ANSP 181143, 1 (unsexed 27.2 mm SL), Maynas, at mouth of caño Chincana & Emerald Forest Lodge, approximately 25 miles S of Iquitos. **Río Itaya basin,** PERU, LORETO: ANSP 181142, 1 (unsexed 25.1mm SL), Maynas, [lower Itaya river] at bridge on Iquitos-Nauta highway, approximately 25 miles SSW of Iquitos. **Río Ucayali basin,** PERU, CUSCO, LA CONVENCION: USNM 358986, 37 (21 males 27.2-35.3 mm SL, 16 unsexed 24.9-30.6 mm SL), Echarate, río Urubamba, quebrada Pakiria. USNM 358987, 14 (1 male 29.1 mm SL, 13 unsexed 28.3-34.6 mm SL), Echarate, Malvinas, cocha Nueva. USNM 358989, 3 (1 male 34.0 mm SL, 2 unsexed 30.8-38.5 mm SL), Echarate, Pagoreni, río Camisea. USNM 358991, 8 (3 males 32.6-34.0 mm SL, 5 unsexed 26.9-35.9 mm SL), Echarate, Malvinas, río Urubamba. USNM 358992, 2 (unsexed 35.3-36.9 mm SL), Echarate, Segakiato, quebrada Prokigiato. USNM 358993, 7 (2 males 31.3-32.0 mm SL, 5unsexed 28.8-35.2 mm SL), Echarate, Segakiato, quebrada Kemariato. USNM 358994, 7 (3 males 29.0-34.6 mm SL, 4 unsexed 31.0-36.6 mm SL), Echarate, Peruanita, río Urubamba. USNM 358995, 26 (9 males 26.8-30.2 mm SL, 17 unsexed 26.3-31.4 mm SL), Echarate, río Urubamba, quebrada Cumarillo.USNM 358997, 9 (5 males 28.3-33.1 mm SL, 4 unsexed 28.2-36.4 mm SL), Echarate, Segakiato, río Camisea. USNM 358998, 3 (1 male 30.0 mm SL, 2 unsexed 27.0-37.2 mm SL), Echarate, Segakiato, quebrada Porocari. USNM 358999, 3 unsexed 27.3-29.0mm SL, Echarate, Malvinas, quebrada Kamagariniato. USNM 359002, 10 (6 males 27.5-33.3 mm SL, 4 unsexed 28.3-34.0 mm SL), Echarate, Peruanita, quebrada Kayonaroato. USNM 359003, 4 (unsexed 30.9-38.1 mm SL), Echarate, Pagoreni, quebrada Cumaginaroato. USNM 359007, 233 (110 males 26.1-33.7 mm SL, 9 females, 31.1-32.6 mm SL, 114 unsexed 25.3-32.4 mm SL, Echarate, río Urubamba, Quebrada Pakiria. HUÁNUCU: USNM 280563, 5 unsexed 23.8-27.4 mm SL, Coronel Portillo, main channel and side pools of río Ucayali, approximately 10 km upstream of Pucallpa, 08°31'S 74°22'W. USNM 316607, 1m (unsexed 29.2mm SL), río Sungaroyacu [or

Fig. 17. Holotype of *Holoshesthes* n. sp. "p", MZUSP 87763, female 38.0 mm SL (bottom), and paratype MZUSP 26150, male 37.7 mm SL (top).

Sugaro, lower río Pachitea drainage]. USNM 384418, 11 (unsexed 19.0-26.3 mm SL), Coronel Portillo, Yarinacocha, side caño, 08°16’S 74°36’W. LORETO: MCP 35584, 1 (unsexed 28.9 mm SL), río Pacaya, cocha Yanayacu. MCP 35584, 1 (unsexed 26.3 mm SL), río Pacaya, Cocha Yanayacu. UCAYALI: MZUSP 26065, 4 (unsexed 31.8-37.0 mm SL), Pucallpa-Huánucu, río Huacamayo, MZUSP 26474, 1m (unsexed 32.8 mm SL), río Neshuya, Estrada Pucallpa-Huánucu. MZUSP 26475, 1m (female 39.2 mm SL), same locality as MZUSP 26474. USNM 358996, 6 (3 males 27.6-28.4 mm SL, 3 unsexed 26.7-28.4 mm SL), Atalaya, lower río Urubamba, M. D. Nueva Italia. USNM 359000, 6 (unsexed 26.0-30.4 mm SL), Atalaya, lower río Urubamba, left margim, quebrada San Jose. USNM 359001, 24 (unsexed 19.5-26.5 mm SL), Atalaya, lower río Urubamba, quebrada Anuau. USNM 359004, 75 (15 males 26.2-30.1 mm SL, 60 unsexed 24.2-31.1 mm SL), Atalaya, Sepahua, quebrada Pulija, bajo Urubamba. USNM 362040, 1 (male 26.7 mm SL), Atalaya, quebrada Pulija, bajo Urubamba. **Río Marañon basin,** PERU, HUÁNUCU: MCP 15071, 1 (unsexed 39.8 mm SL), vicinity of Tingo Maria, backwater near Puerto Nuevo, flowing into río Tullamayo & mainstream río Tullamayo, formerly ASNP 149674. LORETO: FMNH 113499, 30 (8m, 7 unsexed 28.7-31.4 mm SL, 1 unsexed 30.4 mm SL c&s) laguna Rimachi [or lago Rimachi or Rimachuima, río Pastaza, middle río Marañon basin], 04°24’52”S 76°39’24”W. **Rio Juruá basin,** BRAZIL, ACRE: MPEG 6789, 30 unsexed (6m, 5 unsexed 29.0-32.5 mm SL, 1 unsexed 30.4 mm SL c&s), Tarauacá, rio Tarauacá. MZUSP 30364, 106 (5m, 1 male 31.7 mm SL, 1 female 31.3 mm SL c&s, 3 unsexed 27.3-25.2 mm SL), Tarauacá, rio Tarauacá. MZUSP 30365, 2m (unsexed 32.8-34.4 mm SL), Tarauacá , rio Tarauacá. MZUSP 42841, 5 (unsexed 19.9-21.8 mm SL), Tarauacá, rio Tarauacá, lago da Esperança. MZUSP 30372, 2 (unsexed 21.7-22.4 mm SL), same locality as MPEG 6789.

Diagnosis. Two characters differ *Holoshesthes* n. sp. "p" from all other *Holoshesthes* species, the autapomorphic presence of elongate unbranched dorsal-, pectoral-, pelvic-, and anal-fin rays in mature females [104-1*] (Fig. 17, 18), and the absence of hooks on first unbranched pelvic-fin ray in males [137-0]. Although none syntopic specimens were found, *Holoshesthes* n. sp. “p” and *Holoshesthes* n. sp. “k” occur in the río Pastaza basin, being addittionally distinguished by: (1) the lower number of branched anal-fin rays 20-24, mostly 21-23 in *Holoshesthes* n. sp. “p”, *vs.* 21-25, mostly 23-24, in *Holosheses* n. sp. “k” (Fig. 10); (2) higher number of gill rakers, 7-9 on upper branch and 14-16 on lower branch in *Holoshesthes* n. sp. “p”, *vs.* 6-8 (mostly 6-7) on upper branch and 12-15 on lower branch in *Holoshesthes* n. sp. “k” (Fig. 11). There is a tendency to a high number of lateral line scales, 37 or 38, in *Holoshesthes* n. sp. “p”, differing it from all other *Holoshesthes* species that have a range of 33 to 37 lateral line scales (Fig. 19).

Fig. 18. Holotype of *Holoshesthes* n. sp. "p", MZUSP 87763, female 38.0 mm SL, showing elongate unbranched dorsal-, pectoral-, pelvic-, and anal-fin rays.

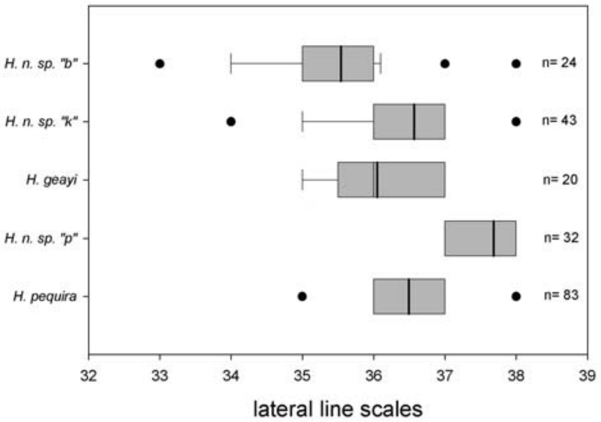

Fig. 19. Lateral line scales counts of the *Holoshesthes* species.

Description. Morphometric data are given in Table 2. Largest male 37.7 mm SL, female 38.8 mm SL, both paratypes. Body elongate and compressed. Males with more compressed and elongate bodies. Greatest body depth at dorsal-fin origin. Snout blunt. Head profile nearly straight from snout to posterior tip of supraoccipital bone. Predorsal profile slightly convex posterior tip of supraoccipital bone to dorsal-fin origin, than straightly to caudal peduncle. Ventral profile convex from mouth tip to anal-fin origin. Anal-fin base straight. Caudal peduncle slightly longer than deep.

Head relatively small. Posterior margin of opercle sinusoidal with upper posterior margin concave and lower posterior margin convex. Mouth terminal. Lower jaw profile slight projected on head profile. Obliquously positioned maxilla ending at vertical through anterior border of eye and at horizontal below inferior eye border. Premaxillary teeth 6-7 with 3-6 cusps, median cusp pointed and larger than laterals (Fig. 15). One to 3 maxillary teeth with 3-7 cusps, similar in shape of the premaxillary teeth**.** Dentary teeth 10-12 bearing 1-3 or 5 cusps: anterior 4 largest teeth with 3 large compressed central cusps and 2 lateral small cusps; 6-8 posterior teeth gradually decreasing in size and cusp number, 5 cusps to conic (5-6 conical teeth). Anterior 3-4 largest dentary teeth with large compressed central cusps oriented distally. Smaller lateral cusps of anteriormost dentary teeth overlapping lateral cusps of adjacent tooth.

Dorsal fin rays **ii 9**(63). Dorsal fin behind midlength of body, posterior to pelvic-fin origin. Second unbranched dorsal-fin ray elongate in mature males and females, extending beyond dorsal-fin distal profile. Anal-fin rays: iv(2), **v**(53), vi(8), 20(2), 21(15), 22(29), 23(14), **24**(3). Anal-fin distal border concave, anterior 6-7 branched rays longest. Posteriormost unbranched anal-fin ray elongate in one female (holotype). Pectoral-fin rays **i**(63), 10(2), 11(18), **12**(41), 13(2). Pectoral fin reaching or slightly through pelvic-fin origin. In mature females unbranched pectoral-fin ray elongate beyond pelvic-fin origin. Pelvic-fin rays **i**(63), 6(3), **7**(60). Pelvic fin slightly pointed, straight distal borders. Unbranched pelvic-fin ray elongated in mature males and females beyond beginning of anal fin. Lateral border of unbranched pectoral-fin ray and unbranched pelvic-fin ray thickened in mature males and females, bearing thin laterodorsal projection of hard tissue covered with soft tissue. Principal caudal-fin rays **19**(62), 20(1). Dorsal procurrent caudal-fin rays **11**(7), 12(29), 13(22), or 14(4), ventral procurrent caudal-fin rays **9**(5), 10(37), 11(17), or 12(3). Caudal-fin ray flaps: ventraly on 3rd-8th (mostly 4th) rays of upper lobe, dorsally on 12th -16th rays of lower lobe. Adipose fin at vertical through last anal-fin ray insertion.

Paired and unpaired retrorse acute hooks on posterior anal-fin ray borders. One to 2 hooks per segment of lepidotrichia on last unbranched anal-fin ray and on 1st-7th branched anal-fin rays, mid-distally positioned. Single retrorse acute hooks on posterior pelvic-fin ray borders. One or two hooks per segment along 1st-7th branched pelvic-fin rays, from the longer basal segment to fin ray tips. One unpaired hook per segment on anterior border of branches of pelvic-fin rays.

Scales cycloid: lateral line complete 37(10), or 38(22); predorsal row 10(6), **11**(18), 12(23), or 13(1); scale rows between lateral line and dorsal-fin origin 6(42); scale rows between lateral line and anal-fin origin 3(6),or **4**(44); scale rows around caudal peduncle **14**(40).Triangular modified scale on pelvic fin base extended posteriorly covering 2 scales. Scales on anal-fin base 5, **6**, 7, 8, 9.

Cleared and stained specimens (7): supraneurals 4-5; precaudal vertebrae, 16-17; caudal vertebrae 19-20. Gill rakers (31 specimens, 7 c&s), upper **7**(7), 8(26), or 9(5), lower **14**(14), 15(20), or 16(4) (3 on hypobranchial). Upper gill rakers practically plain, none denticles, or with 1-2 recurved denticle on anterolateral border; lower gill rakers similarly without denticles or with 1-4 on anterolateral border (Fig. 20). Denticulation mainly on basal portion of gill rakers.

Color in alcohol. Holotype, paratypes MZUSP 26150, and MZUSP 41087 without chromatophores. Color based on other paratypes, and examined specimens. General ground body color pale yellow or beige. Dorsum from head to caudal peduncle with dark chromatophores mostly on border of scales. Pigmented scales extending laterally above longitudinal stripe, also on pseudotympanum area or not. Dark chromatophores on 1st and 2nd unbranched dorsal-fin rays, and 1st-8th branched dorsal-fin rays, more concentrated on middistal portion of 1st-4th branched fin rays**.** Anal fin mostly clear, posterior faint pigmentation on the base of pterygiophores of 6th-19th branched anal-fin rays. Some specimens with chromatophores on the base and mid portion of 1st-5th branched anal-fin rays. Pectoral-fin mostly hyaline, dark chromatophores on 1st unbranched fin ray and 1st branched fin ray. Pelvic-fin and adipose fin clear. Caudal-fin rays with scarce scattered dark chromatophores on both caudal-fin lobes. Rounded caudal-fin spot, reaching only upper border of caudal peduncle.

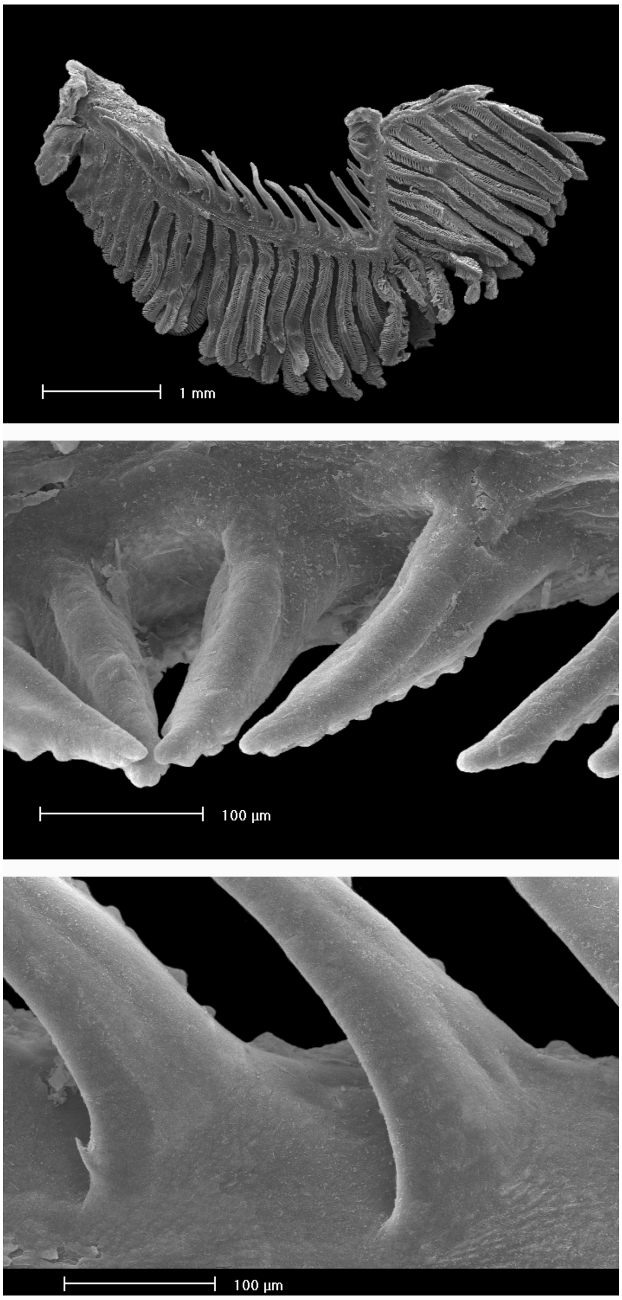

Fig. 20. First left side gill arch of *Holoshesthes* n. sp. "p", paratype MZUSP 26150, male 35.8 mm SL showing gill gland (top), in detail gill rakers on upper branchial branch (middle), and gill rakers on lower branchial branch (bottom). Scanning electron micrographs (SEM).

Dark chromatophores on snout, upper and lower lips, anteriormost portion of maxilla, anteriormost dentary portion, 1st-2nd infraorbitals**.** Top of head with a few dark chromatophores on frontals and parietals, and deep-lying over brain membrane below frontals and parietals, and epidermis covering fontanel. Clearer interorbital region. Faint dark and silver midlateral stripe beginning at vertical through dorsal fin-origin, and extending to caudal spot. Guanine on eye iris, opercle, preopercle, subopercle and interopercle, 2nd to 6th infraorbitals, isthmus, laterally exposed portion of cleithrum, and on belly between pectoral and pelvic fins. Below lateral line, belly faint without pigmentation surrounding pectoral and pelvic fins, scarse chromatophores above anal-fin base not forming chevron shaped markings.

Sexual dimorphism. Mature females with uniquely derived presence of elongate unbranched dorsal-, pectoral-, pelvic-, and anal-fin rays; males with only elongate dorsal- and pelvic-fin rays (Figs. 17, 18). Males with hooks on anal- and pelvic-fin rays, in contrast to the absence of these features in females. The gill gland, as described in Bührnheim & Malabarba (2006) to *Odontostilbe* species, is present in mature males on first gill arch, covering about 8-9 anterior branchial filaments (Fig. 20). Snout length longer in males, depth at dorsal-fin larger in females (Table 2).

Distribution. Mainly found in the río Ucayali basin, but present in some tributaries of the upper río Amazonas, includind upper rio Juruá basin, and one record in the río Marañon basin (Fig. 14). Despite *Holoshesthes* n. sp. "p", and *Holoshesthes* n. sp. "k" occur in the río Marañon basin, none syntopic specimens where found.

Table 2. Morphometrics of *Holoshesthes* n. sp "p" (holotype MZUSP 87763; paratypes, 5 of FMNH 101038, 14 of MZUSP 26150, 4 of MZUSP 41087, 1 of USNM 358990, 5 of USNM 359005, 5 of MUSM 28002, 3 of USNM 358988, 2 of MUSM 28001, 1 of USNM 362042) (non-paratypes (NP) 8 of FMNH 113499, 5 of MPEG 6789, 1 of MZUSP 26474, 1 of MZUSP 26475, 5 of MZUSP 30364, 2 of MZUSP 30365, 1 of USNM 316607).

	Holotype	Paratypes - Males				Paratypes - Females				Paratypes - Unsexed				NP	NP - Unsexed			
	female	n	Low	High	Mean	n	Low	High	Mean	n	Low	High	Mean	Male	n	Low	High	Mean
standard length	38.0	11	31.8	37.7	34.5	20	32.3	47.6	37.2	8	26.2	30.9	29.0	31.7	22	27.3	39.2	30.8
Percentages of standard length																		
head length	23.9	11	24.1	25.2	24.6	20	23.5	25.7	24.4	8	24.9	26.6	25.5	24.3	22	23.2	26.2	24.8
snout-anal fin origin	61.1	11	58.8	62.6	61.0	20	61.8	65.8	63.2	8	60.8	65.0	62.1	61.8	22	60.9	64.0	62.2
snout-dorsal fin origin	50.0	11	47.9	49.6	48.9	20	48.2	51.6	50.1	8	49.2	51.6	50.3	48.3	22	49.0	52.0	50.8
snout-pelvic fin origin	45.3	11	42.9	45.0	44.0	20	43.8	47.7	45.7	8	45.1	46.5	45.9	44.2	22	44.1	46.2	45.0
dorsal-fin base	13.9	11	13.7	14.8	14.1	20	13.2	15.1	14.1	8	13.6	14.6	14.0	12.9	22	13.0	15.4	13.9
anal-fin base	29.2	11	27.4	30.1	28.7	20	27.7	30.1	29.0	8	26.6	29.4	28.0	28.4	22	26.9	29.9	28.4
caudal peduncle length	12.6	11	12.8	15.0	13.9	20	11.9	14.3	13.3	8	11.8	14.2	12.9	14.5	22	12.2	14.6	13.0
caudal peduncle depth	11.3	11	10.7	12.1	11.3	20	10.7	12.6	11.6	8	9.4	12.0	10.5	9.8	22	9.9	12.1	10.7
depth at dorsal-fin origin	34.2	11	28.3	32.2	29.5	20	30.6	37.4	33.8	8	23.3	33.0	27.8	24.9	22	23.6	32.6	29.3
dorsal-fin length	35.3	11	30.8	36.0	33.0	15	28.9	32.6	30.7	4	29.0	30.7	29.8	28.7	19	27.1	30.5	28.6
pelvic-fin length	25.8	11	20.8	26.0	23.4	20	18.4	24.2	20.4	8	16.7	20.1	18.2	16.7	22	16.0	18.3	17.1
pectoral-fin length	37.1	11	20.4	23.5	22.3	19	22.2	31.7	26.7	8	20.5	27.1	22.8	20.5	21	19.6	21.6	20.7
snout-pectoral-fin origin	23.2	11	23.4	25.4	24.3	20	22.5	25.4	23.9	8	23.3	26.2	25.0	24.9	22	22.2	26.2	24.7
Percentages of head length																		
snout length	20.9	11	22.2	26.0	23.9	20	20.0	24.4	21.9	8	20.8	23.7	21.8	22.1	22	18.4	22.4	20.9
upper jaw length	34.1	11	33.0	38.6	35.9	20	32.6	39.8	35.2	8	35.1	39.4	37.6	36.4	22	30.3	39.7	36.2
horizontal eye diameter	36.3	11	32.2	36.9	34.9	20	34.1	38.6	36.2	8	35.7	40.3	37.7	36.4	22	35.9	42.1	38.5
least interorbital width	30.8	11	29.8	32.2	30.9	20	27.7	33.0	30.2	8	28.2	31.8	30.0	29.9	22	29.1	32.5	30.5

Clade *Holoshesthes* n. sp. "k" + (*Holoshesthes geayi* + (*Holoshesthes* n. sp. "b" + *H. hemigrammus*)

Diagnosis. This clade is supported by two derived characters: (1) 3-6 cusps, usually 3-5, in the first to third medial premaxillary teeth [40-1], and usually one or none teeth in the maxilla [54-3] (Fig. 21).

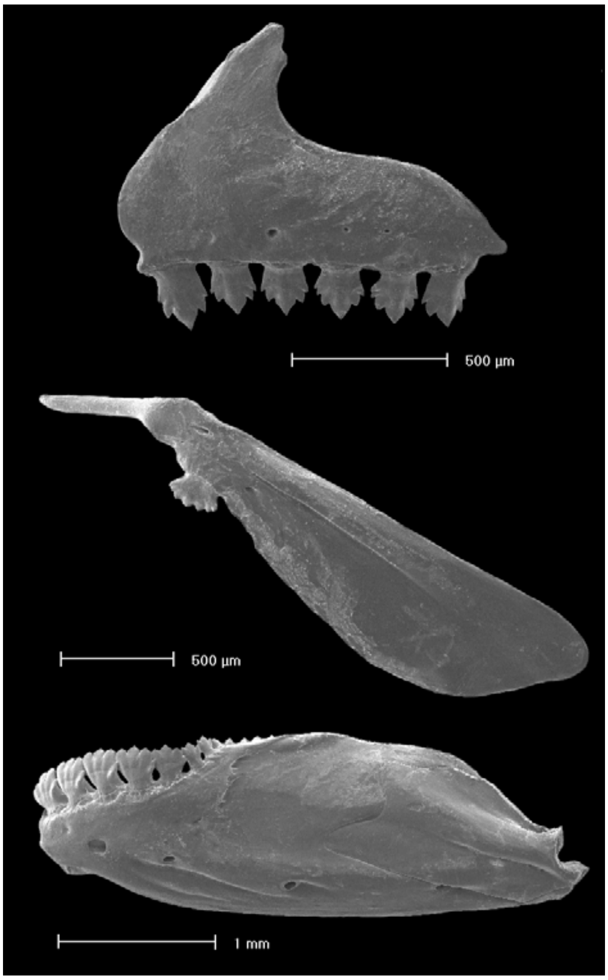

Fig. 21. Dentition of *Holoshesthes* n. sp. "k", KU 13509, female 41.7 mm SL: left side premaxilla (top), maxilla (middle), and dentary (bottom). Scanning electron micrographs (SEM).

Holoshesthes "k", new species

Fig. 22

Holotype. FMNH 116457, 1 (male 41.3mm SL), Ecuador, Pastaza, río Kankua just behind rocky bar in río Pastaza and lateral branch, [upper río Pastaza], 02°17'54"S 77°08'35"W, R. Barriga *et al*., 16 Jul 1999.
Paratypes. Río Napo basin, ECUADOR, NAPO [now partly SUCUMBÍOS]: ANSP 130422, 11 (6m males 35.8-40.0 mm SL, 5 females 38.8-41.7 mm SL), río Aguarico at Santa Cecilia, W. G. Saul & J. D. Lynch, 28 Jun 1967. MCP 14950, 5m (3 males, 35.8-39.2 mm SL, 2 females 38.5-41.0 mmSL), río Aguarico at Santa Cecilia, , W. G. Saul *et al*., 12 Jun 1967. MCP 38418, 10m (1 male 32.1 mm SL, 1 female 38.9 mm SL, 1 female 35.1 mm SL c&s, 1 female 27.7 mm SL c&s, 6 unsexed 29.6-30.1 mm SL), Laguna Manduro Cocha, about 4.5 km NE of Coca, drains via quebrada into río Coca 3.4 km upstream from mouth, 00°25'54"S 76°58'42''W, 24 Sep 1981, D. Stewart *et al*. FMNH 113500, 12 (unsexed 23.2-35.1 mm SL), same data as MCP 38418. KU 13508, 20m (3 males, 37.2-37.7 mm SL, 14 females 43.9-37.4 mm SL, 1 female 39.9 mm SL c&s, 1 male 38.5 mm SL c&s, 1 unsexed 34.8 mm SL), río Aguarico at Santa Cecilia, W. G. Saul & W. E. Duellman, 3 Mar 1967. KU 13509, 20m (1 male 39.4 mm SL, 18 females 49.1-37.7 mm SL, 1 female 41.7 mm SL c&s), río Aguarico at Santa Cecilia, W. G. Saul & L. G. Trueb, 22 Mar 1967. MZUSP 38701, 10m (3 males 28.2-29.5 mm SL, 1 female 38.5 mm SL, 6 unsexed 27.6-35.0 mm SL), río Aguarico, near field camp CEPE, Quarumo, 00°01'S 76°37'05''W, D. Stewart & M. Ibarra, 20 Dec 1981. **Río Pastaza basin**, ECUADOR, PASTAZA: FMNH 113498, 65 (10m, 5 of 30 males 32.9-41.2 mm SL, 2 females 43.4 -44.7 mm SL, 2 unsexed 36.0 -37.4 mm SL), same data as holotype. MEPN 1640, 1m (unsexed 39.2 mm SL), [upper río Pastaza basin], río Lliquino, 1700m on south of pozo Villano, 01°35'15"S 77°18'11"W, R. Barriga & A. Villacis, 29 Oct 2002.

Non-type material. Río Napo basin, ECUADOR, NAPO: ANSP 141501, 1 (female 36.2 mm SL), mouth of río Shushu Fundi. FMNH 116456, 1 (unsexed 35.5 mm SL), río Napo, cocha of mainstream, at and 1.2 km downstream from mouth of río Suyunoyacu (*ca.* 16 km from Coca), 00°32'36''S 77°04'54''W. MHNG 2224.34, 3 (unsexed 24.1-24.6 mm SL), [San Pablo de Kantesiya], río Aguarico, small stream. USNM 311350, 1 (unsexed 27.6 mm SL), Estero Culiyacu 20 min. to Ignacio Alvarado's house, left margin of río Tiputini**.** USNM 327237, 2 (unsexed 28.4-28.8 mm SL), río Payamino and tributary 3-4 miles upriver from mouth into río Coca. PERU, LORETO: INHS 100594, 1 (unsexed 15.9 mm SL), [lower] río Napo, 1.03 km NE Mazán. USNM 329359, 7 (unsexed 22.5-24.4 mm SL), Maynas, Arcadia, middle río Napo, Padre Isla, cocha Chica. USNM 330865, 20 (unsexed 20.5-33.3 mm SL), Maynas, Arcadia, río Napo, isla. USNM 330959, 9 (unsexed 16.8-22.2 mm SL), Maynas, Arcadia, río Napo, Cocha de Conchas. USNM 358568, 4 (unsexed 18.8-20.3 mm SL), Maynas, Arcadia, río Napo, quebrada Isla. USNM 328535, 1 (unsexed 23.5 mm SL), Maynas, Arcadia, río Napo, Padre Isla, cocha Chica. **Río Marañon basin,** ECUADOR, MORONA: ANSP 150047, 2r (unsexed 27.6-27.8mm SL), [upper río Morona basin], Gosulima cocha. PERU, LORETO: NRM 24062, 5m (unsexed 28.7-31.9mm SL), río Tigre drainage, San Jacinto, quebrada at km 45.5. NRM 50320, 1m (unsexed 30.0 mm SL c&s), same data as NRM 24062.

Fig. 22. Holotype of *Holoshesthes* n. sp. "k", FMNH 116457, male 41.3mm SL (top), and paratype FMNH 113498, female 43.4 mm SL (bottom).

Diagnosis. *Holoshesthes* n. sp. "k" and its sister species *H. geayi* are very similar when immature, though not sympatric. However, *Holoshesthes* n. sp “k” has a marked shorter upper jaw length (32.6-39.0% SL) than *H. geayi* (33.8-43.2% SL) (graphic under *H. geayi* diagnosis), and lower number of gill rakers, on upper branch 6-8 (mostly 6-7), on lower branch 12-15 (mostly 13-14) than *H. geayi*, which has 7-9 (mostly 8-9) gill rakers on upper branch, and 14-16 (mostly 15-16) on lower branch (Fig. 11).

Description. Morphometric data are given in Table 3. Largest male 41.3mm SL, female 49.1 mm in SL. Body elongate and compressed. Males with more compressed and elongate bodies. Greatest body depth in the dorsal-fin origin. Snout blunt, more pointed in small specimens less than 30.0mm SL. Head profile straight from snout to posterior tip of supraoccipital bone. Predorsal profile slightly convex between posterior tip of supraoccipital bone and dorsal-fin origin, then straight from dorsal-fin origin to caudal peduncle. Ventral profile convex from mouth to anal-fin origin. Anal-fin base straight. Caudal peduncle slightly longer than deep.

Head relatively small. Posterior margin of opercle sinusoidal with upper posterior margin concave and lower posterior margin convex. Mouth terminal. Lower jaw profile slight projected on head profile. Obliquously positioned maxilla ending at vertical on or sligth posterior to anterior eye border and at horizontal below inferior eye border. Premaxillary teeth 6 with 4-6 cusps, midcentral cusp very pointed and longest. The posterior 2nd and 3rd premaxillary teeth are slighthly smaller than surrounding teeth (Fig. 21). One to 2 maxillary teeth with 3-7 cusps. Dentary teeth 10-14 bearing 1-3 and 5 cusps: anterior 4-5 largest teeth with 3 large compressed central cusps; 5-9 posterior teeth gradually decreasing in size and cusp number, 5 cusps to conic (4-5 conical teeth). Anterior 3-4 largest dentary teeth with large compressed central cusps oriented distally. Smaller lateral cusps of anteriormost dentary teeth overlapping lateral cusps of adjacent tooth.

Dorsal fin rays **ii9**(81). Dorsal fin behind midlength of body, posterior to the beginning of pelvic fins. 2nd unbranched dorsal-fin ray elongated in males. Dorsal-fin border almost straight. Anal-fin rays: iv(1), v(68), or **v**i(12), 21(4), **22**(16), 23(29), 24(23), or 25(9). Anal-fin distal border concave, anterior 6-7 branched rays longest. Pectoral-fin rays: **i**(81), **10**(20), 11(47), 12(13), or 13(1). End of pectoral fin pointed, outer margin slightly convex, inner margin bowed. Pectoral fin reaching or through pelvic-fin origin. Pelvic-fin rays: **i**(81), 6i (13), **7**(67), or 7i(1). Pelvic fin slightly pointed, straight distal borders. Unbranched pelvic-fin ray elongated in males reaching or extending beyond anal-fin origin. Lateral skin border of unbranched pectoral-fin ray and unbranched pelvic-fin ray thickened in mature males, bearing thin laterodorsal projection of hard tissue covered with soft tissue. Principal caudal-fin rays **19**(80), or 20(1). Dorsal procurrent caudal-fin rays 10(3), 11(24), 12(39), 13(12), or **14**(3), ventral procurrent caudal-fin rays 8(2), 9(28), 10(41), 11(8), or **12**(2). Caudal-fin ray flaps: ventrally on 3rd (mostly 4th) to 8th rays of upper lobe, dorsally on 12th -16th rays of lower lobe. Adipose fin at vertical through last anal-fin ray insertion

Paired and unpaired retrorse acute hooks on posterior anal-fin ray borders. One to 3 hooks per segment of lepidotrichia on last unbranched anal-fin ray and on 1st-12th branched anal-fin rays, middistally positioned. Single retrorse acute hooks on posterior pelvic-fin ray borders. 1-3 hooks per segment along 1st-7th branched pelvic-fin rays, on the longer basal segment to fin ray tips. 2 specimens with 1 tiny paired or unpaired hooks per segment (2-3 segments) on unbranched pelvic-fin ray, median positioned. Rare 1-2 unpaired and paired hooks per segment on anterior border of branches of anal-fin rays. 1-2 unpaired hooks per segment on anterior border of branches of pelvic-fin rays.

Scales cycloid: lateral line complete 34(1), 35(4), 36(6), 37(22), or **38**(2); predorsal row 10(5), 11(53), **12** (11), or 13(1); scale rows between lateral line and dorsal-fin origin **5**(17), 6(48); scale rows between lateral line and anal-fin origin 3(10), **4**(64); around caudal peduncle **14**(47). Triangular modified scale on pelvic fin base extended posteriorly covering 2 scales. Scales on anal-fin base **7** (in some paratypes).

Cleared and stained specimens (4), and radiographs (2): supraneurals 4-5; precaudal vertebrae 15-16; caudal vertebrae 19-20. Gill rakers (19 specimens, 4 c&s), upper 6(5), 7(17), or **8**(1), lower 12(1), 13(10), 14(10), or **15**(2) (2, 3 on the hypobranchial). Upper gill rakers with 4-12 recurved denticles somewhat irregularly distributed on anterolateral border to posterolateral border; lower gill rakers with 0-7 recurved denticles on anterolateral border, and none to 4 denticle on posterolateral surface; and posteriormost lower gill raker with none to 5 denticles on anterolateral border, and none to 6 on posterolateral border (Fig. 23). Denticulation mainly on basal portion of gill rakers.

Color in alcohol. General ground body color pale beige. Dorsum from head to caudal peduncle with dark chromatophores mostly on scales border. This pigmentation extends laterally on 1-3 series of longitudinal scales, above lateral line, also on pseudotympanum area or not. Dark chromatophores on 1st -2nd unbranched dorsal-fin rays and 1st-6th branched dorsal-fin rays. In fresher specimens chromatophores extending on 1st-8th branched dorsal-fin rays. Anal fin mostly clear, faint and scarse chromatophores on the pterygiophore base. Three unsexed specimens from río Pastaza basin, FMNH 113498, with scarse chromatophores along 1st-4th branched anal-fin rays, plus one female and two unsexed specimens with chromatophores middistally on last two unbranched anal-fin rays and 1st-7th branched anal-fin rays. Pectoral-fin mostly hyaline, faint chromatophores along the 1st unbranched fin ray and first 1-2 branched fin rays. Pelvic-fin and adipose fin clear. Caudal-fin rays covered with scattered cromatophores on both caudal-fin lobes, except on middle portion of fin near caudal spot. Rounded dark to brown spot on base of caudal-fin, anteriorly contacting longitudinal stripe and posteriorly on proximal base of middle caudal-fin rays, reaching weakly or not the upper border of peduncle, never reaching the lower border of it.

Numerous dark chromatophores on snout, upper and lower lips, anteriormost tip of maxilla, anteriormost dentary portion**.** Top of head with dark chromatophores on frontals, parietals, deep-lying over brain below frontals and parietals, and epidermis covering fontanel, but interorbital region clear with scarce chromatophores. Black and silver midlateral stripe, with dark chromatophores, begininng posterior to pseudotympanum, above lateral line, reaching caudal-fin spot. Guanine on eye iris, opercle, antorbital, infraorbitals, isthmus, and on belly between pectoral and pelvic. Below lateral line, ventral body faint without pigmentation surrounding pectoral- and pelvic-fins, and above anal fin base not forming chevron shaped markings.

Sexual dimorphism. Males with hooks on anal- and pelvic-fin rays, and elongate dorsal- and pelvic-fin rays (Fig. 22), in contrast to the absence of these features in females. The gill gland, as described in Bührnheim & Malabarba (2006) to *Odontostilbe* species, is present in mature males on first gill arch, covering about 10 anterior branchial filaments (Fig. 23). Snout length longer in males, depth at dorsal-fin larger in females (Table 3).

Distribution. *Holoshesthes* n. sp. "k" is mainly from the río Napo basin, but also recorded in the río Marañon basin, not sympatric with *Holoshesthes* n. sp. "p" (Fig. 14).

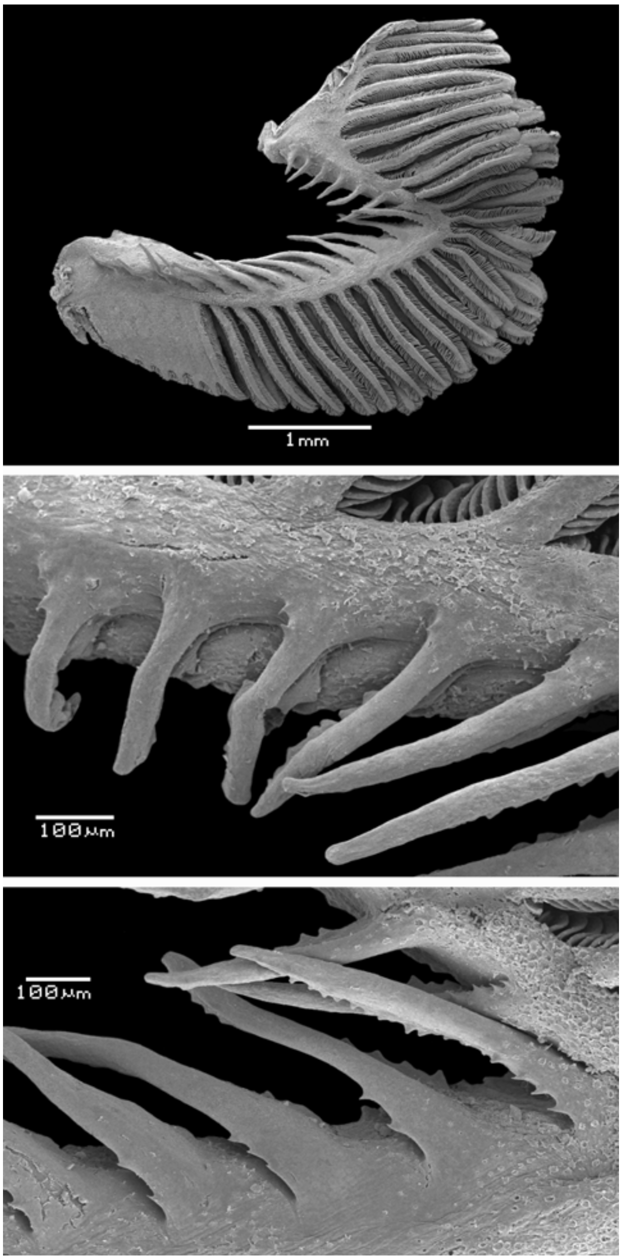

Fig. 23. First left side gill arch of *Holoshesthes* n. sp. "k", paratype KU 13508, male 37.7 mm SL showing gill gland (top), in detail gill rakers on upper branchial branch (middle), and gill rakers on lower branchial branch (bottom). Scanning electron micrographs (SEM).

Table 3. Morphometrics of *Holoshesthes* n. sp. "k" (holotype FMNH 116457, paratypes 6 of ANSP 130422, 10 of MCP 38418, 5 of MCP 14950, 1 of MEPN 1639, 9 of FMNH 113498, 10 of MZUSP 38701, 20 of KU 13508, 20 of KU 13509).

	Holotype	Paratypes - Males				Paratypes - Females			
	Male	n	Low	High	Mean	n	Low	High	Mean
standard length	41.3	23	29.0	41.2	36.6	58	27.6	49.1	38.1
Percentages of standard length									
head length	23.7	23	22.9	25.2	23.9	58	21	25.5	23.1
snout-anal fin origin	60.3	23	57.7	61.2	59.7	58	58.5	63.5	60.8
snout-dorsal fin origin	49.6	23	47.7	50.8	49.2	58	43.0	52.3	50.4
snout-pelvic fin origin	43.8	23	42.1	58.3	43.9	57	42.2	49.7	44.5
dorsal-fin base	14.0	23	12.7	15.1	14.0	58	12.6	15.7	14.2
anal-fin base	28.8	23	28.6	32.2	30.3	58	29.1	33.3	31.1
caudal peduncle length	13.1	23	12.0	14.3	13.2	58	11.5	13.9	12.9
caudal peduncle depth	10.7	23	10.0	12.0	10.9	58	9.4	12.2	11.0
depth at dorsal-fin origin	29.5	23	26.0	30.9	29.1	58	27.4	37.2	33.1
dorsal-fin length	32.7	12	28.0	39.7	34.0	50	28.2	33.4	30.8
pelvic-fin length	22.5	21	17.5	29.3	23.2	57	16.2	20.7	18.2
pectoral-fin length	21.3	22	20.4	24.3	22.0	58	19.8	24.3	21.8
snout-pectoral-fin origin	23.7	23	21.8	25.2	23.4	58	20.7	25.3	22.9
Percentages of head length									
snout length	23.5	23	19.6	24.7	22.6	58	18.0	23.9	20.9
upper jaw length	36.7	23	32.6	37.6	35.1	58	32.0	39.0	35.5
horizontal eye diameter	36.7	23	36.1	47.9	39.1	58	32.2	43.3	39.8
least interorbital width	31.6	23	28.4	33.8	31.7	58	29.4	33.8	31.5

Clade *Holoshesthes geayi* + (*Holoshesthes* n. sp. "b" + *H. hemigrammus*)

Diagnosis. Four derived characters support this clade: (1) anteromedial process of the mesethmoid short, not extending or partially extending between premaxillae, not reaching anterior tooth bearing border of the premaxillae [1-1]; (2) premaxillary teeth spaced, space between teeth nearly equal to one tooth [42-1]; (3) very short anterodorsal ascending rod-like process of the maxilla, articulated to the premaxilla, more than 6 times in the total length of the maxilla [44-2]; (4) long maxilla, almost reaching the posterior border of lower jaw, contacting the posteroventral portion of the angulo-articular, below anterodorsal extension of the angulo-articular, and beyond vertical through the mid-distal portion of the infraorbital 2 [53-0].

Holoshesthes geayi (Schultz. 1944), new combination

Figs. 24, 25

Cheirodontops geayi Schultz, 1944: 319-322 (type species by original designation; type locality: río Guárico and tributaries between San Sebastián and San Casimiro, Estado de Aragua, Venezuela; holotype: USNM 121507; paratypes: USNM 121508, 3 specimens; UMMZ 145039, 1 specimen; MCZ 37235, 1 specimen; CAS 18144, 1 specimen).

Holoshesthes geayi. -Böhlke, 1954: 135-137 [in key, type locality: río Guárico and tributaries, Orinoco system, Venezuela].

Type material examined. Holotype USNM 121507, 1 (female 36.6 mm SL). Venezuela, Aragua, río Guarico and tributaries between San Sebastián and San Casimiro, L. P Schultz, G. Zuloage, W. Phelps & R. Sherman, 12 May 1942. Paratypes: USNM 121508, 3 (2 males 34.2 -35.0 mm SL, 1 female 39.2 mm SL), same data as holotype.

Fig. 24. Holotype of *Holoshesthes geayi*, USNM 121507, female 36.6 mm SL (bottom), and paratype USNM 121508, male 34.2 mm SL (top).

Fig. 25. Paratypes of *Holoshesthes geayi*, MCP 38147, male 31.7 mm SL (top), and female 32.4 mm SL (bottom).

Non-type material. Río Orinoco basin, VENEZUELA, DELTA AMACURO: USNM 233161, 3 (unsexed 20.6-23.0 mm SL), río Orocopiche, around 15 km from mouth in río Orinoco, downstream from route 19 bridge. MONAGAS: USNM 320061, 4 (unsexed 23.3-25.5mm SL), inlet on north side of isla Varadero downstream from Barrancas, 142 nautical miles from sea Buoy, 08°42’03’’N 62°10’00’’W. **Río Apure basin,** VENEZUELA, APURE: ANSP 139540 1 (female 22.2mm SL), río Apure, S bank and backwater areas downstream side of bridge at San Fernando de Apure. ANSP 140747, 6 (25.4-33.5 mm SL), same locality as ANSP 139540. . COJEDES: MCNG 13744, 8 unsexed 26.9-36.5 mm SL, río Tinaco in El Baul. MCNG 14197, 201 (78 males 26.0-32.5 mm SL, 123 females 23.2-35.2 mm SL), río Pao at el Caserio, El Pueblito. MCP 38147, 30 (7m of 15 males, 30.0-32.7 mm SL, 7m of 15 females 31.1-35.5 mm SL), formerly MCNG 14197. GUARICO: ANSP 139542, 22 (5m, 2 males 30.2 mm SL and 31.2 mm SL, 1 female 33.9 mm SL, 2 unsexed 29.7 mm SL and 31.7 mm SL)**,** tributary of río Paya (tributary of río Guarico), 23 km S of San Juan de los Morros on Federal highway 2. ANSP 139551, 15 (1m, unsexed 32.9 mm SL)**,** río Orituco, tributary of río Guarico, 15 km SSE of Calabozo on Cazorla road. ANSP 141555, 18 (4m, 2 males 29.4 - 31.8 mm SL, 2 unsexed 31.5-34.6 mm SL), same locality as ANSP 139551. CAS 64344, 66 (6m, 1 female 30.0 mm SL, 1 unsexed 21.1 mm c&s, 4 unsexed 27.3-34.3 mm SL), Portuguesa, río Maria, at bridge on Guanare-Acarigua highway. USNM 260603, 12 (unsexed 19.3-26.8 mm SL), caño Falcón *ca.* 5 km north of RPV 83-4, río Portuguesa drainage basin, *ca.* 08°14’N 67°35’W. USNM 260606, 43 (6m, 1 male 30.9 mm SL, 5 unsexed 26.5-31.5 mm SL), río Orituco where crossed by road from Calabozo, *ca.* 08°52’N 67°18’W. PORTUGUESA: MCNG 9226, 17 (2 males 29.9-31.3 mm SL, 15 unsexed 28.8-33.8 mm SL), río Tucupido at Los Hierros. MCNG 13307, 26 (11 males 25.8-29.5 mm SL, 15 unsexed 25.2-28.7 mm SL), río Las Marias, same locality as MCNG 13307. MCNG 38544, 3 (unsexed

29.3-30.0 mm SL), río Las Marias. USNM 349386, 6 unsexed 21.9-28.4 mm SL, río Portuguesa, just upstream of highway 5, 11km Wnw of Guanare. USNM 349409, 13m (1 male 29.8 mm SL, 1 male c&s 29.6 mm SL, 11 unsexed 28.0-34.3 mm SL), Quebrada Seca (Town), río Las Marias, approximately 45 min. upstream by car from highway 5, 22 km NNW Guanare. TACHIRA: MCNG 1292, 24 (3 males 28.3-31.8 mm SL, 17 unsexed 26.2-36.8 mm SL), cañito near dam of río Caparo, [upper río Apure basin]. MCNG 11674**,** 1 (unsexed 30.8 mm SL), caño El Tigre via Puerto Vivas. **Río Meta basin,** COLOMBIA, META: ANSP 128349, 7 (unsexed 22.4-25.8 mm SL), Hacienda Mozambique, río Metica, near bottom of first loop in river, just SW of Lake Mozambique. ANSP 128348, 9 (unsexed 26.8-32.5 mm SL), río Metica, *ca.* 1.5 km E of Rajote. ANSP 139458, 2 (1 male 28.8 mm SL & 1 female 33.2 mm SL), río Negrito, midway between La Argelia and La Balsa (Plancha 267 - río Guayuriba), 04°04’N 73°4’W. ANSP 131646, 3 (unsexed 25.7-28.1 mm SL), río Metica, *ca* 3 km SE of Hacienda, Mozambique. ANSP 131647, 3 (unsexed 25.4-30.4 mm SL), same locality as ANSP 131646. ANSP 139459, 1 (unsexed 32.4 mm SL), same locality as ANSP 131646. ANSP 139817, 1 (female 29.4 mm SL), Lake Mozambique, Mozambique ranch, at shoreline on N side of lake, 03°58'N 73°04W. MCP 14954, 3m (unsexed 27.1-28.5mm SL), Laguna El Batin *ca*. 4 km SW upstream of Lake Mozambique, S side of río Metica. MCP 14968, 2 (unsexed 23.6-32.4 mm SL), same locality as ANSP 139458. **Río Guaviare basin,** COLOMBIA, META: CAS 150332, 7m (3 males, 27.1-29.0 mm SL, 4 unsexed, 26.1-30.1mm SL), near Los Micos at north end of Cordillera Macarena, 3°20’0” N 70°56’0”W. CAS 150333, 1 (unsexed 25.0 mm SL) alizarin stained, same data as CAS 150332. CAS 153719, 7 (unsexed 22.6-28.3 mm SL), río Losada, Cordillera Macarena, 02°12’N 74°00’W.

Diagnosis. *Holoshesthes geayi* differ from all other *Holoshesthes* species by one autapomorphy, the 1-3 posteriormost premaxillary teeth larger than the preceding teeth [37-1*] **(Fig. 2).** Although not sympatric, but similar when immature, *H. geayi* has larger upper jaw length (33.8-43.2% SL) than *Holoshesthes* n. sp. "k" (32.6-39.0% SL) (Fig. 26). *H. geayi* and *Holoshesthes* n. sp. "b" are sympatric in the río Orinoco basin. Additional distinguishing characters to them are: (1) snout length larger in *H. geayi* remarked in mature males 20.5-26.8% SL *vs*. in *Holoshesthes* n. sp. "b", males 18.0-22.6% SL (Fig 27); (2) smaller anal-fin base in *H. geayi*, 26.5-31.1% SL *vs* in *Holoshesthes* n. sp. "b", 29.6-34.3% SL (Fig. 28); and (3) lower number of anal-fin rays 19-22 in *H. geayi vs*. 19-26, mostly 22-24, in *Holoshesthes* n. sp. "b" (Fig. 10).

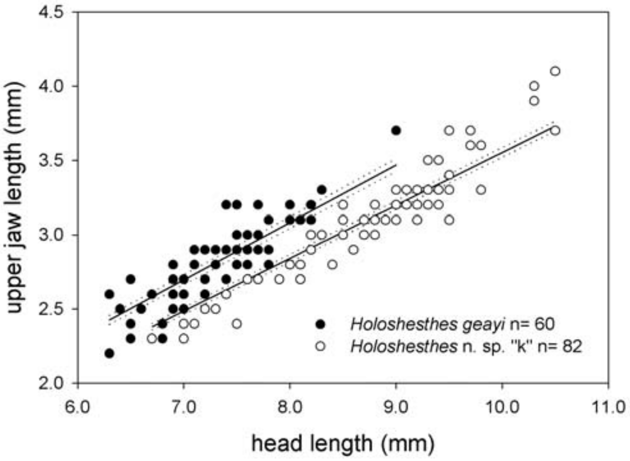

Fig. 26. Upper jaw length as a function of head length for *Holoshesthes geayi* against *Holoshesthes* n. sp. "k".

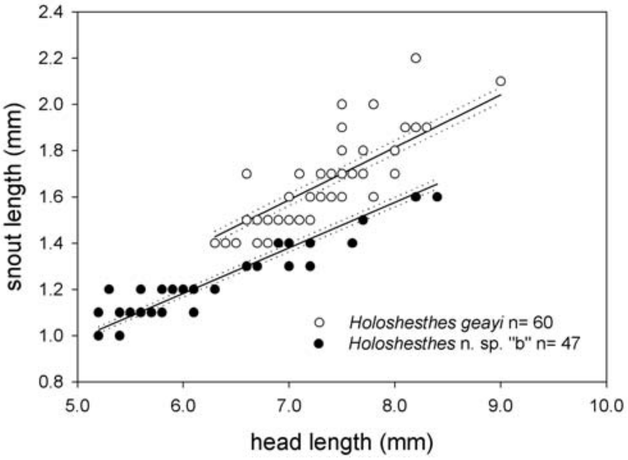

Fig. 27. Snout length as a function of head length for *Holoshesthes geayi* against *Holoshesthes* n. sp. "b".

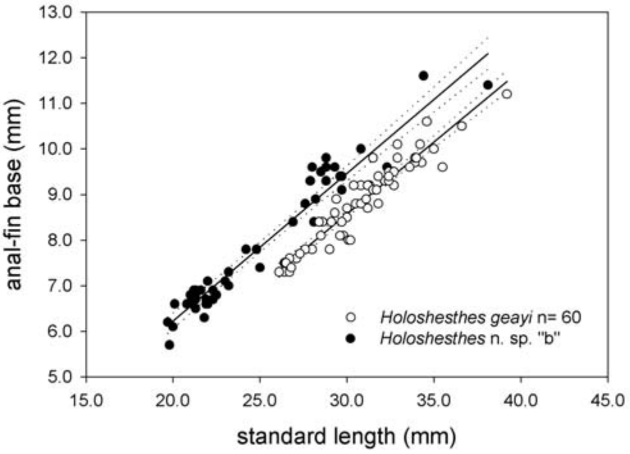

Fig. 28. Anal-fin base as a function of standard length for *Holoshesthes geayi* against *Holoshesthes* n. sp. "b".

Description. Morphometric and meristic data are given in Table 4. Largest male a paratype reaching 34.2 mm in SL, largest female a paratype 39.2 mm in SL. Greatest body depth at dorsal-fin origin. Snout blunt, protruded in mature males. Head profile gently convex from snout to posterior tip of supraoccipital bone. Predorsal profile slightly convex to straight between to posterior tip of supraoccipital bone and dorsal-fin origin, then straight from dorsal-fin origin to caudal peduncle. Ventral profile convex from mouth to anal-fin origin, and nearly straight along anal-fin base. Caudal peduncle elongate, longer than deep.

Head relatively small. Posterior margin of opercle sinusoidal with upper posterior margin concave and lower posterior margin convex. Mouth terminal. Lower jaw profile slight projected on head profile. Obliquously positioned maxilla ending at vertical through anterior border of eye and at horizontal below ventral border of eye. Premaxillary teeth 6 with 3-4 cusps, central cusp acute and longer than lateral cusps (Fig. 2). Conspicuous medial premaxillary tooth, longer than following posterior teeth. One or two posteriormost premaxillary teeth with cusps slightly turned backward. One maxillary tooth with 3-4 cusps, similar in shape to premaxillary teeth. Dentary teeth 11-12 bearing 1-5 cusps: anterior 3, rarely 4, largest teeth with 3 large compressed central cusps; 8-9 posterior teeth gradually decreasing in size and cusp number, 5 cusps to conic (5-7 conical teeth). Anterior 3-4 largest dentary teeth with large compressed central cusps oriented distally. Smaller lateral cusps of anteriormost dentary teeth overlapping lateral cusps of adjacent tooth. Skin fringed at ventral border of maxilla.

Dorsal-fin rays **ii**(60), 8(1), or **9**(59). Dorsal-fin origin at midlength of body, posterior to vertical through pelvic-fins origin. Second unbranched dorsal-fin ray elongate in mature males, extending beyond dorsal-fin distal profile**.** Anal-fin rays iv(4), **v**(49) or vi(7); 19(3), 20(9), 21(35), or **22**(13). Anal-fin distal border concave, anterior 6-7 branched rays longest. Pectoral-fin rays **i**(60), 10(16), **11**(37), 12(6), or 13(1). Pectoral-fin not reaching pelvic-fin origin. Pelvic-fin rays: **i**(46), 6 (2), or **7**(58). Unbranched pelvic-fin ray longer in mature males, crossing origin of anal fin. Lateral skin border of unbranched pectoral-fin rays and unbranched pelvic-fin rays thickened in mature males. Principal caudal-fin rays **19**(60). Dorsal procurrent caudal-fin rays 10(1), 11(9), **12**(34), 13(8), or 14(6), ventral procurrent caudal-fin rays 9(10), **10**(27), or 11(20). Caudal-fin ray flaps extending ventrally on 3rd-8th (mostly 5th-7th) rays of upper lobe, and extending dorsally on 12nd-16th (mostly 13th-14th) rays of lower lobe. Adipose-fin at vertical through last anal-fin ray insertion.

Males with posterior margin of anal-fin rays bearing paired or unpaired slightly retrorse hooks. One or 2 hooks per segment of lepidotrichia, on last unbranched and 1st-11th branched anal-fin rays, positioned at distal half length and not extending to ray tip. Single retrorse pointed hooks on mid fin-ray border along all branched pelvic-fin rays (in fewer rays in some specimens); hooks usually along midlength portion, and scarce on basal fin ray segments.

Scales cycloid: lateral line complete 35(5), 36(9), **37**(6); predorsal row **10**(5), 11(25), 12(11); scale rows between lateral line and dorsal-fin origin **5**(13), 6(33); scale rows between lateral line and anal-fin origin 3(12), **4**(33); longitudinal series of scales around peduncle **14**(23). Triangular modified scale on pelvic-fin base extended posteriorly covering 2 scales. Scales on anal-fin base 6, **7** (on right side of the holotype, 6 in two paratypes).

Cleared and stained specimens (4): supraneurals 4(2), 5(2), thin and elongate; precaudal vertebrae, 16(3); caudal vertebrae 19(3), 20(1). Gill rakers (26 specimens, 4 c&s), upper 7(4), **8**(17), 9(8), lower 14(1), **15**(15), 16(13) (3-4 on the hypobranchial. Upper gill rakers with 0-2 recurved denticles on anterolateral border (Fig. 29). Lower gill rakers with 0-2 similar denticles on lateral border, also mainly on basal portion of gill rakers. The posteriormost lower gill raker with 0-1 denticles on the opposite. Denticulation mainly on basal portion of gill rakers.

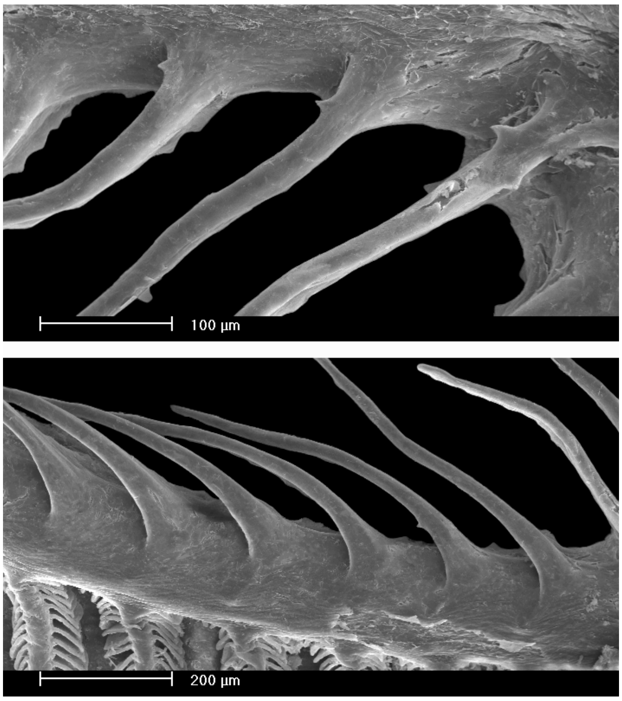

Fig. 29. Gill rakers on upper branchial branch (top) and on lower branchial branch (bottom) of *Holoshesthes geayi*, ANSP 141555, male 29.4 mm SL. First left side gill arch. Scanning electron micrographs (SEM).

Color in alcohol. General ground body color pale beige. Dorsum darker with black chromatophores concentrated on scales border, from head to caudal peduncle. Pigmented scales extending laterally on body, scarcely pigmented on pseudotympanum area, over lateral line and midventral body portion. Dark chromatophores along the two unbranched dorsal-fin rays, more pigmented distally on 2nd unbranched fin ray, and along distal half-length of 1st-5th branched fin rays. Dark chromatophores along posteriormost two unbranched anal-fin rays and along 1st-4th branched anal-fin rays, except at fin rays base. Pectoral fin with dark chromatophores along the first unbranched fin ray, gradually fading along the next branched rays, but remaining pigmented at the base of branched fin rays. Caudal fin with scattered chromatophores along upper and lower lobes and weakly pigmented on median fin rays near caudal-fin spot. Rounded black spot on base of caudal fin, reaching weakly or not upper border of caudal peduncle and not reaching the lower border; in old-preserved specimens only a peculiar elongate and central spot.

Snout and anterior portions of upper and lower jaws covered with scattered dark chromatophores. Ventral and posterior orbital border marked with a pigmented black line. Top of the head on frontals and parietals pigmented, with deep-lying chromatophores over brain membrane, and epidermis covering fontanel. A dark and eventually silver stripe along the middle longitudinal body axis, above lateral line, from behind of pseudotympanum to caudal-fin spot. Guanine pigments on eye iris, opercle, and isthmus (as in original description). Body lighten ventrally, pigmentation absent surrounding pelvic fins. A few or none chromatophores above anal fin base, not forming chevron shaped markings.

Some males and females MCNG 14197 with reddish pigmentation on opercle, pseudotympanum area, anal-fin base, and caudal-fin base (Fig. 25).

Sexual dimorphism. Males with hooks on anal- and pelvic-fin rays, and elongate dorsal- and pelvic-fin rays (Figs. 24, 25), in contrast to the absence of these features in females. The gill gland, as described in Bührnheim & Malabarba (2006) to *Odontostilbe* species, is present in mature males on first gill arch, covering about 9 anterior branchial filaments (Fig. 4). Snout length longer in males, depth at dorsal-fin larger in females (Table 2).

Remarks on type material. Holotype a female well-preserved, almost complete dentition present, lacking maxillary teeth on left side, but with one maxillary teeth on right side. The maxillary teeth is also present in the dentition of paratypes. Schultz (1944: 319) missed this maxillary teeth, using the "lacking all traces of teeth on maxillaries" to diagnose his new genus *Cheirodontops* from *Holoshesthes*. Paratype USNM 121508, male 34.2 mm SL (Fig. 24) with elongate 2nd unbranched dorsal-fin ray, but posterior filamentosous portion of this elongate fin ray fragile attached, halfly broken. After the photographing proccess this filament broke. Paratype USNM 121508, male 35.0 mm SL also with the 2nd unbranched dorsal-fin ray broken. Both these males paratypes have only one of the elongate unbranched pelvic-fin rays entire. Schultz (1994: 322) refers to "a small humeral spot more or less develped", which is probably the pseudotympanum, not an humeral spot. Scales of holotype and paratypes are mostly lacking and insertions of scales are tentatively counted to lateral line of the holotype and paratype male 35.0 mm SL. Type material practically lacking pigmentation.

Distribution. *Holoshesthes geayi* is probably widely distributed in the río Orinoco basin, but here mainly recorded in the río Apure basin, and río Meta basin, with fewer records to río Guaviare basin, and to the mouth of the río Orinoco (Fig. 14).

Table 4. Morphometrics of *Holoshesthes geayi* (holotype USNM 121507, paratypes USNM 121508) (non-types 5 of ANSP 139542, 1 of ASNP 139551, 4 of ANSP 141555, 7 of CAS (SU) 50332, 6 of CAS 64344, 14 of MCP 38147, 6 of USNM 260606, 13 of USNM 349409).

	Holotype	Paratypes			Males				Females				Unsexed			
	Female	Male	Male	Female	n	Low	High	Mean	n	Low	High	Mean	n	Low	High	Mean
standard length	36.6	34.2	35	39.2	18	26.7	34.6	30.4	10	30.0	35.5	32.8	28	26.1	34.3	29.8
Percentages of standard length																
head length	22.4	23.7	23.4	23.0	18	21.7	25.3	24.1	10	22.5	24.1	23.5	28	22.2	25.4	23.7
snout-anal fin origin	60.7	60.5	59.7	63.3	18	58.4	61.8	60.0	10	60.9	64.2	62.1	28	58.6	62.5	60.7
snout-dorsal fin origin	51.1	48.8	49.1	50.5	18	47.3	50.9	49.0	10	49.1	52.5	50.6	28	47.8	52.1	49.7
snout-pelvic fin origin	44.3	44.2	42.6	45.4	18	42.0	45.0	43.5	10	44.0	47.5	45.7	28	41.9	44.7	43.6
dorsal-fin base	14.5	13.5	13.7	13.3	18	12.5	15.0	13.8	10	13.4	15.1	14.2	28	12.7	14.9	14.0
anal-fin base	28.7	29.5	28.6	28.6	18	26.5	30.6	28.3	10	27.0	30.7	28.8	28	26.6	31.1	28.8
caudal peduncle length	14.2	15.8	14.6	14.5	18	12.9	15.9	14.6	10	12.2	15.5	13.9	28	12.4	15.6	14.4
caudal peduncle depth	12.0	11.4	10.9	11.2	18	9.8	11.4	10.6	10	10.6	11.6	11.1	28	9.1	11.6	10.7
depth at dorsal-fin origin	35.2	29.5	27.4	33.7	18	25.2	30.5	27.4	10	28.0	36.6	33.2	28	26.8	30.5	28.4
dorsal-fin length	-	31.0	31.4	30.4	15	25.4	42.2	33.4	8	26.8	29.4	28.3	25	26.4	31.6	28.3
pelvic-fin length	18.3	24.9	23.4	17.6	18	16.2	29.9	22.1	10	16.3	18.2	17.3	26	16.5	20.7	17.7
pectoral-fin length	21.3	20.5	20.9	21.7	17	19.6	22.3	20.6	10	19.0	21.2	20.1	27	18.9	22.2	20.3
snout-pectoral-fin origin	23.0	24.6	22.9	23.2	18	21.7	25.8	23.9	10	22.3	24.1	23.4	28	22.2	24.9	23.8
Percentages of head length																
snout length	23.2	23.5	23.2	23.3	18	20.8	26.8	23.5	10	20.5	24.0	22.3	28	20.6	23.9	22.0
upper jaw length	37.8	38.3	35.4	41.1	18	33.8	42.7	37.8	10	37.3	40.3	39.0	28	34.9	43.2	38.7
horizontal eye diameter	39.0	35.8	34.1	36.7	18	32.9	38.7	36.3	10	34.2	38.8	37.0	28	34.2	39.7	37.5
least interorbital width	32.9	32.1	32.9	32.2	18	29.2	34.8	31.8	10	28.8	32.5	31.4	28	28.6	32.9	30.7

Clade *Holoshesthes hemigrammus* + *Holoshesthes* n. sp. "b"

Diagnosis. Six synapomorphies support this clade: (1) anteromedial process of the mesethmoid short, not extending or partially extending between premaxillae, not reaching anterior tooth bearing border of the premaxillae [1-1]; (2) anterior maxillary teeth tricuspid [55-1] (Fig. 30); (3) absence of the elongate second dorsal-fin ray in males [103-0] (Fig. 32); (3) absence of elongate unbranched pelvic-fin ray in males [104-0] (Fig. 32); (4) hooks on fins of males distributed in dorsal-, pectoral-, pelvic-, anal-fin, and caudal-fin rays [138-1*]; (5) caudal-fin hooks on almost all principal caudal-fin rays, 2-18 [150-3*]. This latter character was uncoded to *H. hemigrammus* by Bührnheim & Malabarba (in manuscript), and most parcimoniosly assumed to support this clade.

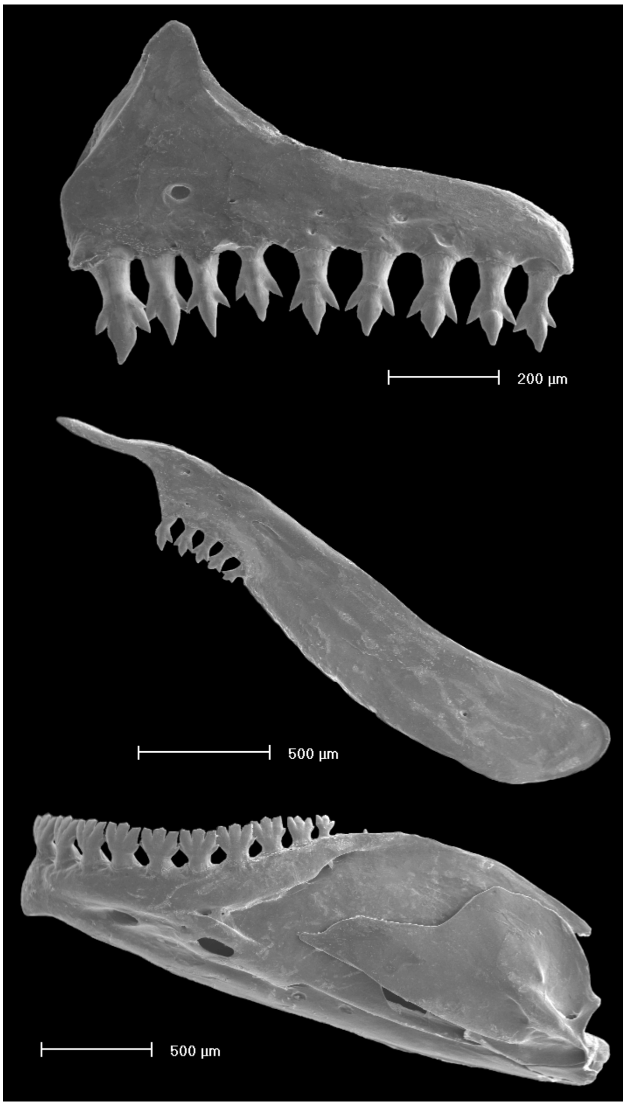

Fig. 30. Dentition of *Holoshesthes hemigrammus*, NRM 17307, male 28.2 mm SL: left side premaxilla (top), maxilla (middle), and dentary (bottom). Scanning electron micrographs (SEM).

Holoshesthes hemigrammus (Eigenmann, 1915)

Fig. 31, 32

Aphyocheirodon hemigrammus Eigenmann, 1915: 58-60, Fig. 18, Pl. IX (fig. 2) (type by original designation, type locality: Jaquara [Jaguara, rio Grande, upper rio Paraná basin, Minas Gerais, Brazil], holotype: CM 6802, now FMNH 57819; 28 paratypes: from 26 CM 6803 in original description, **2,** SU 17517, now CAS 117517, **3** now CAS 75171, **18** now FMNH 57820 (originally 20 specimens, 2 exchanged to SU) same data as the holotype, **4** CM 6804a-d, now FMNH 57821, Mogy Guassú [Mogi-Guaçú, São Paulo, Brazil], **1** CM 6805a, now FMNH 57822, Ribeirão Azul, 12 miles from Tieté [rio Tietê drainage, São Paulo, Brazil].* CAS note: tags for IU 14133 (=IU 13622) found in jar but none specimens.

Type material examined. *Aphyocheirodon hemigrammus*. Paratypes: CAS 75171, 3m, x (unsexed 32.9-36.7 mm SL), Brazil, Minas Gerais, [Jaguara, rio Grande, upper rio Paraná basin], 18 August 1908, J. D. Haseman. CAS 17157, 2m, x (unsexed 34.8-36.0 mm SL), same data as CAS 75171.

Fig. 31. *Holoshesthes hemigrammus*, NRM 17307, male 29.9 mm SL

Fig. 32. Paratype of *Holoshesthes hemigrammus*, CAS 75171, unsexed 36.7 mm SL.

Non-type material. Rio Tietê basin. BRAZIL, SÃO PAULO: MZUSP 17303, 4 (1m unsexed, 21.8 mm SL), Sales, Fazenda Sabino. MZUSP 18482, 2m (females 33.1-31.2 mm SL), Botucatu, Fazenda Edgardia. MZUSP 39863, 1m (unsexed 27.0 mm SL, Botucatu, rio Capivara. MZUSP 39801, 2 (unsexed 24.3- 27.2 mm SL, Botucatu, rio Alambari, Vitoriana. MZUSP 40349, 2m (unsexed 24.3-27.2 mm SL), Botucatu, rio Alambari 1 (Vitoriana). MZUSP 28620, 1m (unsexed 30.5 mm SL), Botucatu, Fazenda Edgardia. MNRJ 19470, 8m of 9 (1 female 31.8 mm SL c&s, 7 unsexed 24.6-34.7 mm SL), Botucatu, Tietê river basin. NRM 17307, 15 (7m males 27.2-29.9 mm SL, 1m male 28.2 mm SL c&s, 7 unsexed 26.2-31.9 mm SL), [Promissão], rio Tietê drain: BR-153 below Usina de Promissão, isolated pool between road and left bank of rio Tietê. NRM 23393, 1 m (unsexed 34.6 mm SL), [Promissão], rio Tietê drainage: muddy pool below Usina de Promissão. **Rio Paraná basin.** BRAZIL, MATO GROSSO DO SUL: MZUSP 16982, 1 (female 36.7 mm SL), Jupiá, marginal pools of rio Paraná. MZUSP 16989, 2 (unsexed 25.4-25.7 mm SL), Jupiá, marginal pools of rio Paraná. MZUSP 16994, 1 (unsexed 23.4 mm SL), Três Lagoas, marginal pool on mouth of rio Sucuriú. **Rio Grande basin**. BRAZIL, SÃO PAULO: MCP 9152, 4 (1c unsexed 21.7 mm SL, 3 unsexed 18.6-21.7mm SL), Pirassununga, lagoa da Aeronáutica, upper stream of Cachoeira das Emas, rio Mogi-Guaçú, rio Grande drainage, 21°54'S 047°23'W. MZUSP 16637, 2 (unsexed 18.4-15.6 mm SL), Porto Ferreira, lagoa do pesqueiro "Paris", [rio Mogi-Guaçú]. MZUSP 16645, 2 (unsexed 19.0-20.5 mm SL), Pirassununga, Lagoa do Scatolin. MZUSP 18588, 1 (unsexed c&s), [near rio Icém], Marimbondo (Represa), rio Grande, CETESB. MZUSP 16645 2c (unsexed 19.0-20.5 mm SL), Pirassununga, Lagoa do Scatolim, rio Mogi-Guaçú.

Diagnosis. *Holoshesthes hemigrammus* differ from all other *Holoshesthes* species by 24 autapomorphies, though 19 are homoplasies independently acquired in other lineages of the Cheirodontinae (Bührnheim & Malabarba, in manuscript). Among these, 19 characters are related to upper and lower jaw dentition. Following, the 24 autapomorphies: (1) lateral wings of the mesethmoid almost indistinct or absent [6-1]; (2) posteroventral process of the orbitosphenoid absent, or presence of a tiny posteroventral process associated to a small posterior concavity in the orbitosphenoid[10-0]; (3) longitudinal branch of the laterosensory canal of parietal posteriorly not contiguous to the transverse laterosensory canal of the parietal, divided by a gap, and anteriorly contiguous to the laterosensory canal of frontal [11-1]; (4) laterosensory canal of frontal posteroventral branch of the laterosensory canal of frontal interrupted, or absent, not contiguous to the laterosensory canal of pterotic [12-1]; (5) laterosensory canal of the first infraorbital absent or nearly absent at the posterior portion of the first infraorbital, never reaching to about half length of the longest axis [15-1]; (6) anterodorsal border of the second infraorbital without pointed projection or not as state 1 [18-0]; (7) posteroventral border of the third infraorbital not contacting the laterosensory canal of preopercle, leaving a naked area between the posterolateral border of the third infraorbital and the laterosensory canal of preopercle [19-2]; (8) fourth infraorbital reduced [20-0]; (9) anterior border of the sixth infraorbital with the anterior lamella small, reduced, once in laterosensory tube width, in a somewhat small lingual-like shape [22-1]; (10) dorsal border of opercle ascendant, posterior portion elevated, protruded [25-2]; (11) preopercular sensory canal short, preopercular canal reaching the posterior condylar articular surface of hyomandybular [27-1]; (12) ectopterygoid teeth present [28*-1]; (13) 8-11 premaxillary teeth [41-0] (Fig. 30); (14) premaxillary teeth juxtaposed, practically without space between teeth [42-0] (Fig. 30); ((15) absence of the longitudinal groove just below dorsolateral border of the maxilla [46-0] (Fig. 30); (16) usually five or six maxillary teeth [54-1] (Fig. 30); (17) lateral ridge absent or almost absent of the upper portion of the angulo-articular, on posterolateral portion of the lower jaw, near the posterior portion of the maxilla, observed in dorsal view [57-0]; (18) lower border of the dentary approximately straight [58-0] (Fig. 30); (19) large anterior dentary teeth with 3 central cusps larger, nearly equal in size, compressed and aligned at their distal tips in a row forming a sharp cutting edge; cusp tips of lateral cusps lateral [72*-3] (Fig. 33); (20) 8 to 10 anteriormost dentary teeth larger and following teeth decreasing in size posteriorly [73*-2] (Fig. 30);; (21) less than 12 gill rakers in the lower branch of the first gill arch [90-1] (Fig. 34a); (22) laterosensory canal of the lateral line not extended between caudal-fin rays, not reaching to the caudal-fin base [114-0]; (23) absence of hooks on the first unbranched pelvic-fin ray in males [137-0]; (24) scattered black chromatophores on entire or almost entire dorsal-fin [158-0].

An addittional character only observed in *H. hemigrammus*, among all *Holoshesthes* species, is the adipose fin with faint dark chromatophores in some specimens.

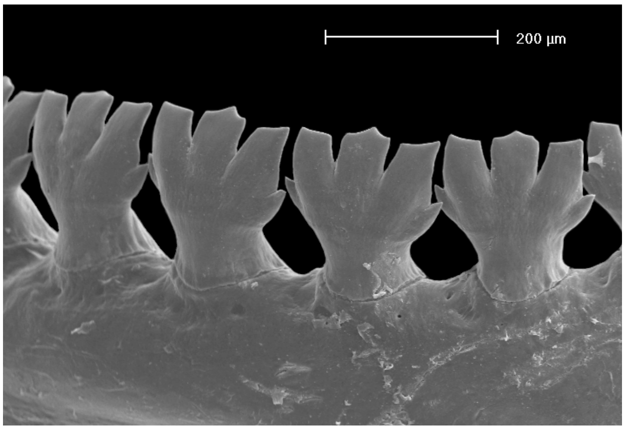

Fig. 33. Dentary teeth of *Holoshesthes hemigrammus*, NRM 17307, male 28.2 mm SL Scanning electron micrograph (SEM).

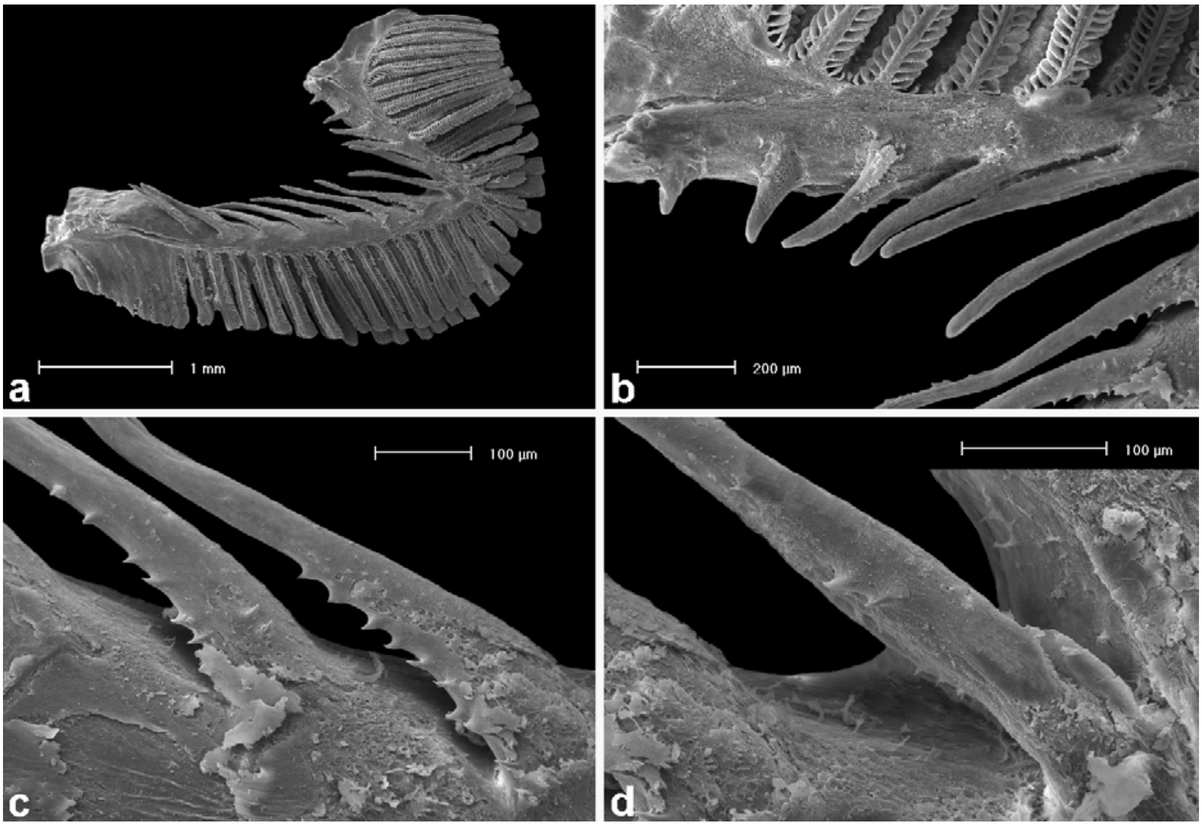

Fig. 34. First left side gill arch of *Holoshesthes hemigrammus*, NRM 17307, male 29.0 mm SL showing gill gland (a), in detail gill rakers on upper branchial branch (b), and gill rakers on lower branchial branch (c-d). Scanning electron micrographs (SEM).

Description. Morphometric data are given in Table 5. Largest male 29.9 mm SL, female 33.1 mm SL. Greatest body depth at dorsal-fin origin and area anterior to dorsal-fin at vertical above belly. Snout short. Head profile almost straigh from snout to posterior tip of supraorbital. Predorsal profile almost straight or slightly convex to dorsal-fin origin, then straight to caudal peduncle. Ventral profile convex from mouth to anal-fin base. Anal-fin base straight. Caudal peduncle slight longer than deep.

Head relatively small. Posterior margin of opercle sinusoidal, upper posterior margin concave and lower posterior margin convex. Mouth terminal. Lower jaw profile slight projected on head profile. Well-developed obliquous maxilla extended behind to anterior border of eye, below ventral border of eye, and at vertical through middistal portion of second infraorbital. Premaxillary teeth 8-11, with 3-5 cusps, central cusp larger than lateral ones, acute cusp tips (Fig. 30). Maxilla with 4-5 teeth bearing 3 cusps equally sized. Dentary teeth 13-14 bearing 1 to 5 cusps: anterior 9 largest teeth with 3 large compressed central cusps and 2 lateral small cusps, 1 medium sized tricuspid tooth, and 3-4 smaller tricuspid to unicuspid conical teeth. Anterior 9 largest dentary teeth with cusps border centrally acute, the two lateral cusps with straight borders, oppositely and laterally directed. Smaller lateral cusps of anteriormost dentary teeth overlapping lateral cusps of adjacent tooth.

Dorsal-fin rays **ii**(43), 8(1), or **9**(42). Dorsal fin behind midlength of body, posterior to pelvic-fin origin. Anal-fin rays **v**(30), vi(12), or **vii**(1), **20**(1), **21**(3), **22**(11), 23(9), 24(12), 25(7), 26(2), or 28(1). Anal-fin distal border concave, anterior 6-7 branched rays longest. Pectoral-fin rays **i**(43), **10**(16), **11**(22), 12(5). End of pectoral-fin slightly rounded to pointed, 1st unbranched fin ray and 1st -3rd branched fin rays longest. Pectoral fin slightly beyond pelvic-fin origin, excepting in one mature female. Pelvic-fin rays **i**(23), 6i (5), or **7**(18). Pelvic fin pointed, straight borders, reaching or slightly through anal-fin origin. Principal caudal-fin rays **19**(40). Dorsal procurrent caudal-fin rays 9(1), 10(2), **11**(12), **12**(20), or **13**(6), ventral procurrent caudal-fin rays 9(6), **10**(29), or **11**(5). None evident caudal-fin ray flaps. Adipose-fin at vertical through last anal-fin ray insertion.

Eight males with hooks on fins, though mostly not well developed, and 2 sexed females, but no other sexual dimorphic characters. Males with acute, elongate, retrorse hooks on posterior border of pelvic- and anal-fin rays. One to 2 paired and unpaired hooks per segment of lepidotrichia, on last unbranched anal-fin ray, and 1st-14th (one specimen reaching to 16th, and with 1 pair of hook on 20th) anal-fin branched rays, positioned at distal half length. One unpaired hooks per segment of lepidotrichia positioned at distal half length of 1st-7th branched pelvic-fin rays. One male 29.9 mm SL with one unpaired hook per segment of lepidotrichia on second unbranched dorsal-fin rays and 1st-6th branched dorsal-fin rays, and one unpaired hook per segment of lepidotrichia on 1st to 4th branched pectoral-fin rays. Another male 27.2 mm SL with one unpaired hook per segment of lepidotrichia positioned at distal portion on caudal-fin rays of upper and lower lobe (1st-6th caudal-fin rays and 15th-19th caudal-fin rays).

Scales cycloid: lateral line incomplete 6(6), 7(10), **8**(20), 9(3), 10(1); longitudinal row 34(12), **35**(16), **36**(6); predorsal row **11**(2), **12**(4); scale rows between lateral line and dorsal-fin origin **6**(35); scale rows between lateral line and anal-fin origin **4**(40); scale rows around peduncle 14 (17). Triangular modified scale on pelvic-fin base extended posteriorly covering 1 scale. Scales on anal-fin base 5-6 (missing or partially missing in paratypes).

Cleared and stained specimens (3): supraneurals 5; precaudal vertebrae 15, caudal vertebrae 19(2), or 20(1). Gill rakers (9 specimens, 3 c&s), upper **5**(6), **6**(7), lower **10**(10), **11**(3) (1 on the hypobranchial). Upper gill rakers with 2-5 recurved denticles on anterolateral border to posterolateral border, and anteriormost upper gill rakers with none or 2 denticles on posterolateral border; lower gill rakers with 0-10 recurved denticles on anterolateral border, and none to 2 denticles on posterolateral surface; and posteriormost lower gill raker with none to 3 denticles on anterolateral border, and none on posterolateral border (Fig. 34). Denticulation mainly on basal portion of gill rakers.

Color in alcohol. General ground body color pale beige. Dorsum with scarce chromatophores mostly on scale border, laterally reaching lateral line, and on pseudotympanum area or not. Dorsal fin mostly clear with dark chromatophores scattered along 1st- 2nd unbranched dorsal-fin rays, at distal half length on 1st-5th branched fin rays, gradually fading to last fin ray. Most pelvic fin clear, a few chromatophores on all fin rays, but gradually fading to last fin ray. Anal fin entirely scattered with faint chromatophores along all fin rays. Pectoral fin with faint chromatophores, decreasing in number from 1st unbranched fin ray to last branched fin ray. Adipose fin pigmented, dark chromatophores on anteriormost portion, or clear. Caudal fin rays with scattered dark chromatophores along both fin lobes, except most hyaline midcentral 8th-11th principal caudal-fin rays, near caudal-fin spot. Black caudal-fin spot, reaching upper and lower borders of caudal peduncle.

Dark chromatophores on head, snout, upper and lower lips (forming a line on lower lip), anterior to middle portion of maxilla, and lower anteriormost dentary portion, dorsal to central portion of opercle. Top of the head pigmented on frontals, and parietals, dark chromatophores deep-lying over brain below frontals and parietals, and epidermis covering fontanel. Faint black and silver midlateral stripe, with scarce dark chromatophores, begininng posterior to pseudotympanum, above lateral line, reaching caudal-fin spot. Guanine on eye iris, laterally on dentary under posterior portion of maxilla, opercle, preopercle, subopercle and interopercle, antorbital, 2nd-5th infraorbitals, isthmus, laterally exposed portion of cleithrum, and on belly between pectoral and pelvic fins, and on belly between pectoral and pelvic. Below lateral line, ventral body faint almost without pigmentation surrounding pectoral- and pelvic-fins. Above anal fin base 8 to 12 chevron shaped markings and faint line of dark chromatophores on pterygiophores area of anal fin.

Sexual dimorphism. Males with hooks on all fins, despite a few hooks not developed on dorsal, pectoral, and caudal-fin rays of available males as above referred. None elongate fin rays or other dimorphic character. The gill gland, as described in Bührnheim & Malabarba (2006) to *Odontostilbe* species, is present in mature males on first gill arch, covering about 8-10 anterior branchial filaments (Fig. 34a).

Remarks on examined paratypes. The two largest specimens of CAS 75171 and the unsexed 32.9 mm SL well-preserved, excepting the smaller specimen of CAS 17517, probably once dehydrated. The largest paratype CAS 75171, 36.7 mm in SL (Fig. 33), has some dark chromatophores bordering anteriormost portion of adipose fin. Dentition almost complete in all specimens examined.

Distribution. *Holoshesthes hemigrammus* is distributed in the upper rio Paraná basin, mainly recorded from rio Tietê and rio Grande drainages, in São Paulo, Brazil (Fig. 35). Two collections from the upper rio Paraná, in Mato Grosso do Sul.

Fig. 35. Distribution of *Holoshesthes hemigrammus* (circles) and *Holoshesthes* n. sp. "k" (lozenges) in South America. Type localities respectively: *H. hemigrammus* (open circles) and *Holoshesthes* n. sp. "b" (open lozenge). Some symbols represent more than one lot, and more than one locality.

Table 5. Morphometrics of *Holoshesthes hemigrammus* (paratypes and non-types 2 of MZUSP 16989, 1 of MZUSP 16994, 1 of MZUSP 16982, 1 of MZUSP 17303, 2 of MZUSP 18482, 1 of MZUSP 39863, 2 of MZUSP 40349, 8 of MNRJ 19470,15 of NRM 17307, 1 of NRM 23393,).

	Paratypes					Males				Females				Unsexed			
	CAS 75171			CAS 17517		n	low	high	mean	n	low	high	mean	n	low	high	mean
standard length	36.7	33.6	32.9	36	34.8	8	27.2	29.9	28.7	3	31.2	33.1	32.0	23	21.8	36.7	28.5
Percentages of standard length																	
head length	27.0	27.4	27.7	26.1	27.9	8	26.5	27.4	27.0	3	27.0	28.1	27.7	23	25.7	29.8	27.7
snout-anal fin origin	61.9	62.8	61.7	60.0	59.8	8	55.9	61.1	58.6	3	57.2	58.9	58.1	23	55.9	61.1	58.1
snout-dorsal fin origin	55.3	53.3	55.0	54.2	55.2	8	52.1	55.4	53.4	3	52.8	54.2	53.6	23	50.6	56.4	53.6
snout-pelvic fin origin	46.0	45.2	45.9	45.6	45.4	8	42.8	46.3	44.5	3	44.0	44.9	44.4	23	42.3	45.9	44.4
dorsal-fin base	13.6	13.7	13.4	13.1	12.9	8	12.3	14.5	13.7	3	13.5	13.6	13.5	23	12.8	15.0	13.6
anal-fin base	30.2	31.0	29.8	30.3	31.3	7	32.1	35.5	33.5	3	33.0	35.6	34.2	23	30.6	35.7	33.3
caudal peduncle length	13.9	12.5	14.0	14.4	13.2	7	11.3	14.4	12.7	3	12.3	12.8	12.5	23	11.1	14.0	12.5
caudal peduncle depth	12.3	11.9	12.2	11.9	12.4	8	9.5	11.4	10.8	3	10.7	11.8	11.1	23	9.3	11.9	10.7
depth at dorsal-fin origin	36.2	35.7	33.7	36.4	35.3	8	31.6	36.1	33.5	3	29.2	35.6	33.4	23	26.7	35.9	31.6
dorsal-fin length	28.9	27.7	28.9	-	-	7	0.0	29.4	24.5	3	26.6	26.9	26.7	20	26.1	32.1	28.9
pelvic-fin length	18.0	15.5	17.3	15.6	-	8	15.2	17.4	16.4	1	16.4	16.4	16.4	22	15.4	17.9	16.7
pectoral-fin length	21.0	19.6	21.3	19.2	19.0	8	19.6	21.6	20.8	3	20.2	21.4	20.6	21	19.0	21.6	20.5
snout-pectoral-fin origin	27.0	27.4	26.7	26.1	27.0	8	25.8	27.0	26.2	3	27.2	27.8	27.5	23	24.4	28.9	26.9
Percentages of head length																	
snout length	20.2	21.7	22.0	21.3	20.6	8	19.2	22.5	20.3	3	21.5	22.1	21.8	23	20.0	23.1	21.6
upper jaw length	42.4	42.4	41.8	41.5	41.2	8	38.5	42.5	40.7	3	41.9	43.7	42.5	23	38.4	44.6	41.6
horizontal eye diameter	32.3	32.6	33.0	30.9	32.0	8	34.1	37.2	36.2	3	32.6	34.5	33.5	23	29.3	37.2	34.8
least interorbital width	30.3	28.3	28.6	29.8	27.8	8	27.3	30.6	28.8	3	28.0	29.1	28.6	23	25.6	31.4	28.7

Holoshesthes n. sp. "b", new species

Fig. 36, 37

Holotype. ANSP 185104, 1 (male, 21.0 mm SL), Colombia, Meta, Meta drainage, lake Mozambique, Mozambique ranch, north side, 03°58'N 73°04W, Luis & Ramero, 27 May 1969.

Paratypes. COLOMBIA: ANSP 173724, 30 (15m, 7 males 23.2-20.0 mm SL, 5 females 23.2-19.8 mm SL; 1 female 22.5 mm SL c&s, 2 males 22.3-20.1 mm SL c&s), same data as holotype. IAvHP, 4 (2 males, 2 females), same data as holotype. ICNMHN 16375, 4 (2 males, 2 females), same data as holotype. VENEZUELA: ANSP 156876, 46 (19m, 13 males 27.6-29.7 mm SL, 1 male 28.1 mm SL c&s, 1 females 30.8 mm SL, 1 female 34.4 mm SL c&s, 4 unsexed 24.2-38.1 mm SL), [Guarico], lagoon Flores Mocadas [lagoon Flores Moradas, rio Guarico, Apure drainage], 80 km S Calabozo, F. Bond, 15 Feb 1938. INHS 69500, 5m (3 males 24.8-26.9 mm SL, 1 male 28.1 mm SL damaged, not measured, 1 female 26.4 mm), Guarico, río Los Aceites, Orituco-Guarico-Apure drainage, 15 km SSE of Palenque, D. C. Taphorn *et al.*, 21 Jan 1985. MCNG 54108, 1 male 26.4 mm SL, Cojedes, río Pao at el Caserio, El Pueblito, D. Taphorn et al., 28 Jul 1985. MCNG 54109**,** 1 male 22.5 mm SL, Tachira, caño El Tigre via Puerto Vivas, D. Taphorn et al., 9 Nov 1981. MCNG 55590, 6 (5 males 19.3-25.8 mm SL, 1 male 26.1 mm SL c&s), Barinas, Puerto Nutrias, flooded zone, D. Taphorn, 27 July 1980. USNM 327250, 1 (male 24.7 mm SL), [Portuguesa], caño Falcón, [affluent of río Portuguesa], J. Baskin, 24 Aug 1974. USNM 327302, 3 (males 24.3-25.3 mm SL), same data as USNM 327250.

Fig. 36. Holotype of *Holoshesthes* n. sp. "b", ASNP 185104, male 21.0 mm SL (top), and paratype ASNP 173724, 1 female 23.2 mm SL (bottom).

Fig. 37. Paratype of *Holoshesthes* n. sp. "b", male USNM327250, 24.7 mm SL.

Non-type material. Río Meta basin, COLOMBIA: ANSP 163163 1 (female 24.2 mm SL), Meta, Laguna “Doctor Sanchez”, a cut-off oxbow, entrance *ca.* 5 km SW from inlet to Lake Mozambique, 03°56'N 73°08W. **Río Orinoco basin,** VENEZUELA: USNM 233188, 18 (unsexed 16.7-25.4 mm SL), [Delta Amacuro], isolated lagoon on isla Tapatapa, at Los Castillos, between Puerto Ordaz and Barrancas, 163 nautical miles from Sea Buoy. **Río Apure basin.** VENEZUELA: ANSP 139541, 20 (unsexed 18.8-25.7 mm SL), [Guárico], Camaguan swamp, on W side of highway to San Fernando de Apure, *ca.* 2 km N of Camaguán, 08°14'N 67°36W. ANSP 185105, 3 (1 male 27.6 mm SL, 1 female 25.7 mm SL, 1 unsexed 20.3 mm SL), Guarico, río Orituco, tributary of río Guarico, 15 km SSE of Calabozo on Cazorla Road. ANSP 150437, 11 (unsexed 17.7-22.3 mm SL), same data as ANSP 185105. MCNG 54109, 1 (male 22.5 mm SL), Tachira, caño El Tigre via Puerto Vivas. MCNG 33790, 7 (1 male 20.2 mm SL, 6 females 18.0-23.8 mm SL), Apure, Paez, via al' El Nula sector caño Rico, 400 meters of village Liberdad. MCP 15072, 1 (female 20.9 mm SL), [Guárico], Camaguan swamp, on W side of highway to San Fernando de Apure, *ca*. 2 km N of Camaguan, 08°14'N 67°36W, formerly ANSP139544). USNM 327244, 22 (unsexed 18.1-29.5 mm SL), [Portuguesa], caño Falcón, [affluent of río Portuguesa]. USNM 327258, 10 (2 males 24.9-26.1 mm SL, 8 unsexed 18.6-22.0 mm SL), same data as USNM 327244.

Diagnosis. *Holoshesthes* n. sp. "b" is diagnosed by the following seven autapomorphies: (1) palatine regular rectangular, well developed [30-1]; (2) main cusps of the posteriormost teeth almost perpendicular to the ventral border of premaxilla [38-0]; (3) first to third medial premaxillary teeth usually conical tooth or conical tooth with a small lateral cusp [40-0] (Fig. 38); (4) maxilla short, terminating at mid portion of lower jaw, contacting the anterodorsal extension of the angulo-articular or at mid portion of the angulo-articular, and reaching beyond the vertical through the contact area between the infraorbitals 1 and 2 or up to the mid portion of the infraorbital 2 [53-1]; (5) anterior maxillary teeth unicuspid [55-2] (Fig. 38); (6) fin hooks straight or practically straight, distal tip perpendicular to anal-fin ray long axis. [149*-1]; (6) caudal-fin hooks on almost all caudal-fin rays, 2-18 [152*-3].

Holoshesthes n. sp. "b" is also readily distinct by the contrasting rounded head profile of mature males *vs*. more pointed in females (Fig. 37; male of Fig. 39 with open mouth) and by the mouth slightly upturned, among all Cheirodontinae.

As noted before in *H. geayi* diagnosis, *Holoshesthes* n. sp. "b" is sympatric with it, differing in: (1) snout length larger in *H. geayi* remarked in mature males 20.5-26.8% SL *vs*. in *Holoshesthes* n. sp. "b", males 18.0-22.6% SL (Fig 27).; (2) smaller anal-fin base in *H. geayi*, 26.5-31.1% SL *vs* in *Holoshesthes* n. sp. "b", 29.6-34.3% SL (Fig. 28); and (3) lower number of anal-fin rays 19-22 in *H. geayi vs*. 19-26, mostly 22-24, in *Holoshesthes* n. sp. "b" (Fig. 10). Juveniles of *Holoshesthes* n. sp. "b" are very similar to *H. geayi*, just differing in premaxillary dentition (3-4 cusps in *H. geayi*, 1-2 cusps in *Holoshesthes* n. sp. "b").

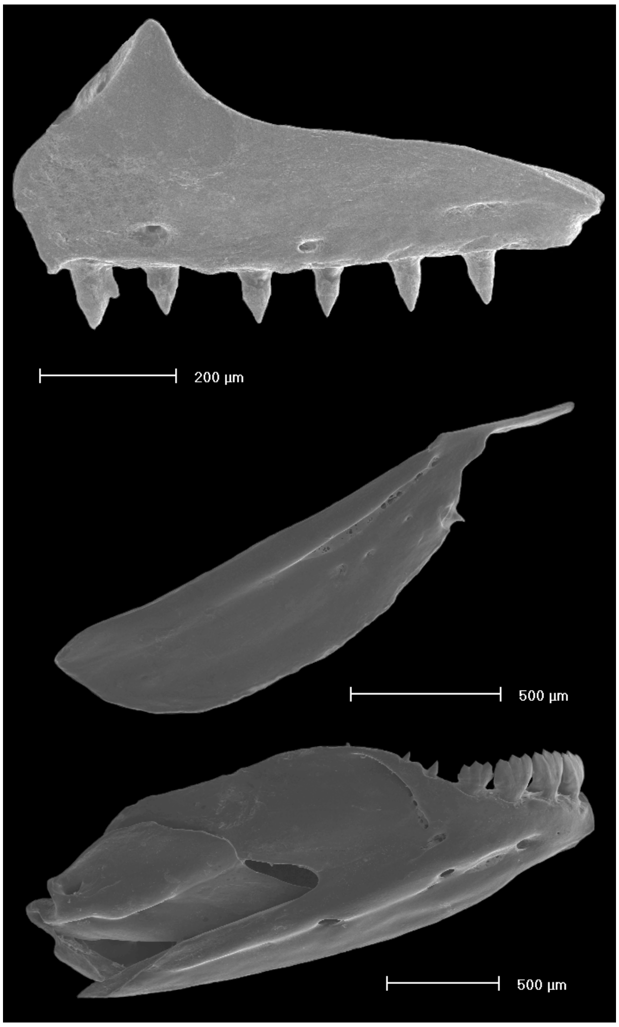

Fig. 38. Dentition of *Holoshesthes* n. sp. "b", ASNP 156876, male28.1 mm SL: left side premaxilla (top), and rigth side maxilla (middle) and dentary (bottom). Originally seven premaxillary teeth, posteriormost premaxillary teeth lacking,. Scanning electron micrograph (SEM).

Description. Morphometric and meristic data are given in Table 6. Largest male 38.1 mm SL, female 34.4 mm in SL. Greatest body depth at dorsal-fin origin corresponding to most elevated point in dorsal profile; greatest body depth in front of dorsal fin in females when the belly is expanded. Snout very short, approximately twice in horizontal eye diameter. Dorsal body profile slightly convex from snout to dorsal-fin origin, and posteriorly descending straight or slightly concave to caudal peduncle. Ventral profile convex from mouth to anal-fin origin. Anal-fin base straight. Caudal peduncle slightlylonger than deep.

Head relatively short, rounded profile in males, more pointed profile in females. Posterior margin of opercle sinusoidal, upper posterior margin concave and lower posterior margin convex. Mouth slightly upturned. Lower jaw profile slight projected on head profile. Well-developed oblique positioned maxilla ending at vertical through anterior eye border and below inferior eye border. Premaxillary teeth 5-8, conical or with one small lateral cusp (Fig. 38). Maxilla without teeth or with an unique conical tooth. Dentary teeth 8 bearing 1-5 cusps: anterior 3 teeth largest with 3 large compressed central cusps; 1 median size tricuspid tooth and 4 small conic teeth.

Dorsal fin rays **ii**(47), 8(4), or **9**(43). Dorsal-fin origin midlength of body, posterior to vertical through pelvic-fins origin. Posterior dorsal-fin border almost straight. Anal-fin rays **iv**(8), v(36), vi(3), 20(1), 21(2), 22(21), **23**(15), 24(6), 25(1), 26(1). Anal-fin distal border concave, anterior 6-7 branched rays longest. Pectoral-fin rays **i**(47), 9(2), **10**(41), 11(4). Pectoral fin slightly rounded at tip, 1st unbranched fin ray and anteriormost 3 branched fin rays longer; lateral margin straight to slightly convex, posterior margin nearly straight. Pectoral fin reaching or slightly beyond pelvic-fin origin. Pelvic-fin rays **i**(47), 6i(17), **7**(30). Pelvic fin slightly pointed, straight borders, reaching to or slightly beyond anal-fin origin. Principal caudal-fin rays **19**(42). Dorsal procurrent caudal fin rays 11(4), 12(14), **13**(21), 14(2), or 15(1), ventral procurrent caudal fin rays 8(1), 9(9), **10**(21), or 11(8). Small caudal-fin ray flaps: dorsally on 4th-6th rays of upper lobe, ventrally on 13th-15th rays of lower lobe or none flaps. Adipose-fin at vertical through last anal-fin ray insertion.

All fins of males with small paired or unpaired hooks perpendicular to fin ray axes, mostly on posterior borders, but also some on anterior and lateral borders. One or 2 hooks per ray segment on 2nd unbranched and on all or anterior 7-8 branched dorsal-fin rays, mid-distally positioned. One or 2 hooks per ray segment on last two unbranched anal-fin rays and on all or almost all branched anal-fin rays, mid-distally positioned. One or 2 hooks per ray segment on first unbranched and on all branched pectoral-fin rays, more distally positioned. Hooks on pectoral-fin rays also on anterior border of fin rays. One or 2 hooks per ray segment on unbranched and branched pelvic-fin rays, including last one unbranched fin ray when present, mid-distally positioned. One or 2 hooks per ray segment on most principal caudal-fin rays from 2nd-18th fin rays, distally disposed on ray branches; no hooks on 1st -19th principal caudal-fin rays. Hooks of upper caudal fin lobe on lower border of fin rays, hooks of lower caudal-fin lobe on upper border of fin rays, hooks of middle fin rays 10-11th on both fin ray borders.

Scales cycloid, lateral line complete 33(2), 34(1), 35(7), **36**(12) 37(1), 38(1), interrupted in a few specimens, with 12(2), 15(1), 20(1) perforated scales; predorsal row **11**(16), 12(15), 13 (1); between lateral line and dorsal-fin origin **5**(33), 6(7); between lateral line and pelvic-fin origin **3**(44), 4(2); longitudinal series of scales around caudal peduncle **14**(32). Triangular modified scale on pelvic fin base extended posteriorly covering 2 scales, almost 1. Scales on anal-fin base **6**, 7.

Cleared and stained specimens (4): supraneurals 4(1), or 5(3); precaudal vertebrae 16; caudal vertebrae 19. Gill rakers (4 specimens, 4 c&s), upper **8**(7), 9(1), lower 13(1), 14(1), **15**(5), or 16(1) (3 on the hypobranchial). Upper gill rakers with none to 5 recurved denticles on anterolateral border, and anteriormost upper gill rakers with none to 2 similar denticles on posterolateral border; lower gill rakers with none to 3 denticles on anterolateral border, and the posteriormost lower gill raker with none to 2 denticle on anterolateral border, and none to 4 denticles on posterolateral border (Fig. 39). Denticulation mainly on basal portion of gill rakers. In specimens of smaller size around 20.0 mm SL the gill rakers have relatively less denticulation than those in larger specimens around 30.0 mm SL.

Anomalies. Paratype ANSP 173724, female 21.9 mm SL with numerous irregular osseous unicuspid tooth-like structures along unbranched pectoral-fin ray and 1st-3rd branched pectoral-fin rays, laterally positioned on the base and median portion of ray fin tips. Paratypes ANSP 173724, male 20.1 mm SL, and MCNG 55590, male 19.3 m SL, with numerous osseous unicuspid tooth-like structures distributed on the anterior lower surface of left dentary**.** Paratype INHS 69500, male 24.8 mm in SL without adipose fin. Four males of ANSP 156876 with incomplete lateral line, one male with respectively 12 perforated scales on the left side and 15 on the right side, the three others with 12, 15 and 20 perforated scales on the left side.

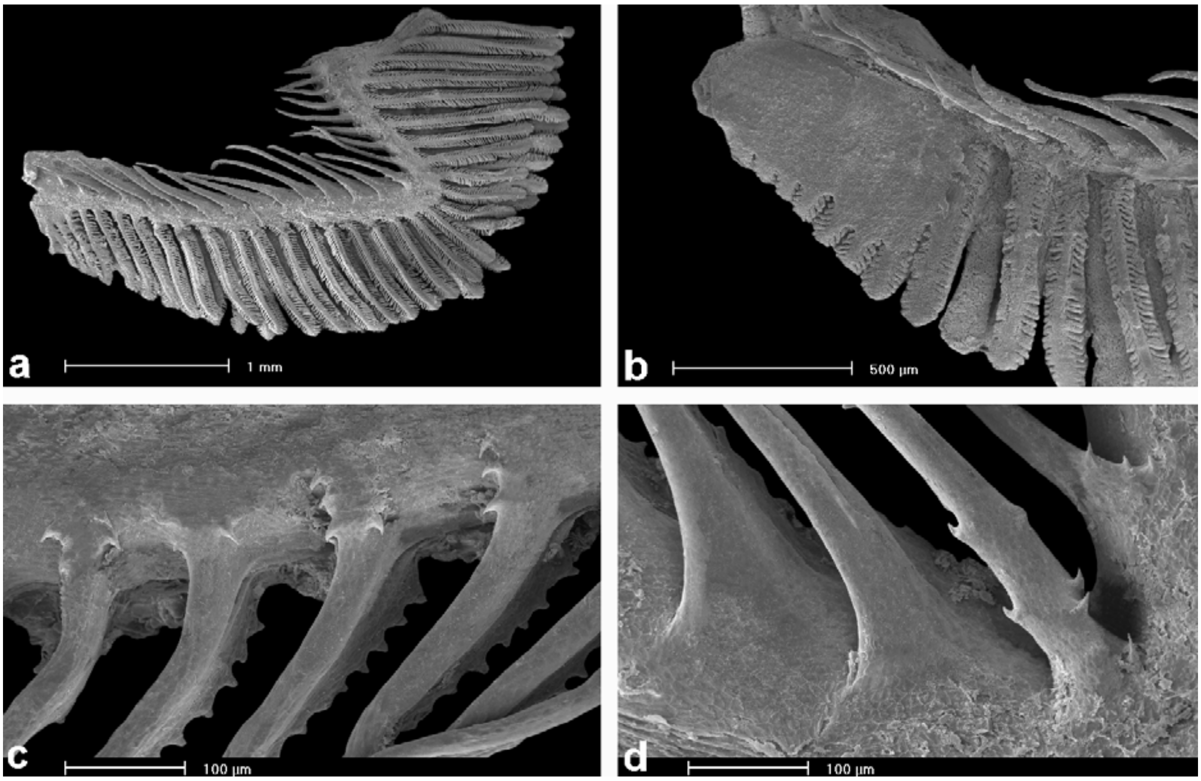

Fig. 39. First left side gill arch of *Holoshesthes* n. sp. "b", paratype ANSP 156876, male 29.6 mm SL (a), paratype ASNP 173724, male 21.6 mm SL, showing gill gland (b) in detail gill rakers on upper branchial branch of paratype ANSP 156876, male 29.6 mm SL (c), and gill rakers on lower branchial branch of the same specimen (d). Scanning electron micrographs (SEM).

Sexual dimorphism. Males with hooks on all fins, in contrast to absence of them in females. None elongate fin rays. Mature males with gill gland on first gill arch, covering about 10 anterior branchial filaments of the lower gill arch (Fig. 39b). Principal component analysis grouped males and females separated with ten measurements loading heaviest on PC2 (Fig. 40). Males are particularly distinct by higher values of dorsal-fin base, pelvic-fin length, pectoral-fin length, least interorbital width, and anal-fin base than females, while females have higher values of depth at dorsal-fin origin, snout-pelvic-fin origin, snout-anal-fin origin, and snout-dorsal-fin origin than males (Table 6). Caudal peduncle-length loaded heaviest on PC2, which would correspond to a higher mean value to this measurement in females than males, but this is not seen in Table 6 because it also loaded heaviest on PC 3. This happened because two of the males positioned on the top of the PCA are outliers in this variable, having exceptional larger caudal-peduncle length values among all males. Dorsal-fin length was removed from this analysis because 9 males and 5 females had broken dorsal fins.

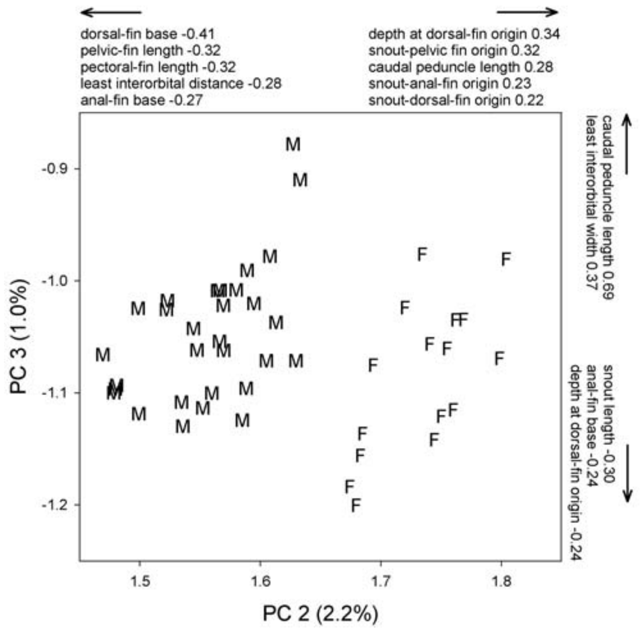

Fig. 40. Principal component analysis of the 17 morphometric data of males (M) and females (F) of *Holoshesthes* n. sp. "b". Stronger loadings on the second and third principal components (PC2, PC3).

Color in alcohol

General ground body color light yellowish beige. Most specimens, including holotype (Fig. 36), without distinct pigmentation on body, except a midlateral stripe reduced to a faint irregular line beginning behind the pseudotympanum, above lateral line, and reaching caudal spot. Dorsal fin scarcely brown pigmented on distal portion of 2nd unbranched fin ray and 1st-3rd branched fin rays. Anal-, pectoral-, pelvic- and adipose fins hyaline. Caudal fin mostly hyaline. Rounded brownish caudal spot on base of caudal fin. A few chromatophores on snout and anteriormost tip of lower jaw. Top of head pigmented on posterior portion of frontals and parietals with deep-lying dark chromatophores over brain membrane below frontals and parietals, and posterior fontanel. Guanine on eyes, opercle, third infraorbital and isthmus.

Only paratypes of USNM 327302, 3 males, and USNM 327302, a male (Fig. 37), well-pigmented, but instead without guanine. Dorsum with dark chromatophores mostly on distal border of scales forming reticulated pattern. Pigmented scales extended laterally on body, also on pseudotympanum area. Dark midlateral stripe, below lateral line and behind pseudotympanum, reaching to caudal spot; more evident at vertical below dorsal fin. Almost entire dorsal fin with scattered dark chromatophores, except the posterior 6-9th dorsal-fin rays mostly hyaline. Pectoral fin ligth, but dark chromatophores on unbranched fin ray and the 1st-4th branched fin rays. Pelvic fin hyaline. Anal fin with some dark chromatophores along 1st-5th branched fin rays, and on base of most fin rays. Adipose fin hyaline. Caudal fin with dark chromatophores scattered, except clear area near caudal fin spot. Caudal fin spot reaching upper border of caudal peduncle and clearer on lower border. Dark chromatophores scattered on snout, upper and lower lips, anteriormost tip of dentary, infraorbitals, opercle, and maxilla. Top of head uniformly covered with chromatophores, including membrane below fontanels. Belly faint. None chevron shaped markings on the region above anal fin, but a thin dark line parallel to anal-fin base.

Distribution. *Holoshesthes* n. sp. "b" probably is widespread in the río Orinoco basin, but here mainly recorded from río Apure basin, only two registers to the upper río Meta basin, and one at the mouth of the río Orinoco (Fig. 35). *H. geayi* is sympatric and syntopic with *Odontostilbe pulchra, O. splendida,* and *O. pao* (Bührnheim & Malabarba, in manuscript).

Table 6. Morphometrics of *Holoshesthes* n. sp. "b" (holotype ANSP 185104, paratypes 23 of ANSP 173724, 16 of ANSP 156876, 4 of INHS 69500).

		Paratypes - Males				Paratypes - Females			
	Holotype	n	Low	High	Mean	n	Low	High	Mean
standard length	21	30	19.7	29.7	25.0	13	19.8	34.4	23.9
Percentages of standard length									
head length	26.2	30	22.9	26.9	24.8	13	23.4	26.8	25.6
snout-anal fin origin	58.6	30	56.3	60.9	58.6	13	59.4	62.6	61.0
snout-dorsal fin origin	51.9	30	49.5	53.8	52.1	13	51.9	55.5	54.0
snout-pelvic fin origin	45.7	30	41.0	46.5	44.3	13	44.2	49.5	47.4
dorsal-fin base	14.3	30	11.7	15.3	13.8	13	12.1	14.2	12.9
anal-fin base	32.4	30	29.6	34.3	31.8	13	28.4	33.7	30.6
caudal peduncle length	14.3	30	12.4	16.4	13.5	13	11.9	14.6	13.6
caudal peduncle depth	12.4	30	9.5	12.2	11.0	13	10.1	12.0	11.1
depth at dorsal-fin origin	31.4	30	26.9	31.5	29.7	13	29.5	33.8	32.2
dorsal-fin length	29.0	19	27.1	30.6	28.9	11	28.2	31.5	29.2
pelvic-fin length	17.1	29	16.2	18.1	17.2	13	14.6	17.4	16.2
pectoral-fin length	23.3	30	19.4	24.3	22.2	13	19.7	21.6	20.9
snout-pectoral-fin origin	26.2	30	22.6	27.0	24.9	13	23.9	27.8	26.3
Percentages of head length									
snout length	20.0	30	18.0	22.6	19.8	13	19.0	21.4	19.8
upper jaw length	32.7	30	30.9	38.8	35.3	13	31.7	38.9	34.3
horizontal eye diameter	38.2	30	34.8	39.7	37.3	13	34.1	39.7	37.1
least interorbital width	30.9	30	27.8	34.8	30.8	13	25.9	30.6	27.6

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CAPÍTULO III

Neotrop. Ichthyol., 4(2):167-196, 2006

Redescription of the type species of *Odontostilbe* Cope, 1870 (Teleostei: Characidae: Cheirodontinae), and description of three new species from the Amazon basin

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The widespread Neotropical cheirodontine *Odontostilbe fugitiva* is reviewed, and three new species of the genus are described from the Amazon basin. A neotype is designated for *O. fugitiva*, from the mouth of the río Mazán, upper río Amazonas basin, Peru. Three nominal species are herein considered as synonyms of *O. fugitiva*: *O. madeirae*, *O. drepanon*, and *O. caquetae*. The three new species are respectively *O. ecuadorensis* from the río Napo basin, *O. nareuda* from the rio Madeira basin, and *O. parecis* from the rio Guaporé basin (rio Madeira basin). Among other diagnostic characters, gill rakers are especially informative in distinguishing species. Description of gill raker denticulation is provided for the first time for species of the Cheirodontinae. Secondary sexually dimorphic characters are described for all species.

O queirodontíneo neotropical *Odontostilbe fugitiva*, de ampla distribuição, é revisado e três espécies novas são descritas para o gênero na bacia Amazônica. Um neótipo é designado para *O. fugitiva*, da boca do rio Mazán, alto rio Amazonas, Peru. Três espécies nominais são consideradas sinônimas de *O. fugitiva*: *O. madeirae*, *O. drepanon* e *O. caquetae*. As três espécies novas são, respectivamente, *O. ecuadorensis* da bacia do rio Napo, *O. nareuda* da bacia do rio Madeira e *O. parecis* da bacia do rio Guaporé (bacia do rio Madeira). Entre outros caracteres diagnósticos, os rastros branquiais são especialmente informativos para distinguir as espécies. Uma descrição da denticulação dos rastros branquiais é apresentada pela primeira vez para espécies de Cheirodontinae. Caracteres de dimorfismo sexual secundário são descritos para todas as espécies.

Key words: Neotropical, Neotype, Systematics, *Odontostilbe madeirae*, *Odontostilbe drepanon*, *Odontostilbe caquetae*.

Introduction

The Cheirodontinae contains about 15 genera and 47 species of small Neotropical characid fishes, usually attaining 30-40 mm in standard length (Malabarba, 2003; Malabarba *et al.*, 2004). *Odontostilbe* Cope, 1870 was originally defined based on the presence of a complete lateral line, *versus* interrupted in *Cheirodon* Girard, 1855. The genus initially comprised only *Odontostilbe fugitiva* Cope, 1870 from "Pebas, Eastern Equador". Currently, Pebas is a city in the Departamento de Loreto in Peru, not Ecuador. The taxonomic history of the discussion of the validity of *Odontostilbe versus Cheirodon* dates back to the work of the danish zoologist Christian F. Lütken. While redescribing *Poecilurichthys pulcher* Gill, 1858, Lütken (1875: 236-237) noted that "technically the species of Trinidad is properly an *Odontostilbe* Cope, but this genus only differs from the known [*Chirodon*] G. in the lateral line which is not complete …" [our translation], referring the species as *Chirodon* (*Odontostilbe*) *pulcher* (Gill, 1858). Subsequently, Steindachner (1882a, 1882b) described *Chirodon pequira*, and designated the type species of *Odontostilbe* as *Chirodon* (*Odontostilbe) fugitiva*. Subsequent works alternated usage of *Odontostilbe* as valid (*e.g.* Eigenmann & Eigenmann, 1892, in a preliminary list of freshwater fish of South American listed *Odontostilbe fugitiva* and recognized *Odontostilbe pulcher*), or as synonym of *Cheirodon* (*e.g.* Ulrey, 1895, when examining "Characinidae" collected by Charles F. Hartt in Brazil listed *Cheirodon fugitiva* and *Cheirodon pulcher*, along with five other species of *Cheirodon*).

Retaining the original diagnostic character of lateral line complete, Eigenmann (1915) recognized *Odontostilbe* with eight species, included in his new subfamily Cheirodontinae:

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O. fugitiva, *O. drepanon* Fowler 1913, *O. madeirae* Fowler 1913, *O. microcephala* Eigenmann, 1907, *O. paraguayensis* Eigenmann & Kennedy, 1903, *O. pulchra*, *O. hastata* Eigenmann, 1913, and *O. melandeta* Eigenmann, 1912. Eigenmann (1915), however, further indicated that *O. hastata*, and *O. melandeta* would be probably moved to other genera. In fact, *O. hastata* was afterwards moved into the genus *Saccoderma* (Schultz, 1944), and *O. melandetum* into the genus *Aphyocharacidium* (Géry, 1960). Subsequent alternate views on the validity of *Odontostilbe versus Cheirodon* based on the completeness of lateral line were presented by Fink & Weitzman (1974), who considered *Odontostilbe* as a synonym of *Cheirodon*, and by Fowler (1913, 1940, 1943), Böhlke (1954), and Géry (1964, 1972a, 1972b, 1977), who considered *Odontostilbe* as valid. Uj (1987) proposed a new diagnosis for *Odontostilbe versus Cheirodon* based on some osteological characters and included a rearrangement of some species of both genera, but his hypothesis was not accepted by subsequent studies (*e.g.* Malabarba, 1998, 2003).

Since the establishment of the monophyly of Cheirodontinae and the proposal of a phylogenetic diagnosis of all included genera (Malabarba, 1998), *Odontostilbe* is considered valid with *Holoshesthes* Eigenmann, 1903 as a synonym. *Cheirodon* Girard, 1855 was restricted to six species from southern South America, and included in the tribe Cheirodontini. Six new genera were proposed, and a new tribe Compsurini was proposed. However, *Odontostilbe* and four other genera were left *incertae sedis* in Cheirodontinae. More recently, Malabarba (2003) refers ten species to *Odontostilbe*: *O. dialeptura* (Fink & Weitzman, 1974), *O. fugitiva*, *O. gracilis* Géry, 1960, *O. littoris* Géry, 1960, *O. microcephala*, *O. mitoptera* (Fink & Weitzman, 1974), *O. paraguayensis*, *O. pequira*, and *O. roloffi* Géry, 1972. Two of them from Central America, *O. mitoptera* and *O. dialeptura*, were temporarily referred to *Odontostilbe*, because both were found to be inseminators, thus belonging to the tribe Compsurini (Malabarba & Weitzman, 1999, 2000).

Herein we provide a redescription of the type species of *Odontostilbe, O. fugitiva,* including the designation of a neotype, a discussion of its synomyms, and morphological variation of populations across the Amazon basin. In order to present a better diagnosis for the type-species of the genus, we also describe herein three new species putatively related to *O. fugitiva* from major tributaries of the Amazon basin, one from upper río Napo and río Putumayo, in Ecuador, and two from rio Madeira basin, in Brazil and Peru. This is part of a major systematic study of *Odontostilbe*.

Material and Methods

Counts and measurements follow Fink & Weitzman (1974), primarily on the left side of the specimen. Head length is the distance between the tip of the snout and the posterior end of subopercle, which is slight posterior to the margin of the opercle. Total vertebrae number includes the four vertebrae of the Webberian apparatus, and the terminal "half centrum" as outlined by Malabarba & Weitzman (1999). The gill raker at the junction of the ceratobranchial and the epibranchial is referred as the posteriormost gill raker of the lower branch of the arch, and counted jointly with the gill rakers on the lower branch. Specimens were cleared and stained according Taylor & Van Dyke (1985), and/or radiographs were used for counting vertebrae, teeth, and gill rakers. Scanning Electron Microscope (SEM) images were obtained from teeth and denticulation of gill rakers. Values of the holotypes and neotype of *O. fugitiva* are marked in bold in descriptions.

The following institutions provided material for the study: AMNH - American Museum of Natural History, New York, USA; ANSP - Academy of Natural Sciences, Philadelphia, USA; CAS - California Academy of Sciences, San Francisco, USA; CBF - Colección Boliviana de Fauna, La Paz, Bolívia; FMNH - Field Museum of Natural History, Chicago, USA; INHS - Illinois Natural History Survey, Illinois, USA; INPA - Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; KU - University of Kansas, Kansas, USA; MCP - Museu de Ciências e Tecnologia, Porto Alegre, Brazil; MCNG - Museo de Ciencias Naturales de Guanare, Guanare, Venezuela, MEPN - Museo de la Escuela Politénica Nacional, Quito, Ecuador; MHNG - Muséum d'histoire naturelle, Geneva, Switzerland, MNHN - Muséum d'historie naturelle, Paris, French; MPEG - Museu Paraense Emílio Goeldi, Belém, Brazil; MUSM - Museo de Historia Natural de la Universidad Nacional Mayor de San Marcus, Lima, Peru; MZUSP - Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; NRM - (Naturhistoriska Riksmuseet) Swedish Museum of Natural History, Stockholm, Switzerland; ROM - Royal Ontario Museum, Toronto, Canada; UF - University of Florida, Gainsville, USA; USNM - National Museum of Natural History, Smithsonian Institution, Washington D.C., USA. Abbreviatures given along with the number of specimens are the following: m - morphometrics and meristics; c - only meristics; x - meristics taken from x-rays; c&s - cleared and stained specimens.

As demonstrated by Gonçalves *et al.* (2005) in the characid *Aphyocharax*, sexual dimorphism may start development at different body sizes, according to gonadal maturation, and so, body size itself does not allow assuming a given specimen lacking male sexually dimorphic features is a female. So, males and females are recognized only when dissected, or when showing sexual dimorphism in specimens of similar size in the same collecting lot. Specimens smaller than the smallest specimen showing sexual dimorphism in each lot are termed as unsexed. Specimens of any size belonging to lots where sexual dimorphism is absent are termed as unsexed.

Statistical analyses. Principal component analysis (PCA) was used to check overall variation among samples, looking for differences in morphometrics among species or between sexes, being an input to multiple regressions (Johnson & Wichern, 1998). PCA on covariances of logarithmically transformed measurements were obtained using Past version 1.28 2004, and Sigma Plot version 6.10 2000. The first principal component was partitioned out, considering that it mostly accounts for size variation (Strauss, 1985).

Multiple linear regressions were applied to describe morphometric differences among species or between sexes. An "overall test for coincidental regressions" as described by Zar (1996: 368,431), and Souza (1998:72-77) was used to determine whether the regressions of two set of data are estimating two species or sexes (H1) or the same population regression (Ho). The test was applied when regression lines showed overlapping in confidence limits. The null hypothesis is that there is a single population underlying all *k* regressions. The following formulae were used: F= ((SSR1 - SSR2 / 2) / (SSR2 / n-4)), where n= number of x, y cases, and n-4 means the sum of the two residual degrees of freedom. The F value is obtained by calculating sum of squared residuals (SSR) of each linear regression of any two supposed different species (or between males and females) (SSRsp1+SSRsp2=SSR2), and the pooled sum of squared residuals (SSR1) obtained of a unique linear regression for the same data. The SSR2 < SSR1 indicates two regression lines are better adjusted to the linear model. Considering two separated regression lines would better describe the function between dependent and independent variables of two hypothesized different species than an unique regression line for the same data, the F statistic would be higher than Fisher's F (alpha= 0.05), rejecting Ho. Associated p values were obtained using a F-table.

Results

Odontostilbe fugitiva Cope, 1870

Fig. 1

Odontostilbe fugitiva Cope, 1870: 566 [original description; dentition figured; type locality: "Pebas, Eastern Equador", actually Pebas, Loreto, Peru, in the Ampiyacu-Amazonas drainage]. -Eigenmann & Eigenmann, 1891: 54 [listed, Pebas, Villa Bella, Santarém]. -Eigenmann, 1910: 429 [listed, habitat: Ecuador (following Cope, 1870; currently Peru)]. -Fowler, 1913: 529, 532 [comparison to *O. madeirae* and *O. drepanon*]. -Eigenmann, 1915: 90 [redescription based on specimens of San Antonio de rio Madeira, Amazon basin; erroneous distribution from Panama and Trinidad to La Plata and Peruvian Amazon; in key]. -Eigenmann & Allen, 1942: 45, 265 [listed for the Amazon basin between lower Marañon, Pongo de Manseriche, to Tabatinga; annotated list in Pebas region, lower Marañon]. -Fowler, 1945a:134 [listed, Pebas, Peru]. -Fowler, 1948: 195 [listed, rio Amazonas, Brazil, Equador (following Cope, 1870; actually Peru)]. -Böhlke, 1954: 137-139 [listed, *Odontostilbe fugitiva* as possible synonym of *Odontostilbe pulchra*]. -Géry, 1972a: 20-21 [*O. caquetae* Fowler, 1943, *O. madeirae* Fowler, 1914 and *O. drepanon* Fowler, 1914 as a probable

Fig. 1. Neotype of *Odontostilbe fugitiva*, MUSM 27501, male 34.6 mm SL (top), and specimen NRM15719, female 35.2 mm SL (bottom).

synonyms of *O. fugitiva*, table with measurements and meristics of type material of *O. madeirae* Fowler and *O. drepanon* Fowler]. -Géry, 1977: 555, 558 [in key, *O. madeirae*, *O. drepanon* and *O. caquetae* as synonyms of *Odontostilbe fugitiva*, compilation of Fowler's drawings of *O. madeirae* and *O. drepanon*]. -Sánchez-Botero & Araújo-Lima, 2001: 440 [listed] - Petry *et al*., 2003: 562, 565, 575 [habitat, listed].

Chirodon fugitivus. -Lütken, 1875: 237 [listed; Amazon basin, Pebas].

Chirodon (Odontostilbe) fugitiva. -Steindachner, 1882: 39 [redescription based on specimens from Amazon basin, Villa Bella, Santarém].

Cheirodon fugitiva. -Ulrey, 1895: 288-290 [in key; erroneous compilation of distribution in Petras (= Pebas), and Brazil]. -Ortega & Vari, 1986: 8 [listed, Amazon basin, distribution compiled from Géry (1964)].

Odontostilbe madeirae Fowler, 1913: 527-529 [description, type locality: tributary of rio Madeira, near Porto Velho, Brazil; fig. 6, illustrated specimen; holotype ANSP 39193, 16 paratypes ANSP 39194-209: 12 ANSP 39194, 1 ANSP 39206, 1 c&s ANSP 39207, 1 ANSP 39208, now Géry collection, 1 missing ANSP 39209, same data as holotype]. -Fowler, 1948: [in list; 197-198, rio Madeira; compilation of drawing of original description]. -Böhlke, 1954: 138 [in list].

Odontostilbe drepanon Fowler, 1913: 529-532 [description, type locality: tributary of rio Madeira, near Porto Velho, Brazil; fig. 7, illustrated specimen; holotype ANSP 39210, 6 paratypes ANSP 39211-16, same data as holotype]. -Fowler, 1948:195-196 [in list; rio Madeira; compilation of drawing of original description]. -Böhlke, 1954: 138 [in list].

Odontostilbe caquetae Fowler, 1943: 230-232 [description, type locality: Florencia, río Orteguasa, Colombia; fig. 13, illustrated specimen; holotype ANSP 70495]. -Fowler, 1948: 194-195 [in list; Alto Amazonas, Colombia; compilation of drawing and original description]. -Böhlke, 1954: 138 [in list].

? *Odontostilbe fugitiva*. -Géry, 1964:18-19 [incorrect date of Cope's description 1871, description of one specimen near Iquitos].

Neotype [by present designation]. MUSM 27501, 1 (male 34.6 mm SL), Peru, Loreto, Amazon basin, [lower] río Napo drainage, Yuto cocha on right bank of río Mazán, 3°30'53''S 73°10'05''W, S. O. Kullander, J. Cruz, N. Sarmiento & A. Hogeborn, 16 Aug 1984.

Type material examined. *Odontostilbe madeirae*. Holotype ANSP 39193, 1m, x (female 32.1 mm SL), Brazil, tributary of rio Madeira, near Porto Velho, E. A. Smith, Jan 1913. Paratypes: ANSP 39194, 8x, c of 12 females (females 25.3-29.2 mm SL,), same data as ANSP 39193; ANSP 39206, 1 (female 33.0 mm SL), same data as ANSP 39193; ANSP 39207, 1 (female c&s), same data as ANSP 39193. *Odontostilbe drepanon*. Holotype ANSP 39210, 1m, x (male 30.5 mm SL), Brazil, tributary of rio Madeira, near Porto Velho, E. A. Smith, Jan 1913. Paratypes: ANSP 39211, 6m, x (males 25.2-28.8 mm SL), same data as ANSP 39210. *Odontostilbe caquetae.* Holotype ANSP 70495, 1m, x (unsexed 28.0 mm SL). Colombia, Caquetá, Florencia, río Orteguasa Basin, Amazon watershed [rio Caquetá-Japurá], N. Maria, 1932.

Non-type material. Río Ucayali basin, PERU, UCAYALI: CAS 70915, 8 (unsexed 23.8-27.5 mm SL), lago Cashiboya, cut off lake of río Ucayali above Contamana, connected to river by narrow channel. MZUSP 26039, 1 (unsexed 23.8 mm SL), Coronel Portillo, Iamiricocha, Masisea, [near mouth of río Pachitea]. MZUSP 26066, 1 (male 33.1 mm SL, 3 unsexed 31.2-34.9 mm SL), río Huacamayo, road Pucallpa-Huánuco. MZUSP 26145, 1 (female 34.7 mm SL), Coronel Portillo, Bagazán [Nuevo Bagazán, río Ucayali]. MZUSP 26151, 16m (11 males, 32.7-37.8 mm SL, 5 females, 34.0-35.9 mm SL), same data as MZUSP 26151. MZUSP 26389, 4 (unsexed 28.8-33.0 mm SL), Pucallpa, Ucayali, río Ucayali. MZUSP 26473, 6m (females 32.1-40.5 mm SL), río Neshuya, road Pucallpa-Huánucu. USNM 280627, 2 (unsexed 25.9-26.3 mm SL), Coronel Portillo, main channel and side pools of río Ucayali, approximately 10 km upstream of Pucallpa, 08°31'S 74°22'W. USNM 324110, 2 (unsexed 20.4-21.3 mm SL), same locality as USNM 280627. PERU, LORETO: NRM 15720, 2m (unsexed 30.3-30.5 mm SL), quebrada Copal at km 15 on road Jenaro Herrera-Colonia Angamos, 04°57'S 73°32'W. MCP 27380, 5m of 18 (unsexed, 28.3-37.1 mm SL), Maynas, Reserva Nacional Pacaya-Samiria, caño Yarina, Pacaya tributary, 5°20'34''S 74°30'01''W. MCP 35585, 1 (unsexed 27.1 mm SL), río Pacaya, cocha Yanayacu, río Ucayali drainage. MCP 35586, 5 (unsexed 24.5-27.4 mm SL), same locality as MCP 35585. MCP 27378, 4 (unsexed 26.5-29.9 mm SL), Maynas, río Pacaya, on the road of lagoons Shauinto and Yanayacu, Reserva Nacional Pacaya-Samiria, 5°16'59''S 74°25'29' 'W. MCP 35587, 1 (unsexed 28.8 mm SL), río Pacaya, PV2, caño, lago Yarina, río Ucayali drainage. PERU, JUNÍN: AMNH 20910, 1 (female 40.8 mm SL), Osherato, either río Tambo, brook Osherato or brook Onkoneni, [río Tambo basin or río Ene-Tambo, upper río Ucayali]. PERU, PASCO: MCP 14974, 10 (4 males 25.3-27.4 mm SL, 3 females 35.8-38.7 mm SL, 3 unsexed 26.4-29.5 mm SL), Puerto Bermudez, upper río Pachitea. **Upper río Ucayali, río Urubamba basin,** PERU, CUSCO, LA CONVENCIÓN, ECHARATE: USNM 362022, 8m of 34 (15 males 30.2-38.6 mm SL [4m males 32.0-38.6 mm SL], 6 females 33.9-37.2 [4m females 33.9-36.8 mm SL], 13 unsexed 26.1-36.6 mm SL), río Urubamba, quebrada Pakiria. USNM 362027, 3 (females 35.9-38.3 mm SL), Segakiato, quebrada Prokigiato. USNM 362028, 6 (2 males 36.9-38.0 mm SL, 4 unsexed 28.8-35.9 mm SL), Segakiato, río Camisea. USNM 362029, 2 (females 35.3-35.8 mm SL), Malvinas, Cocha Nueva. USNM 362034, 4 (1 male 38.9 mm SL, 2 females 38.7-39.5 mm SL, 1 unsexed 28.9 mm SL), Peruanita, cocha, Konkariari. USNM 362035, 1 (unsexed 33.8 mm SL), Segakiato, quebrada Anuintoniato. PERU, UCAYALI, ATALAYA: USNM 362024, 6 (4 males 35.1-40.2 mm SL, 2 unsexed 32.3-38.7mm SL), Sepahua, quebrada Shamboyacu. USNM 362031, 8 (unsexed 26.1-34.2 mm SL), lower río Urubamba, Nueva Itália. USNM 362041, 9 (unsexed 27.9-37.8 mm SL), Sepahua, quebrada Pulija, lower río Urubamba. USNM 362043, 10 (2 males 29.7 mm SL & 33.7 mm SL, 7 females 31.9-38.5 mm SL), Sepahua, río Urubamba, quebrada Shambuyacu. **Rio Marañon basin,** ECUADOR, PASTAZA: FMNH 113504, 2 (unsexed 35.9-36.2 mm SL), stream about 100 m from beach called Waama, río Pastaza drainage, 02°16'56"S 77°11'05"W. MZUSP 87746, 11m (1 male 37.2 mm SL, 8 unsexed 33.4-43.1 mm SL, 2 females 36.2 -39.3 mm SL c&s), dead arm of río Pastaza, 02°17'75"S 77°10'13"W. ECUADOR, MORONA-SANTIAGO: FMNH 113515, 12m of 26 (6 males 36.4-45.1 mm, 6 unsexed 34.2-42.7 mm SL), tributary of río Pastaza at [Puerto] Pakintsa, 02°15'46"S 77 °14'17"W. PERU, LORETO: ASNP 150016, 14m of 24 (7 males 28.1-35.3 mm SL, 7 females 28.8-33.1 mm SL), río Huallaga, Yurimaguas creek. FMNH 113503, 11 (unsexed 24.0-34.2 mm SL), río Huitoyacu [río Pastaza drainage], about 0.5 km upstream from the mouth, 04°11’54"S 76°32’38"W. INHS 54760, 6 (unsexed 21.2-25.4 mm SL), floodplain along south bank of south channel of río Marañon due south of Nauta, 04°30.6’S 73°34.1’W. MCP 14944, 5 (2 males 29.5-30.7 mm SL, 3 females 30.6-33.6 mm SL), same data as ANSP 150016. MZUSP 77834, 5m of 49 (28.1-31.3 mm SL), cocha Huanayo, 4°10’50’’S 76°33’5 ’’W. MZUSP 77843, 5m of 147 (23.0-26.1 mm SL), laguna Huayruri, 3°37’32 ’’S 76°24’48’’W. NRM 15756, 19 unsexed of 100 (unsexed 14.3-22.7 mm SL), Teniente López, beach and meadows on left bank of río Corrientes, [río Tigre drainage]. NRM 15653, 1 (female 32.5 mm SL), Nuevo Andoas, pools on Isla Yanayacu and right bank sandy beach in río Pastaza. NRM 50321, 13m (3 males 31.4-34.8 mm SL, 4 females 34.2-39.1 mm SL, 6 unsexed 32.3-34.6 mm SL), río Tigre drainage, San Jacinto, quebrada at km 45.5. PERU, MORONA: ANSP 150047, 4 (2 males 34.1-35.6 mm SL, 2 unsexed 21.9-27.7 mm SL), [río Morona basin], Gosulima Cocha. PERU, HUÁNUCO: ANSP 136951, 4 (females 47.0-48.7 mm SL), Huánuco, vicinity of Tingo Maria, main stream of río Tullamayo, near Puerto Nuevo. **Río Yanayacu basin,** PERU, LORETO: ASNP 178383, 2m (unsexed 20.4-21.9 mm SL), Maynas, at mouth of caño Chincana & Emerald Forest Lodge, approximately 25 miles south of Iquitos. **Río Itaya basin,** PERU, LORETO: ANSP 178908, 12m (5 males 31.7-35.5 mm SL, 1 female 36.9 mm SL, 1 female 35.5 mm SL c&s, 5 unsexed 29.8-34.7 mm), Maynas, [lower río Itaya] at bridge on Iquitos-Nauta highway, approximately 25 miles SSW of Iquitos. INHS 40226, 1 (unsexed 22.5 mm SL), quebrada Mazana, around 1 km up from confluence with río Itaya, S of Belém, Iquitos. **Lower río Napo basin, río Mazán,** PERU, LORETO: NRM 15719, 6m (3 males 32.2-34.0 mm SL, 3 unsexed 32.8-35.2 mm SL), same data as neotype. **Río Ampiyacu basin,** PERU, LORETO: ANSP 131535, 1m (unsexed 30.8 mm SL alizarin stained), near Pebas, Chancho caño. CAS 136607, 1m (unsexed 32.8 mm SL), caño Chancho. CAS 136608, 1m (unsexed 35.2 mm SL), caño Chancho [lower río Ampiyacu basin, near Pebas]. USNM 175990, 1m (unsexed 35.8 mm SL), caño [Chancho]. USNM 207666, 1 (unsexed 21.1 mm SL), near [Pevas], río Ampiyacu drainage. **Río Orosa basin,** PERU, LORETO: INHS 39313, 2 (unsexed 20.0-20.7 mm SL), Mayuruna Cocha, around 30 minutes by boat downstream of mouth of caño Tonche, 71.7 miles east Iquitos. INHS 39789, 1 (unsexed 23.8 mm SL), lago Pabellon, around 40 minutes upstream by boat from Paucarillo base camp 57.1 miles east Iquitos. **Río Yavari / Javari basin,** PERU, LORETO: NRM 15671, 3m of (unsexed 26.8-30.6 mm SL), Colonia Angamos, quebrada behind school building. **Upper río Amazonas basin,** PERU, LORETO: ANSP 136955, 6 (unsexed), vicinity Iquitos, río Nanay opposite naval base, backwater pools off coche, 4 miles above Amazon. ANSP 136958, 3 (unsexed), same data as ANSP 136955. ASNP 178239, 1m (unsexed 35.5 mm SL), Maynas, río Amazonas main channel along W bank, *ca.* 30-45 min. upstream from inlet to Iquitos (=mouth río Itaya). CAS 70897, 1 (unsexed 26.6 mm SL), Iquitos, río Amazonas. INHS 39852, 1 (unsexed 21.2 mm SL), río Amazonas, across from Puebla Gallito, 7.68 miles SE Iquitos. INHS 540237, 1 (unsexed 22.9 mm SL), río Amazonas, *ca.* 10 & 40 minutes upstream from mouth caño Zapatilla, near town of Yanashi. COLOMBIA, AMAZONAS: FMNH 85346, 27 (unsexed 19.9-25.5 mm), black water river at Yauacaca and first tributary upstream from Leticia on the Colombian side. MCP 14949, 8m of 10 (1 male 33.4 mm SL, 2 females 32.7-34.2mm SL, 5 unsexed 31.9-34.0mm SL), Leticia, backwater (the lakes) area cut off from río Amazonas, formerly ANSP 135937. MCP 35263, 2 (males 32.4-34.0 mm SL), same data as MCP 14949, formerly ANSP 135975. ROM 56384, 6 (unsexed 24.2-31.0 mm SL), 10-60 miles upstream from Letícia, río Amazonas, 4°09’S 69°57’W. ROM 56443, 42 (9 males 31.8-33.4 mm SL, 33 unsexed 31.3-33.9 mm SL), same place as ROM 56384. **Río Putumayo basin,** PERU, LORETO: NRM 26365, 4m (unsexed 21.8-24.4 mm SL), Estrecho, río Putumayo right bank, 02°28’S 72°42’W. COLOMBIA, AMAZONAS: NRM 26430, 3m (unsexed 29.5-32.1 mm SL), río Putumayo drainage, Buenaventura, flooded river margin. **Rio Jutaí basin,** BRAZIL, AMAZONAS**:** MZUSP 17585, 8 (unsexed 21.4-28.1 mm SL), rio Içapó, mouth of rio Jutaí. **Rio Juruá Basin,** BRAZIL, ACRE: MPEG 1951, 3 (unsexed 21.0-23.8 mm SL), Marechal Taumaturgo, rio Juruá, Seringal do Oriente. MPEG 6790, 10m of 30 (unsexed 29.4-32.9 mm SL), Tarauacá, rio Tarauacá. MZUSP 30372, 4m (3 unsexed 20.0-24.7 mm SL, 1 female 32.2 mm SL), same locality as MPEG 6790. MZUSP 31820, 1 (unsexed 22.8 mm SL), same locality as MPEG 6790. MZUSP 42842, 21 (unsexed 18.5-22.0 mm SL), same locality as MPEG 6790. MZUSP 87749, 2m (unsexed 21.6-29.7 mm SL), same locality as MPEG 6790. **Rio Japurá Basin,** BRAZIL, AMAZONAS: MZUSP 27760, 13 (unsexed 17.9-28.0 mm SL), Tefé, Costa Japão, lower rio Japurá. MZUSP 74964, 22 (unsexed 22.0-31.6 mm SL), Serrinha, rio Japurá in Serrinha, right margin. MZUSP 77466, 2 (unsexed 34.9-36.4 mm SL), Vila Bitencourt. MZUSP 77535, 9 of 19 (unsexed 24.8-28.7 mm SL), rio Japurá in Serrinha. **Rio Purus Basin,** BRAZIL, ACRE: MCP 37473, 1 (unsexed 38.5 mm SL), small affluent of rio Iaco, road Sena Madureira-Rio Branco, about 8 km of Sena Madureira. MCP 38106, 2 (unsexed 25.6-24.3 mm SL), rio Acre, Xapuri. MZUSP 49580, 3 (unsexed 20.8-22.4 mm SL), rio Acre. MZUSP 49669, 1 (unsexed 28.2 mm SL), Porto Acre, rio Acre, Seringal Bom Destino (1 hour upper Porto Acre), Instituto. MZUSP 49767, 2 (unsexed 23.0-27.3 mm SL), rio Acre, between Seringal Paraíso and lago Amapá. MZUSP 87754, 29 (unsexed 23.0-33.4 mm SL), Manoel Urbano, rio Purus. BRAZIL, AMAZONAS: MZUSP 49512, 11 of 22 (unsexed 21.4-27.2 mm SL), Boca do Acre, rio Acre. **Rio Solimões basin,** BRAZIL, AMAZONAS: MCP 38314, 20 (unsexed 22.5-30.9 mm SL), stream in Jacaré, near Fonte Boa. MZUSP 6315, 1 (unsexed 24.7 mm SL), lago Castro, mouth of rio Purus. MZUSP 9644, 2 (unsexed 23.4-26.6 mm SL), lago Supiá in front of Codajás. MZUSP 9647, 5 (unsexed 16.2-19.5 mm SL), same data as MZUSP 9644. MZUSP 16690, 1 (unsexed 23.8 mm SL), Benjamin Constant, [rio Solimões]. MZUSP 17344, 8 (unsexed 18.8-25.3 mm SL), rio Solimões, Ilha Sorubim, above Coari. MZUSP 17415, 10 (unsexed), same data as MCP 38314. MZUSP 17421, 175 (unsexed 17.9-31.6 mm SL), same data as MCP 38314. MZUSP 17438, 3 (unsexed 18.1-24.9 mm SL), igarapé Manduaçú, paraná de Iupiá, NW Fonte Boa. MZUSP 17498, 5 (unsexed 18.0-37.9 mm SL), rio Solimões, near Ilha de Baruruá, above mouth of rio Jutaí. MZUSP 17395, 33 (unsexed 16.5-28.1 mm SL), rio Solimões. MZUSP 17520, 2 (unsexed 22.1-30.5 mm SL), Santo Antônio do Içá, mouth of rio Içá. MZUSP 17632, 4 (unsexed 28.7-31.0 mm SL), Fonte Boa, rio Solimões. MZUSP 27751, 13 (unsexed 15.4-24.3 mm SL), Benjamin Constant, paraná do Capacete, rio Solimões. MZUSP 78108, 11 of 23 (unsexed 15.5-21.1 mm SL), Costa do Anori, pool, rio Solimões, near mouth of rio Purus. MZUSP 78109, 3 (unsexed 18.9-21.5 mm SL), same data as MZUSP 78108. USNM 310856, 3 (2 males 34.1-34.4 mm SL, 1 unsexed 33.6 mm SL), muddy igarapé connecting rio Solimões and blackwater lake *ca.* 15 miles west of Coari. BRAZIL, AMAZONAS, municipality of Manaus and proximities (including municipalities of Iranduba or Careiro): INPA 18461, 9 (8 males 32.6 mm SL, 1 female 35.1 mm SL), lago Janauacá, mouth of channel. INPA 18465, 66m of 73 (34 males 33.0-36.5 mm SL, 2 males 34.9-37.2 mm SL c&s, 13 females 32.9-38.1 mm SL, 2 females 34.5-38.4 mm SL c&s, 15 unsexed 29.7-35.9 mm SL), Ilha da Marchantaria. INPA 18467, 25 (7 males 31.7-34.4 mm SL, 18 unsexed 22.5-36.3 mm SL), same locality as INPA 18465. INPA 18506, 10m of 50 (1 male 32.4 mm SL c&s, 1 female 33.9 mm SL c&s, 1 unsexed 23.7 mm SL c&s, 7 unsexed 22.2-24.4 mm SL), paraná do Xiborena. INPA 18510, 132 (unsexed 19.1-29.2 mm SL), lago Pirapora, Catalão. INPA 18512, 1m (male 34.9 mm SL c&s), same locality as INPA 18510. MCP 35775, 110 (61 males 30.0-36.2 mm SL, 45 females 30.9-36.9 mm SL, and 4 unsexed 28.8-30.0 mm SL), Janauari, lago Terra Preta. MCP 35777, 12m of 36 (6 males 30.6-36.6 mm SL, 6 females 34.5-37.2 mm SL), same locality as MCP 35775. MZUSP 6047, 1 (unsexed 26.9 mm SL), lago do Rei, Ilha do Careiro. MZUSP 18736, 2 (unsexed 26.3-33.7 mm SL), lago Janauacá, left margin of rio Solimões. MZUSP 18743, 1 (unsexed 33.0 mm SL), lagoon linked to channel of lago Janauacá, left margin of rio Solimões. USNM 307448, 21 (14 males 32.5-36.7 mm SL, 7 females 37.9 mm SL), São José, lago do Castanho, Janauacá. USNM 308329, 20 (7 males 31.2-34.4 mm SL, 13 unsexed 27.9-34.3 mm SL), lago Terra Preta, Janauari. USNM 310851, 2 (males 31.0-31.4 mm SL), lower rio Negro: igarapé Xiborena *ca.* 30 km east Manaus. USNM 315907, 29 (unsexed 20.7-26.9 mm SL), lago Murumuru, cattle enclosure. USNM 332135, 1 (male 32.6 mm SL), near Manaus, lago Janauari, lago Terra Preta. USNM 323629, 3 (unsexed 27.0-29.9 mm SL), northwest shoreline of Ilha Paciência, rio Solimões, southeast of Manaus. **Lower rio Amazonas basin,** BRAZIL, AMAZONAS: MZUSP 76436, 2 (unsexed 34.4-35.4 mm SL), Parintins, São José, rio Amazonas, left margin, stream mouth. MZUSP 76437, 1 (unsexed 37.6 mm SL), same as MZUSP 76436. BRAZIL, PARÁ: ANSP 150113, 5 (3 males 35.1-35.3 mm SL, 2 females 35.7-36.9 mm SL), paraná-Mirim, lagoa Grande, east of Óbidos. ANSP 149979, 4 (unsexed 34.6-35.6 mm SL), Centro Comercial, brook into lago Grande [near Santarém]. MCP 14959, 4 (3 males 32.6-36.2 mm SL, 1 female 39.2 mm SL), same as ANSP 150113. MZUSP 9498, 7 (unsexed 18.3-24.2 mm SL), Monte Alegre, rio Amazonas. MZUSP 16565, 2 (unsexed 27.0-27.3 mm SL), Oriximiná, Paissandu, [mouth of rio Trombetas]. **Rio Madeira Basin,** BRAZIL, RONDÔNIA, CALAMA: MCP 38482, 12m (5 males 32.1-33.1 mm SL, 7 unsexed 30.9-35.4 mm SL), paraná do Caraparú, rio Madeira. MPEG 3211, 1 (female 38.6 mm SL), same locality as MCP 38482. MPEG 3213, 1 (female 36.7 mm SL), paraná do Flechal. MZUSP 30212, 1 (unsexed 21.2 mm SL), beach of rio Madeira. MZUSP 30213, 1 (unsexed 24.9 mm SL), same locality as MCP 38482. MZUSP 30216, 1 (female 42.5 mm SL), same data as MPEG 3213. MZUSP 30218, 37 (23 males 29.4-32.8 mm SL, 14 unsexed 29.7-34.3 m SL), same data as MCP 38482. MZUSP 30219, 1 (unsexed 29.2 mm SL), rio Madeira, mouth of rio Machado. MZUSP 30220, 1m (male 33.0 mm SL). MZUSP 30221, 1 (unsexed 31.4mm SL), rio Madeira. MZUSP 31784, 1 unsexed 30.9 mm SL, same locality as MCP 38482. MZUSP 35600, 11 (unsexed 21.8-34.2 m SL). MZUSP 42838, 11 (unsexed 15.1-27.6 mm SL), poço da Angélica, rio Madeira. BRAZIL, AMAZONAS: MZUSP 6961, 3 (unsexed 19.7-27.7 mm SL), 25 km below Nova Olinda. MZUSP 18658, 20 (unsexed 19.1-27.2 mm SL), igarapé Xicanga, 5 km from Humaitá, east part of Transamazônica. MZUSP 35591, 3 (unsexed 27.3-29.1 mm SL), mouth of igarapé Puruzinho, rio Madeira. MZUSP 35618, 20 (unsexed 21.2-27.9 mm SL), ilha do Puruzinho, rio Madeira. MZUSP 55922, 3 (unsexed 19.2-20.1 mm SL), rio Madeira, 17.3 km below paraná do Maracá, 3°40’48"S 59°5’30"W. MZUSP 57082, 1 (unsexed 25.6 mm SL), rio Madeira, 15.9 km below paraná do Maracá, 3°43’6"S 59°5’56"W. USNM 310855, 19 (unsexed 18.6-25.2 mm SL), same data as MZUSP 18658. BRAZIL, RONDÔNIA: FMNH 57880, 3 (unsexed 27.7-33.4 mm SL), Santo Antonio, rio Madeira. MZUSP 31821, 1 (unsexed 19.0 mm SL), rio Madeira, cachoeira de Teotônio. MZUSP 35605, 2 (unsexed 26.7-31.4 mm SL), rio Madeira, cachoeira de Santo Antônio. MZUSP 35610, 2 (unsexed 23.4-27.7 mm SL), same data as MZUSP 35605. MZUSP 42840, 22 (unsexed 16.3-26.9 mm SL), rio Madeira, cachoeira de Teotônio. MZUSP 74227, 30 of 233 (unsexed 22.0-28.3 mm SL), rio Machado near mouth. MZUSP 74321, 30 of 455 (unsexed 23.2-27.9 mm SL), same data as MZUSP 74227. MZUSP 76551, 1 (unsexed 26.0 mm SL), Santo Antônio, rio Machado, beach. MZUSP 76829, 1 (unsexed 27.5 mm SL), Santo Antônio, rio Machado, beach. MZUSP 80041, 30 of 91 (unsexed 22.6-28.6 mm) SL, same data as MZUSP 74227.

Diagnosis. The combination of the following characters distinguish *Odontostilbe fugitiva* from all the other species of the genus: (1) mouth terminal, mouth slit nearly at horizontal through middle of eye (*vs.* subterminal, mouth slit at horizontal near lower eye edge in *O. euspilura* and *O. microcephala*; or slightly subterminal, mouth slit at horizontal below middle of eye in *O. dierythrura*); (2) in males snout not very protruding, but slightly pointed or blunt (*vs.* very protruded in *O. euspilura*, *O. microcephala*, and *O. dierythrura*); (3) usually 7 large dentary teeth, with seven cusps (*vs.* 4 large dentary teeth with 3 large and compressed central cusps and 2, 3 lateral small cusps in *O. pequira*); (4) elongation of 2nd unbranched dorsal-fin ray (*vs.* no elongation in *O. euspilura*, or very short elongation in *O. pulchra*); (5) pectoral-fin never extending beyond pelvic-fin origin (*vs.* extending beyond in males of *O. pulchra*); (6) branched anal-fin rays 19-24 (mostly 21-22) [*vs.* 16-20 (mostly 17-18 in *O. microcephala*, and 17-20 (mostly 18-19) in *O. euspilura*]; (7) 1st to 9th (mostly 6th-7th) anal-fin branched rays of males with hooks, positioned at distal half-length of fin rays, tiny hooks occasionally present distally up to 19th anal-fin branched ray (*vs.* well-developed hooks on 1st to 22nd anal-fin branched rays at distal half length of fin rays in *O. pulchra*); (8) no hooks found on 1st unbranched pelvic-fin rays (*vs.* 1-2 unpaired hooks per segment on 1st unbranched pelvic-fin ray occasionally present in *O. euspilura* and *O. pulchra*); (9) gill rakers on upper branch usually 6-7, lower branch usually 12-13 (*vs.* usually 10-12 on upper branch and 14-16 on lower branch in *O. microcephala*; 11-12 on lower branch in *O. dierythrura* and *O. pulchra*; 5-6 on upper branch and 9-10 on lower branch in *O. euspilura*; and 7-8 on upper branch and 13-15 on lower branch in *O. pequira*); and (10) 4 separate supraneurals (*vs.* supraneurals partially fused in *O. paraguayensis*). Upper gill raker counts differ *O. fugitiva* (5-6) from *O. ecuadoriensis*, *O. nareuda*, and *O. parecis* (6-7).

Description. Morphometric data in Table 1. Largest male 45.1 mm SL, female 48.7 mm SL. Body elongate and compressed. Males with more compressed bodies than females. Greatest body depth at dorsal-fin origin. Snout slightly pointed or blunt in males. Head profile gently convex from snout to posterior tip of supraoccipital bone. Predorsal profile slightly convex to straight between posterior tip of supraoccipital bone and dorsal-fin origin, then straight from dorsal-fin origin to caudal peduncle. Ventral profile convex from mouth tip to anal-fin origin. Anal-fin base straight. Caudal peduncle slightly longer than deep.

Head relatively small. Posterior margin of opercle sinusoidal with upper portion concave and lower portion convex. Mouth terminal, mouth slit nearly at horizontal through middle of eye. Obliquously positioned maxilla ending at vertical near or at anterior border of eye and at horizontal on inferior eye border, not crossing these limits. Dentition (based on 10 c&s specimens and 17 alcohol specimens). Premaxillary teeth 5-6, bearing 6-11 cusps (usually 8, 9, and 10); midcentral cusp longer than others; smaller lateral cusps of each tooth overlap cusps of adjacent teeth, except anteriormost teeth (Fig. 2). Premaxillary teeth juxtaposed external to dentary teeth, leaving premaxillary tooth cusps exposed when mouth closed. Maxilla with 2-3 teeth bearing 1-9 cusps (mostly 7-9), decreasing cusp number toward posterior tip of maxilla. Dentary teeth 8-10 bearing 1-9 cusps, gradually decreasing in size posteriorly, first 6-7 teeth largest with 5-9 cusps (mostly 7), 1 medium-sized tooth with 4-7 cusps and last 1-3 teeth very small, conic or with 2-5 cusps. Smaller cusps of dentary teeth overlaping adjacent tooth cusps, usually not in posteriormost teeth. All dentary tooth cusps upwardly pointed or slightly recurved towards interior of mouth.

Dorsal-fin rays **ii**(259), 8(1), or **9**(258). Dorsal-fin origin slightly posterior to midlength of body, and slightly posterior to pelvic-fin origin. First unbranched dorsal-fin ray in females and immature males about half length of second unbranched dorsal-fin ray. Second unbranched dorsal-fin ray slightly elongate in mature males, extending beyond dorsal-fin distal profile. Anal-fin rays **iv**(14), v(241) or vi(4), 19(14), 20(57), 21(103), **22**(57), 23(23), or 24(5). Anal-fin distal border concave, anterior 6-7 branched rays longest. Pectoral-fin rays **i**(259), 9(1), 10(11), **11**(135), 12(105), or 13(7). Unbranched pectoral-fin ray reaching or not pelvic-fin origin, never extending beyond that point. Pelvic-fin rays **i**(259), 6(4), **7**(244), 7i(7), or 8(4). Unbranched pelvic-fin ray longest in mature males, extending beyond origin of anal fin. Lateral skin border of unbranched pectoral-fin ray and unbranched pelvic-fin ray thickened in mature males, bearing thin laterodorsal projection of hard tissue covered with soft tissue. Principal caudal-fin rays **19**(254), rarely 16(1), 17(1), 18(7) or 20(2). Procurrent caudal-fin rays: dorsal 10(34), **11**(113), 12(96), 13(9), or 14(4); ventral 7(1), 8(14), 9(133), **10**(94), or 11(14). Anterior 1 or 2 ventral procurrent caudal-fin rays sometimes laterally expanded, bifurcated, or S-shaped. Caudal-fin ray flaps ventrally on 2nd-8th (mostly 4th-7th) branched rays of upper lobe, and dorsally on 12th-16th (mostly 13th-15th) branched rays of lower lobe. Adipose-fin at vertical through last anal-fin ray insertion.

Males with acute, elongate, retrorse hooks on posterior margin of pelvic- and anal-fin rays. One or two (rarely 3) paired and unpaired hooks per segment of lepidotrichia, on last unbranched anal-fin ray, and 1st to 8th (mostly 6th-7th) anal-fin branched rays, positioned at distal half-length and not extending to ray tip; tiny hooks can be present distally up to 19th anal-fin branched rays in very developed males (*e.g.* INPA 18506, ANSP 178908, ANSP 15006, and neotype). One or two (rarely 3) unpaired and long hooks per segment of lepidotrichia along almost all length of 1st to 7th branched pelvic-fin rays, reaching distal tip of fin ray (expect on 1st branched pelvic-fin ray, on midlength portion). No hooks found on 1st unbranched pelvic-fin ray. One to 3 unpaired hooks sometimes present on anterior border of anal- and pelvic-fin rays branches.

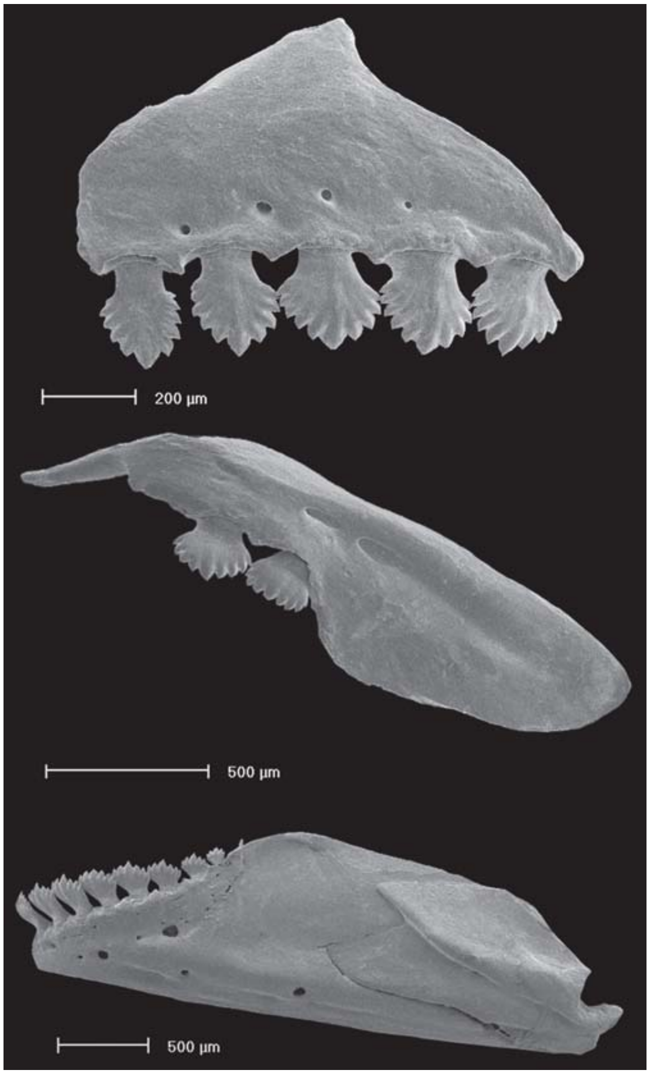


Fig. 2. Dentition of *Odontostilbe fugitiva*, ANSP 178908, female 35.5 mm SL. SEM photograph of left side premaxilla (top), maxilla (middle), and dentary (bottom).

Scales cycloid; lateral line complete 34(3), 35(21), **36**(90), 37(4), or 38(1); predorsal row 9(4), 10(98), **11**(122), or 12(6); scale rows between lateral line and dorsal-fin origin 5(31), **6**(190), or 7(5); scale rows between lateral line and anal-fin origin **4**(238) or 5(5); scale rows around caudal peduncle **14**(186). Triangular modified scale on pelvic fin base extends posteriorly covering 1-3 scales (mostly 2). Scales on anal-fin base 5, **6**, or 7.

Cleared and stained specimens (11): supraneurals 4-5(11); precaudal vertebrae 16(9) or 17(2); caudal vertebrae 18(3), 19(7), or 20(1); gill rakers, upper 6(1) or 7(5), lower 12(6) (2-3 on hypobranchial). Alcohol specimens (174): gill rakers, upper 6(83), **7**(89), or 8(2), lower 11(15), 12(119), **13**(36), or 14(4). Upper gill rakers with 1-5 recurved denticles on anterolateral

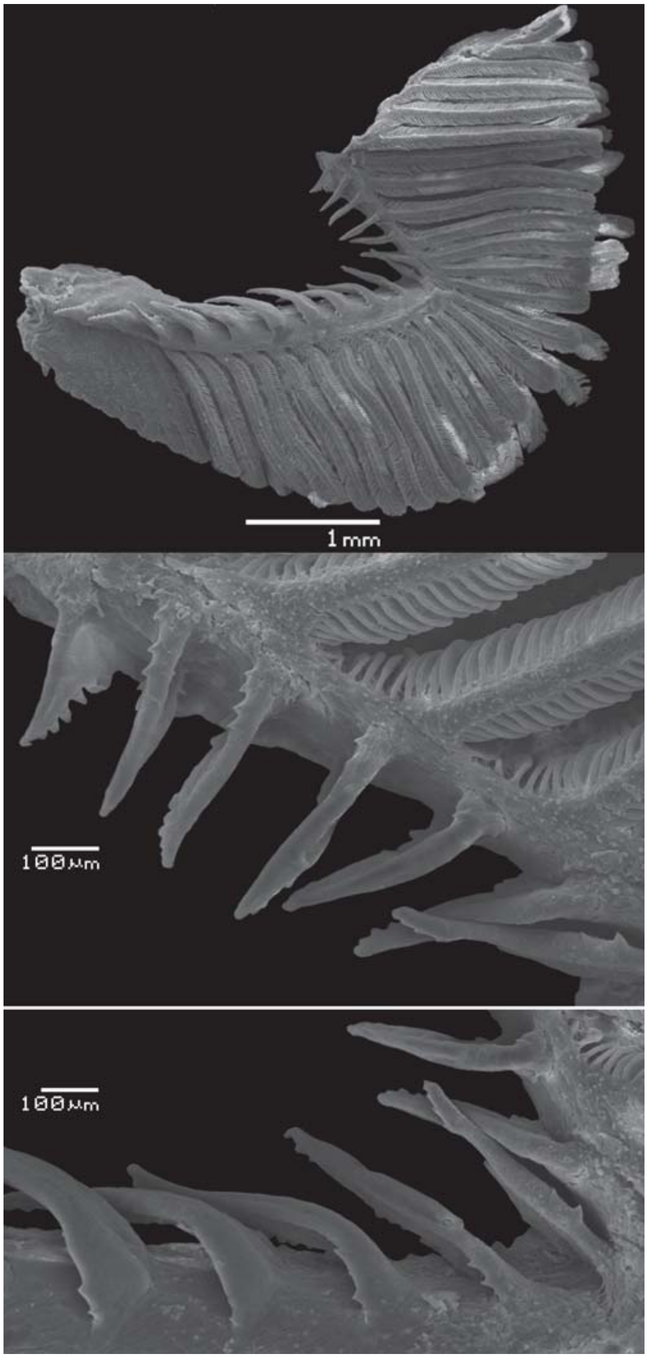


Fig. 3. First gill arch of *Odontostilbe fugitiva*, MCP 35777, male 35.7 mm SL. SEM photographs of the first left side gill arch showing gill gland (top), in detail gill rakers on upper branchial branch (middle), and gill rakers on lower branchial branch (bottom). Lateral view.

border, and anteriormost upper gill rakers with none or 1 similar denticle on posterolateral border; lower gill rakers with 1-4 denticles on anterolateral border, and none or 1 on posterolateral surface; and posteriormost lower gill raker with none or 1 recurved denticle on anterolateral border, and none, 1 or 2 similar denticles on posterolateral border (Fig. 3). Denticulation mainly on basal portion of gill rakers.

Color in alcohol. General ground body color brownish or pale yellow. Dark dorsum pigmentation from head to caudal peduncle, dark chromatophores mostly on border of scales forming reticulated pattern. Pigmented scales extend laterally on body below longitudinal stripe, also on pseudotympanum area or not. Dorsal fin entirely scattered with dark chromatophores along fin rays, densely along 1st-2nd unbranched dorsal-fin rays. Dark chromatophores along 1st-9th dorsal branched fin rays, except almost hyaline 9th branched fin ray. Pectoral and pelvic fins with scattered dark chromatophores, more numerous on anteriormost portions of fins. Fresh specimens only with 7th branched pelvic-fin ray hyaline. Neotype with 1-5th branched pelvic-fin rays pigmented. Pelvic fin mainly hyaline in old-preserved specimens. Anal fin with dark chromatophores spread on all fin rays or on more central branched anal-fin rays, except at tips of last unbranched fin rays and 1st branched fin ray. Adipose fin not pigmented. Caudal fin almost entirely covered with diffuse dark chromatophores along fin rays, except clear areas on base of caudal-fin lobes just behind caudal-fin spot. Rounded black to brown spot on base of caudal fin, reaching upper and lower border of peduncle, or upper border only, sometimes extending little onto proximal portion of 7th to 12th central principal caudal-fin rays.

Numerous dark chromatophores, somewhat contiguous, on snout, upper and lower lips, anteriormost portion of maxilla, and 1st, 2nd, and 6th infraorbitals. Top of head on frontals and parietals pigmented, with deep-lying dark chromatophores over brain membranes below frontals and parietals, and fontanel. Body with faint dark and silver midlateral stripe, sometimes forming black line along middle longitudinal body axis, beginning behind or on pseudotympanum, above lateral line, and reaching caudal spot. Guanine on eye iris, opercle, isthmus, and most of 3rd infraorbital. Below lateral line, belly faint almost without pigmentation, chromatophores above anal-fin base forming 12 to 15 chevron shaped markings.

Color in life. Life color of specimen from lower Ucayali drainage (Fig. 4). One red spot on base of each caudal fin lobe, just posterior to caudal fin black blotch. Red and yellow pigments most on dorsal and anal fins. White pigment on tips of last unbranched and 1st-2nd branched anal-fin rays, and of unbranched and first branched pelvic-fin rays.

Sexual dimorphism. Males with hooks on anal- and pelvic-fin rays, and elongate dorsal- and pelvic-fin rays, in contrast to absence of these features in females. A gill gland (Burns & Weitzman, 1996) present in mature males on first gill arch, covering about 8 to 10 anterior branchial filaments (Fig. 3). Sexual dimorphism in general body shape is also recognized by principal component analysis performed on measurements of males and females (Fig. 5). Principal component 2 (PC2) grouped males and females separately. It was affected strongly and negatively by pelvic-fin length, snout length, and dorsal-fin length; and positively by depth at dorsal-fin origin. Males are particularly distinct from females in all of these characters, having higher values of pelvic-fin length, snout

Fig. 4. *Odontostilbe fugitiva* from lower río Ucayali drainage. Photo by William Crampton (Ucamara Project).

length, and dorsal-fin length than females, while females have higher depth values at dorsal-fin origin than males (Table 1). Principal component 3 (PC3) was affected strongly and positively by snout length and upper jaw length, and negatively by pelvic-fin length and dorsal-fin length. Variation on PC3 seems to be related to the level of development of pelvic- and dorsal-fin rays, snout protusion (snout length, and upper jaw length) in males, because males with higher values for these features are located upper on PC3 axis (Fig. 5).

Remarks on the holotype of *Odontostilbe fugitiva*. The short description of *O. fugitiva* by Cope (1870) makes no reference to type specimens. Most type-specimens of fishes described by Cope were deposited at ANSP, although some at USNM and some are missing (Böhlke, 1984; Vari & Howe, 1991). Henry W. Fowler was the first full-time curator of the fish collection at ANSP, and one of his first tasks was the cataloging of the extensive collection of Edward D. Cope (Böhlke, 1984). During his stay at ANSP, Fowler (1913: 529, 532) described *O. madeirae* and *O. drepanon* and Fowler (1940) *O. dierythrura* and *O. hasemani*, but he did not mention any type specimens for *O. fugitiva*. Finally, when describing *O. caquetae*, Fowler (1943: 232) stated that the type of *O. fugitiva* was lost. Géry (1972a) also affirmed the holotype of *O. fugitiva* was lost after visiting ASNP to study Fowler's type material. Vari & Howe (1991) did not list *O. fugitiva* among characiform type specimens at USNM.

Böhlke (1984: 46) indicated ANSP 8059 as the holotype of *O. fugitiva*, and noticed that "original Cope label and catalog indicate this to be type of *O. fugitiva*". However, in the same publication, Böhlke (1984: 46) remarked the same lot (ANSP 8059) was listed by Fowler (1906) as the holotype of *Aphyocharax filigerus*, valid as *Prionobrama filigera* (Cope, 1870). Examination of ANSP 8059 confirmed this is a specimen of *P. filigera*. Both authors have fruitlessly searched the ANSP and USNM fish collections after the type material of *O. fugitiva* [including the lot ANSP 8073 listed by Fowler (1906) as cotypes of *Aphyocharax filigerus*].

Neotype designation. *Odontostilbe fugitiva* is the type species of *Odontostilbe*, and the designation of a neotype, as well as establishment of the identity of the type species is essential in solving nomenclatural questions among cheirodontines. The neotype was not caught at Pebas, the original type locality of *O. fugitiva*. Pebas is located at the confluence of río Ampyiacu with río Amazonas, Loreto, Peru. The neotype is a mature male from an affluent of lower río Napo basin, río Mazán, upper rio Amazonas, Loreto, Peru. Río Mazán is to the west of the type locality, being the nearest site (Fig. 6) with the best preserved mature male (Fig. 1) available, being in conformity with ICZN (1999). Since secondary sexually dimorphic characters are important to distinguish *Odontostilbe* and other Cheirodontinae genera, a mature male is preferred as the neotype. The chosen male has entire elongate 2nd unbranched dorsal-fin ray and unbranched

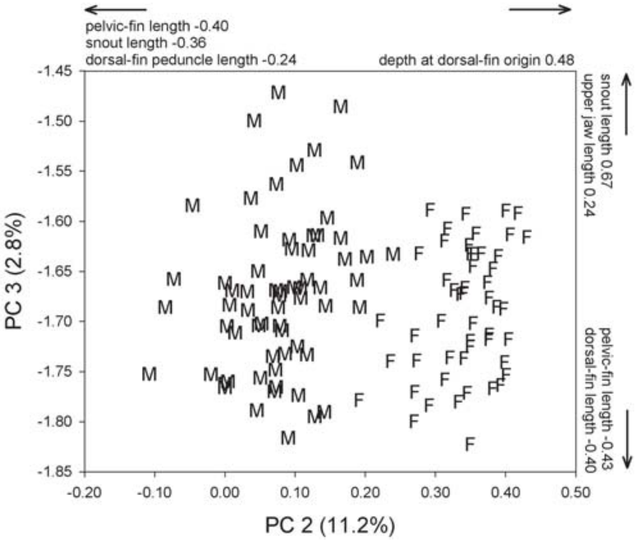


Fig. 5. Principal component analysis of the 18 morphometric data of males (M) and females (F) of *Odontostilbe fugitiva*. Stronger loadings on the second and third principal components (PC2, PC3).

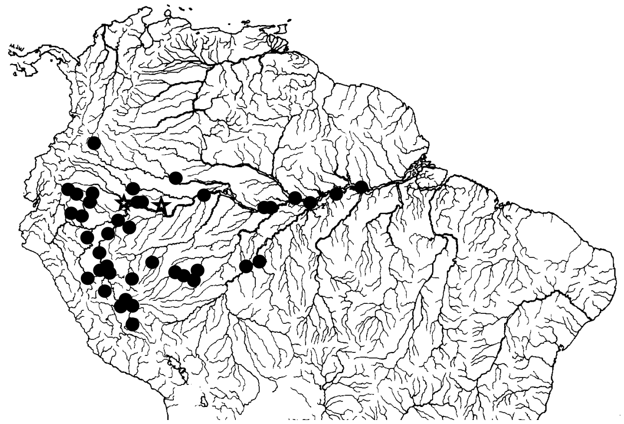


Fig. 6. Distribution of *Odontostilbe fugitiva* in central and northen South America. Circles (material examined, symbols can represent more than one lot, and more than one locality), and stars (type locality of neotype on the rigth and of the lost holotype on the left).

pelvic-fin rays, well-developed acute retrorse hooks on pelvic- and anal-fin rays, preserved scales, and well-preserved color pattern (Fig. 1). Cope (1870: 566) referred to a "transverse line [of scales] at vent 11; at ventral fins 5-5". Although distinct from the counts of the neotype, these counts are included in the range found herein for the species (5-7 between lateral line and dorsal-fin origin and 4-5 between lateral line and anal-fin origin).

The status of *Odontostilbe madeirae* and *Odontostilbe drepanon*. Both species were described in the same paper by Fowler (1913). The holotype (Fig. 7) and all paratypes but one of *O. drepanon* have the dimorphic characters unique to males of *Odontostilbe*: elongation of 2nd unbranched dorsal-fin ray and 1st unbranched pelvic-fin rays, and presence of hooks on pelvic-fin rays and anal-fin rays. On the other hand, the holotype (Fig. 7) and all paratypes of *O. madeirae* lack these characters, and have higher body depth, the diagnostic features for females (see Table 1 and description under Sexual Dimorphism above). The two species described by Fowler (1913) overall match the *O. fugitiva* diagnosis, and this is a case of misunderstanding dimorphic males and females as two different species. Fowler (1913: 529) remarked that the absence of "the dark-edged silver lateral band" in *O. madeirae* is a character to distinguish it from *O. fugitiva*. The holotype and paratypes of *O. madeirae* actually have a faded longitudinal line of chromatophores posterior to the pseudotympanum.

The holotype of *O. madeirae* has few dentary teeth remaining, but laterally 4 teeth remain, each with 7 cusps. Premaxillary teeth 5 with 7-8 cusps and maxillary teeth 2 with 7 cusps. The holotype of *O. drepanon* also lacks most dentary teeth, but on the right side four teeth remain each with about 7 cusps. Premaxillary teeth 5 with 7-9 cusps, and maxillary teeth 2 with 7 cusps. The 2nd unbranched dorsal-fin ray is broken.

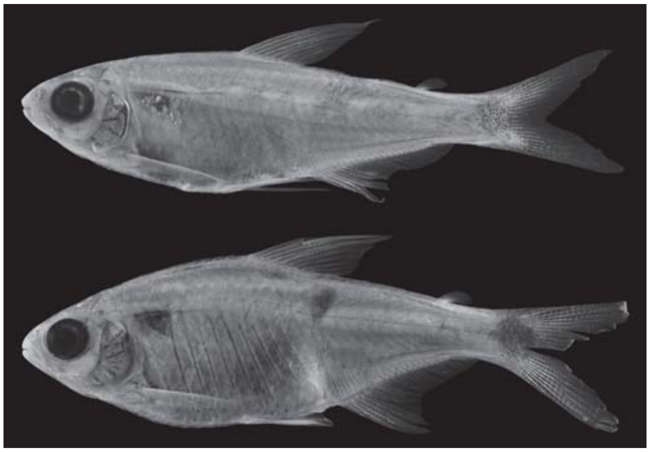


Fig. 7. Holotypes of *Odontostilbe madeirae*, ANSP 39193, female 32.1 mm SL (top), and *Odontostilbe drepanon*. ANSP 39210, male 30.5 mm SL (bottom - The darkned area below dorsal fin is a preservation artifact).

The status of *Odontostilbe caquetae*. *Odontostilbe caquetae* was described from a single immature specimen (28.0 mm SL). Fowler diagnosed *O. caquetae* comparing the holotype with data available in the short redescription of *O. fugitiva* by Eigenmann (1915:93), which was based on four specimens examined from "San Antonio de Rio Madeira", measuring "largest 41 mm". Following Fowler's diagnosis, *O. caquetae* would have a smaller head, smaller eye and larger snout than *O. fugitiva*. However, measurements and counts of the holotype of *O. caquetae* overlap those of *O. fugitiva* (Table 1), not supporting any of Fowler's diagnostic characters. For that reason, we consider *O. caquetae* as a synonym of *O. fugitiva*.

The holotype is now dark colored and damaged with most dorsal-fin rays and caudal-fin rays broken (Fig. 8). Infraorbitals 2-5 are lacking on the left side. Premaxilla probably would have five teeth, but just two of them remain on each left and right sides, bearing 8-7 cusps. Right maxilla with 2 teeth bearing 8-9 cusps, and left maxilla with only one tooth with 8 cusps. Four dentary teeth remain on each side bearing 5-6 cusps. This dentition is similar to that found in smaller specimens of *O. fugitiva, O. pulchra*, *O. euspilura* or *O. ecuadorensis*. The type locality of *O. caquetae* is Florencia, río Portuguesa, río Caqueta drainage, where *O. euspilura* occurs (Fowler, 1945b). The main reason for not considering *O.*

Fig. 8. Holotype of *Odontostilbe caquetae*, ANSP 70495, unsexed 28.0 mm SL.

caquetae as synonym of *O. euspilura* is the terminal mouth in the former, against the inferior mouth in the latter.

The first right gill arch of the holotype was found cut off from branchial apparatus, but kept under the operculum. Both first gill arches have 6 gill rakers on upper branch and 11 on lower branch. Fowler (1943: 232) described 7+11 gill rakers and it is possible the first gill raker was lost in the damaged upper branches of both gill arches. Specimens of *Odontostilbe* examined from rio Japurá, the Brazilian name for mid and lower río Caqueta, match *O. fugitiva* in measurements and counts, including 6, 7 gill rakers on upper gill arch and 12 on lower (one among 10 examined specimens of rio Japurá has 6+11 gill rakers as the holotype of *O. caquetae*). Therefore we consider *O. caquetae* as synonym of *O. fugitiva*. However, we consider this synonym provisional since no mature males of *Odontostilbe* were available from upper río Caqueta or rio Japurá.

Distribution and geographical variation. *Odontostilbe fugitiva* is the most widespred *Odontostilbe* species in the Amazon basin, occurring from the major western tributaries to the lower rio Amazonas (Fig. 6). More extense records are from the río Ucayali, río Marañon, rio Amazonas and rio Madeira basins. Records from western major tributaries of the Amazon, Purus and Juruá systems, are relatively scarce. Predominantly, the species occurs in major whitewater rivers of the Amazon basin, being not so far identified from the rio Negro, rio Trombetas, rio Tapajós, rio Xingu, rio Tocantins-Araguaia. The well-sampled fish fauna of the rio Negro did not reveal *O. fugitiva* (Goulding *et al.*, 1988), though they listed 12 specimens of "*Cheirodon* sp." (not found at INPA collection). Chao (2001) also did not include *O. fugitiva* in a list of fishes of rio Negro basin and lower rio Branco caught by Project Piaba. Personal searches [CMB] at INPA and Project Piaba fish collections failed in finding *O. fugitiva* in rio Negro material. Lowe McConnell (1991) listed *O.* cf. *fugitiva* from a tributary of the rio Araguaia, the rio das Mortes. However, the examination of material from the rio Araguaia basin failed to reveal any *O. fugitiva*.

Specimens from upper río Marañon, upper río Ucayali drainages, and middle rio Amazonas (rio Solimões) showed some variation in morphometry. This seems to be related to some exceptionally developed males and females in samples from upper portions of Marañon and Ucayali. Indeed, the largest mature specimens of *O. fugitiva* come from upper río Pastaza**,** Ecuador (FMNH 113515), and upper río Huallaga, Peru (ANSP 136951), both upper affluents of Maranõn, with some comparable size specimens only from río Urubamba, upper Ucayali. Noteworthy, males from río Marañon basin (río Pastaza, río Tigre, and río Huallaga) show a tendency to have longer snout lengths and upper jaw lengths than males of most populations of upper río Amazonas basin (río Putumayo, río Itaya, río Mazán, río Ampyiacu, río Yavari, and the río Amazonas). However, no additional differences were found to support the recognition of a separate species for río Marañon basin**.** Some specimens from the upper río Pastaza (FMNH 113515) show a somewhat subterminal mouth similar to *O. dierythrura* and other undescribed species from río Madre de Dios, upper rio Madeira basin. *Odontostilbe dierythrura* and this undescribed species, however, possess larger upper jaw length (Fig. 9), and more pronounced snouts than *O. fugitiva*, including the Marañon population.

Males of río Ucayali basin also had differences in snout and upper jaw length when contrasted with males from the main rio Amazonas basin, having snout length difference statistically significant in the coincidental regression test ($F_{(2, 74)}$= 11.8, $p<0.00$) (Fig. 10). When compared to *O. fugitiva*, *O. dierythrura* and *Odontostilbe* n. sp. from Madre de Dios, the upper jaw length of the population from río Urubamba, upper Ucayali, remains at an intermediate range between *O. fugitiva* and the other two species (Fig. 11). Again, considering there

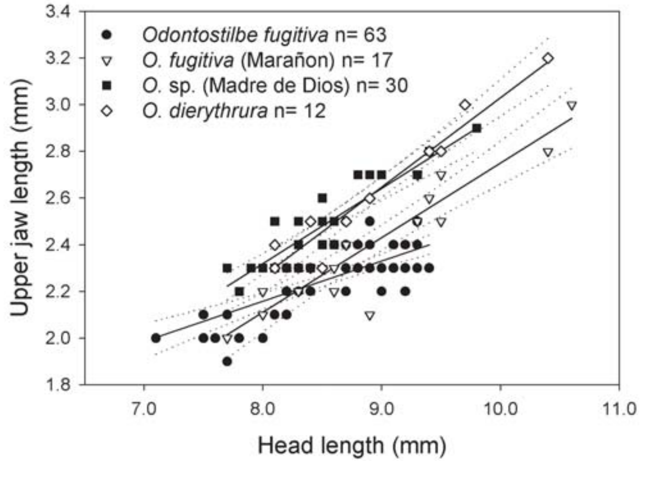


Fig 9. Upper jaw length as a function of head length for males of *Odontostilbe fugitiva*, specimens widely distributed on rio Amazonas, and upper and middle río Maranõn basin, against *O. dierythrura* and *Odontostilbe sp.* of río Madre de Dios basin.

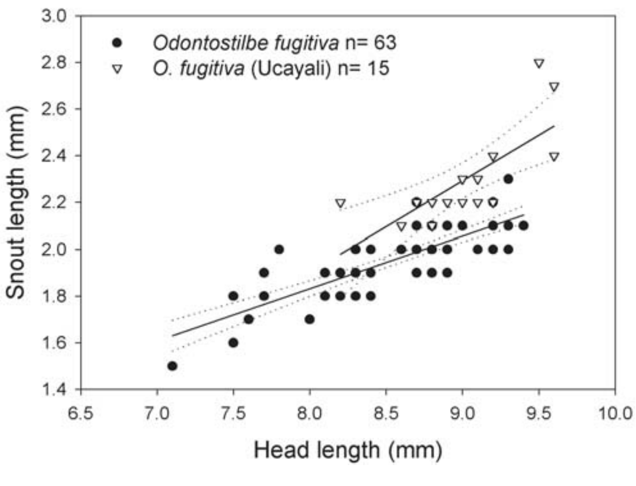


Fig 10. Snout length as a function of head length for males of *Odontostilbe fugitiva*, specimens widely distributed on rio Amazonas basin against specimens of río Ucayali basin.

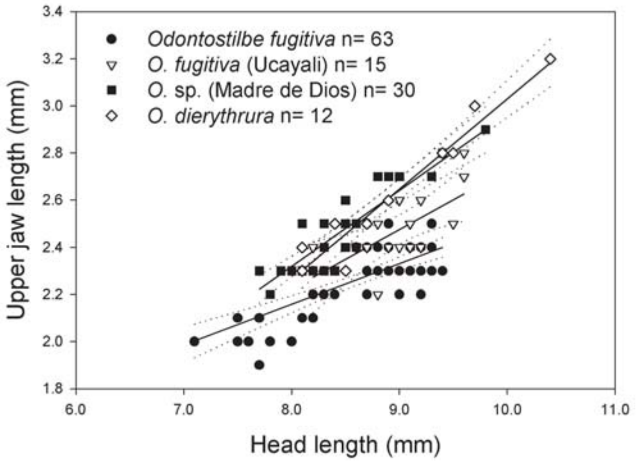


Fig 11. Upper jaw length as a function of head length for males of *Odontostilbe fugitiva*, specimens widely distributed on río Amazonas basin, and specimens of río Ucayali basin, against *O. dierythrura* and *Odontostilbe* sp. of río Madre de Dios basin.

were no additional characters differing these populations, and the overlaps in statistics for snout length and upper jaw length, the Ucayali population is considered to be *O. fugitiva*.

A significant statistical difference in measurements was also found when comparing rio Solimões samplings from the region near Manaus to overall *O. fugitiva* material from upper rio Amazonas basin, including río Ucayali and río Marañon systems. Not only males, but females and unsexed specimens jointly, show differences in snout to pectoral-fin length ($F_{(2, 200)} = 85.6$, $p<0.00$) (Fig. 12). This difference is also considered a variation among *O. fugitiva* populations. However, there is a lack of mature males and females among specimens available from an extensive portion of the rio Solimões between Letícia, Colombia, and Manaus, Brazil. Most samples from Solimões consisted of material caught near Manaus by Peter Bayley in 1970s or more recently by INPA researchers.

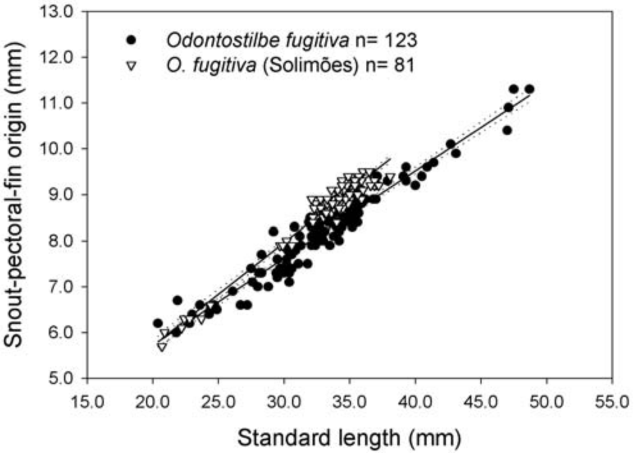


Fig. 12.. Snout to pectoral-fin length as a function of standard length for males, females, and unsexed specimens of *Odontostilbe fugitiva*, specimens widely distributed in rio Amazonas basin against specimens of rio Solimões basin (middle rio Amazonas).

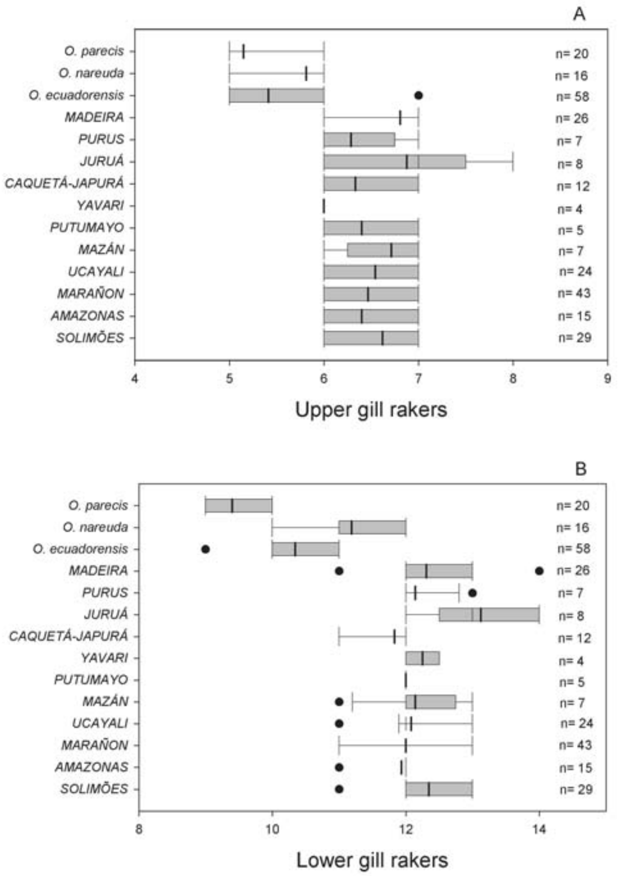


Fig. 13. Upper and lower gill rakers counts of *Odontostilbe fugitiva* populations, and three new species *Odontostilbe ecuadorensis*, *Odontostilbe nareuda*, and *Odontostilbe parecis*.

Examined specimens from rio Juruá basin are unsexed, probably juveniles. Exceptionally, two specimens among 8, have 8 upper gill rakers, and 3 specimens have 14 lower gill rakers (Fig. 13a). Higher gill raker counts occur in *O. dierythrura* and in an undescribed species from Madre de Dios. However, the upper jaw lengths of the avaliable specimens of Juruá fit that of *O. fugitiva*. One specimen of *O. fugitiva* from the rio Madeira also has 14 lower gill rakers (Fig. 13b). Similarly, specimens examined from rio Purus contain only unsexed specimens. In the lack of fully developed, mature specimens, we tentatively assign Juruá and Purus specimens to *O. fugitiva*.

Ecological notes. Recorded mainly from whitewaters; blackwater as "black-muddy" is cited only for FMNH 85346, a stream near Leticia, Colombia. Sánchez-Botero & Araújo-Lima (2001) referred to *Odontostilbe piaba*, *Odontostilbe* sp. and *Odontostilbe fugitiva* in a list of species associated with roots of aquatic macrophytes during high water period at three floodplain lakes of rio Solimões. Sánchez-Botero *et al.* (2003)

Table 1. Morphometrics of *Odontostilbe fugitiva*, upper rio Amazonas basin (río Ucayali, río Marañon, río Putumayo, río Itaya, río Mazán, río Ampyiacu, río Amazonas, río Yavari, rio Juruá, rio Madeira, rio Solimões). Neotype MUSM 27501 of río Mazán, affluent of mouth of río Napo. Separately, the holotype ANSP 70495 of *Odontostilbe caquetae* syn. from the río Caquetá basin, the holotype ANSP 39193 of *O. madeirae* syn., and holotype ANSP 39210 of *O. drepanon* syn., plus six paratypes ANSP 39211 from the rio Madeira basin.

	Males					Females				Unsexed				*O. caquetae*	*O. madeirae*	*O. drepanon*				
	Neotype	n	Low	High	Mean	n	Low	High	Mean	n	Low	High	Mean	Holotype	Holotype	Holotype	n	Low	High	Mean
Standard length	34.6	88	28.1	45.1	34.3	60	28.8	48.7	35.5	102	20.4	43.1	31.1	28.0	32.1	30.5	6	25.2	28.8	27.2
Percents of standard length																				
head length	24.3	88	23.1	27.5	25.8	60	22.1	27.2	25.0	101	22.7	30.1	25.6	24.3	24.6	25.6	6	25.9	28.4	27.0
snout-anal fin origin	63.6	88	60.6	66.9	63.8	60	62.9	70.2	66.2	102	60.9	68.1	64.8	63.6	65.7	63.0	6	62.8	64.3	63.6
snout-dorsal fin origin	48.0	88	47.1	51.4	49.0	60	47.4	52.8	50.7	102	48.3	53.6	50.4	49.6	48.9	46.6	6	47.2	50.7	49.2
snout-pelvic fin origin	45.4	88	43.7	49.6	46.3	60	45.3	51.3	48.0	102	44.4	49.3	47.1	45.0	47.7	44.9	6	44.8	47.1	46.3
dorsal-fin base	13.6	88	13.2	15.7	14.2	60	13.1	15.4	14.5	102	12.9	16.6	14.4	13.2	14.6	13.8	6	13.5	15.9	14.5
anal-fin base	27.5	88	23.5	28.9	26.7	60	24.3	28.9	26.6	101	24.0	29.4	26.7	24.3	26.2	26.9	6	25.3	27.6	26.4
caudal peduncle length	13.6	88	11.3	15.3	13.3	60	10.9	13.9	12.4	102	10.8	14.4	12.5	14.3	13.1	12.5	6	13.1	14.0	13.6
caudal peduncle depth	10.4	88	9.0	12.5	11.1	60	10.1	13.0	11.5	102	9.0	12.7	10.9	10.4	10.9	11.1	6	9.9	11.8	11.1
depth at dorsal-fin origin	28.3	88	26.6	35.5	31.7	60	29.6	41.3	35.9	102	28.6	37.6	32.2	29.6	35.5	30.8	6	29.0	33.1	30.1
dorsal-fin length	29.8	71	27.6	37.1	31.5	50	27.4	32.3	30.0	91	27.7	32.8	30.0	21.4	30.8	31.8	6	28.5	37.2	33.5
pelvic-fin length	20.2	88	16.9	26.8	21.2	60	16.9	19.5	18.2	102	15.4	23.4	17.9	17.5	18.4	24.3	6	18.2	25.7	22.6
pectoral-fin length	21.7	88	19.3	24.2	22.2	60	18.8	22.8	21.2	102	19.3	24.3	21.1	17.5	21.2	21.6	6	22.1	23.5	22.5
snout-pectoral-fin origin	24.0	88	23.1	27.1	25.6	60	22.1	26.8	24.8	102	23.0	30.6	25.6	25.0	25.9	24.6	6	25.0	27.9	26.1
Percents of head length																				
snout length	22.6	88	21.3	29.5	23.6	60	19.1	24.7	22.0	101	18.0	25.6	21.4	20.6	22.8	25.6	6	19.4	24.7	22.1
upper jaw length	26.2	88	23.6	29.3	26.6	60	24.0	30.0	26.7	101	23.4	29.9	26.7	27.9	27.8	28.2	6	25.3	28.2	26.5
horizontal eye diameter	36.9	88	32.3	38.6	35.3	60	34.0	41.3	36.9	101	33.7	41.8	37.8	41.2	34.2	34.6	6	28.9	35.8	33.6
least interorbital width	32.1	88	29.3	35.8	32.7	60	30.0	36.5	32.9	101	28.8	37.0	32.7	32.4	32.9	32.1	6	29.8	32.0	30.8

listed *Odontostilbe aff. piaba* caught under macrophytes *Eichhornia azurea* and *Eichhornia crassipes* in lago Camaleão, considering *Odontostilbe* among the typical fish genera associated to *Eichhornia* spp., along with *Ctenobrycon, Synbranchus*, *Hemigrammus*, *Moenkhausia, Mylossoma*, and *Hoplias*. Some of the fish collected by Sánchez-Botero & Araújo-Lima (2001) were examined at INPA. Three distinct species of Cheirodontinae were identified by those authors as "*O. fugitiva*", including two *Serrapinnus* species, plus *O. fugitiva.* That is not surprising, since *O. piaba* [actually *Serrapinnus piaba*] for example is used in the literature as a misidentification of several *Serrapinnus* spp. In any case, Sánchez-Botero & Araújo-Lima (2001) results pointed out a high abundance of the cheirodontine *O. fugitiva* and at least three *Serrapinnus* spp. (*Serrapinnus micropterus*, *Serrapinnus* gr. *microdon*, and *Serrapinnus* n. sp., our identifications) in lakes from the rio Solimões floodplain. Peter Bayley fish collections undertaken during the late 1970's from the same lakes were also extensively examined (material at ANSP, MCP, and USNM), confirming that *O. fugitiva* is very common in these floodplain lakes. At the same localities, Marchantaria Isle (lago Camaleão), Janauacá, and Janauari, *O. fugitiva* was caught associated with macrophytes *Echinochloa polystachya*, *E. crassipes*, *Paspalum repens*, *Panicum* sp., or unvegetated places, and considered as omnivorous (Petry *et al.*, 2003).

Two new cheirodontine species provisionally treated as "*Odontostilbe*", but not described herein, are sympatric and have been found mixed with *O. fugitiva* in some jars. One of these new species mostly occurs in the río Ucayali basin and the second in the río Marañon basin.

***Odontostilbe ecuadorensis*, new species**

Fig. 14

Holotype. ANSP 170608, 1 (male 45.7 mm SL), Ecuador, Napo, Santa Cecilia, río Aguarico, 00°06'N 76°51W; W. G. Saul & F. B. Cross, 14 Jun 1968.

Paratypes. ECUADOR, SUCUMBÍOS: ANSP 130574, 12m (1 male 45.6 mm SL, 9 females 42.7-46.7 mm SL, 1 female 49.1 mm SL c&s, 1 unsexed 35.1 mm SL), backwater of río Aguarico at Santa Cecilia, 00°06'N 76°51'W, W. G. Saul, 30 Jun 1967. MCP 38419, 12m (5 males 32.7-38.6 mm SL, 1 female 40.1 mm SL, 6 unsexed 24.1-36.2 mm SL), río Napo, beach on south bank, 2.7 km upstream from bridge at Coca, 00°29'S 77°24'W, D. Stewart, M. Ibarra, R. Barriga & Uquillas, 2 Oct 1981. FMNH 113512, 74 unsexed (4 males 32.4-33.4 mm SL, 70 unsexed 28.6-35.0 mm SL), same data as MCP 38419. KU 13524, 15m of 32 (7 males 36.3-45.8mm SL, 2 males 43.3 mm SL and 43.5 mm SL c&s, 2 females 41.7 mm SL and 45.2 mm SL, 1 female 45.2 mm SL c&s, 3 unsexed 33.6-34.8 mm SL), Aguarico, isolated pool at backwater of río Aguarico at Santa Cecilia, W. G. Saul, 27 Jun 1968. KU 13526, 3m (1 male 44.0 mm SL, 2 females, 47.7-50.2 mm SL), río Aguarico at Santa Cecilia, W. G. Saul, 13 Mar 1967. MEPN 1517, 2m (1 female 45.2 mm SL, 1 female 43.6 mm SL c&s), Sucumbíos, río Duguno, 2 km on south of indian group Cofán del Duguno, Aguarico [drainage], 00°08'15"N 76°45'18"W, R. Barriga & S. Criollo, 1 May 1995. ECUADOR, NAPO: FMNH 113511, 1m (7 males, 38.2-45.5 mm SL), río Napo, cocha of mainstream, at and 1.2 km downstream from mouth of río Suyunoyacu (*ca.* 16 km from Coca), 00°32'36''S 77°04'54''W, 22 Sep 1981. FMNH 113513, 11m (unsexed 29.6-32.5 mm SL), río San Miguel at Tipishca, km 54.5, [upper río Putumayo], 00°12'30''S 76°13' W, D. Stewart, M. Ibarra & R. Barriga., 4 Oct 1983. FMNH 113514, 5m (4 males 40.6-43.2 mm, 1 male 43.5 mm SL c&s, 1 female 40.3 mm SL), Napo, quebrada Capihuara, distributary of río Payamino, [río Coca, río Napo drainage], 00°30’S 76°14’30’’W, D. Stewart, M. Ibarra & R. Barriga., 13 Nov 1983.

Non-type material. Río Napo basin, ECUADOR, SUCUMBÍOS: ANSP 141496, 2m (unsexed 27.8-28.8 mm SL), [río Pañayacu], 00°25’S 76°07’W. ANSP 141506, 12m (unsexed 27.0-31.2 mm SL), Napo, near mouth of río Cuyabeno, 00°16’S 75°53’W. ECUADOR, NAPO: ANSP 141508, 1m (female 36.0 mm SL), mouth of río Shushu Fundi, 00°18’S 76°21’W. PERU, LORETO, MAYNAS, ARCADIA: USNM 379440, 1 (unsexed 28.5 mm SL), middle río Napo, Padre Isla, cocha Chica. USNM 379469, 1 (unsexed 21.2 mm SL), middle río Napo quebrada Negra 1, en la quebrada Norte. USNM 384420, 1 (unsexed 22.3 mm SL), same data as USNM 379440. USNM 384822, 1 (unsexed 18.0 mm SL), río Napo, cocha de Conchas. PERU, LORETO, MAYNAS, CASTANA: USNM 328553, 5 (unsexed 17.0-18.1 mm SL), middle río Aguarico, quebrada Castana Negra. **Lower río Napo,** PERU, LORETO: ANSP 178148, 2m (unsexed 33.7 -40.9 mm SL), Maynas, beach & backwater along right bank just upstream from mouth río Mazán, near town of Mazán, 03°29’10’’S 73°06’24’’W. INHS 36600, 2m (unsexed 30.4-32.0 mm SL), mouth of río Mazán, near town of Mazán. INHS 36658, 1m (unsexed 37.6 mm SL), 1 km upstream mouth of río Mazán, 3 km west town of Mazán. INHS 36668, 1m (unsexed 30.6 mm SL), 1 km upstream mouth of río Mazán, 3 km west town of Mazán.

Diagnosis. Characters that diagnose *Odontostilbe ecuadorensis* are: (1) upper gill rakers 5-6, lower 9-11, mostly 10-11 (*vs.* upper gill rakers 6-8, mostly 6-7, and lower 11-14, usually 12 in *O. fugitiva* (Fig. 13a-b); (2) denticulation of gill rakers more numerous in *O. ecuadorensis* than in *O. fugitiva* (in specimens larger than 32.5 mm SL), mainly on posteriormost gill raker of lower arch (5-6 denticles on basal portions of gill raker in *O. ecuadorensis vs.* 0-2 in *O. fugitiva* (Figs. 3, 16); (3) elongate 2nd unbranched dorsal-fin ray (*vs.* not elongate in *O. euspilura* and very short elongate in *O. pulchra*); (4) no hooks on unbranched pelvic-fin ray (*vs.* 1-2 unpaired hooks per segment on 1st unbranched pelvic-fin ray occasionally present in *O. euspilura* and *O. pulchra*); (5) 1-3 paired or unpaired hooks per segment on last unbranched anal-fin ray, and 1st to 16th anal-fin branched rays (small hooks like knots on anal-fin ray branches, usually on 10th branched fin ray and following rays) (*vs.* well-developed hooks on 1st to 22nd anal-fin branched rays at distal half length of fin rays in *O. pulchra*); and (6) usually seven large dentary teeth, with seven cusps (*vs.* 4 large dentary teeth with 3 large and compressed central cusps and 2, 3 lateral small cusps in *O. pequira*). *Odontostilbe ecuadorensis* differs from sympatric *O. euspilura* by its terminal mouth (*vs.* subterminal mouth).

Description. Morphometric data given in Table 2. Slender and large *Odontostilbe* species, largest male (holotype) 45.7 mm SL, largest female 47.7 mm SL. Body elongate and compressed, more compressed in males than females. Greatest body depth at dorsal-fin origin. Snout pointed in males, rounded in females. Head profile slightly convex from snout to dorsal-fin origin; profile descends from that point almost straight to caudal peduncle. Ventral profile convex from lower jaw to caudal peduncle. Anal-fin base straight. Caudal peduncle slightly longer than deep.

Head relatively small. Posterior margin of opercle sinusoidal with upper portion concave and lower portion convex. Mouth terminal. Maxilla short terminates at vertical near or at anterior eye border, horizontal to lower eye border. Dentition (based on 6 c&s specimens and 28 alcohol specimens). Premaxillary teeth 4, 5, or 6, bearing 5-9 cusps (usually 7, 8, or 9); midcentral cusp longest, lateral cusps overlap cusps of adjacent teeth (Fig. 15). Premaxillary teeth juxtaposed external to dentary teeth, leaving premaxillary tooth cusps exposed when mouth closed. Maxilla with 2 or 3 teeth bearing 1-9 (usually 7) cusps, decreasing cusp number toward posterior tip of maxilla. Dentary teeth 8-9 gradually decreasing in size posteriorly, anterior 6 teeth large bearing 5-7 cusps (usually 7), and posterior teeth small, conic or with 2-5 cusps. Smaller cusps of dentary teeth overlap cusps of adjacent teeth, usually not in posteriormost teeth.

Dorsal-fin rays **ii**(89), **9**(89). Dorsal fin slightly posterior to mid body length, and slightly posterior to pelvic-fin origin. First unbranched dorsal-fin ray in females and immature males about half length of second unbranched dorsal-fin ray. Second unbranched dorsal-fin ray elongate in mature males, extending beyond dorsal-fin distal profile. Anal-fin rays iii(1), iv(8), **v**(78), vi(2); 18(3), 19(15), 20(34), 21(31), or **22**(6). Anal-fin distal border concave, anterior 6-7 branched rays longest. Pectoral-fin rays **i**(89), 10(8), **11(**55), or 12(26). Unbranched pectoral-fin ray reaching or not pelvic-fin origin, never extending beyond pelvic-fin origin. Pelvic-fin rays **i**(89), 6(1), **7(**87), or 8(1). Unbranched pelvic-fin rays longest in mature males, extending beyond origin of anal fin. Lateral skin border of unbranched pectoral-fin rays and unbranched pelvic-fin rays thickened in mature males, bearing thin laterodorsal projection of hard tissue covered with soft tissue. Principal caudal-fin rays **19**(89). Procurrent caudal-fin rays: dorsal 8(1), 9(3), 10(5), 11(31), 12(44), or **13**(5); ventral 8(5), 9(33), 10(41), **11**(9), or 12(1). Sometimes 1-2 anterior ventral procurrent caudal-fin rays laterally expanded, bifurcated, or S-shaped. Caudal-fin ray flaps ventrally on 3rd-8th rays of upper lobe, dorsally on 12th-16th rays of lower lobe. Adipose-fin at vertical through to last anal-fin ray insertion.

Males with robust, elongate, retrorse hooks on posterior border of pelvic- and anal-fin rays. One to 3 paired or unpaired hooks per segment on last unbranched anal-fin ray, and 1st to 16th branched anal-fin rays, more developed from 1st to usually 7th rays and very small like knots usually on 10th branched fin ray and following rays. Hooks on middle portion of anterior rays and on distal portion after 3rd branched anal-fin ray. One to 3 unpaired acute, elongate hooks per segment of lepidotrichia along almost entire length of 1st to 7th branched pelvic-fin rays, and reaching tip of fin rays (except on 1st branched pelvic-fin ray, on midlenght portion). No hooks found on 1st unbranched pelvic-fin ray. One or two hooks on anterior border of branches of anal-fin rays. One or two hooks on anterior border of branches of pelvic-fin rays.

Scales cycloid; lateral line complete 35(6), 36(42), 37(11), or **38**(2); predorsal row 10(37), **11**(48), or 12(2); upper trans-

Fig. 14. Holotype of *Odontostilbe ecuadorensis*, ANSP 170608, male 45.7 mm SL (top), and paratypes MEPN 1517, 1 female 45.2 mm SL (middle) with exceptionally developed ovaries, ANSP 130574, female 46.6 mm SL (bottom).

verse rows 5(9), **6**(76), or 7(2); lower transverse rows **4**(87) or 5(1); scale rows around caudal peduncle **14**(73). Triangular modified scale on pelvic fin base extends posteriorly covering 2, 3 scales. Scales on anal-fin base **6**-8.

Cleared and stained specimens (5): supraneurals 4; precaudal vertebrae, 16(4) or 17(1); caudal vertebrae 18(1), 19(2), or 20(2); gill rakers, upper 5(2) or 6(3), lower 10(2) or 11(3) (2 on hypobranchial). Alcohol specimens (58): gill rakers, upper 5(35), **6**(22), or 7(1), lower 9(1), **10**(36), or 11**(**21). Upper gill rakers with 1-6 recurved denticles on anterolateral border, and 1-3 similar denticles on posterolateral border; lower gill rakers with 1-6 recurved denticles on anterolateral border (1-4 anteriormost lower gill rakers with opposing 1-3 denticles); excepting posteriormost lower gill raker with 3-6 recurved denticles irregularly placed on anterior border, and 4-6 similar denticles on posterior border (Fig. 16a-d). Less numerous in small specimens (one specimen 27.1 mm SL, with none to 3 denticles on lateral border of upper gill rakers, and

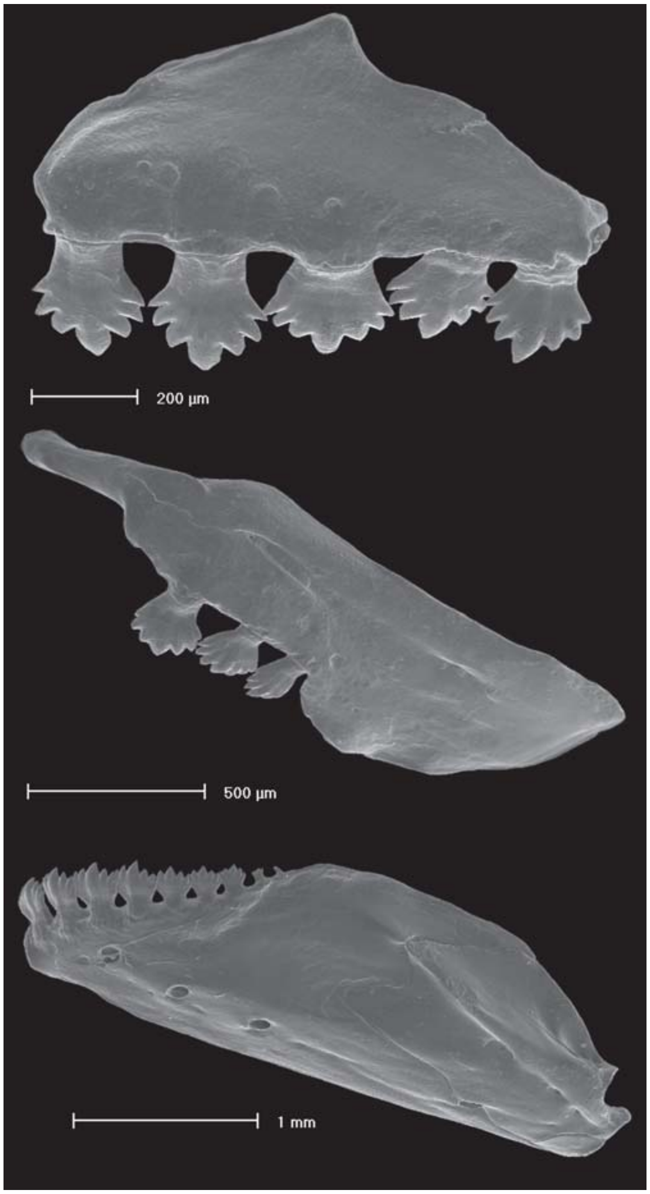


Fig. 15. Dentition of *Odontostilbe ecuadorensis*, KU 13524, male 43.5 mm SL. SEM photograph of left side premaxilla (top), maxilla (middle), and dentary (bottom).

none to 3 on lateral border of lower gill rakers). All denticulation mostly on basal portion of gill rakers.

Color in alcohol. General ground body color brownish yellow. Dark dorsum pigmentation from head to caudal peduncle, chromatophores mostly on border of scales. Pigmented scales extend laterally on body above longitudinal stripe, sometimes on pseudotympanum area in well-pigmented specimens. Dark chromatophores on all dorsal-fin rays, along 1st and 2nd unbranched fin rays and faint on 1st-8th branched dorsal-fin rays, almost hyaline on 9th branched ray. Dark chromatophores on 1st unbranched pectoral-fin ray, less numerous on 1st and 2nd branched fin rays, following branched rays practically hyaline. Pelvic fins usually hyaline, with some dark chromatophores on unbranched pelvic-fin ray. Anal fin mostly clear with few dark chromatophores. Some specimens bearing dark chromatophores on distal portion of middle branched anal-fin rays. Adipose fin not pigmented. Caudal fin almost entirely covered with diffuse dark chromatophores along fin rays, except light areas on base of caudal-fin lobes just behind caudal-fin spot. Somewhat rounded brownish caudal spot on base of caudal fin, reaching upper border of peduncle, but never reaching lower border, sometimes extending on proximal portion of 7th to 12th central caudal-fin rays (specimens from río Cuyabeno). Holotype is not well-pigmented, with pelvic and anal fins hyaline.

Black chromatophores on snout, upper lip, sometimes on lower lip, anteriormost portion of maxilla, and 1st, 2nd, and 6th infraorbitals. Pigmentation on top of head on frontals, and parietals with deep-lying dark chromatophores over brain membranes below frontals and parietals, and fontanel. Body with faint dark and silver midlateral stripe, sometimes reduced to one or two parallel lines, along middle longitudinal body axis, beginning above pseudotympanum, above lateral line, and reaching caudal spot. Guanine on eye iris, opercle, isthmus, and most of 3rd, 4th, and 5th infraorbitals. Below lateral line, belly faint, chromatophores just above anal fin-base forming 6 to 10 chevron shaped markings.

Sexual dimorphism. Males with hooks on anal- and pelvic-fin rays, elongate dorsal- and pelvic-fin rays, in contrast to absence of these features in females (see description). Gill gland (Burns & Weitzman, 1996) presents on first gill arch in mature males, covering about 8 to 12 anterior branchial filaments (Fig. 16). Principal component analysis of morphometric data of males and females denotes sexual dimorphism in general body shape (Fig. 17). Principal component 2 (PC2) grouped males and females separately, being affected strongly and negatively by snout length, pelvic-fin length, and caudal peduncle length; and positively by depth at dorsal-fin origin. Males are distinguished from females in all these characters, showing higher values of snout length, pelvic-fin length, and caudal peduncle length than females, while females have higher values of body depth at dorsal-fin origin than males (Table 2). Principal component 3 (PC3) was affected strongly and positively by snout length and upper jaw length, and negatively by pelvic-fin length and dorsal-fin length. Some males have well-developed dorsal and pelvic-fin rays, and protuding snouts (greater snout length, and upper jaw length). This correlates with their heaviest loadings in PC3 forming a group on upper left corner of the graph (Fig. 17).

Distribution. Río Napo, río Putumayo, and río Pastaza basins (a single lot known for the latter) (Fig. 18). Nearly all material from Ecuador, and some lots from Peru on border with Ecuador. The species is also recorded on lower río Napo basin in sympatry with *O. fugitiva*.

Etymology. The epithet *ecuadorensis* refers to the country where the species was first discovered.

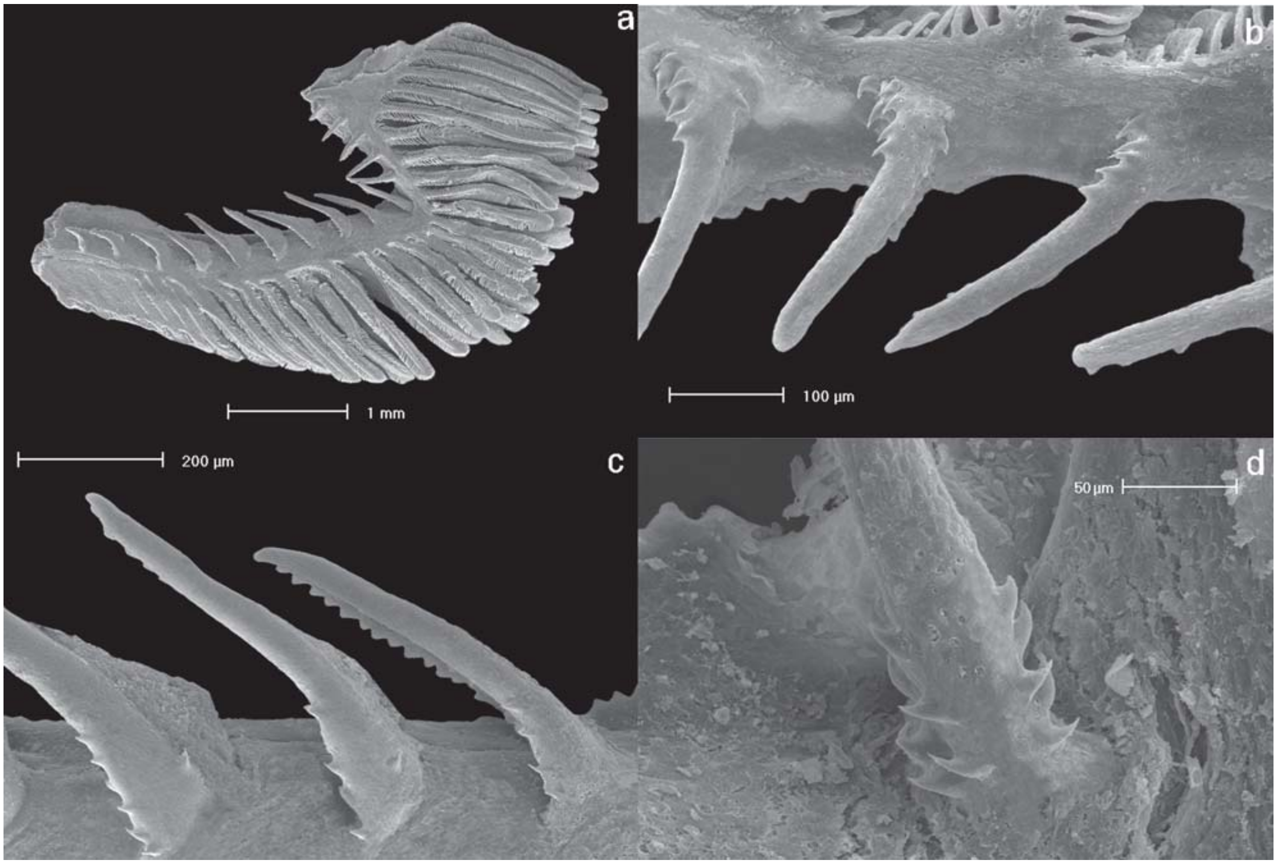


Fig. 16. First gill arch of *Odontostilbe ecuadorensis*, FMNH 113514, male 40.6 mm SL (photos a, b, d). SEM photographs of the left side gill arch showing gill gland (a), in detail gill rakers on upper branchial branch (b), gill rakers on lower branchial branch (FMNH 113513, unsexed 32.5 mm SL) (c), and the posteriormost gill raker on the lower branch in detail (d). Lateral view.

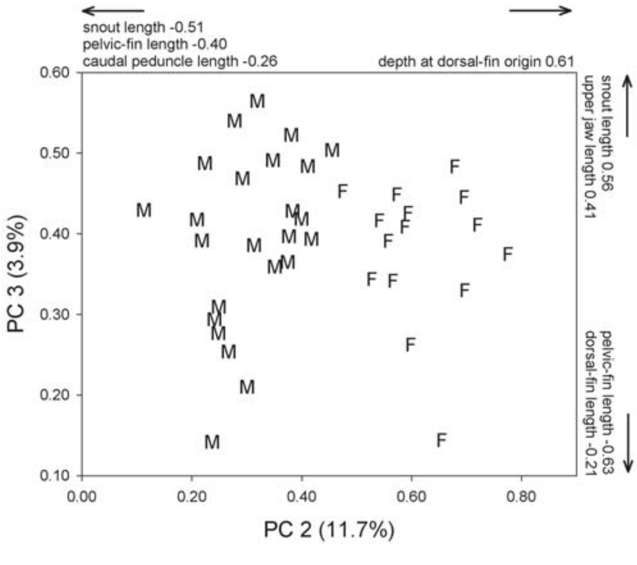
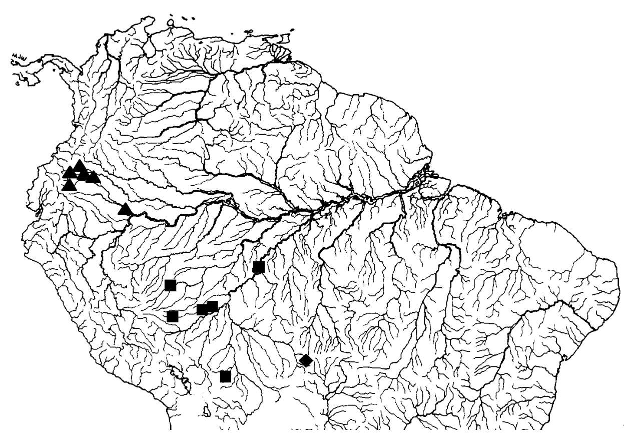


Fig. 17. Principal component analysis of the 18 morphometric data of males (M) and females (F) of *Odontostilbe ecuadorensis*. Stronger loadings on the second and third principal components (PC2, PC3).

Ecological notes. Saul (1975) identified *Odontostilbe cf. madeirae* Fowler, 1913, and *Holoshesthes heterodon* Eigenmann, 1915 as two cheirodontine species commonly taken together in the río Aguarico, the former primarily feeding on algae and plant material, and the latter on insects and insect larvae. However, examination of Saul's (1975) material proved the species named *O. cf. madeirae* to be a mix of *O. ecuadorensis* described herein and *O. euspilura*. The material he named *H. heterodon* consist of an undescribed cheirodontine. Part of the specimens caugth by W. Saul was selected herein as type material for *O. ecuadorensis*. These Ecuadorian species are reported to occur in clearwater, blackwater or turbid waters, riverine sandy-beaches (Stewart *et al.*, 2002), or lagoons and associated tributaries (Galacatos *et al*., 1996). All the material examined for this study came from altitudes between 200-500 m. Galacatos *et al.* (1996) recognized two altitudinal regions in Ecuadorian Amazon, lowland between 200 m and 220 m, and piedmont between 235 m and 295 m, where most *Odontostilbe* species were caught, preferentially in lagoons rather than streams.

Table 2. Morphometrics of *Odontostilbe ecuadorensis* n. sp. (holotype ANSP 170608, 12 of ANSP 130574, 2 of MEPN 001517, 15 of KU 13524, 3 of KU 13526, 7 of FMNH 113511, 11 of FMNH 113513, 5 of FMNH 113514).

	Males					Females				Unsexed			
	Holotype	n	Low	High	Mean	n	Low	High	Mean	n	Low	High	Mean
Standard length	45.7	27	32.7	45.8	41.4	18	31.2	50.2	43.8	43	24.1	46.6	32.5
Percents of standard length													
head length	23.9	27	23.2	26.0	24.3	18	22.2	25.3	23.2	43	22.7	27.5	25.3
snout-anal fin origin	63.2	27	62.0	67.1	64.7	18	64.5	70.8	66.8	43	62.9	68.3	65.8
snout-dorsal fin origin	47.3	27	46.9	50.5	48.6	18	48.9	52.2	50.4	43	48.6	52.4	50.5
snout-pelvic fin origin	45.7	27	44.2	49.0	46.5	18	45.8	51.8	47.8	43	46.0	49.7	47.7
dorsal-fin base	14.0	27	13.2	14.5	13.9	18	13.2	14.9	14.1	43	12.6	15.6	14.3
anal-fin base	26.7	27	23.4	27.1	25.6	18	24.8	26.7	25.6	43	23.4	27.3	25.4
caudal peduncle length	14.2	27	12.3	14.8	13.6	18	11.4	13.8	12.6	43	10.9	14.0	12.8
caudal peduncle depth	11.8	27	9.6	12.5	11.0	18	10.6	12.5	11.5	43	9.7	12.1	11.0
depth at dorsal-fin origin	30.6	27	27.0	34.1	29.7	18	32.1	43.8	36.1	43	27.0	36.7	31.8
dorsal-fin length	32.8	23	27.7	34.9	30.3	15	28.1	32.1	29.7	40	27.6	31.9	29.7
pelvic-fin length	23.0	27	17.1	24.8	19.9	18	17.0	19.0	18.1	43	16.6	19.7	17.9
pectoral-fin length	21.7	27	20.1	23.5	21.7	18	20.1	23.0	21.2	43	19.1	22.5	21.1
snout-pectoral-fin origin	23.2	27	23.0	25.7	24.2	18	22.1	25.3	23.4	43	23.3	27.7	25.2
Percents of head length													
snout length	25.7	27	22.8	28.6	25.0	18	19.0	23.9	21.6	43	19.4	24.1	22.1
upper jaw length	24.8	27	23.1	28.3	26.4	18	23.0	28.0	26.0	43	23.5	29.2	27.0
horizontal eye diameter	32.1	27	33.3	38.1	35.6	18	33.9	39.1	36.9	43	35.8	40.7	37.8
least interorbital width	33.9	27	30.6	35.6	32.9	18	30.9	36.5	34.0	43	29.6	36.3	32.1



Figs. 18. Distribution of *Odontostilbe ecuadorensis* (triangles), *Odontostilbe nareuda* (squares), and *Odontostilbe parecis* (losangles). Symbols can represent more than one lot, and more than one locality.

Odontostilbe nareuda, new species

Fig. 19

Holotype. CBF 09621, 1 (male 33.1 mm), Bolivia, Pando, [río Orthon - rio Madeira basin], lake on right bank of río Nareuda, around 3-4 km above mouth of río Tahuamanu, H. Ortega *et al.*, 10 Sep 1996.

Paratypes. BOLIVIA, PANDO: FMNH 106433, 4m of 17 (2 males 29.4-31.4 mm SL, 1 male 31.6 mm SL c&s, 1 female? 32.3 mm SL, 13 unsexed 19.5-27.1 mm SL not measured), same data as holotype. FMNH 106428, 1m (unsexed 30.9 mm SL), rio Madeira basin, lake on the right bank of río Nareuda, *ca.* 3-4 km above mouth of río Tahuamanu, H. Ortega *et al.*, 10 Sep 1996. FMNH 106430, 1m (unsexed 38.0 mm SL), rio Madeira basin, lake on the right bank of río Nareuda, *ca.* 5 km from mouth of río Tahuamanu, J. Sarmiento & S. Barrera, 11 Sep 1996. BRAZIL, RONDÔNIA: MCP 38417, 20 (1 male 28.8 mm SL, 19 unsexed 24.0-28.6 mm SL), [Calama], poço da Angélica, rio Madeira, M. Goulding, 12 Dec 1980, formerly MZUSP 42837. MZUSP 87759, 1m (female 35.3 mm SL), Calama, M. Goulding, 2 Feb 1981. MZUSP 87760, 5m (4 unsexed 27.0-34.5 mm SL, and 1 unsexed c&s 27.5 mm SL), same data as MCP 38417.

Non-type material. Río Madeira basin, BRAZIL, AMAZONAS**:** MZUSP 42837, 200 **(**unsexed 21.5-28.3 mm SL), [Calama], poço da Angélica, rio Madeira. **Río Mamoré basin,** BOLIVIA, MOTACUSAL**:** MNHN 1989-1465, 10 of 112 (7 unsexed 21.5-25.7 mm SL, 3m unsexed- 26.7-28.7 mm SL), río Isiboro, río Mamoré basin. **Río Purus basin,** BRAZIL, ACRE: MZUSP 87752, 2 (unsexed 26.3-26.8 mm SL), rio Acre, between Seringal Paraíso and lago Amapá. MZUSP 87753, 1 (unsexed 33.1 mm SL), Manoel Urbano, rio Purus. **Río Orthon - lower Río Beni basin,** BOLIVIA, PANDO: FMNH 106429, 1 (unsexed 20.0 mm SL), lake on the right bank of río Nareuda, around 3-4 km above mouth of río Tahuamanu. FMNH 106432, 3 (unsexed 21.9-30.9 m SL), approx. 2-3 km above mouth of río Muyumanu. FMNH 106434, 2 (unsexed 29.2-29.2 mm SL), right bank of stream Filadelfia, approx. 10 km from mouth of río Nareuda. FMNH 106435, 2 (unsexed 21.0-21.5 mm SL), hidden lake on right bank of río Tahuamanu, approx. 500 m from mouth of río Nareuda. FMNH 106436, 1 (unsexed 23.2 mm SL), río Tahuamanu at rocks and island archipelago and rapids, 68 km below mouth of río Nareuda. FMNH 106462, 1m (unsexed 28.3 mm SL), río Nareuda at camp, altitude 250 m.

Diagnosis. *Odontostilbe nareuda* basically differs from all other species by larger anal-fin base length, 30.6-32.8% SL (*e.g. vs.* 23.5-29.4% SL in *O. fugitiva*, Fig. 20, or 23.1-28.5% SL in *O. dierythrura*), and higher anal-fin counts, 24-26 (*vs.* 16-24

Fig. 19. Holotype of *Odontostilbe nareuda*, CBF 09621, male 33.1 mm (top), and paratype FMNH 106433, possibly a female 32.3 mm SL, not showing dimorphic characters of males (bottom).

for all other species). Adittionaly, gill raker counts on upper branch 5-6 and lower branch 11-12 of *O. nareuda* differ from sympatric species *O. fugitiva* with mostly 6-7 on upper and 12-13 on lower (Figs. 13a-b).

Description. Morphometric data given in Table 3. Largest male 33.1 mm SL; female 32.3 mm SL. Body elongate and compressed. Greatest body depth at dorsal-fin origin. Snout usually pointed; not protuded in males. Dorsal profile ascends slightly convex from snout to dorsal-fin origin, and descends straight from that point to caudal peduncle. Ventral profile convex from lower jaw to anal-fin origin, and straight along anal-fin base. Caudal peduncle slightly longer than deep.

Head relatively small. Posterior margin of opercle sinusoidal with upper portion concave and lower portion convex. Mouth terminal. Maxilla short, oblique; posterior tip reaching near or to vertical at anterior eye border, and ending at level of inferior eye border. Cleared and stained specimens (2). Premaxillary teeth 5, bearing 7-9 cusps; midcentral cusp longer than lateral cusps; smaller lateral cusps of each tooth overlap cusps of adjacent teeth, except anteriormost teeth (Fig. 21). Premaxillary teeth juxtaposed externally to dentary teeth, leaving premaxillary tooth cusps exposed when mouth closed.

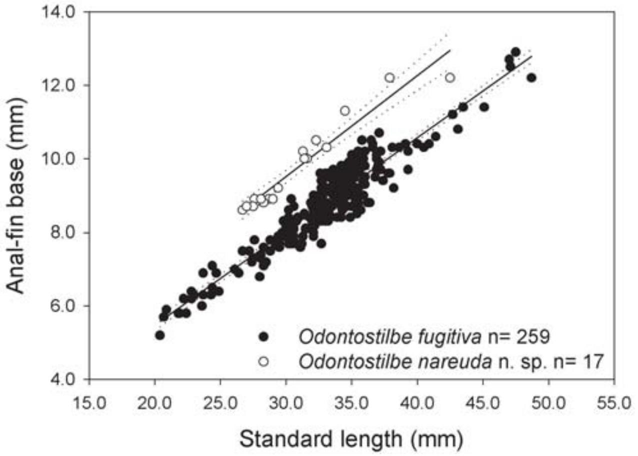


Fig. 20. Anal-fin base as a function of standard length for males, females and unsexed specimens of *Odontostilbe fugitiva* against *Odontostilbe nareuda*.

Maxilla with 2 teeth bearing 2-8 cusps, usually decreasing cusp number to posterior tip of maxilla. Dentary teeth 8-11 bearing 1-7 cusps, gradually decreasing in size posteriorly; anterior 6 teeth large with 5-7 cusps, and remainder small with 1-4 cusps. Smaller cusps of dentary teeth overlaping adjacent tooth cusps, usually not in posteriormost teeth. All dentary tooth cusps slightly recurved towards interior of mouth.

Dorsal-fin rays **ii**(17) or **9**(17). Dorsal-fin origin slightly posterior to midlength of body, and slightly posterior to vertical through pelvic-fin origin. Anal-fin rays **v**(16), vi(1), 23(3), **24**(9), 25(4), or 26(1). Anal-fin distal border concave, about 7

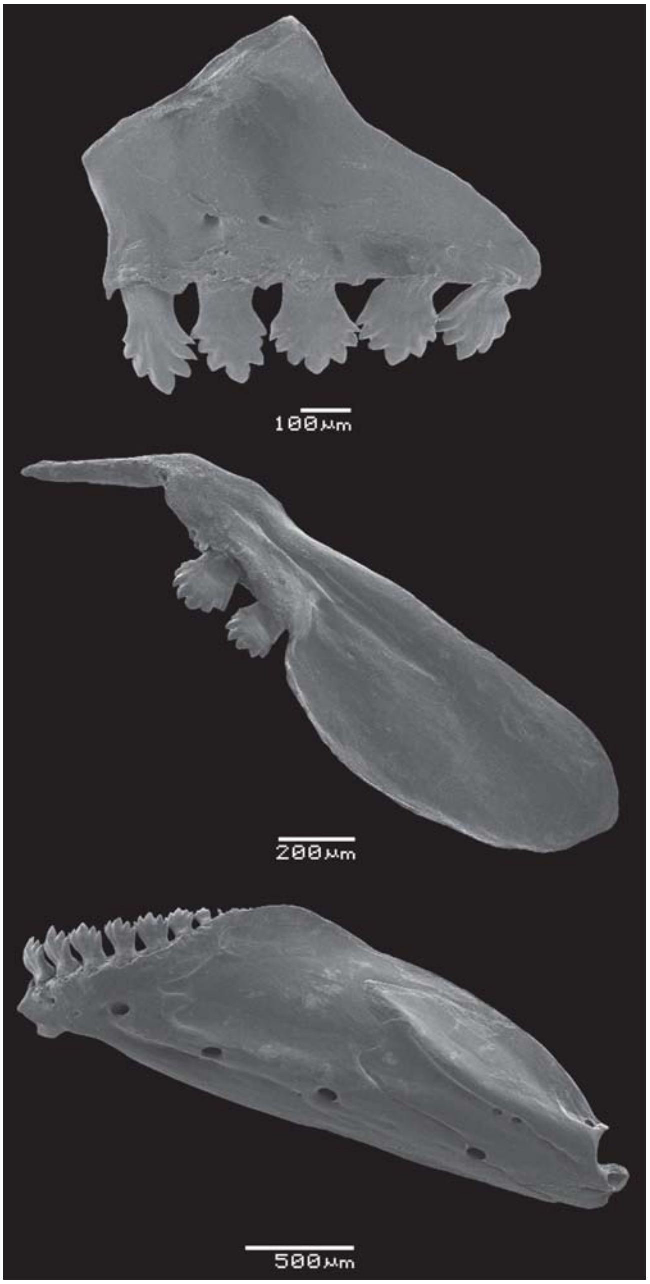


Fig 21. Dentition of *Odontostilbe nareuda*, FMNH 106433, male 31.6 mm SL. SEM photograph of left side premaxilla (top), maxilla (middle), and dentary (bottom).

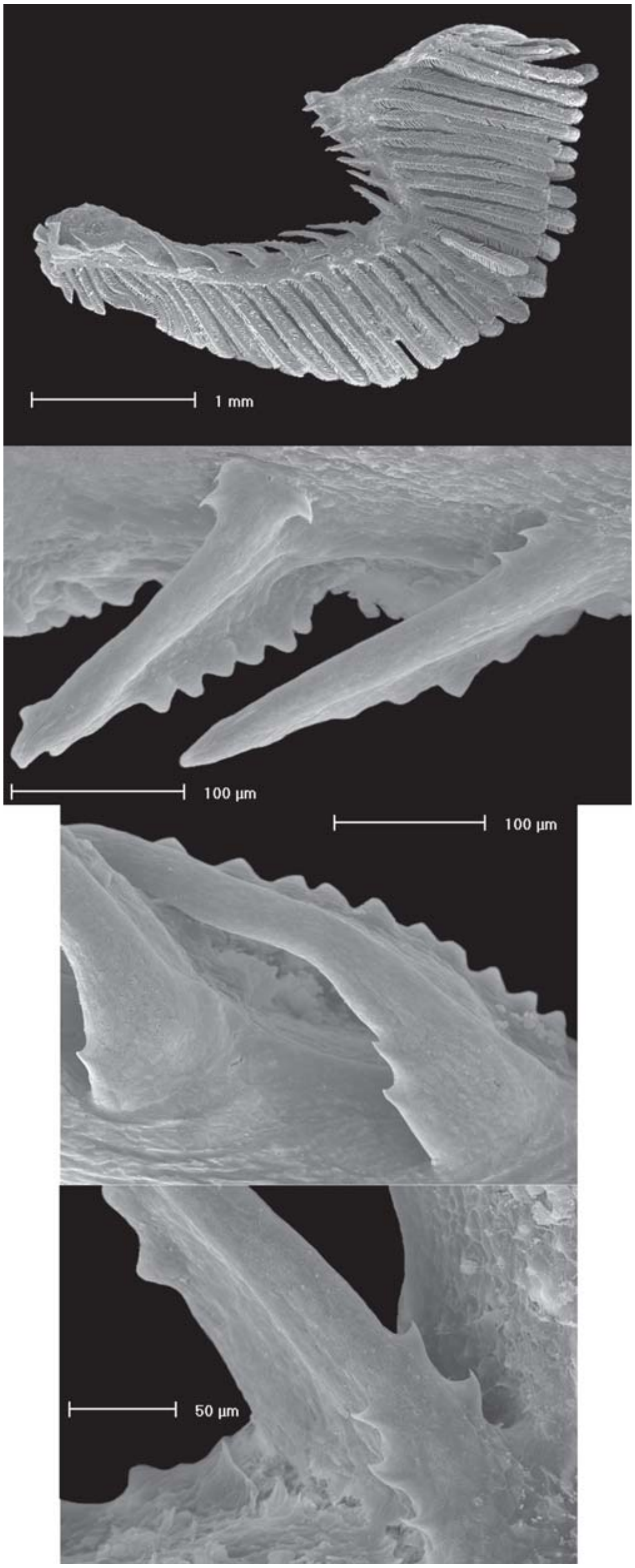


Fig. 22. First gill arch of *Odontostilbe nareuda*, FMNH 106433, unsexed 29.2 mm SL. SEM photographs of the left side gill arch (top), in detail gill rakers on upper branchial branch (middle), and gill rakers on lower branchial branch (bottom). Lateral view.

Table 3. Morphometrics of *Odontostilbe nareuda* n. sp. (holotype CBF 09621, paratypes 5 of FMNH 106433, 1 of MZUSP 87759, 5 of MZUSP 87760, non-paratypes 3 of MNHN 1989–1465, 1 of FMNH 106428, 1 of FMNH 106430, and 1 FMNH 116462).

	Males					Unsexed			
	Holotype	n	Low	High	Mean	n	Low	High	Mean
Standard length	33.1	3	29.4	31.6	30.8	13	26.7	37.9	30.3
Percents of standard length									
head length	25.1	3	25.0	25.9	25.3	13	24.1	26.1	25.4
snout-anal fin origin	59.5	3	58.9	60.8	60.0	13	59.9	62.0	60.7
snout-dorsal fin origin	49.5	3	50.0	51.0	50.5	13	49.1	52.2	50.6
snout-pelvic fin origin	43.5	3	43.9	44.9	44.3	13	42.8	45.9	44.2
dorsal-fin base	13.6	3	13.6	15.0	14.2	13	13.5	15.6	14.2
anal-fin base	31.1	3	31.3	31.8	31.6	13	30.6	32.8	31.8
caudal peduncle length	13.0	3	12.4	13.0	12.7	13	11.3	13.1	12.3
caudal peduncle depth	11.2	3	10.2	10.9	10.6	13	9.4	11.5	10.5
depth at dorsal-fin origin	30.5	3	30.4	31.3	31.0	13	30.3	34.8	31.9
dorsal-fin length	30.8	2	30.9	33.0	31.9	7	30.4	32.4	31.4
pelvic-fin length	18.1	3	17.8	18.4	18.1	13	16.5	18.0	17.2
pectoral-fin length	22.1	3	21.3	22.4	22.0	13	18.7	21.1	20.4
snout-pectoral-fin origin	25.1	3	25.3	25.9	25.5	13	24.1	26.1	25.7
Percents of head length									
snout length	22.9	3	22.8	23.7	23.1	13	19.8	21.6	20.6
upper jaw length	27.7	3	27.8	29.1	28.6	13	25.7	29.6	27.1
horizontal eye diameter	38.6	3	40.5	42.1	41.0	13	37.6	41.4	39.7
least interorbital width	31.3	3	31.6	31.6	31.6	13	29.6	33.3	31.1

anterior branched rays longer than posterior rays. Pectoral-fin rays **i**(17), 9(1), 10(9), or **11**(7). Unbranched pectoral-fin ray reaching or not reaching pelvic-fin origin, extending beyond pelvic-fin origin in mature males**.** Pelvic-fin rays **i**(20), 6(1), or **7**(19). No evident elongation of unbranched dorsal or pelvic-fin rays in males. Lateral skin border of unbranched pectoral-fin rays and unbranched pelvic-fin rays thickened in mature males, bearing thin laterodorsal projection of hard tissue covered with soft tissue. Principal caudal-fin rays **19**(20). Procurrent caudal-fin rays: dorsal **11**(7), 12(8), or 13(2); ventral 9(7) or **10**(10). Sometimes anterior ventral procurrent caudal-fin rays modified, distally bifurcated. Caudal-fin ray flaps ventrally on 4th-7th rays of upper lobe, and dorsally on 14th-15th rays of lower lobe. Adipose-fin at vertical through last anal-fin ray insertion.

Holotype and paratype males of FMNH 106433 are unique, all having not totally developed hooks. Males with acute, retrorse hooks on posterior margin of pelvic and anal-fin rays. One or two paired or unpaired hooks per segment of lepidotrichia on last unbranched anal-fin ray, and 1st to 9th anal-fin branched rays, positioned at middistal length of rays. One or two unpaired hooks per segment of lepidotrichia along almost entire length of 1st to 7th branched pelvic-fin rays, and reaching tip of fin rays (except on 1st branched pelvic-fin ray, on midlenght portion).

Scales cycloid; lateral line complete 35(1) or **36**(6); predorsal row 10(6) or **11**(10); scale rows between lateral line and dorsal-fin origin **5**(7) or 6(6); scale rows between lateral line and anal-fin origin **4(**15), scale near pelvic-fin origin usually smaller than others); scale rows around caudal peduncle **14**(7). Triangular modified scale on pelvic-fin base extends posteriorly covering 1-3 scales. Scales on anal-fin base 6-**7**.

Cleared and stained specimens (2): supraneurals 4(1) or 5(1); precaudal vertebrae, 16(2); caudal vertebrae 19(2). Gill rakers (counted in 15 alcohol specimens, and 2 c&s), upper 5(3) or **6**(13); lower 10(3), 11(7), or **12**(6) (1-2 on hypobranchial). Upper gill rakers with 1-3 recurved denticles on anterolateral border, and none or 1 similar denticle on posterolateral border; lower gill rakers with none to 3 recurved denticles on anterolateral border (1-4 anteriormost lower gill rakers with none or 1 denticle on posterolateral border); posteriormost lower gill raker with 3 denticles on anterolateral border, and 1-2 similar denticles on posterolateral border (Fig. 22). All denticulation mainly on basal portion of gill rakers.

Color in alcohol. General ground body color brownish or pale yellow. Dorsal portion of body dark from head to caudal peduncle; dark chromatophores mostly on scale borders, forming reticulated pattern. Pigmented scales not extending laterally on body, no distinct dark chromatophores on pseudotympanum area. Dorsal fin entirely with dark chromatophores scattered along all fin rays, more densely along 1st and 2nd unbranched dorsal-fin rays. Pectoral and pelvic fins with scattered dark chromatophores, more numerous on anteriormost portions of fins. Holotype with pelvic fins hyaline. Anal fin mostly pigmented, dark chromatophores spread on all fin rays, except at tips of last unbranched fin ray and 1st branched fin ray. Adipose fin hyaline. Caudal fin almost entirely covered with diffuse dark chromatophores along fin rays, clear areas on base of caudal-fin lobes just behind caudal-fin spot. Rounded black to brown spot on base of caudal fin, reaching upper and lower border of peduncle, usually lighter near ventral border, sometimes extending little on proximal portion of 7th to 12th central caudal-fin rays.

Numerous chromatophores on snout, as well as upper and lower lips (on lower lip these almost form line). Numerous dark chromatophores on anteriormost portion of maxilla, and 1st infraorbital. Pigmentation on top of head on frontals and parietals, and deep-lying dark chromatophores cover brain membranes below frontals, parietals, and fontanel. Body with faint dark midlateral stripe, sometimes reduced to line along longitudinal body axis, beginning below dorsal fin**,** above lateral line, and extending to caudal spot. Belly pale, almost without chromatophores below lateral line, except above anal-fin base with 7 to 12 chevron shaped markings. Guanine on eye iris, interopercle, opercle, subopercle, isthmus, 2nd to 4th infraorbitals, lateral portion of parietals just behind eye, and belly. Guanine more evident in MCP 38417, and MZUSP 87760 specimens. Holotype with some guanine.

Odontostilbe nareuda seems to have fewer dark chromatophores than similar species such as *O. fugitiva*, *O. dierythrura,* and *O. parecis,* and another new species from río Madre de Dios (in manuscript), all of these occur in the rio Madeira basin. Except for *O. parecis* from rio Guaporé basin, the other three species were found to be sympatric with *O. nareuda*.

Sexual dimorphism. Only three males available, holotype and two paratypes, but these are not fully mature, without completely developed hooks. These males have longer pectoral-fin rays in contrast with specimens with undetermined sex, statistically significant in test for coincidental regressions ($F_{(2, 276)} = 28.5$, $p<0.00$) (Fig. 23). The snout profile of holotype is slightly protruded in comparison with the unsexed paratype FMNH 106433 (Fig. 19). Gill gland not found in males of *O. nareuda*. Absence of this gill gland probably explained by lack of mature males among examined specimens.

Distribution. *Odontostilbe nareuda* is known from the lower río Beni basin, in the ríos Nareuda and Muyumanu, of the ríos Tahuamanu-Orthon drainage that runs parallel to the río Madre de Dios, and the middle rio Madeira (Fig. 18). However, it may be widespread in the rio Madeira basin. Some specimens from the upper rio Mamoré basin were tentatively identified as *O. nareuda*. Also, three specimens from the rio Purus match the larger anal-fin base diagnostic of *O. nareuda*. A somewhat similar distribution was observed for *Creagrutus occidaneus* that occurs in río Madre de Dios and upper rio Purus (Vari & Harold, 2001). Further samples of these regions including mature males and females are needed to assure these distributions.

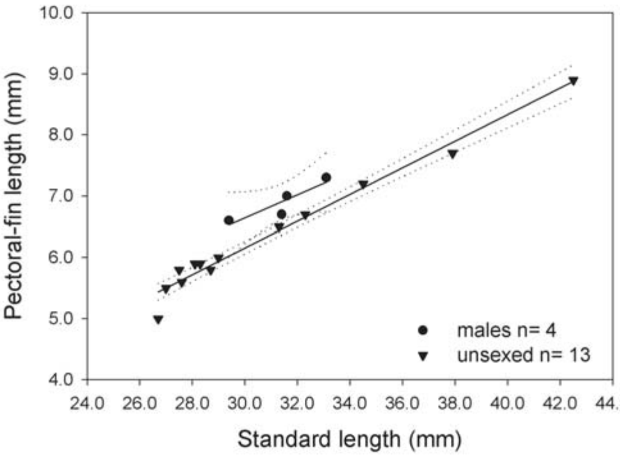


Fig. 23. Pectoral-fin length as a function of standard length for males *versus* unsexed specimens of *Odontostilbe nareuda*.

Etymology. In allusion to the type-locality, in the río Nareuda.

Ecological notes. FMNH field notes for *O. nareuda* indicate that it occurs in oxbow lakes, river or small river habitats in forest, having whitewater or turbid-white water. The bottom was sandy or muddy substrate with sticks, logs, and leaves. Nevertheless the río Nareuda is mostly a blackwater river as noted by Machado-Alllison *et al.* (1999a), all the locality notes of FMNH lots refer to whitewater, except FMNH 106430 which mentions clearwater of brown color. The lower río Nareuda seems to be influenced by whitewaters of the río Tahuamanu - río Orthon basin. The FMNH specimens all came from the AquaRAP expedition in the upper río Orthon basin, Bolívia. These specimens were originally identified as *Cheirodon fugitiva*, *Odontostilbe fugitiva* or *Odontostilbe* sp. (Chernoff *et al.*, 1999; Sarmiento *et al*., 1999). Specimens identified for the AquaRAP expedition as *O. paraguayensis*, and listed as that species by Willink *et al.* (1999) as "believed to be" a new record for the Bolivian Amazon, actually are *O. nareuda* or an undescribed species of cheirodontine. Both species were collected together, being probably syntopic. Machado-Allison *et al.* (1999b) detailed the abundance of species regarding the field station that corresponds to FMNH lots of the holotype and some paratypes (FMNH 106433) and cited "*O. paraguayensis*" as the most abundant species, and "*Cheirodon fugitiva*" the fifth ranked, being "typically from cochas or flooded lakes".

***Odontostilbe parecis*, new species**

Fig. 24

Holotype. INPA 24885, 1 (male 33.0 mm SL), Brazil, Mato Grosso, BR 174, Corredeira Papagaio, [near BR 364, rio Galera, upper rio Guaporé basin], Equipe Rose, V. Py-Daniel *et al*., 3 Oct 1984.

Paratypes. BRAZIL, MATO GROSSO: INPA 21424, 4m of 8 (1 male 35.0 mm SL, 3 unsexed 29.8-36.2 mm SL), same data as holotype. INPA 21425, 1m of 23 (male 30.6 mm SL), rio Novo, BR 174, [near BR 364, rio Novo, rio Galera, upper rio Guaporé basin], Equipe Rose, V. Py-Daniel *et al.*, 2 Oct 1984. MCP 37318, 129 (unsexed 16.7-38.0 mm SL), Nova Lacerda, rio Galera, affluent of rio Guaporé in Balneário Galera, V. Bertaco *et al*., 14°28'59''S 59°35'07''W, 12 Jul 2004. MCP 37319, 14m of 82 (5 males 30.3-39.0 mm SL, 1 male 32.8 mm SL c&s, 4 females 33.6-41.6 mm SL, 1 female 36.8 mm SL c&s, 3 unsexed 31.3-34.4 mm SL), Pontes e Lacerda, affluent of rio Galera about 71 km north of rio Guaporé, 14°39'12''S 59°26'46''W, R. Reis *et al*., 12 Jul 2004.

Non-type material. Rio Madeira - Rio Guaporé basin, BRASIL, MATO GROSSO: MCP 38493, 45 (2 males 31.8-32.3 mm SL, 43 unsexed 15.6-38.7 mm SL), Comodoro, stream affluent of rio Novo on the road BR 174, 14°13'25''S 59°41'27''W.

Fig. 24. Holotype of *Odontostilbe parecis*, INPA 24885, male 33.0 mm SL (top), and paratypes MCP 37319, male 33.0 mm SL (middle), female 41.6 mm SL (bottom).

Diagnosis. Differs from Amazonian species of *Odontostilbe* by: (1) number of lower gill rakers 9-10 (*vs.* 11-14 in *Odontostilbe fugitiva* and *O. dierythrura*, 10-11 in *O. ecuadorensis*, and 10-12 in *O. nareuda*) (Fig. 13a-b); (2) number of branched anal-fin rays (20-21, *vs.* 23-26 in *O. nareuda*); (3) terminal mouth (*vs.* conspicuous subterminal mouth in *O. euspilura*); (4) longer upper jaw length 28.8-32.9% HL (*vs.* 23.4-30.0% HL in *O. fugitiva*, Fig. 25, or *vs.* 23.0-29.2% HL in *O. ecuadorensis*); and (5) larger eye in males 38.9-40.8% HL diameter (*vs.* 28.9-38.6% HL in *O. fugitiva*, Fig. 26, or *vs.* 33.3-38.1% HL in *O. ecuadorensis*). The combination of the characters listed above distinguishes *O. parecis* from all other *Odontostilbe* species.

Description. Morphometric data given in Table 4. Largest male reaching 35.0 mm SL, and female 41.6 mm SL. Body elongate and compressed. Males with more elongate and compressed bodies than females. Greatest body depth at dorsal-

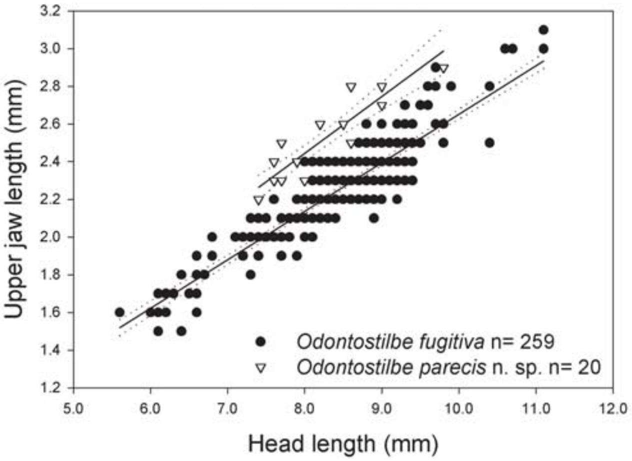


Fig. 25. Upper jaw lenght as a function of head length for males, females, and unsexed specimens of *Odontostilbe fugitiva* and *Odontostilbe parecis*.

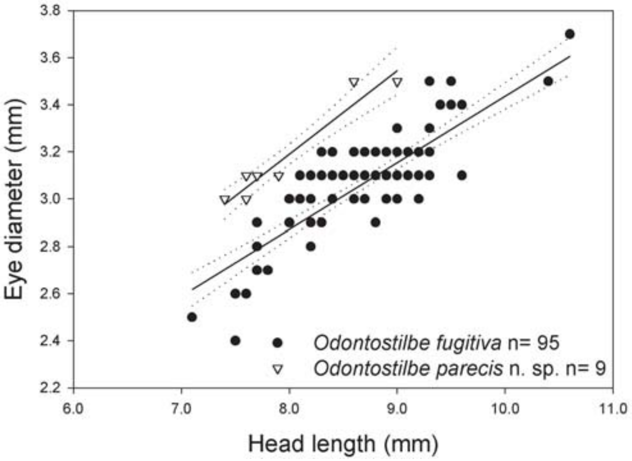


Fig. 26. Eye diameter as a function of head length for males of *Odontostilbe fugitiva* and *Odontostilbe parecis*.

fin origin. Snout blunt, larger in males. Head profile pointed, gently convex from snout to posterior tip of supraoccipital bone. Dorsal profile ascends almost straight from that point to dorsal-fin origin, sometimes with sligth depression at posterior tip of supraoccipital; from dorsal-fin origin descends almost straight to caudal peduncle. Ventral profile convex from lower jaw to anal-fin origin, and straight along anal-fin base. Caudal peduncle slightly longer than deep.

Head relatively small. Posterior margin of opercle sinusoidal with upper portion concave and lower portion convex. Mouth terminal. Maxilla short, terminating posteriorly at vertical near anterior eye border, and ending at level equal to inferior eye border, positioned at 45 degrees angle relative to longitudinal body axis. Cleared and stained specimens (2). Premaxillary teeth 5, bearing 8-10 cusps; midcentral cusp longer than lateral cusps; smaller lateral cusps of each tooth overlap cusps of adjacent teeth (Fig. 27). Premaxillary teeth juxtaposed externally to dentary teeth, leaving premaxillary tooth cusps exposed when mouth closed. Maxilla with 2-3 teeth bearing 7-9 cusps, usually decreasing cusp number to posterior tip of maxilla. Dentary teeth 8-9 bearing 2-7 cusps, gradually decreasing in size posteriorly, first 6-7 teeth large with 6-7 cusps, following 2 small teeth with 2-5 cusps. Smaller cusps of all dentary teeth overlaping adjacent teeth cusps, usually not in posteriormost teeth. All dentary tooth cusps slightly recurved towards interior of mouth.

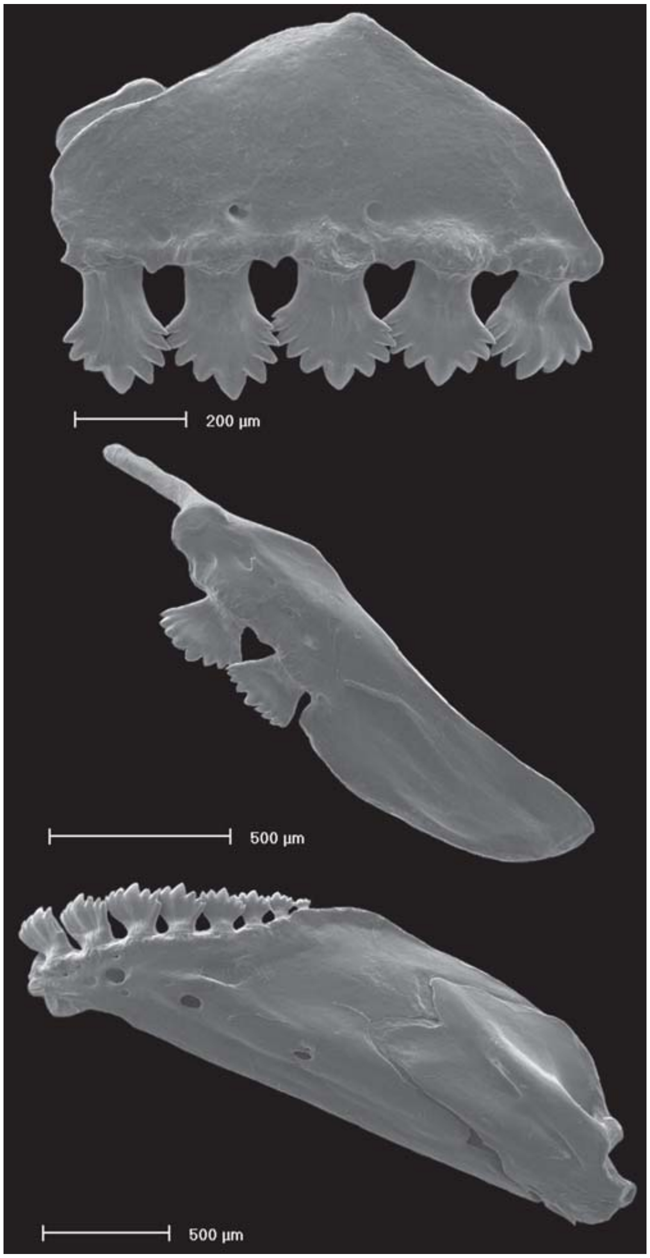


Fig. 27. Dentition of *Odontostilbe parecis*, MCP 37319, male 32.8 mm SL. SEM photograph of left side premaxilla (top), maxilla (middle), and dentary (bottom).

Dorsal-fin rays **ii**(20) or **9**(20). Dorsal-fin origin slightly posterior to midlength of body, and slightly posterior to vertical through pelvic-fin origin. Anal-fin rays **v**(20), 19(5), 20(8), or **21**(7). Anal-fin distal border concave, anterior 6-7 branched rays longest. Pectoral-fin rays: **i**(20), 9(1), 10(7), **11**(10), or 12(2). Unbranched pectoral-fin ray short of reaching or reaching pelvic-fin origin, slightly extending beyond pelvic-fin origin in males. Pelvic-fin rays **i(**20), 6(1), or **7**(19). Unbranched dorsal or pelvic-fin rays not elongate in males. Lateral skin border of unbranched pectoral-fin rays and unbranched pelvic-fin rays thickened in mature males, bearing thin laterodorsal projection of hard tissue covered with soft tissue. Principal caudal-fin rays **19**(20). Procurrent caudal-fin rays: dorsal 10(2), **11**(9), or 12(9); ventral 8(3), **9**(15), or 10(2). Anterior ventral procurrent caudal-fin rays distally bifurcated or not. Caudal-fin ray flaps ventrally on 2nd -8th (mostly 4th-7th) rays of upper lobe, and dorsally on 12th-16th (mostly 13th-15th) rays of lower lobe. Adipose fin at vertical through last anal-fin ray insertion.

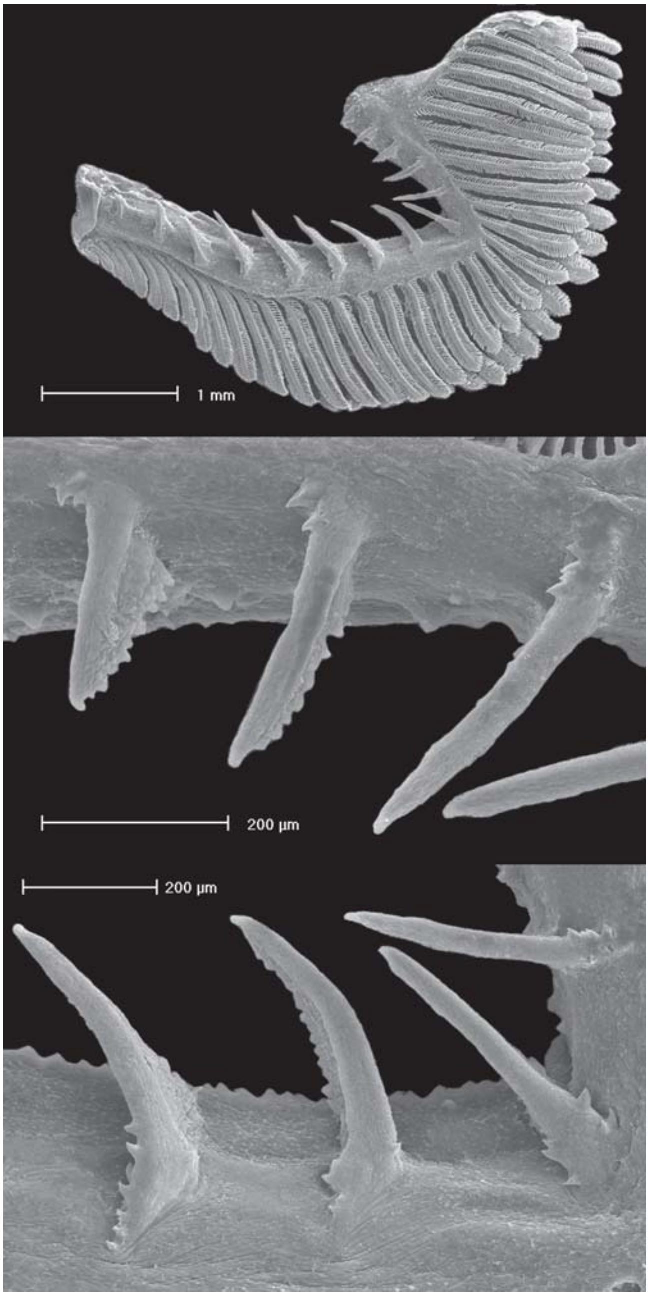


Fig. 28. First gill arch of *Odontostilbe parecis*, INPA 21425, male 30.6 mm SL. SEM photographs of the left side gill arch (top), in detail gill rakers on upper branchial branch (middle), and gill raker on lower branchial branch (bottom). Lateral view.

Males with acute, retrorse hooks on posterior margin of pelvic and anal-fin rays. One or two paired and unpaired hooks per segment of lepidotrichia, on last unbranched anal-fin ray, and 1st to 8th branched anal-fin rays, positioned at middistal length of rays and usually not extending to ray tip; tiny hooks can be present up to 16th anal-fin branched ray, occurring distally on branches (up to 17th anal-fin branched ray in holotype). One or two unpaired hooks per segment of lepidotrichia on 1st to 7th branched pelvic-fin rays, extending almost entirely to distal ray tip (along midlenght of 1st branched pelvic-fin ray). Few mature males available for description of hooks. Type material from INPA contains males with more developed hooks. Holotype with hooks on 2nd to 5th branched pelvic-fin rays. Because available males are not fully mature, this species could have typical elongation of unbranched dorsal and pelvic-fin rays present in of *Odontostilbe* species.

Scales cycloid; lateral line complete 35(7) or 37(1); predorsal row 9(2), **10**(12), or 11(3); scale rows between lateral line and dorsal-fin origin **5**(10) or 6(8); scale rows between lateral line and anal-fin origin **4**(18); scale rows around caudal peduncle 14(10). Triangular modified scale on pelvic fin base extends posteriorly covering 1-2 scales (mostly 2). Scales on anal-fin base 5-7 (partially missing in holotype).

Cleared and stained specimens (2): supraneurals 4(2); precaudal vertebrae, 15(1) or 16(1); caudal vertebrae 19(2). Gill rakers (18 in alcohol, 2 c&s), upper **5**(17) or 6(3), lower 9(12) or **10**(8) (2 on hypobranchial). Upper gill rakers with none or 1-3 recurved denticles along anterolateral border, and none to 2 similar denticles on posterolateral border; lower gill rakers with none to 5 recurved denticles on anterolateral border (1-4 anteriormost lower gill rakers with none to 2 denticles on posterolateral border); excepting posteriormost lower gill raker with 4 recurved denticles irregularly placed on lateral surface (Fig. 28). All denticulation mostly on basal portion of gill rakers.

Color in alcohol. General ground body color brownish or pale yellow. Dorsum dark from head to caudal peduncle, chromatophores mostly on scale borders forming reticulated pattern. Pigmented scales extend laterally on body below longitudinal stripe, also on pseudotympanum area. Dorsal fin with scattered chromatophores along all fin rays, more densely pigmented along 1st and 2nd unbranched dorsal-fin rays. Pectoral and pelvic fins with scattered dark chromatophores, more numerous on anteriormost portions of fins. Holotype with pelvic fin hyaline. Anal fin mostly pigmented with chromatophores spread on all fin rays, except at distal tips of last unbranched fin ray and 1st branched fin ray. Adipose fin hyaline. Caudal fin almost entirely covered with diffuse chromatophores along fin rays, clear areas on base of caudal-fin lobes just posterior to caudal-fin spot. Rounded black to brown spot on base of caudal fin, usually light near lower border, sometimes extending little onto proximal portion of 7th to 12th central caudal-fin rays.

Numerous chromatophores on snout, upper and lower lips, anteriormost portion of maxilla and lower jaw, and 1st-2nd infraorbitals. Pigmentation on dorsal surface of head on frontals and parietals, and deep-lying dark chromatophores over brain membranes below frontals and parietals, and fontanel. Body with faint dark midlateral stripe, sometimes reduced to line, along midlongitudinal body axis, beginning posterior to or on pseudotympanum, above lateral line, reaching caudal spot. Below lateral line, ventral body faint almost without chromatophores. Pigmented area above anal-fin base forming 10 to 11 chevron-shaped markings. Guanine surrounds eye iris, interopercle, opercle, ishtmus, and most 3rd infraorbital. Holotype with some remaining guanine, but fresher specimens of MCP without any guanine.

Sexual dimorphism. Males with anal- and pelvic-fin hooks on rays as previously described, such hooks absent in females. Gill gland (Burns & Weitzman, 1996) present in three mature males of *Odontostilbe parecis*, holotype, and two paratypes (Fig. 28). Holotype of *O. parecis* with gill gland present on first gill arch, covering about 9 anterior branchial filaments. Paratype INPA 21425, a male 30.6 mm SL with a gland including about 7 anterior branchial filaments and paratype MCP 37319, 39.0 mm SL with gland including about 6 anterior branchial filaments. Principal component analysis of morphometric data of males and females plus unsexed specimens shows sexual dimorphism in general body shape (Fig. 29). Principal component 2 (PC2) grouped males and females separately. This affected strongly and negatively by caudal peduncle length, pectoral-fin length, pelvic-fin length, and snout length; and positively by depth at dorsal-fin origin. Principal component 3 (PC3) affected strongly and positively by snout length and caudal peduncle length, negatively by anal-fin base and pectoral-fin length. Males differed from females in all of these characters. Usually males with higher mean values for peduncle length, pectoral-fin length, pelvic-fin length, and snout length, while females and unsexed specimens have higher depth at dorsal-fin origin than males (Table 3). Unsexed specimens were not assumed to be females, because they probably also include immature males. All examined males are probably not fully mature as mentioned in description. Additional material may reinforce sexual morphometric characters described here.

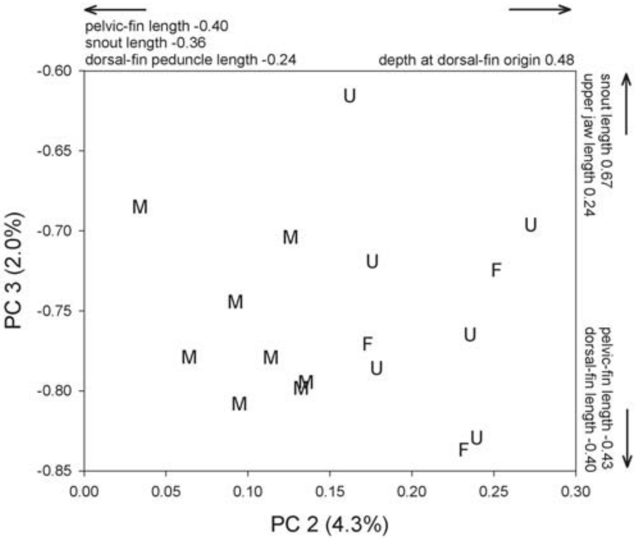


Fig. 29. Principal component analysis of the 18 morphometric data of males (M), females (F), and unsexed specimens (U) of *Odontostilbe parecis*. Stronger loadings on the second and third principal components (PC2, PC3).

Table 4. Morphometrics of *Odontostilbe parecis* n. sp. (holotype INPA 24885, paratypes INPA 21424, and MCP 37319).

	Males					Females				Unsexed			
	Holotype	n	Low	High	Mean	n	Low	High	Mean	n	Low	High	Mean
Standard length	33.0	8	30.3	39.0	32.8	3	36.8	41.6	38.9	8	29.8	36.2	33.3
Percents of standard length													
head length	23.9	8	23.1	24.9	24.2	3	23.4	23.6	23.5	8	23.3	24.8	24.0
snout-anal fin origin	64.5	8	60.4	66.3	63.0	3	63.0	64.3	63.7	8	63.1	66.1	64.7
snout-dorsal fin origin	47.9	8	46.4	48.9	47.7	3	46.9	49.0	47.9	8	47.8	50.7	49.3
snout-pelvic fin origin	45.8	8	43.3	48.0	45.0	3	44.2	45.3	44.6	8	45.1	47.7	46.0
dorsal-fin base	15.2	8	13.7	15.2	14.6	3	14.7	16.1	15.2	8	14.1	15.1	14.7
anal-fin base	28.2	8	25.9	29.0	27.2	3	27.7	28.6	28.1	8	25.5	28.6	26.8
caudal peduncle length	13.0	8	12.8	14.9	13.8	3	12.5	13.9	13.3	8	12.5	14.1	13.0
caudal peduncle depth	10.9	8	10.1	11.2	10.5	3	10.9	11.5	11.2	8	9.9	11.3	10.7
depth at dorsal-fin origin	31.2	8	29.5	33.3	31.3	3	31.5	35.7	33.8	8	29.9	37.1	33.1
dorsal-fin length	32.7	8	31.0	33.1	31.8	3	30.5	31.3	31.0	8	29.8	33.6	31.2
pelvic-fin length	19.4	8	18.0	20.6	19.4	3	17.7	18.3	18.1	8	18.0	19.8	18.5
pectoral-fin length	23.0	8	20.3	23.8	22.3	3	20.3	21.5	20.7	8	20.1	21.5	21.0
snout-pectoral-fin origin	24.2	8	23.5	25.5	24.5	3	23.7	23.9	23.8	8	23.5	25.5	24.5
Percents of head length													
snout length	26.6	8	22.1	26.0	24.4	3	21.4	23.3	22.7	8	22.5	25.9	23.9
upper jaw length	30.4	8	29.1	32.9	30.3	3	29.6	32.6	31.1	8	28.8	32.5	30.8
horizontal eye diameter	39.2	8	38.9	40.8	40.0	3	39.8	41.1	40.5	8	40.0	42.5	41.2
least interorbital width	35.4	8	31.6	34.4	33.4	3	31.4	34.4	33.2	8	31.7	35.3	33.7

Distribution. Upper rio Guaporé drainage, rio Galera and rio Novo.

Etymology. The epithet *parecis* refers to the Chapada dos Parecis, a plateau situated on the east of Guaporé tributaries where the species was discovered.

Ecological notes. The Guaporé-Iténez is a clearwater right-bank tributary of the major rio Madeira (Goulding *et al*., 2003). Field notes record of MCP material: translucent water of quiet to medium flow, sandy bottom with pebbles, and a depth of 1-1.2 m. This was species collected along with *Serrapinnus* sp.

Discussion

Previous phylogenetic diagnosis for the genus *Odontostilbe* among cheirodontines was based on two synapomorphies described in Malabarba (1998), and related to the elongation of the second unbranched dorsal-fin ray and the unbranched pelvic-fin ray of males. These characters were found homoplastic in "*Odontostilbe*" *mitoptera* of the Compsurini. Recognition of *Odontostilbe* separately from genera assigned to the tribes Cheirodontini and Compsurini was also supported by the lack in *Odontostilbe* species of the several synapomorphies dignosing those tribes and their included genera. These synapomorphies consist of primary and secondary sexual characters. The genera *Pseudocheirodon*, *Prodontocharax*, *Aphyocheirodon*, and *Cheirodontops* also lack specialized sexually dimorphic features present in the Compsurini and Cheirodontini and were diagnosed based on jaws and teeth modifications, absent in *Odontostilbe*.

The diagnosis of *Odontostilbe* in the present contribution follows that of Malabarba (1998), based on the analysis of two *Odontostilbe* species only, *O. fugitiva* and *O. pequira*, respectively the type species of the genera *Odontostilbe* and *Holoshesthes*. *Holoshesthes* was placed in the synonym of *Odontostilbe*. We found morphological diversity in *Odontostilbe* much larger than previously known. We recognize in *Odontostilbe* six species of the ten species referred to the genus by Malabarba (2003): *O. fugitiva, O. dierythrura* Fowler, 1940, *O. microcephala* Eigenmann, 1907, *O. paraguayensis* Eigenmann & Kennedy, 1903, *O. pequira* (Steindachner, 1882), and *O. roloffi* Géry, 1972 (actually a synonym of *O. euspilura*, see below). This excludes the two species of Central American compsurins provisionally kept in *Odontostilbe*: "*O.*" *dialeptura* and "*O.*" *mitoptera*. Also, the generic assignment of the two nominal species described by Géry (1960) as *Cheirodon* (*C. gracilis* and *C. gracilis littoris*) and latter transferred to *Odontostilbe* by Planquette *et. al.* (1996), deserve a separate revision and are not included in *Odontostilbe*.

In a comprehensive taxonomic revision of *Odontostilbe* in progress by the first author, 10 additional species of cheirodontines were found related to this genus, in addition to the six species listed above and the three new species described herein. Among these 10 species, 8 are undescribed, one is *Odontostilbe pulchra* (Gill, 1858) [left as *species inquirenda* among Cheirodontinae by Malabarba (2003)], and the last one is *Cheirodontops geayi* Schultz, 1944, type species of *Cheirodontops*. *Cheirodontops geayi* was not previously hypothesized as related to *Odontostilbe*, although Böhlke (1954) pointed out that *Cheirodontops* Schultz, 1944 was solely distinguished from *Holoshesthes* Eigenmann, 1903 by the absence of teeth on the maxillary. The examination of type material of *C. geayi*, and an extensive revision of the species, showed that the teeth are present on the maxilla. Also it was found that the elongation of dorsal- and pelvic-fin rays in mature males that diagnoses *Odontostilbe* is present in *Cheirodontops*. Schultz (1944) observed the resemblance of teeth between *Cheirodontops* and *Holoshesthes*. Malabarba (1998) based on the phylogenetic analysis of Cheirodontinae placed *Holoshesthes* in synonym of *Odontostilbe*, arguing that the character of the presence of dentary teeth with at least five cusps, with the three central cusps larger, compressed and in a row forming a sharp cutting edge, was found to be ambiguous, and independently acquired in four cheirodontine lineages. Eigenmann (1915), and Géry (1977) used this character alone to distinguish *Holoshesthes* of *Odontostilbe*. Additional phylogenetic analysis of *Odontostilbe* is needed to clarify the relationships and taxonomic status of *Holoshesthes* and *Cheirodontops*.

Malabarba (2003) listed *Deuterodon* (*Lobodeuterodon*) *euspilurus* Fowler, 1945, described from upper río Caquetá basin, Colombia, as a junior synonym of *O. fugitiva*. According to work in progress by the senior author, *O. euspilura* (Fowler, 1945) is a valid species, and a senior synonym of *O. roloffi* Géry, 1972 described from upper río Napo, Ecuador. A full redescription of this species will be provided in a forthcoming paper.

Almost all the mature males of the examined *Odontostilbe* related species share both elongations of the unbranched dorsal- and pelvic-fin rays, excepting *Odontostilbe euspilura* and an undescribed species from rio Uruguay basin that lack the elongation of the second unbranched dorsal-fin ray. Two other undescribed species from upper rio Paraná basin lack both elongations, of unbranched dorsal- and pelvic-fin rays, but there are few mature males available of them. *Odontostilbe pulchra* has a slight elongation of the second unbranched dorsal-fin ray only in some specimens, but has the unbranched pelvic-fin ray elongate.

A reevaluation of the diagnosis of *Odontostilbe* is still needed because the discovery of several new species not previously used in a phylogenetic analysis of the genus by Malabarba (1998). The discovery of new data regarding *Cheirodontops geayi* indicating that it shares characters diagnosing *Odontostilbe* (elongation of the dorsal- and pelvic-fin rays) requires a reanalysis of the phylogeny of these genera of the Cheirodontinae. Also, such an analysis should include *Lobodeuterodon* (its type species) and *Holoshesthes*, apparent junior synonyms of *Odontostilbe*.

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CAPÍTULO IV

Redescription of *Odontostilbe pulchra* (Gill, 1858) (Teleostei: Characidae: Cheirodontinae: Odontostilbini), and description of two new species from the Orinoco River basin

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Abstract

Odontostilbe pulchra, before doubtly assigned to the genus or to río Orinoco basin, is redescribed with the rediscovery of two syntypes. Originally described to the Island of Trinidad, *O. pulchra* is widespread in Venezuela, río Orinoco basin, in smaller coastal drainages in the northen South America, in the Lake Valencia system, and río Essequibo basin. A punctual occurrence in the upper rio Negro, nearly southern of the río Orinoco headwaters, extends its distribution to the Amazon basin. Additionally, two new species of *Odontostilbe* from the río Orinoco basin are described.

Key words: Northern South America, Syntypes, Taxonomy, *Poecilurichthys pulcher*.

Introduction

Odontostilbe Cope, 1870 is the most basal and unspecialized genus of the tribe Odontostilbini. It belongs to the subfamily Cheirodontinae, a recognized monophyletic clade of Characidae including about 15 genera and 50 species of small neotropical fishes (Malabarba, 1998, 2003; Malabarba *et al.*, 2004; Bührnheim & Malabarba, submitted). A total of ten species were recognized in *Odontostilbe* by Bührnheim & Malabarba (2006): *Odontostilbe pulchra* (Gill, 1858), *O. fugitiva* Cope, 1870, *O. pequira* (Steindachner, 1882), *O. paraguayensis* Eigenmann & Kennedy, 1903, *O. microcephala* Eigenmann, 1907, *O. dierythrura* Fowler, 1940, *O. euspilura* (Géry, 1972), *O. ecuadorensis* Bührnheim & Malabarba, 2006, *O. nareuda* Bührnheim & Malabarba, 2006, *O. parecis* Bührnheim & Malabarba, 2006, but the genus contains at least other seven undescribed species.

A single species of *Odontostilbe* has been so far assigned to the río Orinoco basin. *Odontostilbe pulchra* was originally described from the Island of Trinidad as *Poecilurichthys pulcher* Gill, 1858. The genus *Poecilurichthys* Gill, 1858 was described in the same paper, being *Poecilurichthys brevoortii* Gill, 1858 [= *Astyanax bimaculatus* (Linnaeus, 1758)] posteriorly designated as the type species of that genus by Eigenmann (1910: 432), and *Poecilurichthys* considered a junior synonym or a subgenus of *Astyanax* Baird & Girard, 1854. Lütken (1875) redescribed the species as *Chirodon* (*Odontostilbe*) *pulcher*. After that, practically all cheirodontine material from the río Orinoco and Trinidad have been referred in the literature as *Cheirodon pulcher*, *Odontostilbe pulcher* or *Odontostilbe pulchra*, but these references seems to include more than one species of *Odontostilbe*, as well as undescribed species of *Odontostilbe*, *Holoshesthes* and *Serrapinnus.*

The poor and not diagnostic original description of *Odontostilbe pulchra*, associated to the use of this specific name for several cheirodontine species, lead Malabarba (2003) to consider "*P. pulchra*" Gill, 1858 as *species inquirenda*. In this paper we redescribe "*P. pulchra*" based on the rediscovery of two syntypes, and review its distribution in Trinidad and in northern South American drainages. Jointly, two new *Odontostilbe* species sympatric to *O. pulchra* in the río Orinoco basin are described.

Material and Methods

Counts and measurements follow Fink & Weitzman (1974), primarily on the left side of the specimen. Head length is the distance between the tip of the snout and the posterior end of subopercle, which is slight posterior to the margin of opercle. Total vertebrae number includes the four vertebrae of the Webberian apparatus, and the terminal “half centrum” according to Malabarba & Weitzman (1999). The gill raker at the junction of the ceratobranchial and the epibranchial is referred as the posteriormost gill raker of the lower branch of the arch, and counted jointly to the gill rakers on this lower branch as in Bührnheim & Malabarba (2006). Specimens were cleared and stained according Taylor & Van Dyke (1985), and/or radiographs were used for counting vertebrae, teeth, and gill rakers. Scanning electron micrographs (SEM) were obtained from teeth and denticulation of gill rakers. Values of the holotype of the new species and of the two syntypes of *O. pulchra* are marked in bold along descriptions. Males and females are recognized only when dissected, or when showing sexual dimorphism in specimens of similar size in the same collecting lot, otherwise they were termed as unsexed (Bührnheim & Malabarba, 2006). The two syntypes of *Odontostilbe pulchra* recognized as females are an exception to this rule, because principal component analysis and regression analyses grouped them with females.

The following institutions provided material for the study: **ANSP -** Academy of Natural Sciences, Philadelphia, USA; **CAS -** California Academy of Sciences, San Francisco, USA; **FMNH** - Field Museum of Natural History, Chicago, USA; **INHS** - Illinois Natural History survey, Illinois, USA; **ICNMNH -** Universidad Nacional de Colombia, Museu de Historia Natural, Bogotá, Colombia; **INPA -** Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; **MCP** - Museu de Ciências e Tecnologia, Porto Alegre, Brazil; **MCNG** - Museo de Ciencias Naturales de Guanare, Guanare, Venezuela; **MHNG** - Muséum d’histoire naturelle, Geneva, Switzerland, **MNHN** - Muséum d’historie naturelle, Paris, French; **MZUSP** - Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; **ROM** - Royal Ontario Museum, Toronto, Canada; **UMMZ** - University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA; **USNM** - National Museum of Natural History, Washington D.C., USA. Abbreviatures given along with the number of specimens are the following: m- morphometrics and meristics taken; c- only meristics taken; x- meristics taken from x-rays; c&s- cleared and stained specimens.

Statistical analyses. Principal component analysis (PCA) was used to check overall variation among samples, looking for differences in morphometrics among species or between sexes, being an input to multiple regressions (Johnson & Wichern, 1998). PCA on covariances of logarithmically transformed measurements were obtained using Past version 1.28 2004, and Sigma Plot version 6.10 2000. The first principal component was partitioned out, considering it mostly accounts for size variation (Strauss, 1985). Multiple linear regressions were applied to describe morphometric differences among species or between sexes.

Results

Odontostilbe pulchra (Gill, 1858)

Fig. 1

Poecilurichthys pulcher Gill, 1858: 419 [new species description, type locality: western portion of the Island of Trinidad].

Tetragonopterus pulcher -Günther, 1864: 317 [new generic combination].

Chirodon (*Odontostilbe*) *pulcher*. -Lütken, 1875: 236-238 [new generic combination, redescription].

Odontostilbe pulcher (Gill). -Eigenmann & Eigenmann, 1892: 54 [new generic combination]. -Eigenmann, 1909: 327 [listed, Trinidad]. -Eigenmann, 1910: 429 [listed, Trinidad]. -Price, 1955: 11, Fig. 3 [map with distribution to Caroni, Caparo, and northen Oropouche drainages in Trinidad, known to occur in Venezuela]. -Boeseman, 1960: 72, 88-89 [listed, synonym list]. -Eigenmann, 1920: 4, 9-10 [listed to the Valencia basin, Venezuela, Maracay, Rio Bue]. –Schultz, 1944: 318-319 [list of synonyms, specimen from Caripito, Venezuela].

Cheirodon pulcher. -Ulrey, 1895: 289-290 [in key, including teeth counts, Trinidad].

Chirodon pulcher. -Regan, 1906: 380, 385, Pl. XXII. Fig. 2 [species redescription, distribution Trinidad, Cumuto, partial designation in key, illustration]. -Guppy, 1906: 378-380, 385, Pl. XXII. Fig. 2 [in key, redescription based on four specimens deposited at Bristish Museum, distribution Cumuto, Trinidad, color in life description]. -Guppy, 1934: 118, 120-122, Fig. 5 [recorded in ponds and water holes in the vicinity of rice fields, compilation of Regan’s 1906 drawing, listed as larvicidal fish, usually in dams, only from Trinidad].

Odontostilbe pulchra. -Eigenmann, 1915: 90, 95-96, Pl. XVII. Fig. 1 [in key, Regan’s characters compilation, reproduction of Regan’s illustration]. -Fowler, 1943: 65-66. Fig. 2 [common name sardine doree, drawing of a specimen]. -Böhlke, 1954: 137-140 [possibly synonym of *Odontostilbe fugitiva*, table with measurements and counts of *O. pulchra* and *O. fugitiva*]. -Géry, 1977: 558 [in key].

Fig. 1. *Odontostilbe pulchra*, syntype MNHN 0000-9593, female 28.7 mm SL (top), a specimen INHS 40101, male 32.3 mm SL from Trinidad (middle top), and specimens MCP 38863, male 28.6 mm SL (middle bottom), and female 32.5 mm SL (bottom) from río Orinoco basin.

Syntypes. MNHN 0000-9593, 2 (females 28.7mm SL and 30.8mm SL), west portion of Trinidad.

Non-type material. Uncertain drainage, TRINIDAD: CAS 70933, 1 (male 24.7 mm SL), 10°37'N 61°13'W. **Cunapo River basin,** TRINIDAD: INHS 40081, 4m (2 females 32.6-33.3 mm SL, 2 unsexed 26.3-29.9mm SL), Quare River, 1km E Valencia on road to Arima. **Caroni River basin,** TRINIDAD: ANSP 70181, 1 (unsexed 18.2 mm SL), sent from Port-of-Spain. INHS 40101, 20m (13 males 29.4-32.7 mm SL, 1 male 32.5 mm SL c&s, 4 females 33.6-34.6 mm SL, 1 female 34.4 mm SL c&s, and 1 unsexed 25.1 mm SL), Cumuto River, 5 km S Brazil on the road to Talparo. ROM 41035, 9 unsexed 17.9-27.6 mm, east side of north-south canal south of Blue river, Caroni swamp. ROM 44764, 20m (6 males 26.2-28.6 mmSL, 11 females 28.4-36.9 mm SL, 3 unsexed 28.3-31.2 mm SL), near Bamboo Grove on Churchill and Roosevelt highway, St. Joseph River. ROM 1082, 2 c&s (1 male, 1 unsexed), near Bamboo Grove on Churchill and Roosevelt highway, St. Joseph River. ROM 1139CS, 1 c&s, near Bamboo Grove on Churchill and Roosevelt highway, St. Joseph River. USNM 290410, 7 unsexed 30.8-37.2 mm SL, Valencia River, [Aripo River drainage, upper Caroni River basin]. USNM 177552, 50 (2c of 10 females 27.1-36.3 mm SL, 11 males 26.6-32.1 mm SL, 6 unsexed 14.6-18.2 mm SL), [Caroni County], Piarco. **O'Meara River basin,** TRINIDAD: ROM 41069, 1m (female 35.0 mm SL), small stream, 13 miles east of Port Spain on Churchill-Roosevelt highway, at B1-13, 10°38'N 61°20'W. **Bejucal River basin,** TRINIDAD: UMMZ 189000, 20 of 40 (20 unsexed 18.5-29.2 mm SL), [Caroni County, Cunupia], Mt. Plaisance Village, BWI. **Tuy River basin - Caribbean coastal drainage,** VENEZUELA: INHS 29318, 16 (3 males 24.8-27.0 mm SL, 1 male 28.9 mm SL, 12 unsexed 12.5-32.0 mm SL), Miranda, Quebrada Querepe, tributary of río Merecure, 5 km NE Caucagua. **Río Unare basin - Caribbean coastal drainage,** VENEZUELA: ANSP 165594, 2 (unsexed 18.9-21.8 mm SL) alizarin stained, [Anzoategui], Laguna at San Pable, L. Encantada. INHS 31295, 5 (1 male 34.0 mm SL, 4 unsexed 20.5-22.9 mm SL), Guarico, quebrada Honda, río Unare, 7 km W Zaraza, hwy. 13. **Lake Valencia basin,** VENEZUELA: CAS 70934, 43 (19 males 28.5-31.3 mm SL, 9 females 31.5-36.4 mm SL, 15 unsexed 24.7-37.9 mm SL), Aragua, [río Bue], Maracay. MCP 14945, 9 (1 male 29.8 mm SL, 8 unsexed 25.1-34.5 mm SL), caño Cambur tributary to Lake Valencia, 11 km S El Valencia, formerly ANSP 150108. INHS 60011, 6 (1 male 29.2 mm SL, 5 unsexed 24.4-29.3 mm SL), Carabobo, río Las Penitas, Vigirima, 10°20'N 67°52'W. **Río Meta basin,** COLOMBIA, META: ANSP 128231, 10 of 41 (7 males 24.6-28.9 mm SL, 3 females 29.5-30.5 mm SL), río Metica *ca.* 3 km SE Mozambique ranch, 03°57'N 73°02'W. ANSP 131976, 21 (5 males 26.4-31.6 mm SL, 16 unsexed 25.1-37.7 mm SL), río Metica, *ca.* 1.5 km E of Rajote. ANSP 131977, 10 (2 males 25.5-31.3 mm SL, 8 unsexed 25.1-32.6 mm SL), same locality as ANSP 131976. ANSP 133239, 2 (unsexed 28.0-32.1 mm SL), caño Rico at Brasília. ANSP 139335, 8 (unsexed 25.1-35.6 mm SL), same locality as ANSP 128231. ANSP 139346, 10x of 15 (6 males 21.2-30.8 mm SL, 2 females 32.0-30.1 mm SL, 7 unsexed 25.3-31.5 mm SL), same locality as ANSP 128231. ANSP 139347, 1 (female 29.6 mm SL), tributary of caño El Chocho *ca.* 5 km N of La Siberia. ANSP 139348, 10 (2 males 23.1 mm SL & 25.0 mm SL, 8 unsexed 24.4-29.5 mm SL), tributary of caño La Raya, 1st caño N of La Siberia. ANSP 139349, 3 (females 29.1-33.5 mm SL), laguna El Batin, *ca.* 4 km SW upstream of lake Mozambique, S side of río Metica. ANSP 139450, 10m of 23 (5 males 24.2-25.9 mm SL, 1 male 24.3 mm SL c&s, 5 females 25.7-27.5 mm SL, 1 female 26.9 mm SL c&s), laguna Doctor Sanchez, a cut-off oxbow, entrance *ca.* 5 km SW from inlet to lake Mozambique, 03°56'N 73°08'W. ANSP 139452, 2 (1 male 25.4 mm SL, 1 female 25.5 mm SL), río Negro, downstream from main Villavicencio-Puerto Lopez highway at La Balsa, W side of river. ANSP 139456, 1 (female 33.8 mm SL), río Negrito at bridge on road joining Puerto Lopez and Villavicencio, 200-400 yd downstream of bridge. ANSP 139469, 4 (2 males 24.2-27.3

mm SL, 2 females 27.1-27.6 mm SL), same locality as ANSP 139349. ANSP 139471, 23 of 63 (11 males 23.1-27.4 mm SL, 12 females 28.4-32.6mm SL), caño Rico at La Defensa, NW of Laguna Mozambique, becomes caño Buenaventura before entering río Negro. ANSP 139472, 94m (4 males 23.0-25.0 mm SL, 4 females 27.2-34.7 mm SL), tributary of La Raya, 1st caño north of La Siberia, 04°50’N 73°05’W. ANSP 139485, 74 (14 males 18.9-23.6 mm SL, 60 unsexed 18.3-24.3 mm SL), Mozambique ranch, lake Mozambique, N shore at main house. ANSP 139572, 3x of 128 (68 males 20.9-31.1 mm SL, 60 unsexed 24.5-33.9 mm SL), río Negrito at bridge at La Balsa. ANSP 139579, 20m of 199 (10 males 16.6-25.7 mm SL, 10 females 23.1-29.2 mm SL), Mozambique ranch, lake Mozambique, N end directly in front of main house. ANSP 140762, 1 (male 24.6 mm SL), Metica river, upstream from entrance to lake Mozambique, halfway to entrance to laguna Arrotas. ANSP 140794, 19 (3 males 20.5-24.5 mm SL, 16 unsexed 18.6-29.8 mm SL), same locality as ANSP 139347. ANSP 140830, 34 (9 males 24.5-28.8 mm SL, 2 females 32.9 mm SL, 23 unsexed 21.7-31.7 mm SL), confluence of río Guayariba and río Metica. FMNH 84037, 4 (1 unsexed 26.7, 3 males 26.6-28.3 mm SL), río Meta, temporary pool near caño Venturosa, at 1 km N Puerto Lopez. ICNMHN 935, 1 (female 40.4 mm SL), Meta, [Cundinamarca], Quebrada Tascona, río Guacavia, [upper río Meta]. INPA 25174, 30 (15 males 23.2-30.0 mm SL, 15 unsexed 24.1-32.0 mm SL), same data as ANSP 139572. MCP 14942, 5 (2 males 27.9-27.6 mm SL, 3 unsexed 23.2-26.8 mm SL), Mozambique ranch, río Metica, just SW of lake Mozambique. MCP 14946, 5 (females 25.7-30.7 mm SL), lake Mozambique, Mozambique ranch N side, formerly 137577. MCP 14952, 5 (females 27.9-32.4 mm SL), same locality as ANSP 139347, formerly ANSP 134733. MCP 14956, 20 (10 males 19.1-24.2 mm SL, 10 unsexed 14.9-23.3 mm SL), formerly ANSP 139579. MCP 14964, 10 (4 males 29.2-31.6 mm SL, 8 unsexed 28.2-32.1 mm SL), formerly ANSP 131977. MCP 14965, 20 (3 males 23.8-26.4, 17 unsexed 22.3-28.0 mm SL), formerly ANSP 139472. MCP 14966, 20 (7 males 25.1-30.8 mm, 13 unsexed 29.6-34.4 mm SL), formerly ANSP 131976. MCP 14975, 20 (1m male 29.5 mm SL, 1m female 29.6 mm SL, 18 unsexed 16.2-23.2 mm SL), formerly ANSP 139485. MCP 38863, 19m of 49 (9 males 22.4-29.9mm SL, 1 male 30.6mm SL c&s, 3 females 32.0-33.4 mm SL, 1 female 30.8 mm SL c&s, and 5 unsexed 24.2-22.8 mm SL), formerly ANSP 139572. MHNG 2171.39, 2 (unsexed 26.7-28.3 mm SL), Villavicencio, upper río Meta. MNHG 2171.82, 2 (unsexed 20.8-21.4 mm SL), floodplains, caño Carupa of río Guachariria. **Golfo de Paria coastal drainage,** VENEZUELA, MONAGAS: ANSP 150112, 9 (1 male 29.7 mm, 8 unsexed 26.7-34.1 mm SL), río Pina, 6 km N of Maturín, [Golfo de Paria]. MCP 14970, 8 (unsexed 25.5-32.2 mm SL), formerly ANSP 150112. INHS 31438, 11 (2 males 27.2-34.7 mm SL, 9 unsexed 18.9-38.4 mm SL), río De Oro, río Guarapiche- río San Juan drainage, 4 km SW Jusepín. INHS 31461, 14 (unsexed 18.8-33.6 mm SL), río Guanipa (Caribbean Sea Dr.), 20 km SSE Maturín on hwy. 10. INHS 31485, 9 (unsexed 19.7-25.9 mm SL), río Tigre, 50 km of Maturín, rt. 10 bridge. USNM 163149, 11 (8 males 27.9-31.9 mm SL, 3 unsexed 31.1-37.3 mm SL), Caicara, Guarapiche river. **Río Orinoco basin,** VENEZUELA, ANZOATEGUI: ANSP 159909, 7 (unsexed 21.9-27.2 mm SL), río Orinoco at Soledad boat launch just below Puente Angostura. INHS 61950, 14 (4 males 23.8-26.8 mm SL, 10 unsexed 20.9-28.3 mm SL), [río Caris], in hato El Moron, SE of El Tigre. VENEZUELA, BOLIVAR: ANSP 160790, 5x of 40 (unsexed 20.0-31.6 mm SL), river and flooded area 15 km N of Maniapure on Caicara - Puerto Ayacucho hwy (río Chaviripa?). ANSP 160819, 20 (1 male 29.2 mm SL, 19 unsexed 20.9-35.1 mm SL), small stream crossing Caicara - Puerto Ayacucho hwy 18 km N of Maniapure. USNM 233520, 95 (unsexed 16.1-23.4 mm SL), río Orocopiche, *ca.* 15 km from mouth in río Orinoco, downstream from route 19 bridge, 08°03’N 63°40’W. VENEZUELA, DELTA AMACURO: USNM 233359, 97 (unsexed 18.3-25.0 mm SL), río Orinoco, small caño on w side just above downstream mouth of caño Remolinos, 74 nautical miles upstream from Sea Buoy. USNM 233652, 37 (unsexed 19.8-31.8 mm SL), río Orinoco, backwater caño Araguao, 112 nautical miles upstream from

Sea Buoy. USNM 233689, 6 (unsexed 23.7-26.7 mm SL), río Orinoco, lagoon at caño Araguaito, *ca.* km 130. VENEZUELA, MONAGAS: USNM 233745, 31 (1 male 25.5 mm SL, 30 unsexed 18.6-26.8 mm SL), río Orinoco, Barrancas, laguna El Guatero, 143 nautical miles upstream from Sea Buoy. **Río Essequibo basin, Cuyuní drainage,** VENEZUELA, BOLIVAR: CAS 70907, 9 (unsexed 19.9-23.6 mm SL), río Carichapo, 30 km E of Upata, 200 km E of ciudad Bolivar. INHS 31574, 5 (unsexed 20.7-27.0 mm SL), río Oronata, río Yuruari drainage, between Upata & El Manteco. INHS 31625, 20 (2 males 24.7-25.2 mm SL, 1 female 26.6 mm SL, 17 unsexed 19.9-25.4 mm SL), tributary of río Yuruari, 3 km W Guasipati via La Pastora. INHS 31662, 7 (unsexed 21.2-26.2 mm SL), tributary of río Yuruari, near La Pastora, W of Guasipati. INHS 31754, 16 (3 males 20.8-23.1 mm SL, 13 unsexed 20.7-28.5 mm SL), río Corumo, E Tumeremo on road to Bochinche. INHS 31718, 23 unsexed 17.9-23.7 mm SL, río Guanare, río Yuruari drainage, El Miamo. INHS 31744, 14 (4 males 21.4-24.5 mm SL, 7 females 22.8-25.5 mm SL, 3 unsexed 21.2-21.6 mm SL), tributary of río Corumo, E Tumeremo on road to Bochinche. **Río Apure basin,** VENEZUELA, GUARICO: ANSP 139544, 7 (unsexed 22.7-25.5 mm SL), Camaguán swamp, on W side of highway to San Fernando de Apure, *ca.* 2 km N of Camaguán. ANSP 141553, 16 (unsexed 16.3-26.6 mm SL), río Orituco, tributary of río Guarico, 15 km SSE of Calabozo on Cazorla Road. ANSP 149992, 4 (2 males 31.0-32.8 mm SL, 2 unsexed 22.4-25.9 mm SL), [upper río Guarico], lagoon 2-15 km SW El Sombrero. ANSP 163489, 7 (3 males 23.2-24.5 mm SL, 4 unsexed 25.6-25.9 mm SL), río Portuguesa; caño Falcón, laguna La Raya near Camaguán. CAS 70882, 3 (2 males 26.1-25.8 mm SL, 1 female 28.0 mm SL), spring brook, a tributary to río Guarico, 5 km south of Calabozo. CAS 70906, 30 of 119 (unsexed 19.0-34.2 mm SL), spring brook, tributary of río Guarico, 6 km southwest of Calabozo. MCP 14961, 6 (unsexed 18.2-25.3 mm SL), formerly ANSP 139544. MCP 14976, 16 (unsexed 16.8-28.4 mm SL), formerly ANSP 141553. USNM 260590, 10 (unsexed 18.8-28.8 mm SL), río Orituco where crossed by road from Calabozo. VENEZUELA, APURE: ANSP 140752, 12 (unsexed 19.0-28.7 mm SL), río Apure, S bank and backwater areas downstream side of bridge at San Fernando de Apure. INHS 28049, 17 (unsexed 18.6-26.7 mm SL), río Arauca overflow pool, upper río Apure, north edge of Elorza. INHS 89783 22 (unsexed of 140 13.5-16.9 mm SL), caño Caicara, río Matiyure drainage., *ca.* 15 km SSW Mantecal on Bruzual-Elorza road. USNM 260598, 28 (16 males 28.3-35.0 mm SL, 11 unsexed 19.4-22.9 mm SL), Centro de Recria M.A.C. – Mantecal, pools along side of road about 2.5 km south of road from Mantecal. USNM 260601, 21 (3 males 21.1-22.2 mm SL, 18 unsexed 21.2-29.5 mm SL), side channel of río Apure *ca.* 5 km west of San Fernando de Apure. USNM 330330, 2 (1 male 25.1 mm SL, 1 female 25.3 mm SL), modulos experimentales de Mantecal. VENEZUELA, PORTUGUESA: CAS 64404, 4 (unsexed 19.3-30.7 mm SL), caño Maraca en el puente 60 km via Guanare-Guanarito road. FMNH 96160, 20 (1 male 31.1 mm SL, 19 unsexed 25.4-31.2 mm SL), Guanare, río Maria, side pool, 800 m upstream from bridge, 4 km E of Guanare. INHS 54553, 20 (unsexed of 48 16.7-22.8 mm SL), caño Maraca, caño Ignes, río Portuguesa drainage, on road from Guanare to Guanarito at 60 km marker. INHS 54650, 3 (unsexed 18.0-19.9 mm SL), río Portuguesa, Hwy. 5 bridge. INHS 56134, 1 (unsexed 20.1 mm SL), río Portuguesa, Hwy. 5 bridge. INHS 89824, 6 (unsexed 13.3-16.8 mm SL), caño Mamón, río Portuguesa drainage, El Mamón, 24 km E Guanare. USNM 332091, 10 (1 male 32.0 mm SL, 9 unsexed 25.6-32.1 mm SL), río Portuguesa, cerca de Nueva Florida. USNM 348669, 1 unsexed (26.3 mm SL), Guanare-Guanarito road at road Km 60, 08°49’39’’N 69°20’42’’W. VENEZUELA, COJEDES:CAS 70884, 45 (1 male 27.6 mm SL, 44 unsexed 22.4-29.8 mm SL), río Tinaquillo, Orinoco basin. CAS 70901, 14 unsexed 25.9-38.2 mm SL, same locality as CAS 70884. VENEZUELA, LARA: CAS 70900, 5 (unsexed 19.5-22.4 mm SL), quebrada Seca near Moran, 25 km. S of Barquisimeto. VENEZUELA, TACHIRA: INHS 28152, 27 (4 males 21.0-22.7 mm SL, 23 unsexed 15.1-24.2 mm SL), tributary of río Doradas, upper río Apure, La Pedrera. VENEZUELA, ARAGUA: INHS 31382, 12 unsexed

26.7-34.7 mm SL, río Guarico, Barbacoas. **Río Guaviare basin,** COLOMBIA, META: ICNMHN 2956, 9 (1 male 27.3 mm SL, 8 unsexed 21.1-35.9 mm SL), La Macarena, alto raudal, río Santo Domingo. SU 50346, 1 (unsexed 34.5 mm SL),Colombia, río Guaviare basin, vicinity of Los Micos, north end of Cordillera Macarena, 03°20’N 73°56’W . USNM 181359, 1 unsexed 20.5 mm SL, llanos, río Guaviare. **Waini River Basin - coastal drainage,** GUYANA: ROM 67867, 5 (unsexed 28.1-31.5 mm SL), Barama River, Chinese Landing at base camp, 73°10’N 59°33’W. ROM 67868, 11 (5 males 25.2-28.3 mm SL, 6 unsexed 26.2-30.1 mm SL), Barama River, Chinese Landing, 1.5 km upstream from store, 72°90’N 59°34’W. ROM 67869, 1 unsexed 29.0 mm SL, same locality as ROM 67867. ROM 67872, 20 (8 males 25.4-28.2 mm SL, 12 unsexed 19.0-31.3 mm SL), Waini River at Kwabanna next to float plane ramp, 73°40’N 59°09’W. **Rio Amazonas basin,** BRAZIL, AMAZONAS: INPA 20980, 1 (male 29.3 mm SL), rio Toototobi, affluent of upper rio Demini, rio Negro drainage, indigenous camp.

Diagnosis. A remarked large anal-fin base (26.0-33.5% HL) differ *O. pulchra* from most other *Odontostilbe* species, *e.g.* from the nearest distributed Amazonian *O. fugitiva* (23.5-29.4% HL) (Fig. 2). Only *O. nareuda* from the rio Madeira basin has similar large anal-fin base length (31.3-32.8% HL), but differs in anal-fin counts (24-26 *vs* 17-24, mostly 19-22 in *O. pulchra*). Furthermore, mature males of *O. pulchra* differs from *O. fugitiva*, *O. ecuadorensis*, *O. dierythrura*, *O. parecis*, *O. paraguayensis*, and *O. microcephala*, and the two new species from the rio Orinoco, *O. splendida*, and *O. pao*, by the presence of hooks on the 1st to 22nd anal-fin branched rays of males, pratically along all branched anal-fin rays (*vs.* 1st to 9th, mostly 6th-7th, anal-fin branched rays of males with hooks); the anal-fin distal border slightly concave to almost straight in mature males (*vs.*, distal border concave); the longer pectoral fin crossing a vertical through pelvic-fin origin (*vs.* shorter pectoral fin reaching to vertical through pelvic-fin origin, *e.g. vs. O. fugitiva* in Fig. 3), almost absence of elongation of the 2nd unbranched dorsal-fin ray (*vs* elongate 2nd unbranched dorsal-fin ray). Adittionally, the longer upper jaw length in males, females and unsexed specimens differs *O. pulchra* (26.8-32.5% SL) from *O. fugitiva* (23.4-30.0% SL) (Fig. 4). Among other characters formerly cited, snout lenght in males distinghishes *O. pulchra* (18.0-26.0% HL, mean 21.8% HL) from the sympatric *O. splendida* (24.1-26.9% HL, mean 25.2% HL), and *O. pao* (26.7-30.6, mean 28.6% HL) (Fig. 5).

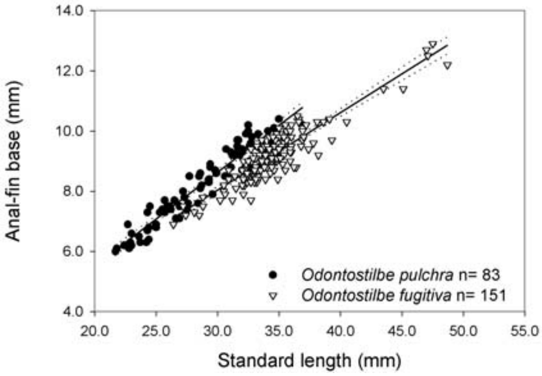

Fig. 2. Anal-fin base length as a function of standard length for males of *Odontostilbe pulchra*, against *O. fugitiva*.

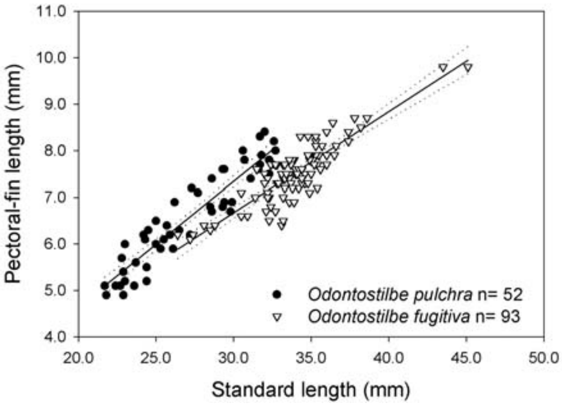

Fig. 3. Pectoral-fin length as a function of standard length for males of *Odontostilbe pulchra*, against *O. fugitiva*.

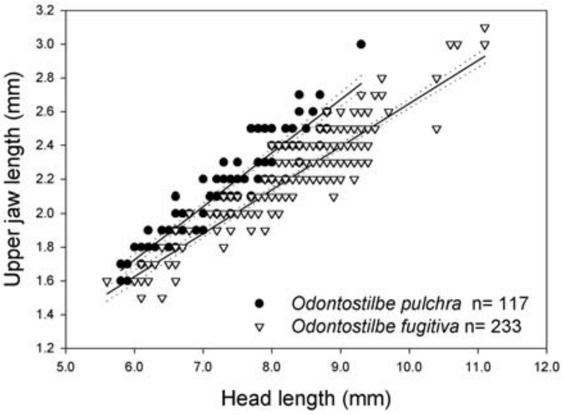

Fig. 4. Upper jaw length as a function of head length for males, females and unsexed specimens of *Odontostilbe pulchra*, against *O. fugitiva*.

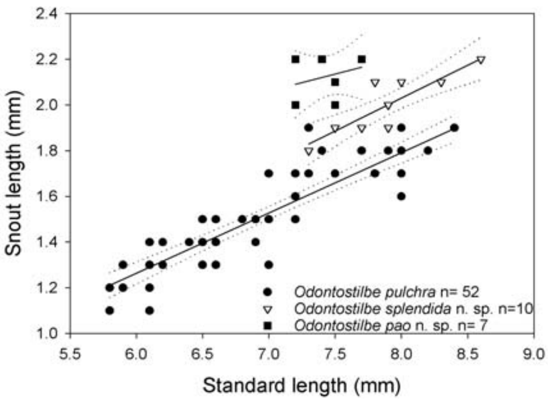

Fig. 5. Snout length as a function of standard length for males of *Odontostilbe pulchra*, against *O. splendida*, and *O. pao*.

Description. Morphometric data are given in Table 1. Largest male 32.7 mm SL, largest female 36.9 mm SL. Body elongate and compressed. Greatest body depth at dorsal-fin origin. Snout short, more blunt in males. Head profile gently convex to straigth from snout to posterior tip of supraoccipital bone. Predorsal profile slightly convex between posterior tip of supraoccipital bone and dorsal-fin origin, then straight from dorsal-fin origin to caudal peduncle. Ventral profile convex from mouth to anal-fin origin. Anal-fin base straight. Caudal peduncle slightly longer than deep.

Dorsal-fin rays: **ii, 9**(117). Dorsal-fin origin slightly behind mid length of body, and slightly posterior to pelvic-fin origin. Second unbranched dorsal-fin ray and 1st-2nd branched dorsal-fin rays longest. Anal-fin rays: **iv**(5), **v**(103) or vi(9); branched 17(1), 18(1), **19**(10), **20**(32), 21(46), 22(21), 23(4), or 24(2). Anal-fin distal border usually concave, slightly concave to almost straight in mature males. Pectoral-fin rays: **i**(117), 10(43), 11(60), or **12** (14). Distal tip of pectoral fin slightly pointed, 1st unbranched pectoral-fin ray and 1st-3rd branched pectoral-fin rays longer, reaching posterior to vertical through pelvic-fin origin in males. Pelvic-fin rays **i**(117), 6(2), 6i(2), **7**(112), or 7i(1). Unbranched pelvic-fin ray slightly elongate, reaching to or slight posterior to anal-fin origin in males. Epitelium from external border of unbranched pectoral-fin ray and unbranched pelvic-fin ray thickened in males. Principal caudal-fin rays 16(1), 18(1), **19**(112), or 20(2). Procurrent caudal fin rays: dorsal **10**(12), **11**(36), 12(51), 13(16), or 14(1), ventral 8(11), **9**(52), 10(43), or 11(8). Some dorsal and ventral procurrent caudal-fin rays laterally expanded or bifurcated. Caudal-fin ray flaps ventraly on 4th-7th rays of upper lobe, dorsally on 13th-16th (most 13th-15th) rays of lower lobe. Adipose-fin at vertical through last anal-fin ray insertion.

Head relatively small. Posterior margin of opercle sinusoidal with upper portion concave and lower portion convex. Mouth terminal. Obliquously positioned maxilla ending at vertical through anterior border of eye**,** and practically at horizontal on inferior border of eye. Premaxillary teeth 5, bearing 7-10 cusps; central cusp longest (Fig. 6). Maxilla with 2-3 (mainly 2) teeth bearing 6-10 cusps, decreasing cusp number to posterior tip of maxilla. Dentary teeth 7-9 bearing 1-7 cusps, gradually decreasing in size; first 5-6 teeth large with 5-7 cusps, 1 medium-sized tooth with 5-6 cusps and posterior teeth very small decreasing from 5 cusps to conical. Smaller cusps of large dentary teeth overlap cusps of adjacent tooth or not.

Males with acute well-developed retrorse hooks on medial margin of pelvic-fin rays and posterior margin of anal-fin rays. One to three paired and unpaired hooks per segment of lepidotrichia at distal half-length of last unbranched anal-fin ray and 1st to 22th branched anal-fin rays. One to three unpaired and long hooks per segment of lepidotrichia on 1st unbranched pelvic-fin rays (3 specimens) on midlength portion, and on 1st-7th branched pelvic-fin rays, on midlenght portion through distal tip of fin ray. One or two unpaired hooks per segment of lepidotrichia on lateral or anterior border of branches in some to several pelvic- and anal-fin rays.

Scales cycloid: lateral line complete **33**(6), **34**(51), 35(28), 36(5), or 37(1); predorsal row 9(3), **10**(84), 11(25), or 12(2); scale rows between lateral line and dorsal-fin origin **5**(49), or 6(64); scale rows between lateral line and anal-fin origin **3**(14), or **4**(102),. Scale rows around peduncle **14**(102). Triangular modified scale on pelvic-fin base extends posteriorly covering 2 scales. Scales on anal-fin base 6, 7.

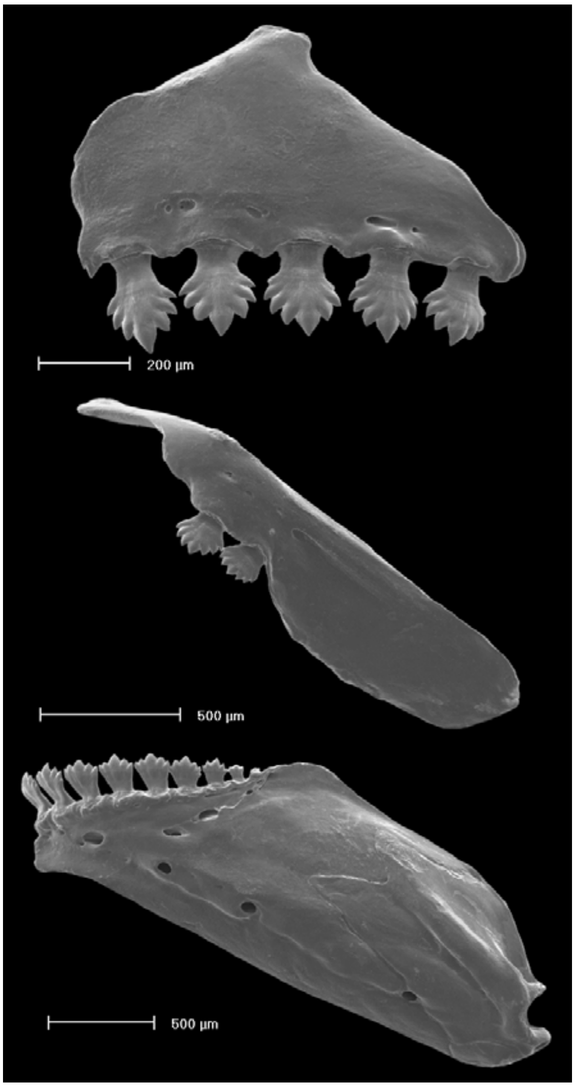

Fig. 6. Dentition of *Odontostilbe pulchra*, INHS 40101, male 32.5 mm SL: left premaxilla (top), maxilla (middle), and dentary (bottom), lateral view. Scanning electron micrograph (SEM).

Cleared and stained specimens (12), x-rays (18): supraneurals 4(18), 5(2); precaudal vertebrae, including Weberian apparatus, 14(1), 15(26), or 16(3); caudal vertebrae 17(9), 18(17), or 19(4); gill rakers (8 c&s), upper 6(3), or 7(5), lower 11(7), or 12(1) (2-3 on hypobranchial). Alcohol specimens (64): gill rakers, upper 5(4), **6**(48), or 7(12), lower 10(4), **11**(45), or **12**(15). Upper gill rakers with 1-4 denticles along anterolateral border, and 1-2 similar denticles on posterolateral border; lower gill rakers with 1-6 denticles on anterolateral border, and none or 1 on posterolateral surface; and posteriormost lower gill raker with none to 2 denticles on posterolateral border, and none to 3 denticles on anterolateral border (Fig. 7). Denticulation mainly on basal portion of gill rakers.

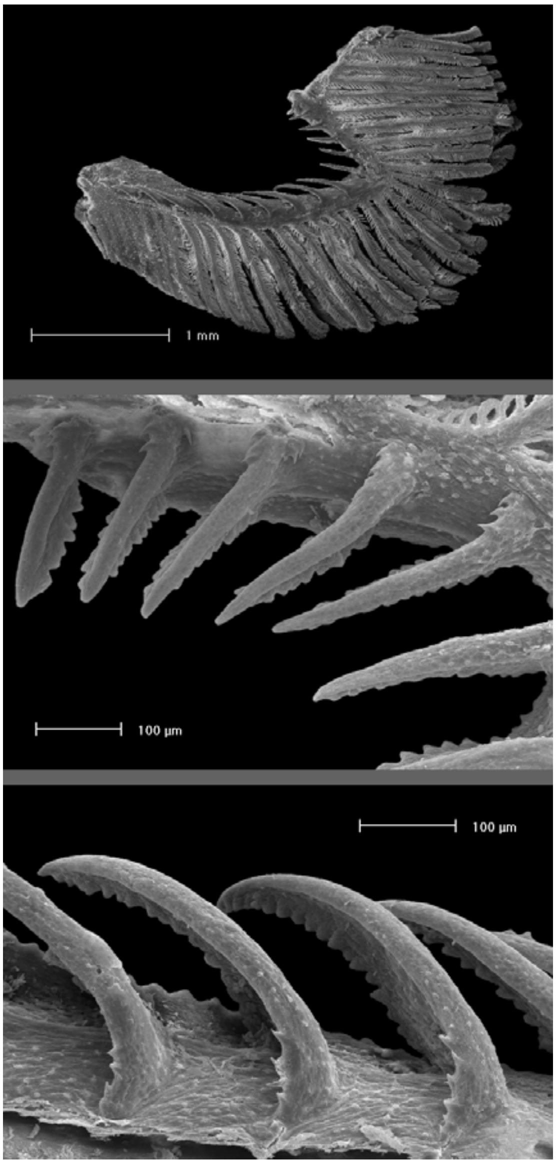

Fig. 7. First gill arch of *Odontostilbe pulchra*: left side, lateral view, showing gill gland (top) of FMNH 84037, male 26.6 mm SL, in detail gill rakers on upper branchial branch (middle), and gill rakers on lower branchial branch (bottom) of MCP 38863, male 27.2 mm SL. Scanning electron micrographs (SEM).

Color in alcohol. General ground body color pale beige, pale orange, or brownish in syntypes. Dorsum with small dark chromatophores from head to caudal peduncle, chromatophores more concentrate on scales border. Scattered dark chromatophores on scales on pseudotympanum area, extending over lateral line. Dark chromatophores along all dorsal-fin rays, except last branched fin ray only pigmented near fin base; 1st and 2nd unbranched dorsal-fin rays strongly pigmented. All anal-fin rays with chromatophores, more concentrated on distal half-length, last unbranched fin ray and 1st branched fin ray less pigmented. All pectoral-fin rays with dark chromatophores, gradually fading to posterior branched rays, 1st unbranched pectoral-fin ray more pigmented. Pelvic fin clearnot pigmente or with some scattered chromatophores (two specimens). Caudal fin almost entirely covered with diffuse dark chromatophores, except light area near caudal-fin spot. Rounded black caudal spot, reaching upper border of caudal peduncle.

Black chromatophores on snout, upper and lower lips, anteriormost portion of maxilla, and anteriormost portion of dentary. Abundant dark chromatophores on fontanel, frontals and parietals, deep-lying chromatophores over brain membrane below frontals and parietals. Body with faint dark and silver midlateral stripe, along middle longitudinal body axis, beginning posterior to pseudotympanum, abovelateral line, and reaching caudal spot.

Guanine on eye iris, opercle, isthmus, and circumorbital series. Below lateral line, belly faint practically without pigmentation, chromatophores just above anal-fin base forming about 10 chevron shaped markings.

The syntypes are dark brown in ground body color, faded chromatophores are present forming the caudal-fin spot, and guanine is preserved forming the remarked silver longitudinal stripe.

Color in life. Notes of UMMZ 189000: orange-red in anal, dorsal and caudal fins; center of caudal fin colorless. Guppy (1906) described: “olivaceous; sides silvery or a silvery longitudinal stripe from operculum to base of caudal; an indistinct dark humeral spot; a blackish spot at the base of caudal, posteriorly ending in a point and margined with yellow above and below; dorsal and anal pink.”

Sexual dimorphism. As anteriorly mentioned males have hooks on anal- and pelvic-fin rays. There is none elongation of the second unbranched dorsal-fin ray, but a slighty elongation of the unbranched pelvic-fin ray, and the anal-fin distal border is less concave than in females (Fig. 1). The pectoral-fin length and snout-dorsal fin origin distance are larger in males than females (Figs. 8-9). The snout is usually more developed in males (Fig. 10). A gill gland is found on the first gill arch of mature males, emcompassing about 8 to 11 anterior branchial filaments (Fig. 7).

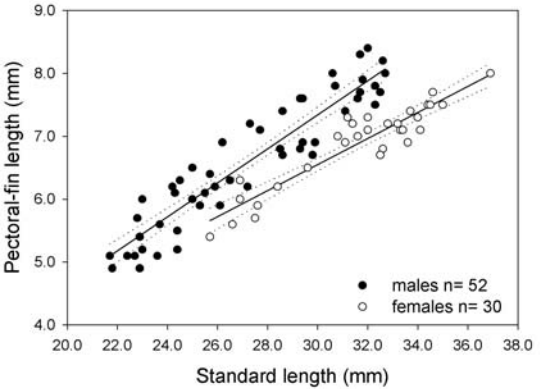

Fig. 8. Pectoral-fin length as a function of standard length for males against females of *Odontostilbe pulchra*.

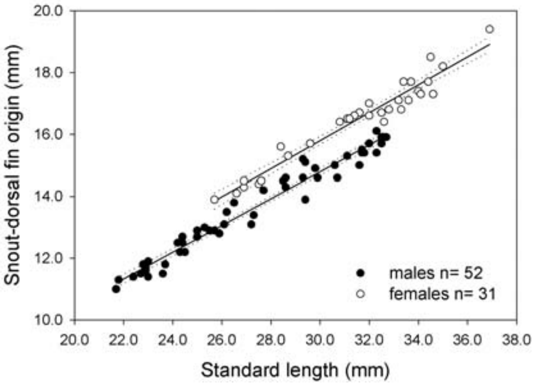

Fig. 9. Snout-dorsal fin origin as a function of standard length for males against females of *Odontostilbe pulchra*.

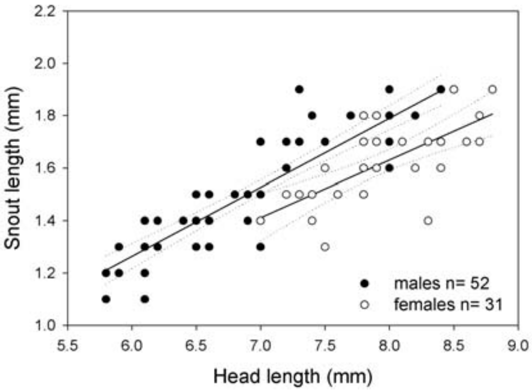

Fig. 10. Snout length as a function of head length for males against females of *Odontostilbe pulchra*.

Remarks on the type material. *Poecilurichthys pulchra* was described by the american naturalist Theodore Gill in the year he traveled to the West Indian Islands. He departed in January, 1858 (Dahl, 1916), and resided in Trinidad for several months “through portions of the spring and summer” (Gill, 1858). The description of *P. pulchra* did not refer to any catalog number, but Gill (1858: 371) remarked: “specimens of most of the species which are being described have been deposited in the museum of the Smithsonian Institution, and in the private cabinets of Messrs. Stewart and Brevoort.” Therefore, not all type specimens would have been deposited at Smithsonian. The Smithsonian catalog of type specimens of Characiformes (Vari & Howe, 1991) not mentioned the type material of *P. pulchra* Gill, 1858, though referred to the syntypes of *Poecilurichthys brevoortii* Gill, 1858, which are the unique type material found at Smithsonian among other new species of characins described by Gill in that year.

Later in 1875, the danish zoologist Christian F. Lütken redescribed *Chirodon* (*Odontostilbe*) *pulchra* from Trinidad, moving it from *Poecilurichthys* Gill to *Chirodon* Girard. Regarding *C.* (*O.*) *pulchra* specimens examined for his work, Lütken explained that they were from Trinidad (1875: 220-221): “From the 11 species of this family – Characinidae - from Trinidad that Prof. Gill carried home, the Museum has obtained about seven through the Judicial Counselor Mr. Riise, and further one that Mr. Gill overlooked: when all of these have been unknown by Günther; and because of insufficient descriptions he has not been able to arrange Tetragonopterins in their systematic place, here these species are the object for some remarks or partly for complete descriptions” [our translation]. Coincidentally, Prof. Gill is the american naturalist that described the species in 1858, and Mr. Riise the man honored in the description of *Corynopoma riisei* Gill, 1858 (Gill, 1858: 427): “Mr. A. H. Riise of the Danish Island of St. Thomas, the gentleman to whom this species has been dedicated, is well known as one of the most active zoologists of the West Indies, and has greatly contributed to our knowledge…, by his contributions to Dr. Louis Pfeiffer, and to Dr. A. Lütken” [our translation]. Further detailing Mr. Riise’s contribution to the Zoological Museum of Copenhagen (ZMUC), Lütken (187: 223) wrote under diagnosis of *Corynopoma* Gill: “In this small collection of fishes from Trinidad, which Prof. Gill gave to Mr. Riise at that time and whom again gave it to the Museum,…” [our translation], or still on foot notes, Lütken (1875: 222): “The Justice Counselor Mr. Riise owed to the Museum eigth species of Characins and four Siluroids from Trinidad” [our translation].

Considering that, Lütken’s (1875) species redescriptions of characins from Trinidad, which had been previously described by Gill (1858), could be based on type material or related material caught at that time Gill was in Trinidad. As Lütken worked at ZMUC from 1852 to 1899 (Alves & Pompeu, 2001), the type material of *Poecilurichthys pulchra* Gill could be donated to him through Riise and Gill. However, the type material of *P. pulchra* Gill is not listed in the “Catalog of fish types of Zoological Museum of Copenhagen” (Nielsen, 1974), and not found in ZMUC (personal communication of Dr. Jörgen G. Nielsen, ZMUC curator).

During this work, two specimens of *O. pulchra* obtained on loan from the Muséum d'histoire naturelle de Paris (MNHN), could be proven to be the Lütken (1875) specimens. The two fishes were donated to MNHN from ZMUC with the following information: "Museum of Copenhague (Reinhardt and Lütken) 1876. Provenance: Trinidad" (Patrice Pruvost, MNHN, personal communication). In Lütken's (1875) redescription, *C.* (*O.*) *pulchra* was redescribed probably on the base of two specimens as indicated by lateral line, dorsal-fin and anal-fin ray counts in p. 238: "…33-34 scales along the entire lateral line,… D: 10.11 (2.8-9); … A: 23-25 (3-4 + 20-21)" [our translation]. These two specimens, MNHN 0000-9593, examined herein match these counts of *C. pulchra* by Lütken (1875) and other characters: a- each dentary with 7 teeth; b- 5 transversal scale series above lateral line; c- 33-34 lateral line scales; d- dorsal fin 10.11, including 1 or 2 unbranched dorsal-fin rays plus 9 branched dorsal-fin rays; e- pectoral fin 12, not including the 1st unbranched fin ray, f- ventral fin 8, including the 1st unbranched pelvic-fin ray; and g- anal fin 23-25 (3-4 +20-21), 4 unbranched fin rays plus 20 unbranched fin rays. The external morphology, and color descriptions of Lütken's specimens fit the two MNHN specimens, for example: "Pectoral fins reach to pelvic fins,...", or "The white lateral band and the dark shoulder and caudal spots are generally enough distinct; however the spots of the shoulder may be lacking" [our translations]. The white lateral band is actually silver, and remains in the two specimens (Fig. 1). The "shoulder spot" is the pseudotympanum. Therefore, MNHN 0000-9593 specimens match those examined by Lütken (1875).

After Lütken's 1875 redescription, there were no more citations found refering to further examinations of Gill's type material. Britski (2001) stated that there is a lower number of type species in the Museum of Zoology of Copenhagen than the number of species described in another Lütken's work about fishes of the Rio das Velhas, and suggested that some type material had been lost or donated to different museums, as the syntypes of *Leporinus reinhardti* Lütken, 1875 and *L. taeniatus* Lütken, 1875 actually deposited at MNHN.

Based on these evidences, mainly the Gill's donation of the characins from Trinidad to Riise, and then to Lütken, the two specimens of MNHN 0000-9593 are recognized here as the syntypes of *Odontostilbe pulchra*. Gill (1858) description of the species seems to be based on one specimen, and matches dorsal-fin, anal-fin and pelvic-fin ray counts of one specimen of MNHN 0000-9593, p. 419: "D. 10. A. 22…V.8.". Probably unbranched and branched fin rays were jointly counted by Gill, and the anal-fin ray count is 20 branched anal-fin rays. Despite of that indication for the existence of an holotype, we prefer considering the two as syntypes because they were collected together, remaining in the same jar after Lütken's examination.

The following incorrect information were found in the label of the two syntypes MNHN 0000-9593: a- Area: Uruguay, Locality: Trinidad; b- Collectors: Reinhardt, Lütken, c- Date: 1976. These data were corrected to: a- Area: none information, Locality: western portion of Trinidad; b- Collectors: unknown; c- Date of determination: 1876 by Johannes T. Reinhardt and Christian F. Lütken; d- Date of collection: 1858. This date of collection is based on the biography of Gill by Dahl (1916), where he confirms that the visit to Trinidad occurred in 1858 between January and August (p315): "Gill sailed in January, 1858...He went to Washington in August 1858...". Notes supporting corrections: (1) the city Trinidad in Uruguay is localized on the margin of río La Plata basin, where there are no cheirodontines with lateral line complete with 34-35 scales, number of ventral procurrent caudal-fin rays 8-11, plus dentary teeth with seven cusps (differing of *Heterocheirodon* spp., *Cheirodon* spp., and *Holoshesthes pequira*, the cheirodontines present in La Plata basin); (2) Lütken examined the syntypes, probably also Reinhardt as he worked with Lütken, but there is no evidence that they had been collecting in Trinidad, Uruguay in 1876; (3) additional information from MNHN files (through Patrice Pruvost personal communication) confirming origin of the material from ZMUC, Denmark.

Syntypes are somewhat damaged with broken fins (Fig. 1, top). Specimen 28.7 m SL lacks most premaxillary and maxillary teeth, but other female 30.8 mm SL has entire dentition preserved on premaxilla and maxila, and some dentary teeth. This female 30.8 mm SL has body bent, difficulting measurements. Scales are relatively well-preserved in both specimens.

Distribution. *Odontostilbe pulchra* occurs in the island of Trinidad, being registered to the western drainages of the Caroni, Bejucal and O'Meara river drainages, and to the eastern Quare river, Cunapo basin (Fig. 11). An uncertain drainage that is probably on the southeast of Trinidad is referred in the geographical coordinates of CAS 70933, not plotted in the map. It is widespread in río Orinoco basin, smaller coastal drainages of Venezuela, Lake Valencia system, and río Essequibo basin (Fig. 11).

Information on the distribution of *Odontostilbe pulchra* based on previous paper is doubtfull, since it appears that several undescribed cheirodontinae species of the genera *Odontostilbe, Serrapinnus* and even *Holoshesthes,* from northern South America have been identified as *O. pulchra*. The species has been described by Price (1955) as "found in Caroni, Caparo and northern Oropouche drainages only and is known occur in Venezuela as well".

Taphorn (1992) provides a map with distribution of "*Cheirodon pulcher*" for the río Apure basin, but it probably is the distribution of an undescribed species of *Serrapinnus* as he mention the lateral line being incomplete in "*C. pulcher*" diagnosis (complete in *O. pulchra*). "*C. pulcher*" (Gill, 1858) is cited in the list of fishes from Venezuela (Taphorn *et. al*., 1997). Lasso *et al.* (2003) cited *C. pulcher* to the Orinoco, Cuyuní, Gulf of Paria, Caribbean, and Lake Valencia; all drainages confirmed by examined material herein. Lasso *et al.* (2004) detailed *C. pulcher* distribution of Orinoco River basin for the following drainages: upper Orinoco, Ventuari, Atabapo, Meta, Cinaruco, Suarape, Capanaparo, Arauca, Apure, Cuchiviero, Zuata, Caura, Pao, Caris, Caroní, Morichal Largo, Delta, and the own Orinoco (most drainages not listed in the material examined herein).

Odontostilbe pulchra is not restricted to río Orinoco basin and the island of Trinidad. There is a punctual occurrence in the upper rio Demini, rio Negro, Amazonas basin, though represented by an unique mature male (Fig. 11). This is a locality near southern headwaters of the río Orinoco basin, indicating that the species is present in the Orinoco-Amazon basin boundaries. Lasso *et al.* (1990) discussed the biogeographic history and faunistic similarity between upper río Caroni and the neighbouring rio Branco, rio Negro, mentioning possible connection between these water systems, which could be previous to Sierra de Pacaraima uplifting, or through divergent Gran Sabana paleoflowings. The rio Demini, where *O. pulchra* is recorded, runs parallel to rio Branco, thus the occurrence of the typical species of Orinoco as *O. pulchra* migth be an evidence of the common biogeographical history for the Orinoco-Amazon basin in this region. The proximate historical relationship between Orinocian and northen Amazonian ichthyofauna is hypothesized to date before Orinoco-Amazonas divide in the Late Miocene by the Vaupes Arch to Guyana Shield on the west to the Serrania de La Macarena (Lundberg *et al*., 1998). However, there is the alternate hypothesis that the Rupununi inundated savannah is a modern dispersal route to the fishfaunas from upper rio Negro and the rio Essequibo (Hubert & Renno, 2006).

Ecologycal notes. As stated above, information of *O. pulchra* based on previous paper is doubtfull, since it appears that several undescribed cheirodontinae species have been identified as *O. pulchra*. In Trinidad, it is described as "found in drains and ravines in the high woods, Cumuto" (Regan, 1906). In Venezuela, Winemiller (1989) referred to "*O. pulcher*" as the numerically dominant species in the estero during wet season caño Maraca, a swamp-creek in the floodplain of the western Venezuelan llanos, Apure-Orinoco drainage. "*O. pulcher*" was found in diets of *Charax gibbosus, Hoplias malabaricus, Pygocentrus notatus,* *Caquetaia kraussii*, and *Gymnotus carapo*, being the main food item for *C. gibbosus* between 50-60 mm (Winemiller, 1989). Fish census at the same caño Maraca, totalled 3182 specimens of "*O. pulcher*", the most numerous fish in the sampled fishfauna (Winemiller & Pianka, 1990). Taphorn (1992) refers to the species *Cheirodon pulcher* as "ubiquitous in the piedmont and llanos", "abundant" in Apure River Basin, "slow moving streams and especially in lowland lentic systems". In a table, Taphorn (1992: 500) classified *C. pulcher* as r1 strategist, omnivorous, occurring in white, clear and blackwaters, abundant, present in both mountains and llanos. R1 strategists are "those species with low juvenile and adult survivorship, low fecundity per reproductive bout, but many bouts per season, a short generation time, and population densities that fluctuate greatly between the wet and dry seasons" (Taphorn, 1992). However, the "*C. pulcher*" studied by Taphorn (1992), as commented before probably is an undescribed species of *Serrapinnus*, as he mention the incomplete lateral line in "*C. pulcher*" diagnosis (complete in *O. pulchra*). Despite of the difficulties in the identification of the

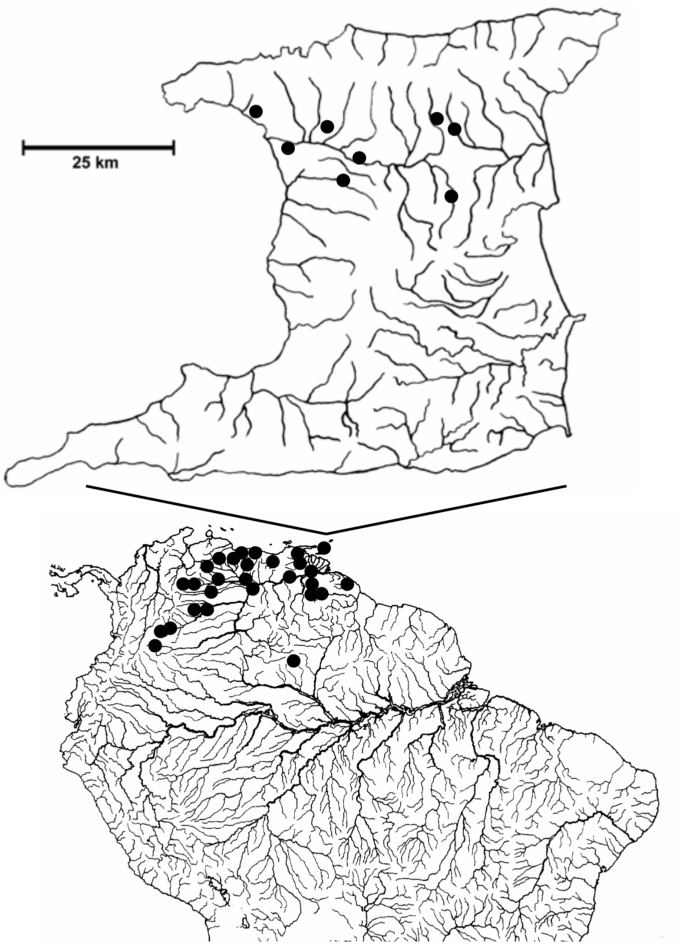

Fig. 11. Distribution of *Odontostilbe pulchra*. Circles (material examined, symbols can represent more than one lot, and more than one locality). In detail Trinidad map, modified from American Geographical Society of New York (1957).

species, probably the species has been studied in many ecological studies as that of Lasso (1992) for the lower Suapure ichthyofauna, listing *O. pulcher* as an important fish in ornamental trade of the Los Pijiguaos region in Venezuela, Flecker (1992) using *C. pulcher*, a dominant "tetra" in río Las Marias in experiments about trophic guilds, or Jepsen (1997) listing "*Chierodon* sp. 1 and sp. 2" among the most common fish species taken from sand bank habitats in the Cinaruco River. Recently, Hoeinghaus *et al.* (2004) reinforces the high abundance of "*C. pulcher*" in the llanos foodplain of the río Portuguesa, remarking it is the most frequently collected species jointly with *Roeboides dayi*.

Table 1. Morphometrics of *Odontostilbe pulchra* (syntypes MNHN 0000-9593) (Trinidad drainages, INHS 40081, INHS 40101, ROM 41069, ROM 44764, USNM 290410; río Orinoco basin, ANSP 139450, ANSP 139579, ANSP 139472, MCP 14975, MCP 38863; rio Amazonas basin, INPA 20980).

	Females		Males				Females				Unsexed			
	Syntypes		n	Low	High	Mean	n	Low	High	Mean	n	Low	High	Mean
Standard length	28.7	31.2	52	21.7	32.7	27.3	29	25.7	36.9	31.6	32	23.1	37.2	28.5
Percentages of standard length														
head length	26.1	25.0	52	24.2	28.9	25.9	29	23.8	27.8	25.2	32	22.9	26.8	25.3
snout-anal fin origin	62.7	64.1	52	58.6	64.0	61.9	29	61.7	67.8	65.0	32	57.9	67.4	63.8
snout-dorsal fin origin	53.3	52.9	52	47.3	52.1	50.0	29	50.0	54.9	52.3	32	46.9	54.5	51.4
snout-pelvic fin origin	44.6	43.6	52	42.3	47.9	44.8	29	44.6	49.6	47.1	32	41.8	50.2	46.0
dorsal-fin base	13.9	15.4	52	12.4	16.5	14.6	29	13.2	15.6	14.2	32	13.0	15.9	14.5
anal-fin base	28.6	29.5	52	26.0	31.4	28.8	29	26.3	30.7	28.1	32	26.0	33.5	28.4
caudal peduncle length	12.2	14.4	52	12.5	16.0	13.8	29	11.4	14.4	13.0	32	10.0	14.3	12.8
caudal peduncle depth	11.8	13.5	52	10.2	12.9	11.6	29	10.5	12.5	11.6	32	9.8	12.4	11.5
depth at dorsal-fin origin	37.3	41.3	52	28.0	35.9	32.7	29	30.7	41.8	37.4	32	29.6	41.3	34.7
dorsal-fin length		33.7	47	28.6	37.5	32.1	29	28.6	33.1	30.9	29	27.4	33.4	31.6
pelvic-fin length	16.7	18.3	51	16.8	26.1	20.4	29	16.0	19.3	17.8	32	16.1	19.9	18.0
pectoral-fin length		23.4	52	21.3	26.4	24.2	29	20.5	23.4	21.7	32	18.8	23.9	21.9
snout-pectoral-fin origin	25.8	23.7	52	23.5	28.7	25.8	29	23.0	27.8	25.1	32	23.3	27.0	25.4
Percentages of head length														
snout length	17.3	19.2	52	18.0	26.0	21.8	28	18.9	23.1	20.6	32	18.2	23.1	20.8
upper jaw length	28.0	28.2	52	27.1	31.8	29.1	29	27.0	32.1	29.2	32	26.8	32.5	29.6
horizontal eye diameter	38.7	41.0	52	34.8	41.9	38.2	29	34.5	41.0	37.6	32	36.6	40.9	39.1
least interorbital width	29.3	33.3	52	27.9	35.0	31.9	29	28.4	34.2	31.4	32	28.4	34.2	31.3

Odontostilbe splendida, new species

Fig. 13

Holotype. ANSP 181040, 1 male (32.7 mm SL), Colombia, Meta, río Negrito at bridge at La Balsa, Meta drainage, J. E. Böhlke *et al*., 27 March 1975.

Paratypes. ANSP 181041, 30m, (8x of 30), (8 males 29.4-36.4 mm SL, 1 male 34.7mm SL C&S, 20 females 31.3-41.6 mm SL, 1 female 32.1mm SL C&S) , same data as holotype. MCP 38862, 27 (13 males 28.9-33.6 mm SL, 1 male 29.5 mm Sl c&s, 13 unsexed 28.5-34.4 mm SL), same data as holotype, formerly ANSP 139572. MCNG 54519, 13 (7 males 29.2-33.2 mm SL, 6 unsexed 30.1-34.4 mm SL), same data as holotype. MBUCV 32890, 13 (7 males 29.3-32.9 mm SL, 6 unsexed 25.8-32.3 mm SL), same data as holotype. ICNMHN

14168, 13 (7 males 29.0-33.0 mm SL, 6 unsexed 31.0-32.8 mm SL), same data as holotype. INPA 25173, 13 (7 males 29.5-32.2 mm SL, 6 unsexed 29.7-34.2), same data as holotype.

Material examined. Río Meta basin, COLOMBIA, META: MNHG 2512.93, 3 (unsexed 22.9-27.0 mm SL), río Humadea, near El Merey basin of río Meta. ANSP 139484, 7 (2 males 32.8-33.9 mm SL, 5 unsexed 29.7-33.6 mm SL), confluence of río Guayariba and río Metica. **Río Apure basin,** VENEZUELA, GUARICO: ANSP 181137, 50 (1 male 31.1 mm SL, 49 unsexed 19.2-37.5 mm SL), tributary of río Guarico, 3 km S of Calabozo on federal highway no. 2, formerly ANSP 139696. MCP 14971, 11 unsexed 17.1-31.7 mm SL, río Apure, San Fernando de Apure, formerly ANSP 150111. VENEZUELA, PORTUGUESA: USNM 349419, 7 unsexed 29.9-33.0 mm SL, río Las Marias, quebrada Seca (town) approximately 45 min. upstream by car from hwy. 5, 22 Km NNW Guanare. **Río Orinoco basin,** VENEZUELA, BOLIVAR: ANSP 181136, 30 (1 male 32.8 mm SL, 29 unsexed 26.2-33.5 mm SL), caño Caiman, at crossing of Caicara - Puerto Ayacucho hwy, 19.2 km W of Ciudad Bolivar-Caicara highway, formerly ANSP 159904..

Fig. 12. Holotype of *Odontostilbe splendida*, ANSP 181040, male 32.7 mm SL, and paratype ANSP 181041, female 32.1 mm SL.

Diagnosis. The anterior position of the adipose fin, at vertical through last 2nd or 3rd anal-fin ray insertions in *O. splendida* (Fig. 13) is noticeably distinct from all the other *Odontostilbe* species, including the sympatric *O. pulchra* (Fig. 1) and *O. pao* (Fig. 23), in which the adipose fin is positioned at vertical through last anal-fin ray insertion. *Odontostilbe splendida* further differs from *O. pulchra* by a group of morphometric characters especially evident in males: snout pointed and longer in *O. splendida* (24.1-26.9% HL) *vs.* short and blunt in *O. pulchra* (18.0-26.0% HL) (Fig. 5), longer pectoral-fin length (20.9-23.5% SL in *O. splendida vs.* 21.3-26.4% SL in *O. pulchra*) (Fig. 13), smaller anal-fin base (24.9-26.8% SL *vs.* 26.0-31.4% SL) (Fig. 14), shorter caudal peduncle length (11.5-13.0% SL *vs.* 12.5-16.0% SL) (Fig. 15), larger snout-pelvic fin origin distance (45.1-48.7% SL *vs.* 42.3-47.9% SL) (Fig. 16), and larger snout-anal fin origin distance (63.7-68.6% SL *vs.* 58.6-64.0% SL) (Fig. 17). Additionally, mature males of *O. splendida* are remarkably distinguished by the presence of hooks on 1st to 6th-7th anal-fin rays, *vs.* hooks on 1st to 22nd anal-fin branched rays in *O. pulchra*. Mature males of *O. splendida* usually have the 2nd unbranched dorsal-fin ray elongate, not present in *O. pulchra*. Females and immature specimens, and not well-developed males of *O. splendida* and *O. pulchra*, how overlapping ranges in many of the ratios cited above, and can be differentiated by the following characters: (1) presence of 3-4 (mostly 3) maxillary teeth in *O. splendida*, against 2-3 (mostly 2) in *O. pulchra*; 36 lateral line scales (one specimen 35) in *O. splendida vs.* 33-37, mostly 34-35 lateral line scales in *O. pulchra.* The number of gill rakers counts on lower branch differs *O. splendida* (averaging 11) from *O. fugitiva* (usually 12) (Fig. 18).

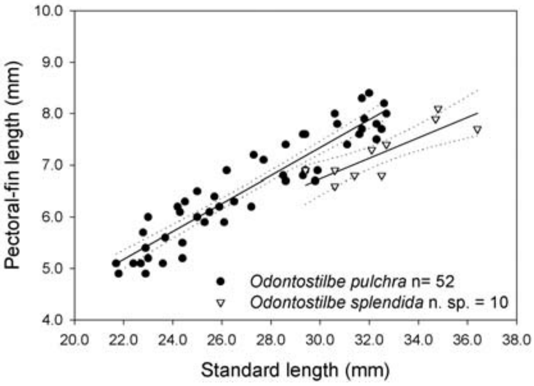

Fig. 13. Pectoral-fin length as a function of standard length for males of *Odontostilbe pulchra*, against *O. splendida*.

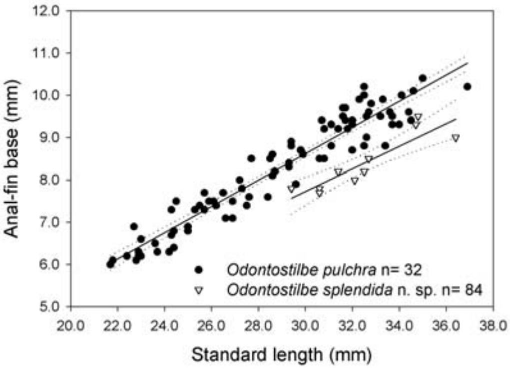

Fig. 14. Anal-fin base as a function of standard length for males of *Odontostilbe pulchra*, against *O. splendida*.

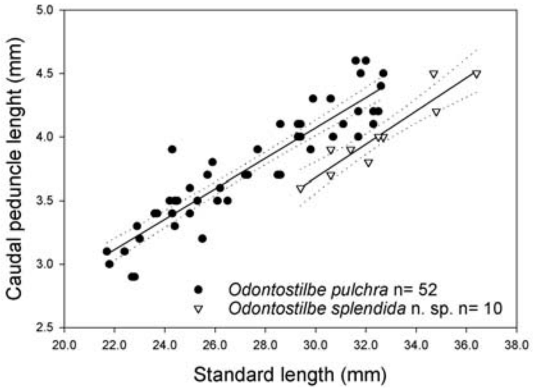

Fig. 15. Caudal peduncle length as a function of standard length for males of *Odontostilbe pulchra*, against *O. splendida*.

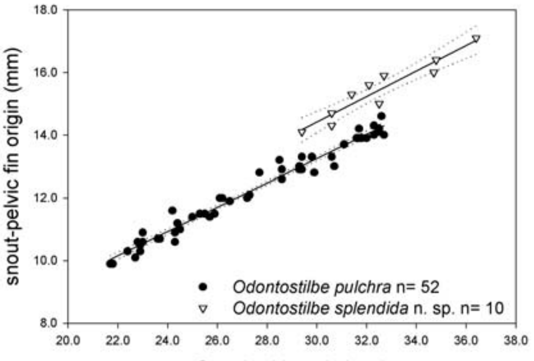

Fig. 16. Snout-pelvic fin origin as a function of standard length for males of *Odontostilbe pulchra*, against *O. splendida*.

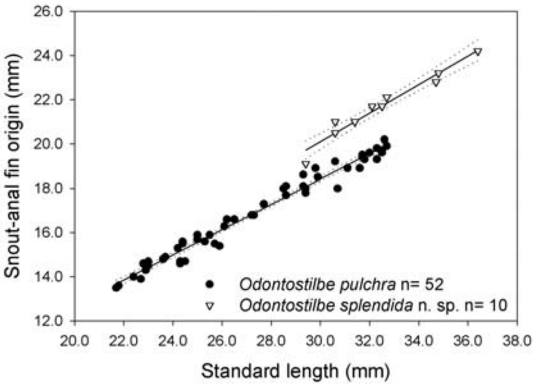

Fig. 17. Snout-anal fin origin as a function of standard length for males of *Odontostilbe pulchra*, against *O. splendida*.

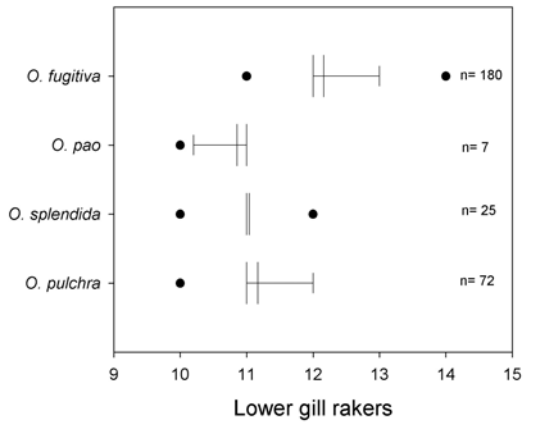

Fig. 18. Lower gill rakers counts of *Odontostilbe pulchra*, *Odontostilbe fugitiva* (data from Bührnheim & Malabarba, 2006), and of two new species *Odontostilbe splendida*, and *Odontostilbe pao*.

Description. Morphometric data are given in Table 2. Largest male 36.4 mm in SL, largest female 41.6 mm in SL. Body elongate and compressed. Body of males slightly more compressed and elongate than females. Greatest body depth in dorsal-fin origin. Snout short, somewhat pointed in males. Head profile pointed, gently convex to straigth from snout to posterior tip of supraoccipital bone. Predorsal profile slightly convex to straight between posterior tip of supraoccipital bone and dorsal-fin origin, straight on dorsal-fin base, and then slight convex to straight from end of dorsal-fin base to caudal peduncle. Ventral profile convex from mouth tip to anal-fin origin. Anal-fin base straight. Caudal peduncle slightly longer than deep.

Head relatively small. Posterior margin of opercle sinusoidal with upper portion concave and lower portion convex. Mouth terminal. Obliquous positioned maxilla ending at vertical through anterior border of eye**,** and at horizontal on inferior border of eye. Premaxillary teeth 5-6, bearing 8-11 cusps; central cusp longest (Fig. 19). Maxilla with 3-4 (mainly 3) teeth bearing 5-9 cusps, decreasing cusp number toward posterior tip of maxilla. Dentary teeth 9-10, gradually decreasing in size, anterior 5-6 teeth large bearing 7-8 cusps, 1 medium-sized tooth with 5-6 cusps, and posterior teeth small, conic or with 2-5 cusps. Smaller cusps of dentary teeth overlap cusps of adjacent tooth.

Dorsal-fin rays **ii,9**(31). Dorsal-fin origin slightly posterior to mid body length, and slightly posterior to pelvic-fin origin. Second unbranched dorsal-fin ray slightly elongate in males (not in holotype), extending beyond dorsal-fin distal profile. Anal-fin rays: iv(6), or **v**(25); branched **19**(9), 20(16), 21(5), or 22(1). Anal-fin distal border concave, anterior 6-7 branched rays longest. Pectoral-fin rays: i(31); branched 9(2), **10**(9), 11(16), or 12(3). Pelvic-fin rays: i(31), branched 6(1), or **7**(30). Unbranched pelvic-fin ray longest ray in mature males, extending beyond origin of anal fin. Lateral skin border of unbranched pectoral-fin ray and unbranched pelvic-fin ray slight thickened in males. Principal caudal-fin rays 19(31).

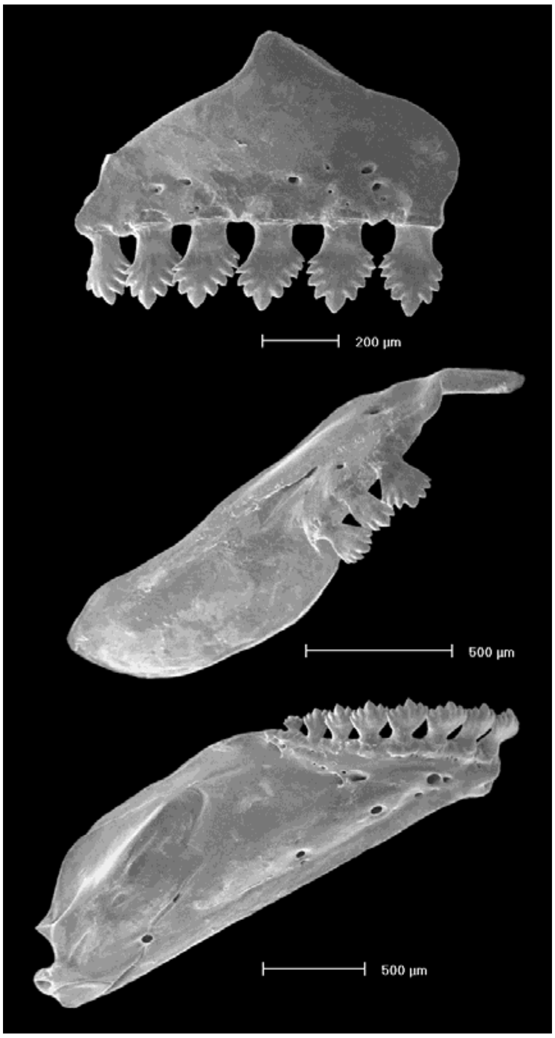

Fig. 19. Dentition of *Odontostilbe splendida*, paratype ANSP 181041, female 32.1 mm SL: right side premaxilla (top), maxilla (middle), and dentary (bottom), lateral view. Scanning electron micrographs (SEM).

Procurrent caudal-fin rays: dorsal 10(1), 11(4), 12(14), **13**(9), or 14(3), ventral 9(3), 10(17), **11**(10), or 12(1). Anterior 1 or 2 ventral procurrent caudal-fin rays sometimes laterally expanded or bifurcated. Caudal-fin ray flaps ventrally on 4nd-8th branched rays of upper lobe, dorsally on 13th -16th branched rays of lower lobe. Adipose-fin at vertical through last 2nd or 3rd anal-fin ray insertions.

Males with acute retrorse hooks on posterior border of pelvic- and anal-fin rays. One or two paired or unpaired hooks per segment of lepidotrichia, at distal half-length of last unbranched anal-fin ray, and 1st to 6th-7th branched anal-fin rays. One or two unpaired long hooks per segment of lepidotrichia along almost entire length of 1st to 7th branched pelvic-fin rays, reaching distal tip of fin ray (except on 1st branched pelvic-fin ray, on midlength portion). One or two unpaired hooks per segment of lepidotrichia on anterior border of branchings of pelvic- and anal-fin rays.

Scales cycloid: lateral line complete 35(1), or **36**(26); predorsal row **10**(10), or 11(20); scale rows between lateral line and dorsal-fin origin **6**(28), or 7(2); scale rows between lateral line and anal-fin origin **4**(15), or 5(15); scale rows around caudal peduncle **14**(29). Triangular modified scale on pelvic-fin base extends posteriorly covering 2-3 scales. Scales on anal-fin base **6**, 7.

Cleared and stained specimens (3), and radiographs (8): supraneurals 4; precaudal vertebrae, including Weberian apparatus, 16(3), or 17(8); caudal vertebrae 17(3), 18(7), or 19(1); gill rakers, upper 5(1), or 6(2), lower 10, 11, or 12 (2-3 on hypobranchial). Alcohol specimens (22): gill rakers, upper 5(2), **6**(18), or 7(2), lower **11**(21), or 12(1). Upper gill rakers with none to 3 denticles on anterolateral border; lower gill rakers with 1-4 recurved denticles on anterolateral border; and posteriormost lower gill raker with none to 7 recurved denticles on posterior border, and 3 denticles on anterior border (Fig. 20). Denticulation mainly on basal portion of gill rakers.

Color in alcohol. General ground body color pale yellow or pale orange. Dorsal part of body darker with chromatophores more concentrate on scales border, from head to caudal peduncle. Dark chromatophores along all dorsal-fin rays. Pectoral fin with chromatophores along 1st unbranched pectoral-fin ray and 1st branched fin rays. Pelvic fin clear. Anal fin with dark chromatophores on central branched anal-fin rays, except at tips of last unbranched fin rays and 1st branched fin ray; hyaline in holotype. Adipose fin clear. Caudal fin almost entirely covered with diffuse dark chromatophores along fin rays, except clear areas on base of caudal-fin lobes just behind caudal-fin spot (chromatophores very faded in type material).

Rounded brown to black spot on base of caudal fin, usually reaching upper border of caudal peduncle.

Dark chromatophores on snout, upper lip, anteriormost portion of maxilla, and 1st to 2nd infraorbitals. Top of head on frontals and parietals pigmented, deep-lying dark chromatophores over brain membranes below frontals and parietals, and fontanels. Body with faint dark and silver midlateral stripe, beginning behind pseudotympanum, above lateral line, and reaching caudal spot. Guanine on eye iris, opercle, ishtmus, and 2nd to 5th infraorbital. Scattered chromatophores on pseudotympanum area, or not. Below lateral line, belly faint usually unpigmented, chromatophores above anal-fin base area forming 10 to 11 chevron shaped markings (faint scattered chromatophores in type material).

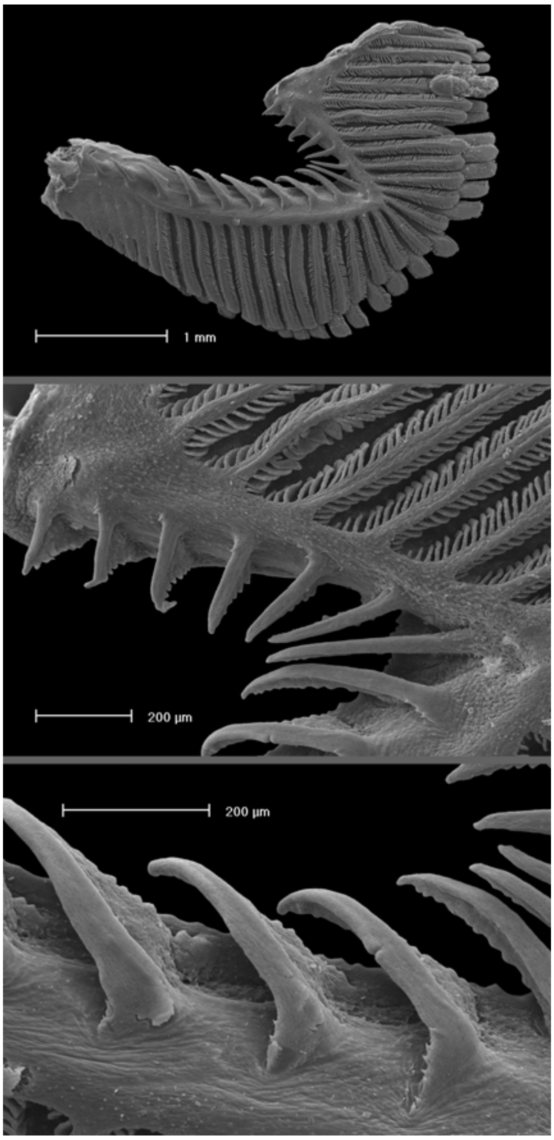

Fig. 20. First gill arch of *Odontostilbe splendida*, MCP 38862, male 29.7 mm SL: left side, lateral view, showing gill gland (top), in detail gill rakers on upper branchial branch (middle), and gill rakers on lower branchial branch (bottom). Scanning electron micrographs (SEM).

Sexual dimorphism. Males have hooks on anal and pelvic-fin rays, and sligth elongation of dorsal- and pelvic-fin rays, in contrast to the absence of these features in females (see description). A gill gland (Burns & Weitzman, 1996) is found in mature males of *Odontostilbe splendida*. The gill gland is present on the first gill arch, covering about 7 to 9 anterior branchial filaments (Fig. 20). Males usually have longer snout length, and caudal peduncle length (Fig. 22).

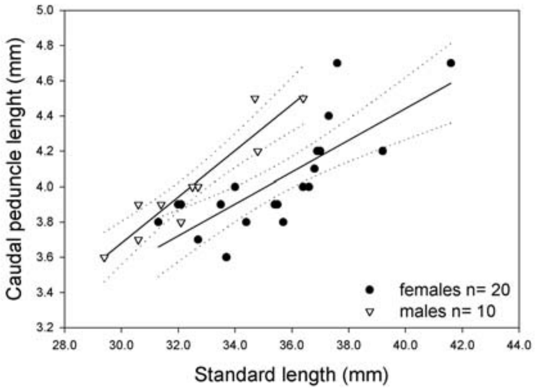

Fig. 21. Caudal peduncle length as a function of standard length for males against females of *Odontostilbe splendida*.

Distribution. Río Orinoco basin (Fig. 22).

Etymology. Refers to the latin word *splendidus*, meaning splendid, grand, admirable.

Ecologycal notes. Field notes of type material indicate bottom with mud and sand, and water depth nearly 3 feet.

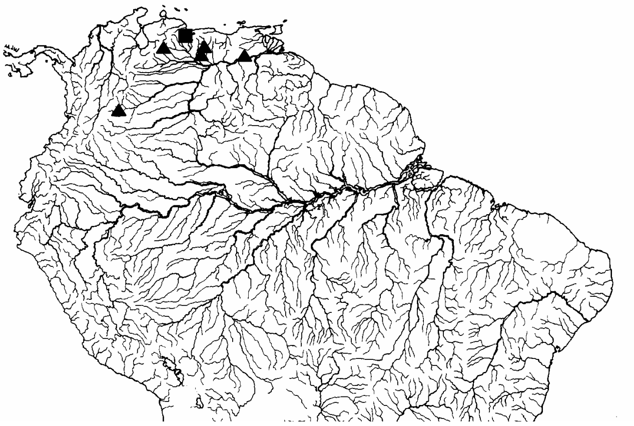

Fig. 22. Distribution of *Odontostilbe splendida* (triangles), and *Odontostilbe pao* (square). Symbols can represent more than one lot, and more than one locality.

Table 2. Morphometrics of *Odontostilbe splendida* (holotype ANSP 181040, and paratypes ANSP 181041.

	Males					Females			
	Holotype	n	Low	High	Mean	n	Low	High	Mean
Standard length	32.7	9	29.4	36.4	32.3	21	31.3	41.6	35.4
Percentages of standard length									
head length	25.4	9	23.1	25.8	24.5	21	22.2	24.6	23.5
snout-anal fin origin	67.6	9	63.7	68.6	66.5	21	66.5	70.9	69.1
snout-dorsal fin origin	51.1	9	47.5	51.6	49.8	21	49.2	52.9	51.8
snout-pelvic fin origin	48.6	9	45.1	48.7	47.3	21	46.6	50.8	48.9
dorsal-fin base	15.3	9	13.8	15.3	14.5	21	13.4	15.5	14.6
anal-fin base	26.0	9	24.9	26.8	25.8	21	24.0	28.3	26.4
caudal peduncle length	12.2	9	11.5	13.0	12.3	21	10.6	13.1	11.5
caudal peduncle depth	13.5	9	11.4	13.5	12.4	21	11.0	13.6	12.6
depth at dorsal-fin origin	36.1	9	33.5	37.1	35.5	21	36.5	42.6	39.9
dorsal-fin length	33.9	8	29.6	33.9	31.7	21	26.2	31.9	29.9
pelvic-fin length	20.2	9	19.0	22.1	20.3	21	16.3	19.4	17.9
pectoral-fin length	22.6	9	20.9	23.5	22.3	21	19.0	22.9	21.2
snout-pectoral-fin origin	24.5	9	21.7	25.2	23.6	21	21.4	24.6	23.1
Percentages of head length									
snout length	25.3	9	24.1	26.9	25.2	21	21.4	25.6	23.7
upper jaw length	30.1	9	29.1	31.5	30.3	20	28.4	32.6	30.8
horizontal eye diameter	38.6	9	36.0	39.0	37.6	21	36.8	41.0	38.4
least interorbital width	36.1	9	33.3	36.1	35.1	21	32.1	39.1	36.3

***Odontostilbe pao*, new species**

Fig. 23

Holotype. MCNG 54497, 1 (male 29.3 mm SL), Venezuela, Cojedes, río Pao at el Caserio, El Pueblito, D. Taphorn *et al*., 28 July 1985.

Paratypes. MCNG 54107, 6 (5 males 27.2-28.7 mm SL, 1 male 28.8 mm SL c&s), same data as the holotype.

Diagnosis. *Odontostilbe pao* differs from the two other species from the río Orinoco basin, by the presence of a remarkable elongation of the 2nd unbranched dorsal-fin ray in males, not found in males of *O. pulchra* (Fig. 1), and short in males of *O. splendida*. Additionally, males of *O. pao* are distinghished from the two Orinocian species by the larger snout length (*O. pao* 26.7-30.6% HL, *O. pulchra* 18.0-26.0% HL, *O. splendida* 24.1-26.9% HL) (Figs. 5, 26), and larger upper jaw length (*O. pao* 32.5-34.7% HL, *O. pulchra* 27.1-31.8% HL, *O. splendida* 29.1-31.5% HL) (Fig. 26). The presence of hooks on 1st to 8th anal-fin branched rays differs *O. pao* from *O. pulchra* (hooks on 1st to 22th anal-fin branched rays). The gill raker counts on lower branch (averaging 11) differs from *O. fugitiva* (usually 12) (Fig. 18). *Odontostilbe pao* differs from all other *Odontostilbe* species by the peculiar shape of the posterior portion of the maxilla, somewhat triangular, short, with midlength portion deeper and gradually narrowing to the posterior tip (Fig. 24), *vs*. maxilla somewhat spatula-like shaped, short or elongate, with a deep midlength and posterior region, and then narrowing abruptly only at posterior tip in all other *Odontostilbe* species (Figs. 6, 19).

Fig. 23. Holotype of *Odontostilbe pao*, MCNG 54497, male 29.3 mm SL.

Description. Only males available. Morphometric data are given in Table 2. Largest male reaching 29.3 mm in SL. Body elongated and compressed. Greatest body depth in dorsal-fin origin. Snout pointed. Head profile gently convex to straigth from snout to posterior tip of supraoccipital bone. Predorsal profile slightly convex between tip of supraoccipital bone and dorsal-fin origin, then straight from dorsal-fin origin to caudal peduncle. Ventral profile convex from mouth to anal-fin origin. Anal-fin base straight. Caudal peduncle slightly longer than deep.

Head relatively small. Posterior margin of opercle sinusoidal with upper portion concave and lower portion convex. Snout pointed. Mouth terminal, premaxilla projects beyond dentary leaving border of teeth cusps exposed. Obliquous positioned maxilla ending at vertical on anterior eye border, and at horizontal slight through inferior eye border. Premaxillary teeth 6, bearing 8-10 cusps; central cusp longest (Fig. 24). Maxilla with 4 similar teeth bearing 3-7 cusps, decreasing cusp number to posterior tip of maxilla. Dentary teeth 11 bearing 1-7 cusps, gradually decreasing in size, first 7 teeth largest with 6-7 cusps, 1 medium-sized tooth with 5 cusps, and last small teeth conical or with 2 cusps. Head relatively small. Posterior margin of opercle sinusoidal with upper portion concave and lower portion convex. Smaller cusps of dentary teeth overlap cusps of adjacent tooth.

Dorsal-fin rays **ii, 9**(7). Dorsal fin slightly behind mid length of body, and slightly posterior to pelvic-fin origin. Second unbranched dorsal-fin ray elongate in males, extending beyond dorsal-fin distal profile. Anal-fin rays: iv(1), **v**(6); branched **18**(1), 19(2), or 20(4). Anal-fin distal border concave. Pectoral-fin rays: i(7); branched **10**(2), 11(4), or 12(1). Pelvic-fin rays: **i**(7), branched **6i**(2), **7**(5). Unbranched pelvic-fin ray longest in mature males, extending beyond origin of anal fin. Lateral skin border of unbranched pectoral-fin ray and unbranched pelvic-fin ray slight thickened in males. Principal caudal-fin rays **19**(7). Procurrent caudal-fin rays: dorsal 11(3), or **12**(4), ventral 9(1), 10(4), or **11**(2). Caudal-fin ray flaps ventrally on 4nd-7th branched rays of upper lobe, and dorsally on 13th -15th branched rays of lower lobe. Adipose-fin at vertical through last anal-fin ray insertion.

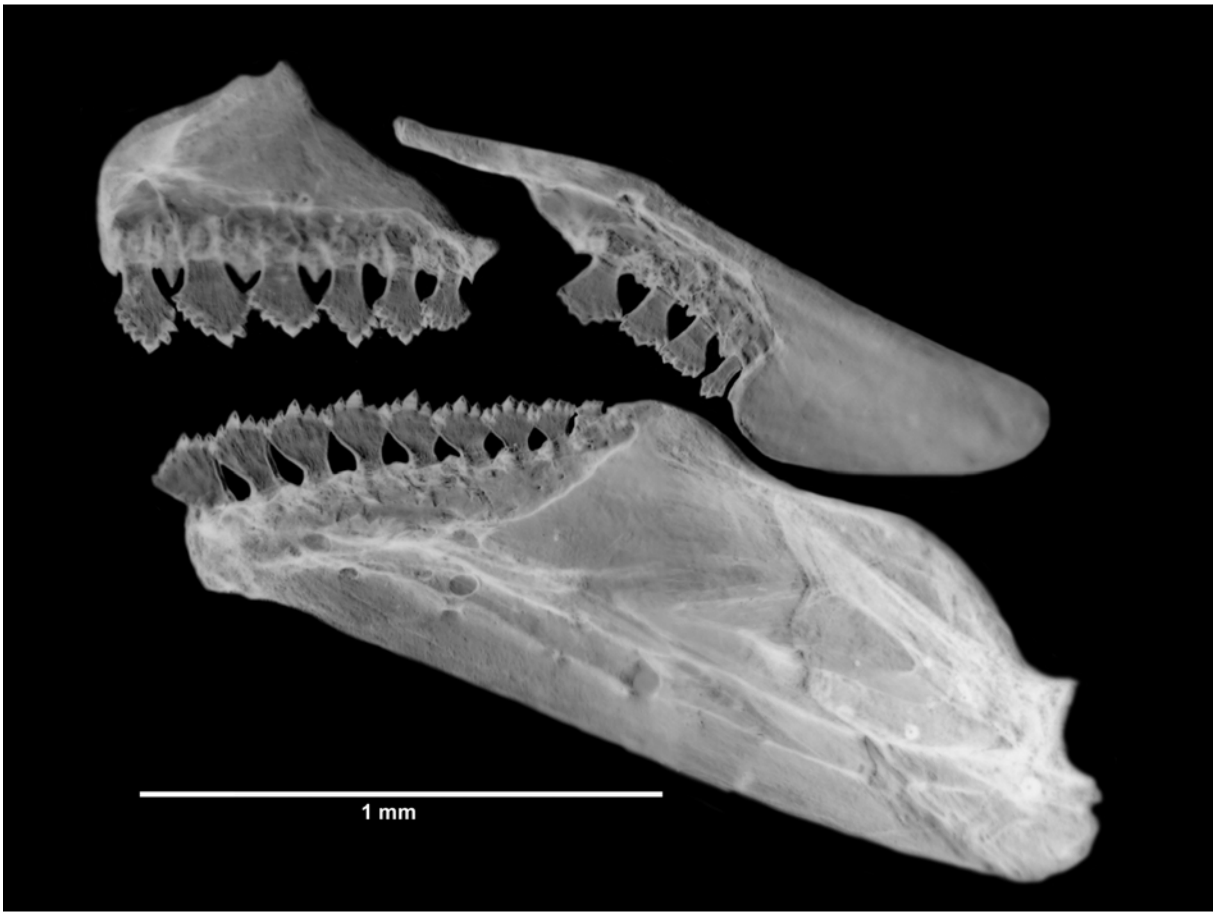

Fig. 24. Dentition of *Odontostilbe pao*, MCNG 54107, male 28.8 mm SL c&s. Photograph of left side premaxilla (top), maxilla (middle), and dentary (bottom), lateral view, under estereosmicroscope.

Males with acute, elongate, retrorse hooks on posterior border of pelvic- and anal-fin rays. 1-2 paired and unpaired hooks per segment on last unbranched anal-fin ray, and 1st to 8th (mostly 6-7th) anal-fin branched rays, mid positioned on fin rays. 1-2 unpaired slender hooks per segment on 1st to 7th branched pelvic-fin rays, extending almost entirely and reaching end tip of fin rays.

Scales cycloid: lateral line complete about 36 (scale insertions counted); predorsal row 10(1), or **11**(2); scale rows between lateral line and dorsal-fin origin **6**(6), or 7(1); scale rows between lateral line and anal-fin origin **4**(4); scale rows around peduncle lacking. Triangular modified scale on pelvic-fin base extends posteriorly covering 2 scales.

Cleared and stained specimens (1): supraneurals 4; precaudal vertebrae, including Weberian apparatus, 16; caudal vertebrae 18; gill rakers, upper 6, lower 11 (2 on hypobranchial). Alcohol specimens (6): gill rakers, upper **6** (6), lower 10(1), or **11**(5). Upper gill rakers with none to 2 denticles on anterolateral border, and none on posterolateral border; lower gill rakers with none or 2 denticles on anterolateral border, and none or 1 denticle on posterolateral border; posteriormost lower gill raker with just 3 denticles on anterolateral border (**Fig. 29**). Denticulation mainly on basal portion of gill rakers.

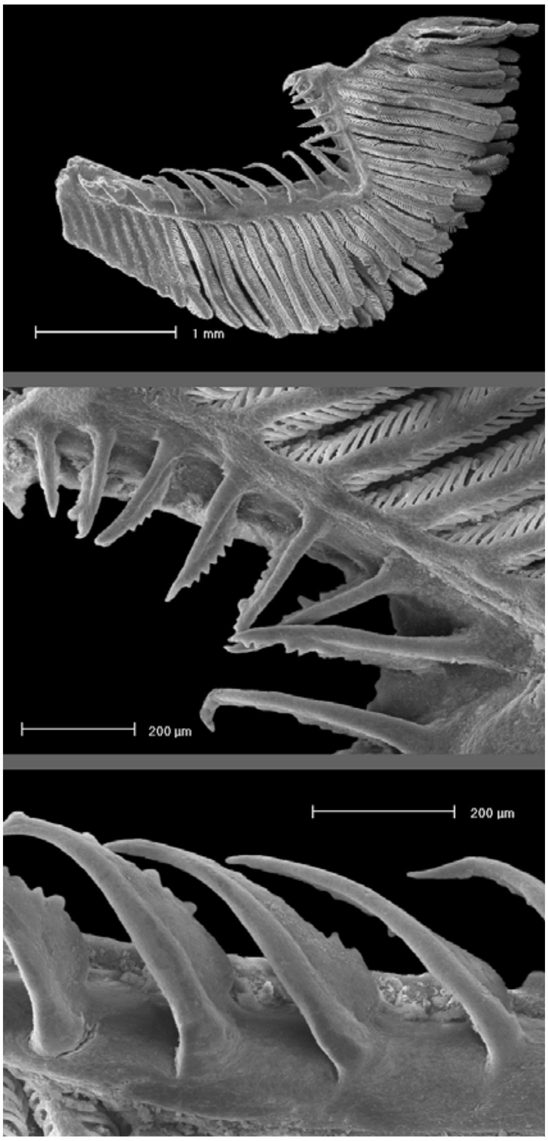

Fig. 25. First gill arch of *Odontostilbe pao*, MCNG 54107, male 28.8 mm SL. SEM photographs of the first gill arch, left side, lateral view, showing gill gland (top), in detail gill rakers on upper branchial branch (middle), and gill rakers on lower branchial branch (bottom).

Sexual dimorphism. Only mature males available, presenting typical dimorphic characters found in other *Odontostilbe* species, like the presence of hooks on pelvic- and anal-fin rays, and the elongation of dorsal- and pelvic-fin rays. The gill gland is present on the first gill arch including 7 to 9 anterior branchial filaments (Fig. 25). Snout well-developed in males, and probably a dimorphic character as found in other *Odontostilbe* species (Bührnheim & Malabarba, 2006).

Color in alcohol. General ground body color beige. Dorsal part of the body from head to peduncle darker with chromatophores more concentrate on scales border. Dark chromatophores along all dorsal-fin rays. Pectoral fin with chromatophores along 1st unbranched pectoral-fin ray and 1st branched fin rays. Pelvic fin hyaline. Anal fin with dark chromatophores on more central branched anal-fin rays, except at the tips of the last unbranched fin rays and the 1st branched fin ray; hyaline in holotype. Adipose fin clear. Caudal fin almost entirely covered with diffuse chromatophores along fin rays, except clearer areas on base of caudal-fin lobes just behind caudal-fin spot (chromatophores very faded in type material). Rounded black to brown spot on the base of caudal fin, reaching upper border of caudal peduncle.

Chromatophores on snout, upper lip, proximal portion of maxilla, infraorbitals 1, 2. Pigmentation of top of head on frontals and parietals, with deep-lying chromatophores over brain membrane below frontals and parietals, and fontanels. Faint dark and silver midlateral stripe, beginning behind pseudotympanum, above lateral line, and reaching caudal spot. Guanine on eye iris, opercle, ishtmus, and most 3rd infraorbital. Below lateral line body faint without pigmentation, a few chromatophores above anal-fin base in holotype.

Distribution. Only known from type locality río Pao, affluent of the río Chirgua-Guanare system, río Portuguesa, río Apure-Orinoco basin (Fig. 22).

Etymology. Refers to the type locality río Pao.

Ecologycal notes. Type material caught in the llanos, savannas, white water, together with the cheirodontines *Cheirodontops geayi* and *Odondostilbe pulchra* (Donald Taphorn personal communication).

Remarks. A principal component analysis with 17 morphometric variables grouped separately males of *O. pao*, *O. splendida*, and *O. pulchra*, excepting for one specimen of *O. splendida*, nearby *O. pulchra* specimens on the PC3 axis (Fig. 26). PC2 was affected most strongly and negatively by snout length, dorsal-fin length, and upper jaw length; and positively by anal-fin base. *O. pao* has larger snout length, dorsal-fin length, and upper jaw length as referred in its diagnosis. PC3 was affected most strongly and negatively by pectoral-fin length, and anal-fin base; and positively by depth at dorsal-fin origin, snout-anal fin origin, and caudal peduncle depth. Actually, *O. pao* and *O. pulchra* have shorter depth at dorsal-fin origin, snout-anal fin origin, and caudal peduncle depth than *O. splendida* (Tables 1-3). In contrast, males of *O. pao*, and *O. pulchra* have larger pectoral-fin length, anal-fin base, and caudal peduncle depth (Tables 1-3). The specimen of *O. splendida* positioned far below has the highest proportion of anal-fin base 26.8 % in SL among all specimens measured, which explains its position nearly *O. pulchra* specimens. This specimen through regression analyses matched *O. splendida* characters. The pelvic-fin length was not considered in the principal component analysis because it increased the overlap between *O. pulchra* and *O. splendida* since pelvic-fin length ranges are similar.

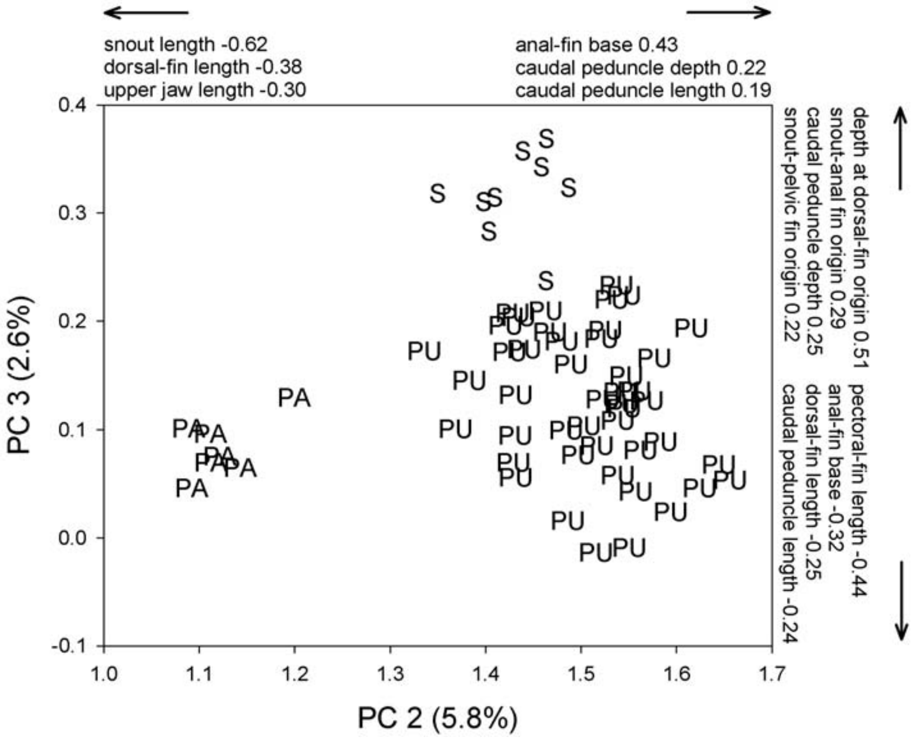

Fig. 26. Principal component analysis of the 17 morphometric measurements of *Odontostilbe pulchra* (PU), *Odontostilbe splendida* (S), and *Odontostilbe pao* (PA). Stronger loadings on the second and third principal components (PC2, PC3).

Table 3. Morphometrics of *Odontostilbe pao* n. sp. (holotype MCNG 54497, and paratypes MCNG 54107).

	males				
	Holotype	n	Low	High	Mean
standard length	29.3	6	27.2	28.8	28.2
Percentages of standard length					
head length	26.3	6	25.9	26.8	26.3
snout-anal fin origin	63.8	6	63.3	66.3	64.7
snout-dorsal fin origin	48.1	6	48.2	50.5	49.5
snout-pelvic fin origin	46.8	6	47.1	48.9	48.2
dorsal-fin base	15.0	6	14.1	16.0	14.8
anal-fin base	24.6	6	25.4	27.1	26.3
caudal peduncle length	14.0	6	12.5	13.3	13.0
caudal peduncle depth	10.9	6	10.4	11.4	11.1
depth at dorsal-fin origin	30.4	6	30.2	32.1	31.1
dorsal-fin length	37.5	6	36.5	42.6	40.1
pelvic-fin length	25.9	6	24.1	28.3	25.9
pectoral-fin length	24.2	6	23.6	25.8	24.6
snout-pectoral-fin origin	25.9	6	25.2	27.0	26.3
Percentages of head length					
snout length	28.6	6	26.7	30.6	28.6
upper jaw length	33.8	6	32.5	34.7	33.5
horizontal eye diameter	33.8	6	36.0	37.8	36.9
least interorbital width	33.8	6	33.3	35.1	34.2

Discussion

Böhlke (1954) suggested the synonym of *Odontostilbe pulchra* with *O. fugitiva* on the base of a single specimen examined of the former, and four topotypes of the latter. This purpose was not confirmed considering the diagnostic characters found differing *O. pulchra* and *O. fugitiva*. Apparently without mature males avaliable, he was not able to identify the remarked differences in anal fins between these species. Furthermore, he did not take measurements of the anal-fin base. The two species are the widespreadest among all *Odontostilbe* species in northern South America, *O. pulchra* in Orinocian waters and *O. fugitiva* in Amazonian waters. The sole occurrence of *O. pulchra* in the rio Toototobi, rio Demini-upper rio Negro system, the major left-side affluent of rio Amazonas, open up a possible sympatry with *O. fugitiva*. However, neither *O. pulchra* nor *O. fugitiva* were assigned to the black water rio Negro, that might be a barrier as most *Odontostilbe* species seems to prefer whitewaters (Bührnheim & Malabarba, 2006).

Odontostilbe pao was found possibly related to *Pseudocheirodon terrabae* and *P. arnoldi*, two Central American cheirodontines, forming the clade A2 in an overall parsimony analysis of the Cheirodontinae by Bührnheim & Malabarba (in manuscript). However, this clade is discussed considering the weak support of that hypothesis versus the strong support of the recognition of a monophyletic clade including only *Pseudocheirodon terrabae* and *P. arnoldi*.

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Conclusões Gerais

A monofilia de Cheirodontinae e de suas tribos Cheirodontini e Compsurini é confirmada com base em uma reanálise filogenética com 53 táxons e 169 caracteres. A subfamília Cheirodontinae é redefinida por 15 sinapomorfias, cinco novas unicamente derivadas. Os gêneros de posição filogenética incerta na subfamília foram agrupados em uma nova tribo, Odontostilbini, sustentada por 13 sinapomorfias. Odontostilbini abrange seis gêneros: *Odontostilbe* Cope 1870, *Holoshesthes* Eigenmann 1903 com *Aphyocheirodon* Eigenmann, 1915 e *Cheirodontops* Schultz, 1994 como seus sinônimos, *Pseudocheirodon* Meek & Hildebrant, 1916, *Lobodeuterodon* Fowler, 1945, *Prodontocharax* Pearson, 1924 e *Amblystilbe* Fowler, 1940. Três destes gêneros são revalidados, *Holoshesthes* e *Lobodeuterodon* saem da sinonímia de *Odontostilbe* e *Amblystilbe* da sinonímia de *Prodontocharax*. Duas novas sinonímias são propostas, *Aphyocheirodon* e *Cheirodontops* como sinônimos de *Holoshesthes*.

O gênero *Odontostilbe* compreende 15 espécies, sendo distribuído amplamente na América do Sul nas grandes Bacias dos rios Amazonas, Orinoco e La Plata. Na análise filogenética a monofilia de *Odontostilbe* não é encontrada. Entretando, o gênero é mantido válido incluindo as espécies presentes em uma politomia basal na nova tribo Odontostilbini e que não possuem as sinapomorfias dos grupos monofiléticos encontrados na tribo. Estes grupos monofiléticos são um clado com seis espécies do gênero *Holoshesthes*, um clado com duas espécies de *Pseudocheirodon* e outro clado formado por *Lobodeuterodon*, *Prodontocharax* e *Amblystilbe*, respectivamente com três espécies, uma em cada gênero.

Holoshesthes é redefinido com base em 21 sinapomorfias e suas seis espécies redescritas e rediagnosticados. A espécie tipo é *Holoshesthes pequira* (Steindachner, 1882), com um lectótipo designado. *Cheirodontops geayi* e *Aphyocheirodon hemigrammus* são redescritas em *Holoshesthes*. Três espécies novas foram descobertas para o gênero. O gênero ocorre nas grandes Bacias dos rios Amazonas, Orinoco e La Plata. A espécie tipo *Odontostilbe fugitiva* Cope, 1870 é redescrita com a designação de um neótipo. Sua distribuição na bacia Amazônica e variações populacionais são esclarecidas. Conjuntamente, três espécies novas foram descritas, *O. ecuadorensis*, *O. nareuda*, e *O. parecis*, também da bacia Amazônica. As espécies de *Odontostilbe* da bacia do río Orinoco incluem uma redescrida e duas novas. *Odontostilbe pulchra* (Gill, 1858), anteriormente como *species inquirenda* em Cheirodontinae e de distribuição confusa, têm dois síntipos redescobertos e ocorre em Trinidad e na Bacia do río Orinoco, com uma ocorrência pontual na Bacia do rio Amazonas.