

Phylogenetic systematics of the driftwood catfishes (Siluriformes: Auchenipteridae): a combined morphological and molecular analysis

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A comprehensive phylogeny of species relationships of the Auchenipteridae is reconstructed here with a large-scale taxon sampling based on combined morphological and molecular datasets. The hypothesized phylogeny includes most species of Auchenipteridae (97 of 124 valid species) and multiple members of siluriform families as an outgroup (32 species) to embrace the diversity of forms among related catfishes. As the first large-scale phylogeny of the Auchenipteridae, comparison between taxa included information from both morphology (264 characters) and mitochondrial and nuclear molecular markers (3490 nucleotides) from five genes: *coI*, *16S*, *rag2*, *myh6* and *SH3PX3*. Trees were generated under two different optimality criteria (Maximum Parsimony and Bayesian Inference). A new classification for the family is presented herein to bring the taxonomy more in line with the new phylogenetic hypothesis. The strict consensus tree corroborates the monophyly of superfamily Doradoidea, family Auchenipteridae and its two subfamilies, Centromochlinae and Auchenipterinae. The new classification scheme proposes nine tribes in Auchenipteridae, based on the monophyly of major groups in both subfamilies. *Centromochlus*, *Glanidium* and *Tatia* are each recovered as paraphyletic. To maintain a monophyletic classification, some species treated as *Tatia* and *Centromochlus* are assigned to genera not previously recognized as valid.

ADDITIONAL KEYWORDS: Amazon basin – Auchenipterinae – Bayesian inference – Centromochlinae – evolution – freshwater – maximum parsimony – Neotropical region – taxonomy.

INTRODUCTION

AN OVERVIEW OF THE AUCHENIPTERIDAE

Neotropical freshwater fishes comprise the richest vertebrate fauna on the planet, including > 5600 known species (Reis *et al.*, 2003; Albert & Reis, 2011) and current estimates of ≤ 9000 species (Reis *et al.*, 2016). Siluriformes is the most diverse order and the most widespread among Ostariophysi, with 39 families and ~3920 species recognized (Fricke *et al.*, 2019). Auchenipteridae, known as the driftwood catfishes, is

a monophyletic group with 124 valid species known to date, arranged in 22 genera (Auchenipterinae with 76 species and Centromochlinae with 48 species; see Table 1). However, several new species still await a formal description (known examples in *Gelanoglanis*, *Glanidium*, *Spinipterus*, *Tatia*, *Trachelyichthys*, *Trachelyopterus* and *Tympanopleura*). Auchenipteridae vary in body size from miniature *Gelanoglanis* species, measuring ≤ 30 mm standard length (SL), to large fishes of ~600 mm SL, such as some species of *Ageneiosus*. Auchenipterid catfishes are widely distributed in South and Central America from Argentina to Panama, occurring in many different freshwater habitats, such as streams, rivers and lakes, and are commonly found among submerged logs. They inhabit mostly freshwater areas, except for some species of *Pseudauchenipterus*, which can also inhabit

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**Richard P. Vari, in memoriam. He died on January 15, 2016.

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Table 1. List of the current names of species of Auchenipteridae and valid names according to the new proposed classification scheme.

| Current name | Valid name |
|---|--|
| <i>Ageneiosus akamai</i> | <i>Ageneiosus akamai</i> Ribeiro, Rapp Py-Daniel & Walsh, 2017 |
| <i>Ageneiosus apiaka</i> | <i>Ageneiosus apiaka</i> Ribeiro, Rapp Py-Daniel & Walsh, 2017 |
| <i>Ageneiosus dentatus</i> | <i>Ageneiosus dentatus</i> Kner, 1857 |
| <i>Ageneiosus inermis</i> | <i>Ageneiosus inermis</i> (Linnaeus, 1766) |
| <i>Ageneiosus intrusus</i> | <i>Ageneiosus intrusus</i> Ribeiro, Rapp Py-Daniel & Walsh, 2017 |
| <i>Ageneiosus lineatus</i> | <i>Ageneiosus lineatus</i> Ribeiro, Rapp Py-Daniel & Walsh, 2017 |
| <i>Ageneiosus magoi</i> | <i>Ageneiosus magoi</i> Castillo & Brull, 1898 |
| <i>Ageneiosus militaris</i> | <i>Ageneiosus militaris</i> Valenciennes, 1836 |
| <i>Ageneiosus pardalis</i> | <i>Ageneiosus pardalis</i> Lütken, 1874 |
| <i>Ageneiosus polystictus</i> | <i>Ageneiosus polystictus</i> Steindachner, 1915 |
| <i>Ageneiosus ucayalensis</i> | <i>Ageneiosus ucayalensis</i> Castelnau, 1855 |
| <i>Ageneiosus uranophthalmus</i> | <i>Ageneiosus uranophthalmus</i> Ribeiro & Rapp Py-Daniel, 2010 |
| <i>Ageneiosus vittatus</i> | <i>Ageneiosus vittatus</i> Steindachner, 1908 |
| <i>Asterophysus batrachus</i> | <i>Asterophysus batrachus</i> Kner, 1857 |
| <i>Auchenipterichthys coracoideus</i> | <i>Auchenipterichthys coracoideus</i> (Eigenmann & Allen, 1942) |
| <i>Auchenipterichthys longimanus</i> | <i>Auchenipterichthys longimanus</i> (Günther, 1864) |
| <i>Auchenipterichthys punctatus</i> | <i>Auchenipterichthys punctatus</i> (Valenciennes, 1840) |
| <i>Auchenipterichthys thoracatus</i> | <i>Auchenipterichthys thoracatus</i> (Kner, 1857) |
| <i>Auchenipterus ambyiacus</i> | <i>Auchenipterus ambyiacus</i> Fowler, 1915 |
| <i>Auchenipterus brachyurus</i> | <i>Auchenipterus brachyurus</i> (Cope, 1878) |
| <i>Auchenipterus brevior</i> | <i>Auchenipterus brevior</i> Eigenmann, 1912 |
| <i>Auchenipterus britskii</i> | <i>Auchenipterus britskii</i> Ferraris & Vari, 1999 |
| <i>Auchenipterus demerarae</i> | <i>Auchenipterus demerarae</i> Eigenmann, 1912 |
| <i>Auchenipterus dentatus</i> | <i>Auchenipterus dentatus</i> Valenciennes, 1840 |
| <i>Auchenipterus fordicei</i> | <i>Auchenipterus fordicei</i> Eigenmann & Eigenmann, 1888 |
| <i>Auchenipterus menezesi</i> | <i>Auchenipterus menezesi</i> Ferraris & Vari, 1999 |
| <i>Auchenipterus nigripinnis</i> | <i>Auchenipterus nigripinnis</i> (Boulenger, 1895) |
| <i>Auchenipterus nuchalis</i> | <i>Auchenipterus nuchalis</i> (Spix & Agassiz, 1829) |
| <i>Auchenipterus osteomystax</i> | <i>Auchenipterus osteomystax</i> (Miranda Ribeiro, 1918) |
| <i>Centromochlus altae</i> | <i>Duringlanis altae</i> (Fowler, 1945) |
| <i>Centromochlus bockmanni</i> | <i>Tatia bockmanni</i> (Sarmiento-Soares & Buckup, 2005) |
| <i>Centromochlus britskii</i> | <i>Tatia britskii</i> (Sarmiento-Soares & Birindelli, 2015) |
| <i>Centromochlus concolor</i> | <i>Tatia concolor</i> Mees, 1974 |
| <i>Centromochlus existimatus</i> | <i>Centromochlus existimatus</i> Mees, 1974 |
| <i>Centromochlus ferrarisi</i> | <i>Ferrarissaoaresia ferrarisi</i> (Birindelli, Sarmiento-Soares & Lima, 2015) |
| <i>Centromochlus heckelii</i> | <i>Centromochlus heckelii</i> (De Filippi, 1853) |
| <i>Centromochlus macracanthus</i> | <i>Balroglanis macracanthus</i> (Soares-Porto, 2000) |
| * <i>Centromochlus megalops</i> Kner, 1857 | <i>Centromochlus heckelii</i> (De Filippi, 1853) |
| <i>Centromochlus meridionalis</i> | <i>Ferrarissaoaresia meridionalis</i> (Sarmiento-Soares, Cabeceira, Carvalho, Zuanon & Akama, 2013) |
| <i>Centromochlus orca</i> | <i>Tatia orca</i> (Sarmiento-Soares, Lazzarotto, Rapp Py-Daniel & Leitão, 2017) |
| <i>Centromochlus perugiae</i> | <i>Duringlanis perugiae</i> (Steindachner, 1882) |
| <i>Centromochlus punctatus</i> | <i>Tatia punctata</i> Mees, 1974 |
| <i>Centromochlus reticulatus</i> | <i>Tatia reticulata</i> Mees, 1974 |
| <i>Centromochlus romani</i> | <i>Duringlanis romani</i> (Mees, 1988) |
| <i>Centromochlus schultzi</i> | <i>Balroglanis schultzi</i> (Rössel, 1962) |
| <i>Centromochlus simplex</i> | <i>Tatia simplex</i> Mees, 1974 |
| * <i>Centromochlus steindachneri</i> Gill, 1870 | <i>Centromochlus heckelii</i> (De Filippi, 1853) |
| <i>Entomocorus benjamini</i> | <i>Entomocorus benjamini</i> Eigenmann, 1917 |
| <i>Entomocorus gameroi</i> | <i>Entomocorus gameroi</i> Mago-Leccia, 1984 |
| <i>Entomocorus melaphareus</i> | <i>Entomocorus melaphareus</i> Akama & Ferraris, 2003 |
| <i>Entomocorus radiosus</i> | <i>Entomocorus radiosus</i> Reis & Borges, 2006 |

Table 1. Continued

| Current name | Valid name |
|--|--|
| <i>Epapterus blohmi</i> | <i>Epapterus blohmi</i> Vari, Jewett, Taphorn & Gilbert, 1984 |
| <i>Epapterus dispilurus</i> | <i>Epapterus dispilurus</i> Cope, 1878 |
| <i>Gelanoglanis nanonoticolus</i> | <i>Gelanoglanis nanonoticolus</i> Soares-Porto, Walsh, Nico & Netto, 1999 |
| <i>Gelanoglanis pan</i> | <i>Gelanoglanis pan</i> Calegari, Reis & Vari, 2014 |
| <i>Gelanoglanis stroudi</i> | <i>Gelanoglanis stroudi</i> Böhlke, 1980 |
| <i>Gelanoglanis travieso</i> | <i>Gelanoglanis travieso</i> Rengifo, Lujan, Taphorn & Petry, 2008 |
| <i>Gelanoglanis varii</i> | <i>Gelanoglanis varii</i> Calegari & Reis, 2016 |
| <i>Glanidium albescens</i> | <i>Glanidium albescens</i> Reinhardt, 1874 |
| <i>Glanidium botocudo</i> | <i>Glanidium botocudo</i> Sarmiento-Soares & Martins-Pinheiro, 2013 |
| <i>Glanidium catharinensis</i> | <i>Glanidium catharinensis</i> Miranda Ribeiro, 1962 |
| <i>Glanidium cesarpintoi</i> | <i>Glanidium cesarpintoi</i> Ihering, 1928 |
| <i>Glanidium leopardum</i> | <i>Gephyromochlus leopardus</i> (Hoedeman, 1961) |
| <i>Glanidium melanopterum</i> | <i>Glanidium melanopterum</i> Miranda Ribeiro, 1918 |
| <i>Glanidium ribeiroi</i> | <i>Glanidium ribeiroi</i> Haseman, 1911 |
| <i>Liosomadoras morrowi</i> | <i>Liosomadoras morrowi</i> Fowler, 1940 |
| <i>Liosomadoras oncinus</i> | <i>Liosomadoras oncinus</i> (Jardine, 1841) |
| <i>Pseudauchenipterus affinis</i> | <i>Pseudauchenipterus affinis</i> (Steindachner, 1877) |
| <i>Pseudauchenipterus flavescens</i> | <i>Pseudauchenipterus flavescens</i> (Eigenmann & Eingenmann, 1888) |
| <i>Pseudauchenipterus jequitinhonhae</i> | <i>Pseudauchenipterus jequitinhonhae</i> (Steindachner, 1877) |
| <i>Pseudauchenipterus nodosus</i> | <i>Pseudauchenipterus nodosus</i> (Bloch, 1794) |
| <i>Pseudepapterus cucuhyensis</i> | <i>Pseudepapterus cucuhyensis</i> Böhlke, 1951 |
| <i>Pseudepapterus gracilis</i> | <i>Pseudepapterus gracilis</i> Ferraris & Vari, 2000 |
| <i>Pseudepapterus hasemani</i> | <i>Pseudepapterus hasemani</i> (Steindachner, 1915) |
| <i>Pseudotatia parva</i> | <i>Pseudotatia parva</i> Mees, 1974 |
| <i>Spinipterus acsi</i> | <i>Spinipterus acsi</i> Akama & Ferraris, 2011 |
| <i>Tatia aulopygia</i> | <i>Tatia aulopygia</i> Kner, 1857 |
| <i>Tatia boemia</i> | <i>Tatia boemia</i> Koch & Reis, 1996 |
| <i>Tatia brunnea</i> | <i>Tatia brunnea</i> Mees, 1974 |
| <i>Tatia carolae</i> | <i>Balroglanis carolae</i> (Vari & Ferraris, 2013) |
| <i>Tatia caudosignata</i> | <i>Tatia caudosignata</i> Do Nascimento, Albornoz-Garzón & García-Melo, 2019 |
| <i>Tatia caxiuuanensis</i> | <i>Tatia caxiuuanensis</i> Sarmiento-Soares & Martins-Pinheiro, 2008 |
| † <i>Tatia creutzbergi</i> | <i>Tatia creutzbergi</i> (Boeseman, 1953) |
| <i>Tatia dunnii</i> | <i>Tatia dunnii</i> (Fowler, 1945) |
| <i>Tatia galaxias</i> | <i>Tatia galaxias</i> Mees, 1974 |
| <i>Tatia gyrina</i> | <i>Tatia gyrina</i> (Eigenmann & Allen, 1942) |
| <i>Tatia intermedia</i> | <i>Tatia intermedia</i> (Steindachner, 1877) |
| <i>Tatia jaracatia</i> | <i>Tatia jaracatia</i> Pavanelli & Bifi, 2009 |
| <i>Tatia marthae</i> | <i>Tatia marthae</i> Vari & Ferraris, 2013 |
| <i>Tatia meesi</i> | <i>Tatia meesi</i> Sarmiento-Soares & Martins-Pinheiro, 2008 |
| <i>Tatia melanoleuca</i> | <i>Tatia melanoleuca</i> Vari & Calegari, 2014 |
| <i>Tatia musaica</i> | <i>Tatia musaica</i> Royero, 1992 |
| <i>Tatia neivai</i> | <i>Tatia neivai</i> (Ihering, 1930) |
| <i>Tatia nigra</i> | <i>Tatia nigra</i> Sarmiento-Soares & Martins-Pinheiro, 2008 |
| <i>Tatia strigata</i> | <i>Tatia strigata</i> Soares-Porto, 1995 |
| <i>Tetranematichthys barthemi</i> | <i>Tetranematichthys barthemi</i> Peixoto & Wosiacki, 2010 |
| <i>Tetranematichthys quadrifilis</i> | <i>Tetranematichthys quadrifilis</i> (Kner, 1857) |
| <i>Tetranematichthys wallacei</i> | <i>Tetranematichthys wallacei</i> Vari & Ferraris, 2006 |
| <i>Tocantinsia piresi</i> | <i>Tocantinsia piresi</i> (Miranda Ribeiro, 1920) |
| <i>Trachelyichthys decaradiatus</i> | <i>Trachelyichthys decaradiatus</i> Mees, 1974 |
| <i>Trachelyichthys exilis</i> | <i>Trachelyichthys exilis</i> Greenfield & Glodek, 1977 |
| <i>Trachelyopterichthys anduzei</i> | <i>Trachelyopterichthys anduzei</i> Ferraris & Fernandez, 1987 |
| <i>Trachelyopterichthys taeniatus</i> | <i>Trachelyopterichthys taeniatus</i> (Kner, 1857) |
| <i>Trachelyopterus albicrux</i> | <i>Trachelyopterus albicrux</i> (Berg, 1901) |

Table 1. Continued

| Current name | Valid name |
|--------------------------------------|---|
| <i>Trachelyopterus amblops</i> | <i>Trachelyopterus amblops</i> (Meek & Hildebrand, 1913) |
| <i>Trachelyopterus ceratophysus</i> | <i>Trachelyopterus ceratophysus</i> (Kner, 1857) |
| <i>Trachelyopterus coriaceus</i> | <i>Trachelyopterus coriaceus</i> Valenciennes, 1840 |
| <i>Trachelyopterus cratensis</i> | <i>Trachelyopterus cratensis</i> (Miranda Ribeiro, 1937) |
| <i>Trachelyopterus fisheri</i> | <i>Trachelyopterus fisheri</i> (Eigenmann, 1916) |
| <i>Trachelyopterus galeatus</i> | <i>Trachelyopterus galeatus</i> (Linnaeus, 1766) |
| <i>Trachelyopterus insignis</i> | <i>Trachelyopterus insignis</i> (Steindachner, 1878) |
| <i>Trachelyopterus lacustris</i> | <i>Trachelyopterus lacustris</i> (Lütken, 1874) |
| <i>Trachelyopterus leopardinus</i> | <i>Trachelyopterus leopardinus</i> (Borodin, 1927) |
| <i>Trachelyopterus lucenai</i> | <i>Trachelyopterus lucenai</i> Bertolotti, da Silva & Pereira, 1995 |
| <i>Trachelyopterus peloichthys</i> | <i>Trachelyopterus peloichthys</i> (Schultz, 1944) |
| <i>Trachelyopterus striatulus</i> | <i>Trachelyopterus striatulus</i> (Steindachner, 1877) |
| <i>Trachelyopterus teaguei</i> | <i>Trachelyopterus teaguei</i> (Devincenzi, 1942) |
| <i>Trachycorystes menezesi</i> | <i>Trachycorystes menezesi</i> Britski & Akama, 2011 |
| <i>Trachycorystes porosus</i> | <i>Trachelyopterus porosus</i> (Eigenmann & Eigenmann, 1888) |
| <i>Trachycorystes trachycorystes</i> | <i>Trachycorystes trachycorystes</i> (Valenciennes, 1840) |
| <i>Tympanopleura atronasmus</i> | <i>Tympanopleura atronasmus</i> (Eigenmann & Eigenmann, 1888) |
| <i>Tympanopleura brevis</i> | <i>Tympanopleura brevis</i> (Steindachner, 1881) |
| <i>Tympanopleura cryptica</i> | <i>Tympanopleura cryptica</i> Walsh, Ribeiro & Rapp Py-Daniel, 2015 |
| <i>Tympanopleura longipinna</i> | <i>Tympanopleura longipinna</i> Walsh, Ribeiro & Rapp Py-Daniel, 2015 |
| <i>Tympanopleura piperata</i> | <i>Tympanopleura piperata</i> Eigenmann, 1912 |
| <i>Tympanopleura rondoni</i> | <i>Tympanopleura rondoni</i> (Miranda Ribeiro, 1914) |

Names in bold indicate generic changes.

*New synonymy.

†Revalidation.

brackish water. Auchenipterids are of some economic interest, because a number of species have been used as a food source, mainly species of *Ageneiosus*. In addition, small species with attractive colour patterns, such as *Auchenipterichthys*, *Centromochlus*, *Tatia* and *Trachelyichthys*, in addition to species with voracious predator behaviour, such as *Asterophysus batrachus* and *Trachycorystes trachycorystes*, are of commercial interest to aquarists, being exported from Brazil, Peru and Venezuela mainly to the USA, Europe and Asia. Auchenipterids generally have a twilight to nocturnal habit, at which times they usually forage near the water surface. Other species can be found active during the day and yet others can live in multispecies shoals (Burgess, 1989; B.B.C., pers. obs.).

Auchenipteridae have a wide variety of feeding behaviours. Some species feed on fruits and seeds, as observed in *Trachycorystes* (Goulding, 1980), whereas other species are predators of insects, crustaceans (Menezes, 1949; Burgess, 1989), small fishes, frogs (B.B.C., pers. obs.) and reptiles (Freitas *et al.*, 2011). Among the Neotropical Siluriformes, one of the most interesting and outstanding characteristics of the Auchenipteridae is that they are inseminating fishes with external development (oviparous *sensu* Nakatani *et al.*, 2001), a distinctive feature otherwise

known among catfishes only in Scoloplacidae and Astroblepidae (Spadella *et al.* 2006, 2012).

Ihering (1937) was the first to report the occurrence of what he called internal fertilization in the Auchenipteridae, reporting observations of the reproduction of *Trachycorystes striatulus* (currently known as *Trachelyopterus striatulus*). Ihering described the reproduction of this species as very peculiar, with the spermatozoa being introduced into the female oviduct through a copulatory organ (i.e. the anal fin of males modified into an intromittent organ) before the maturation of eggs. Consequently, fertilization occurs during spawning without the presence of males. Although the author did not witness the fertilization itself, the morphology of the gonads and the physiology of the spermatozoa reinforce the hypothesis of internal fertilization in the family. The testes are strongly modified, and the spermatozoa are produced only in the anterior portion, whereas the posterior portion of the testis is modified to produce a gelatinous substance. This substance is insoluble, and males inject it into females at the end of copulation immediately after the spermatozoa have been introduced, forming a barrier in the oviduct. In addition, when their spermatozoa are exposed to the water, they suffer deformation and lose mobility, unlike spermatozoa of fishes with external fertilization (Ihering,

1937). However, additional studies should be conducted to determine the exact moment when the spermatozoa fertilize the eggs. For this reason, Auchenipteridae continue to be referred to as inseminating fishes (Spadella *et al.*, 2012). This peculiar reproductive strategy is directly associated with their marked sexual dimorphism, which can involve many morphological changes in mature males: the shape, size and position of the anal fin; development and fusion of the anal-fin pterygiophores; enlargement, elongation and ossification of the maxillary barbel and the dorsal-fin spine; anterior displacement of the dorsal-fin spine; development of serrae on the anterior surface of the dorsal-fin spine; development of a gonopodium; and development of nuptial dermal tubercles (Britski, 1972; Ferraris, 1988; Royero, 1999; Ferraris & Vari, 1999; Akama, 2004; Ribeiro, 2011; Birindelli, 2014; Calegari *et al.*, 2014).

Members of the Auchenipteridae are popularly known as *cangati*, *fidalgo*, *mandubé*, *palmito*, *ximbé*, *porrudo*, *cachorro-de-padre*, *carataí* and *barriga mole* in Brazil; as *manduví*, *novia* and *pinguinos* in other Latin American countries; and as driftwood, woodcat and jaguar catfish in the international community.

EVOLUTIONARY POSITION AND COMPOSITION OF THE DORADOIDEA

Despite the current knowledge of the phylogenetic relationships of Siluriformes, the evolutionary history of some groups remains controversial and even unresolved. Nonetheless, the monophyly of the order is widely corroborated by many authors (Fink & Fink, 1981, 1996; Mo, 1991; de Pinna, 1993; Britto, 2002; Diogo, 2004; Sullivan *et al.*, 2006; Arcila *et al.*, 2017; Betancur-R *et al.*, 2017). The most current phylogenies of Siluriformes based on morphological evidence have found a general consensus regarding the early diversification of Diplomystidae within the order, as the sister group to all remaining catfishes (Mo, 1991; Arratia, 1992; de Pinna, 1998; Britto, 2002; Diogo, 2004; Birindelli, 2014). However, the synapomorphic characters of the non-Diplomystidae catfishes still differ among studies (Grande, 1987; Mo, 1991; de Pinna, 1998; Arratia, 1992; Diogo, 2004). In contrast, recent genomic-based phylogenies (Arcila *et al.*, 2017; Betancur-R *et al.*, 2017) have recovered a different position for Diplomystoidei (Diplomystidae) within Siluriformes as sister taxa to all Siluroidei, with both clades sister to Loricarioidei.

Notwithstanding, the phylogenies of Mo (1991), Lundberg (1993) and de Pinna (1998) agree upon the close relationship of the families Ariidae, Mochokidae, Doradidae and Auchenipteridae. Those authors suggested that the cosmopolitan Ariidae is the sister group to the Doradoidei (Mochokidae, Doradidae and Auchenipteridae). However, it was Regan (1911) who established the first hypothesis of monophyly

for the group formed by the Auchenipteridae and Doradidae (superfamily Doradoidea), proposing its close relationship with the Ariidae based on the absence of the mesocoracoid. In contrast to Regan (1911), the above authors suggested the Mochokidae as the sister group to the clade formed by the Auchenipteridae and Doradidae, a hypothesis strongly corroborated by subsequent authors, including Britto (2002), Diogo (2004) and Birindelli (2014), also based on morphological characters. In addition, molecular results of Sullivan *et al.* (2006, 2008) include the monophyly of a group formed by Auchenipteridae and Doradidae (Doradoidea), corroborating the earliest morphological studies. Furthermore, Sullivan (2006) presented, as the final hypothesis, a tree comprising the concatenation of different results found in distinct analyses, supporting the Aspredinidae as the sister group to the Doradoidea, in contrast to all morphological hypotheses to date (de Pinna, 1998; Britto, 2002; Diogo, 2004; Birindelli, 2014). Corroborating Sullivan *et al.* (2006, 2008) and in light of new technologies, the two most recent genomic-based large-scale phylogenies including major groups of Siluriformes (Arcila *et al.*, 2017; Betancur-R *et al.*, 2017) resulted in the sister-group relationship of Auchenipteridae and Doradidae, with the Neotropical Aspredinidae recovered as their sister taxa. Nevertheless, in a molecular phylogeny of the non-Diplomystidae catfishes seeking the sister group to the Ictaluridae, Hardman (2005) alternatively found the Doradoidea to be a separate clade in a more basal position in Siluriformes, a hypothesis incongruent with all previous reported phylogenies.

HISTORICAL OVERVIEW OF THE SYSTEMATICS OF AUCHENIPTERIDAE

The Auchenipteridae have an extensive and confusing taxonomic and phylogenetic history. Several studies since the 18th century have generated controversial results regarding the composition of the family and its interrelationships. The taxonomy of auchenipterids had long been linked with diverse catfish families, primarily Doradidae and Pimelodidae. The nomenclatural history of auchenipterids began with Linnaeus (1766) in the 12th edition of *Systema Naturae*, in which he described *Silurus inermis* Linnaeus, 1766 and *Silurus galeatus* Linnaeus, 1766 (currently allocated in *Ageneiosus* and *Trachelyopterus*, respectively). Thenceforth, many studies were published on new species and genera and on the classification of large catfish groups. A brief description of the studies that have influenced the history of the Auchenipteridae is below.

Bloch (1794) described several new genera and species, including *Silurus nodosus* Bloch, 1794 (currently valid as *Pseudauchenipterus*). Later, Bloch & Schneider (1801) lumped *Silurus*, Mochokidae and

other siluroids as an order in the class Heptapterygii. Soon thereafter, Lacepède (1803) described the genus *Ageneiosus*, allocating the species previously described by Linnaeus and including *Silurus nodosus*, *Silurus galeatus* and some species from other families (Mochokidae, Ariidae and Pimelodidae) in the genus *Pimelodus*. Rafinesque (1815) was the first author to assign a formal group to the catfishes, the Oplophoria, which included two subfamilies, one comprising loricariids and callichthyids and the other comprising the remaining catfishes.

Cuvier (1817) proposed the first classification and diagnosis of fishes based on anatomy, placing all catfishes together in an exclusive family called ‘Siluroides’, divided into three subgroups, with ‘Silures’ including species of *Ageneiosus* (*Ageneiosus inermis*) and *Trachelyopterus* (*Pimelodus galeatus*). Spix & Agassiz (1829) classified the catfishes into two subfamilies, one called ‘Siluroidei’, to which they allocated *Hypophthalmus*, which at that time contained *Hypophthalmus nuchalis* Spix & Agassiz, 1829 (currently known as *Auchenipterus*) and the second called ‘Gonyodontes’. Cuvier & Valenciennes (1840) modified the nomenclature again, creating several new genera: *Arius* for *Silurus nodosus*; *Auchenipterus* for *Auchenipterus nuchalis* and several new species, namely *Auchenipterus dentatus* Valenciennes, 1840, *Auchenipterus furcatus* Valenciennes, 1840, *Auchenipterus immaculatus* Valenciennes, 1840, *Auchenipterus maculosus* Valenciennes, 1840, *Auchenipterus punctatus* Valenciennes, 1840 and *Auchenipterus trachycorystes* Valenciennes, 1840; and *Trachelyopterus*, including *Trachelyopterus coriaceus* Valenciennes, 1840. Even so, Müller & Troschel (1849) transferred *Silurus nodosus* to *Auchenipterus*.

Kner (1857) also increased the known diversity of auchenipterids and described new genera and species, such as *Asterophysus batrachus* Kner, 1857, *Auchenipterusthoracatus* Kner, 1857 and *Auchenipterus ceratophysus* Kner, 1857 (the latter currently placed in *Trachelyopterus*), *Centromochlus aulopygia* Kner 1857 and *Centromochlus megalops* Kner, 1857. Bleeker (1858, 1862–63) greatly contributed to knowledge of the siluroids, describing new genera and assigning suprageneric groups. In his study (Bleeker, 1862–63), he created the Stirp Pseudoauchenipterini, subdivided into Pseudoauchenipteri (including *Auchenipterichthys*, *Parauchenipterus*, *Pseudoauchenipterus* and *Trachycorystes*), Centromochli (including *Centromochlus*) and Asterophysii (including *Asterophysus*). Additionally, Bleeker created the Stirp Pangasini, including the subdivisions Ageneiosii (*Ageneiosus*, *Pseudogeneiosus* and *Tetranematichthys*) and Auchenipterini (*Auchenipterus*). In the same study, Bleeker (1862–63) designated the subfamily Trachelyopteriformes, including the

Stirp Trachelyopterini (*Trachelyopterus* and *Trachelyopterichthys*).

A reclassification of the catfishes (family Siluridae) was conducted by Günther (1864), encompassing many species of *Ageneiosus*, *Asterophysus*, *Auchenipterus*, *Centromochlus*, *Trachelyopterus*, *Tetranematichthys*, other species of the current families Doradidae and Mochokidae and a few species of Ceptosidae, in an exclusive group called Doradina, belonging to the subfamily Stenobranchiae.

Eigenmann & Eigenmann (1890) also contributed to the taxonomy of the auchenipterids and, in a revisionary study of the Neotropical siluroids, separated the Auchenipteridae into two groups: Ageneiosinae (an exclusive group for the species of *Ageneiosus*) and Auchenipterinae. A new classification of the Siluriformes was proposed by Regan (1911), differing from all previous classifications by the inclusion of a great diversity of catfishes and the use of osteological characteristics instead of external morphology alone (de Pinna, 1998). Regan proposed the group Siluroidea, including members of Ageneiosidae and Auchenipteridae in an expanded Doradidae. In the same year, Miranda Ribeiro (1911) recognized some genera as higher level and proposed the Doradidae, Ageneiosidae (*Ageneiosus*, *Pseudogeneiosus* and *Tetranematichthys*), Trachycorystidae (*Asterophysus*, *Auchenipterichthys*, *Centromochlus*, *Glanidium*, *Pseudoauchenipterus*, *Tatia*, *Trachelyopterus*, *Trachelyopterichthys* and *Trachycorystes*) and Auchenipteridae (*Auchenipterus* and *Epapterus*).

A few years later, a new configuration of catfishes was proposed by Eigenmann (1925), including 16 subfamilies, among which the Auchenipteridae, Ageneiosidae and Doradidae were considered independent. Some years later, Ihering (1937) corroborated Eigenmann (1925) in considering Ageneiosidae and Doradidae as apart from the Auchenipteridae; in addition, the latter was divided into two subfamilies: Auchenipterinae and Trachycorystinae.

Subsequently, controversial considerations of the Auchenipteridae were proposed by many authors, such as Fowler (1940), who included *Ageneiosus* in the Auchenipteridae; Gosline (1945), who considered Ageneiosidae to be separate from the remaining auchenipterids, all allocated to the Doradidae; Eigenmann & Allen (1942), who transferred five genera recognized by previous authors as Auchenipteridae to the Pimelodidae; and Jordan (1929), Berg (1940), Fowler (1951) and Greenwood *et al.* (1966), who considered Ageneiosidae, Doradidae and Auchenipteridae to be independent families among the Siluriformes. Chardon (1968) was another author who corroborated this line of consideration and maintained the separation of these three families,

although he recognized that only one character could distinguish the Doradidae from the Auchenipteridae: the presence of lateral bony plates.

In addition to recognizing the independence of these three families, Chardon (1968) also brought together, for the first time, the Mochokidae, Auchenipteridae, Ageneiosidae and Doradidae into a superfamily called Doradoidea, included in the suborder Bagroidei. His work was based on anatomical studies of the Weberian apparatus, mainly the presence of the elastic spring mechanism (except some species of Ageneiosidae; Walsh, 1990), but also features thought to represent a strong skeletal system, such as the deeply sutured cranial bones and the presence of an additional intermediate nuchal shield, among others (Chardon, 1968: 229). In the same year, based on his father's previous study (Miranda Ribeiro, 1911) and with little explanation, Miranda Ribeiro (1968) split the auchenipterids into four families, Asterophysidae, Auchenipteridae, Centromochlidae and Trachycorystidae, and maintained the Ageneiosidae as a separate family.

Britski (1972) was an important contribution for the first establishment of the internal relationship of the Auchenipteridae and Ageneiosidae and for considering both families to form a natural group within the Siluriformes supported by the presence of sexual dimorphism. He also aimed to define the position of the two families within Doradoidea (*sensu* Chardon, 1968). Britski developed an extensive and detailed study (not published to date), based on the internal anatomy, osteology, reproductive system, sexual dimorphism and gas bladder features, that revealed important features for the systematics of the family. As a result, he suggested splitting Auchenipteridae into four subfamilies: Asterophysinae, Auchenipterinae, Centromochlinae and Trachycorystinae. However, he included the genera *Ageneiosus* and *Tetranematichthys* in the family Ageneiosidae and placed *Wertheimeria* in Doradidae.

Based on a strictly cladistic methodology, Ferraris (1988) conducted what would be the first phylogenetic study of the Auchenipteridae (not published), greatly contributing to the knowledge of the family. His phylogeny was based on 129 morphological characters and proposed Doradidae as a sister group to Auchenipteridae (including members of Ageneiosidae) and Centromochlidae (*Centromochlus*, *Gelanoglanis*, *Glanidium*, *Tatia* and New Genera A and B). The author divided the Auchenipteridae into two subfamilies: Auchenipterinae (*Auchenipterichthys*, *Pseudoauchenipterus* and the tribe Auchenipterini, comprising *Ageneiosus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Tetranematichthys*, *Trachelyichthys* and *Trachelyopterus*) and Trachycorystinae (*Liosomadoras*, *Trachelyopterichthys* and *Trachycorystes*). Furthermore, Ferraris (1988) considered the monotypic

genera *Asterophysus*, *Pseudotatia* and *Tocantinsia* as *incertae sedis* within the family. The decision of Ferraris (1988) to recognize two families, Auchenipteridae and Centromochlidae, was based on differences in the reproductive system reflected by the non-enlargement of the urogenital pore of females of centromochlids. De Pinna (1998) agreed with most of the phylogenetic hypothesis of Ferraris (1988), except for the separation of the Auchenipteridae and Centromochlidae into two families, which he stated should be recognized at the subfamily level (de Pinna, 1998).

Curran (1989) also proposed a phylogenetic hypothesis for Auchenipteridae and developed his study based on only 24 morphological characters (primarily external morphology), examining 20 taxa. Curran proposed a more inclusive Auchenipteridae, including Centromochlidae. However, Curran did not include Ageneiosidae (*Ageneiosus* and *Tetranematichthys*) in his study.

Walsh (1990) focused his study on the phylogenetic relationships of Ageneiosidae (not published), describing several osteological characters and important findings. His study corroborates the inclusion of *Tetranematichthys* in the family and the monophyly of *Ageneiosus*, and was mainly based on features related to the gas bladder encapsulation. Walsh also suggested *Ageneiosus pardalis* as sister to all remaining species of *Ageneiosus*.

Soares-Porto (1998) studied the relationships of Centromochlinae, rearranging its species into *Centromochlus*, *Glanidium* and *Tatia* and considering *Gelanoglanis* as a junior synonymy of *Centromochlus*. That synonymization was later reconsidered by Soares-Porto *et al.* (1999), who resurrected the genus. In the same study, *Glanidium* was proposed as the sister group to the remaining Centromochlinae.

Royero (1999) conducted a valuable phylogenetic study (not published) focused on Auchenipteridae but also encompassing members of Ariidae, Mochokidae and Doradidae to establish the relationships among the arioids. Royero deeply investigated and thoroughly discussed 151 morphological characters, which significantly increased the congruence of the auchenipterid relationships. The author repositioned the Ariidae closest to the Mochokidae, Doradidae, Auchenipteridae and Ageneiosidae, successively. Royero recognized four subfamilies in Auchenipteridae, namely Pseudoauchenipterinae, Trachycorystinae, Centromochlinae and Auchenipterinae, and considered *Pseudotatia* as *incertae sedis*. Additionally, Royero found the clade formed by *Ageneiosus* and *Tetranematichthys* to be the sister group to *Trachelyopterus peloichthys* Schultz, 1944, a species described in his dissertation as a supposed new genus never formally published.

In a comprehensive systematic review of *Parauchenipterus* and *Trachelyopterus*, Akama (2004)

re-evaluated the morphological characters of previous authors and included important characteristics of sexual dimorphism. Based on his results (not published to date), *Parauchenipterus* and *Trachelyopterus* are recognized as monophyletic sister groups. In addition to recognizing the validity of both genera, Akama included in his analyses the new genus of Royero (1999), corroborating that author on the monophyly of this genus, and additionally proposed the allocation of more species (*Parauchenipterus amblops*, *Parauchenipterus fisheri*, *Parauchenipterus insignis* and *Parauchenipterus teaguei*) in that genus. According to his results, this clade is more closely related to *Tetranematichthys* and *Ageneiosus*. Akama considered five species valid in *Parauchenipterus* (*Parauchenipterus ceratophysus*, *Parauchenipterus galeatus*, *Parauchenipterus porosus*, *Parauchenipterus striatulus* and a new species from the central Amazon) and two species in *Trachelyopterus* (*Trachelyopterus coriaceus* and a new species from the Paraná-Paraguay basin).

More recently, Birindelli (2014) published a phylogeny of the Doradoidea, where he conducted an exhaustive and wide compilation of morphological characters, in which he gathered and reviewed a series of characters from previous authors encompassing osteology, sexual dimorphism, myology and the reproductive system. As a result, Birindelli found Doradoidea to be the sister group to Mochokidae, as expected for a morphological phylogeny, corroborating previous studies of the same nature. Additionally, the author recognized two subfamilies in the Auchenipteridae (Centromochlinae and Auchenipterinae), in accordance with the classification proposed by Ferraris (2007) and Soares-Porto (1998). Within Auchenipterinae, Birindelli also found support for two tribes, Auchenipterini (composed of *Ageneiosus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, *Tetranematichthys* and the new genus of Royero, 1999), a clade also found by other authors (Akama, 2004, except for *Epapterus*, which was not included in his study; Ribeiro, 2011), and the tribe Trachelyopterini (composed of *Auchenipterichthys*, *Parauchenipterus*, *Trachelyichthys*, *Trachelyopterichthys*, *Trachelyopterus* and *Trachycorystes*). Although Birindelli (2014) has conducted a comprehensive phylogenetic study, the author focused on higher relationships, and in general, the study included few representative species per genus of the Auchenipteridae.

After Birindelli completed his study but before its publication, Ribeiro (2011) developed a phylogeny focused on the *Ageneiosus* group, which later resulted in the publication of two revisions (Walsh *et al.*, 2015; Ribeiro *et al.*, 2017). His phylogeny, still unpublished, included 237 morphological characters and recognized two tribes in Auchenipterinae (Auchenipterini and Trachelyopterini). As a result, his hypothesis corroborated the monophyly of two genera, *Ageneiosus* s.s. and suggested the

revalidation of *Tympanopleura*. Additionally, the author recommended a series of taxonomic changes, which were recently published in two subsequent revisions. Walsh *et al.* (2015) revalidated *Tympanopleura* Eigenmann, 1912 as a genus encompassing *Tympanopleura cryptica*, *Tympanopleura longipinna*, *Tympanopleura atronasus*, *Tympanopleura brevis*, *Tympanopleura piperata* and *Tympanopleura rondoni*, the latter removed from the synonym of *Ageneiosus brevis*. The last four species were previously included in *Ageneiosus* and the first two were described as new in the same study. Ribeiro *et al.* (2017) revised *Ageneiosus*, recognizing 13 valid species and describing four new ones: *Ageneiosus akamai*, *Ageneiosus apiaka*, *Ageneiosus intrusus* and *Ageneiosus lineatus*. Additionally, the authors proposed *Ageneiosus marmoratus* as a junior synonym of *Ageneiosus inermis* and the revalidation of *Ageneiosus dentatus*.

Akama & Ferraris (2011) have also contributed to the understanding of the diversity of the family by describing a new genus and species of a small fish, *Spinipterus acsi*, from the Peruvian Amazon. Although *Spinipterus* is currently monotypic, at least two more species are known to exist and await formal description.

STATE OF KNOWLEDGE OF AUCHENIPTERIDAE AND RELATED TAXA

In summary, throughout the extensive and complex phylogenetic history of the Auchenipteridae, the monophyly of the superfamily Doradoidea has been agreed upon by all recent authors (since the 1980s) and is supported by a series of synapomorphies. Nevertheless, the propositions of the closest relationship of the Doradoidea with the remaining Siluriformes have varied among the different morphological studies, and there is a contrast between morphological and molecular studies. Hypotheses based on morphological traits have suggested that the Doradoidea plus Mochokidae are more closely related to the Ariidae (de Pinna, 1998) or the Malapteruridae (Diogo, 2004) or that they form a clade encompassing exclusively the Doradoidea (Britto, 2002; Birindelli, 2014). In contrast, hypotheses based on genotypic information have appointed the Aspredinidae as the sister group to the Doradoidea (Sullivan *et al.*, 2006, 2008; Arcila *et al.*, 2017; Betancurt-R *et al.*, 2017).

Several studies since 1766 that included species descriptions have generated controversy regarding the composition of the family. However, there is a notable contribution of many authors to the taxonomy of the family, with geographical reviews (Mees, 1974, auchenipterids from Suriname) or revisions of genera, as follows: *Ageneiosus* (Ribeiro *et al.*, 2017), *Auchenipterichthys* (Ferraris *et al.*, 2005), *Auchenipterus* (Ferraris & Vari, 1999),

Epapterus (Vari & Ferraris, 1998), *Liosomadoras* (Birindelli & Jansen, 2012), *Pseudepapterus* (Ferraris & Vari, 2000), *Tatia* (Mees, 1988; Sarmento-Soares, 2008), *Entomocorus* (Reis & Borges, 2006), *Tetranematichthys* (Vari & Ferraris, 2006) and *Tympanopleura* (Walsh *et al.*, 2015).

With respect to family composition, the recognition of the subfamilies Centromochlinae and Auchenipterinae represents well the diversity of forms in Auchenipteridae, a classification accepted by most authors. However, the various disagreements regarding the internal relationships of the family should be noted. The phylogenetic studies of the family, all unpublished except for Curran (1989), Soares-Porto (1998) and Birindelli (2014), contain distinct hypotheses of interrelationships, especially in Auchenipterinae, demonstrating that hypotheses about its evolutionary history are still controversial.

The Auchenipteridae have an extensive and confusing taxonomic and phylogenetic history, in part because of the nature of the evidence used to reconstruct the interrelationships of Siluriformes and, more particularly, of the family. Studies so far have used either morphological or molecular evidence and far from complete taxonomic sampling, showing several incongruities and suggesting controversial evolutionary histories that could be reconstructed better if based on a combination of those data and a thorough taxonomic sampling.

Seeking to reconstruct the internal relationships of Auchenipteridae and its closest relationship among the Siluroidei, the present phylogenetic study includes as many species of the Auchenipteridae as possible in addition to several representatives of relevant siluroid families to contemplate the greater diversity of forms existing in the suborder, providing a strong comparison among taxa and therefore providing information based on evolutionary evidence from different sources, including morphological and molecular data in a combined approach. The combined dataset aims to generate a hypothesis to establish the interrelationships within the Auchenipteridae, which is crucial for a full understanding of the evolution of the family. A new classification for Auchenipteridae is presented herein to bring the taxonomy more in line with the new phylogenetic hypothesis along with phylogenetic diagnoses, a helpful and easy morphological comparison of each rank and a key for genera of the family.

MATERIAL AND METHODS

TAXON AND CHARACTER SAMPLING

Representatives of all valid genera of Auchenipteridae were included in the phylogenetic analyses. A total of 146 terminals were sampled in the combined analysis,

representing 114 auchenipterids (ingroup). The outgroup included 32 specimens from seven siluriform families: Ariidae (three species), Aspredinidae (five species), Cetopsidae (one species), Doradidae (nine species), Diplomystidae (five species), Pimelodidae (two species) and Mochokidae (seven species). The morphological data were accessible from 97 valid taxa of Auchenipteridae (35 centromochlines and 62 auchenipterines), plus 11 putatively new species and six species tentatively identified using the denomination *affinis* in the name, which were included in the analyses in order to test their generic allocation. The author of each new species, when not of the present authors, is given properly in the Diagnosis section. Outgroup choice was based on the previous higher-level and intrafamilial phylogenetic hypotheses of Siluriformes (de Pinna, 1998; Britto, 2002; Diogo, 2004; Sullivan *et al.*, 2006; Vigliotta, 2008; Marceniuk *et al.*, 2012; Arce *et al.*, 2013; Birindelli, 2014).

Specimens used for morphological study were provided by many institutions, as follows: the Academy of Natural Sciences, Philadelphia (ANSP); American Museum of Natural History, New York (AMNH); Auburn University Natural History Museum, Auburn (AUM); California Academy of Sciences, San Francisco (CAS); Coleção Zoológica Norte Capixaba, São Mateus (CZMZ); Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA); Field Museum of Natural History, Chicago (FMNH); Florida Museum of Natural History, Gainesville (UF); Laboratório de Biologia e Genética de Peixes da UNESP, Botucatu (LBP); Los Angeles County Museum, Los Angeles (LACM); Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCP); Museu Nacional, Rio de Janeiro (MNRJ); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP); Muséum National d'Histoire Naturelle, Paris (MNHN); National Museum of Natural History, Smithsonian Institution, Washington (USNM); Natural History Museum, London (BMNH); Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura/Nupélia da Universidade Estadual de Maringá, Maringá (NUP); Royal Ontario Museum, Ontario (ROM); Texas Natural History Collections (TNHC); Universidade Federal do Rio Grande do Sul, Porto Alegre (UFRGS); and Universidade Federal de Rondônia, Porto Velho (UFRO-I).

Molecular data

A complete list of collection data and GenBank accession numbers for each sample included in the molecular analysis is shown in Table 2. All tissue samples included in this study were collected by

Table 2. Voucher catalogue number, tissue identifier number and GenBank accession numbers for all sequence samples analysed

| Family taxon | Voucher catalogue number | Tissue identifier | col | myh6 | rag2 | SH3PX3 | 16S |
|--------------------------------------|--------------------------|-------------------|----------|----------|----------|----------|-------------------------------|
| Auchenipteridae | | | | | | | |
| <i>Ageneiosus akamai</i> | MCP 46990 | C-105 | MF595206 | MF595282 | MF595363 | MF595443 | MF595113 |
| <i>Ageneiosus dentatus</i> | INPA 35533 | – | MF595213 | MF595283 | MF595365 | – | MF595116 |
| <i>Ageneiosus inermis</i> | UFRO-I 8711 | 3438 | – | MF595284 | MF595366 | MF595445 | MF595117 |
| <i>Ageneiosus militaris</i> | MCP 28423 | – | MF595215 | MF595286 | – | MF595447 | MF595119 |
| <i>Ageneiosus militaris</i> B | MCP 26681 | – | MF595211 | – | MF595364 | MF595444 | MF595114 |
| <i>Ageneiosus polystictus</i> | ROM 66265 | 5010 | MF595217 | MF595287 | MF595368 | MF595448 | MF595120 |
| <i>Ageneiosus polystictus</i> B | ROM 86418 | 7036 | MF595212 | – | – | – | MF595115 |
| <i>Ageneiosus ucayalensis</i> | MUSM 36932 | API46 | MF595219 | MF595288 | MF595369 | MF595449 | MF595121 |
| <i>Ageneiosus uranophthalmus</i> | UFRO-I 17223 | 8482 | – | MF595289 | MF595370 | – | MF595122 |
| <i>Ageneiosus vittatus</i> | UFRO-I uncataloged | 3497 | MF595220 | MF595290 | MF595371 | MF595450 | MF595123 |
| <i>Auchenipterichthys coracoides</i> | MCP 46293 | – | – | – | MF595378 | MF595458 | MF595132 |
| <i>Auchenipterichthys longimanus</i> | MCP 46593 | – | MF595227 | MF595297 | MF595379 | MF595459 | MF595133 |
| <i>Auchenipterichthys punctatus</i> | LBP 4442 | 24314 | – | – | MF595380 | – | MF595134 |
| <i>Auchenipterius ambyiacus</i> | UFRO-I 9593 | 4072 | MF595223 | MF595293 | MF595373 | MF595453 | MF595126 |
| <i>Auchenipterius brachyurus</i> | MUSM 36779 | AP68 | MF595224 | MF595294 | MF595374 | – | MF595127 |
| <i>Auchenipterius demerarae</i> | ROM 84014 | 4348 | MF595225 | MF595295 | MF595375 | MF595454 | MF595128 |
| <i>Auchenipterius dentatus</i> | ROM 85886 | 6312 | MF595226 | – | MF595376 | MF595455 | MF595129 |
| <i>Auchenipterius nigripinnis</i> | MCP 28904 | – | – | MF595296 | – | MF595456 | MF595130 |
| <i>Auchenipterius osteomystax</i> | MCP 45011 | – | MF595205 | – | MF595377 | MF595457 | MF595131 |
| <i>Centromochlus heckelii</i> | UFRO-I 9594 | 4106 | – | MF595299 | MF595381 | MF595461 | MF595136 |
| <i>Centromochlus macracanthus</i> | ROM 94568 | 9743 | MF595229 | – | MF595382 | MF595462 | MF595137 |
| <i>Centromochlus meridionalis</i> | MCP 32975 | – | MF595230 | MF595300 | MF595383 | MF595509 | – |
| <i>Centromochlus orca</i> | MCP 49879 | 219 | MF595280 | MF595344 | MF595421 | – | MF595185 |
| <i>Centromochlus perugiae</i> | MCP 45749 | – | MF595231 | MF595302 | MF595385 | – | MF595139 |
| <i>Centromochlus perugiae</i> B | MUSM 36874 | API29 | MF595207 | MF595301 | MF595384 | – | MF595138 |
| <i>Centromochlus reticulatus</i> | AUM 43534 | P4727 | MF595233 | MF595304 | MF595387 | MF595464 | MF595141 |
| <i>Centromochlus romani</i> | LBP 9945 | 46689 | MF595232 | MF595303 | MF595386 | MF595463 | MF595140 |
| <i>Centromochlus schultzi</i> | MCP 47746 | – | MF595234 | MF595305 | – | MF595465 | MF595142 |
| <i>Entomocorus benjamini</i> | MCP 35774 | – | – | – | MF595390 | – | MF595147 |
| <i>Entomocorus radius</i> | MCP 35903 | – | MF595238 | MF595308 | MF595391 | – | MF595148 |
| <i>Epapterus dispilurus</i> | UFRO-I 10937 | 4841 | MF595239 | MF595309 | MF595392 | MF595469 | MF595149 |
| <i>Gelanoglanis nanonotocolus</i> | ANSP 191344 | – | MF595241 | MF595311 | – | – | MF595152 |
| <i>Gelanoglanis</i> sp. 1 Peru | MUSM 46912 | – | MF595242 | MF595312 | MF595393 | MF595471 | MF595153 |
| <i>Gelanoglanis</i> sp. 2 Peru | ANSP 178425 | – | MF595243 | MF595313 | MF595394 | – | – |
| <i>Glanidium leopardium</i> | ANSP 189104 | 7034 | MF595246 | MF595316 | MF595397 | – | KC555871 ^{aa} |
| <i>Glanidium melanopterum</i> | LBP 6458 | 29124 | – | MF595317 | – | – | – |
| <i>Glanidium</i> RS 1 | MCP 28582 | – | – | MF595318 | – | – | MF595156 |
| <i>Glanidium</i> RS 2 | MCP 25462 | – | MF595247 | MF595319 | – | – | – |

Table 2. Continued

| Family taxon | Voucher catalogue number | Tissue identifier | col | myh6 | rag2 | SH3PX3 | 16S |
|---------------------------------------|--------------------------|-------------------|-------------------------------|----------|-------------------------------|----------|----------|
| <i>Liosomadoras oncinus</i> | MCP 46029 | – | MF595249 | MF595321 | MF595399 | MF595474 | MF595158 |
| <i>Pseudauchenipterus affinis</i> | MCP 48066 | – | – | MF595325 | – | MF595479 | – |
| <i>Pseudauchenipterus nodosus</i> | ROM 66351 | 5053 | MF595254 | MF595326 | MF595403 | MF595478 | MF595165 |
| <i>Pseudepapterus cucuhyensis</i> | MCP 51618 | 217 | MH285825 | – | – | – | – |
| <i>Pseudepapterus hasemani</i> | LBP 9401 | 42552 | MF595255 | MF595327 | MF595404 | – | MF595166 |
| <i>Spinipterus acsi</i> | ANSP 178311 | 1573 | – | – | – | – | – |
| <i>Spinipterus</i> sp. 'oncinha' | UFRGS 21671 | 6598 | – | – | – | MF595442 | MF595171 |
| <i>Tatia aulopygia</i> | INPA, uncataloged | – | MF595260 | MF595331 | MF595407 | MF595483 | MF595172 |
| <i>Tatia brunnea</i> | UFRO 3170 | 787 | MF595268 | MF595340 | MF595417 | – | MF595181 |
| <i>Tatia carolae</i> | ROM 94111 | 9235 | – | MF595341 | MF595418 | – | MF595182 |
| <i>Tatia carolae</i> | USNM 401511 | GY11-2-29 | MF595269 | MF595342 | MF595419 | – | MF595183 |
| <i>Tatia caxiuanensis</i> | LBP 9324 | 43842 | MF595270 | MF595343 | MF595420 | – | MF595184 |
| <i>Tatia intermedia</i> | ROM 86248 | 6450 | MF595272 | MF595346 | MF595423 | MF595491 | MF595187 |
| <i>Tatia neivai</i> | LBP 7356 | 34797 | MF595273 | MF595347 | MF595424 | – | MF595188 |
| <i>Tatia nigra</i> | MCP 46028 | – | MF595274 | MF595348 | MF595425 | MF595492 | MF595189 |
| <i>Tatia</i> sp. 2 | MCP 46589 | – | MF595271 | MF595345 | MF595422 | – | MF595186 |
| <i>Tetranematichthys wallacei</i> | LBP 4096 | 23543 | MF595275 | MF595349 | MF595426 | MF595493 | MF595190 |
| <i>Tocantinsia piresi</i> | ANSP 193048 | B2107 | MF595276 | MF595350 | MF595427 | MF595494 | MF595191 |
| <i>Trachelyichthys exilis</i> | ANSP 178212 | 1525 | MF595277 | MF595351 | MF595361 | MF595441 | MF595192 |
| <i>Trachelyopterichthys taeniatus</i> | ANSP 190499 | 101 | – | – | – | – | – |
| <i>Trachelyopterichthys taeniatus</i> | MCP 46032 | – | MF595278 | – | MF595428 | MF595495 | MF595194 |
| <i>Trachelyopterichthys taeniatus</i> | UFRO-I 8373 | 1992 | – | – | – | – | – |
| <i>Trachelyopterichthys taeniatus</i> | MCP 26674 | – | MF595262 | MF595332 | MF595409 | MF595485 | MF595174 |
| <i>Trachelyopterichthys taeniatus</i> | LBP 11054 | 50662 | – | MF595333 | MF595410 | MF595486 | MF595175 |
| <i>Trachelyopterichthys taeniatus</i> | MHNG 2595.066 | GF98028 | MF595264 | MF595335 | DQ492552 ^{ab} | MF595487 | MF595177 |
| <i>Trachelyopterichthys taeniatus</i> | MHNG 2608.013 | GF98029 | – | – | – | – | – |
| <i>Trachelyopterichthys taeniatus</i> | UFRO-I 2069 | 421 | MF595263 | MF595334 | MF595411 | – | MF595176 |
| <i>Trachelyopterichthys taeniatus</i> | MCP 53164 | C-153 | MF595265 | MF595336 | MF595413 | MF595488 | MF595178 |
| <i>Trachelyopterichthys taeniatus</i> | MCP 28976 | – | – | – | – | – | – |
| <i>Trachelyopterichthys taeniatus</i> | LBP 12 | 3544 | MF595266 | MF595337 | MF595414 | MF595489 | – |
| <i>Trachelyopterichthys taeniatus</i> | LBP 2373 | 16060 | GU702097 ^{ac} | – | – | – | – |
| <i>Trachelyopterichthys taeniatus</i> | MCP 46981 | – | – | MF595339 | MF595416 | – | MF595180 |
| <i>Trachelyopterichthys taeniatus</i> | MCP 46026 | – | – | – | MF595429 | MF595496 | MF595195 |
| <i>Trachycorystes trachycorystes</i> | UFRO-I 5170 | 4049 | – | MF595354 | MF595431 | MF595498 | MF595197 |
| <i>Tympanopleura atronassus</i> | UFRO-I uncataloged | 1002 | MF595210 | MF595355 | MF595432 | MF595499 | MF595198 |
| <i>Tympanopleura brevis</i> | UFRO-I uncataloged | 3978 | MF595209 | MF595356 | – | MF595500 | MF595199 |
| <i>Tympanopleura cryptica</i> | UFRO-I uncataloged | 10283 | MF595214 | MF595357 | MF595433 | MF595501 | MF595200 |
| <i>Tympanopleura longipinna</i> | ROM 86042 | 6989 | MF595216 | MF595358 | MF595434 | MF595502 | MF595201 |

Table 2. Continued

| Family taxon | Voucher catalogue number | Tissue identifier | col | myh6 | rag2 | SH3PX3 | 16S |
|-------------------------------------|--------------------------|-------------------|-------------------------------|-------------------------------|-------------------------------|----------|-------------------------------|
| <i>Tympanopleura rondoni</i> | MCP 46994 | C-128 | MF595218 | MF595359 | MF595435 | – | MF595202 |
| <i>Tympanopleura</i> sp.1 | LBP 10573 | 49290 | – | MF595285 | MF595367 | MF595446 | MF595118 |
| Ariidae | | | | | | | |
| <i>Cathorops spixii</i> | LBP 2918 | 18775 | MF595235 | MF595306 | MF595388 | MF595466 | MF595143 |
| <i>Genidens barbatus</i> | Uncataloged | – | MF595244 | MF595314 | FJ626006 ^{†d} | MF595472 | MF595154 |
| <i>Genidens genidens</i> | LBP 2338 | 11301 | JQ365364 ^{†e} | MF595315 | FJ013211 ^{†f} | MF595473 | MF595155 |
| Aspredinidae | | | | | | | |
| <i>Aspredo aspredo</i> | ANSP 191475 | JGL 205 | KC555595 ^{†a} | MF595292 | – | MF595452 | MF595125 |
| <i>Bunocephalus doriae</i> | MCP 25223/ UFRGS 16333 | –/TEC2771 | MF595228 | MF489484 ^{†g} | – | MF595460 | MF595135 |
| <i>Pseudobunocephalus iheringii</i> | MCP 21656 | WAS061 | MF595256 | MF595328 | – | – | MF595167 |
| <i>Pseudobunocephalus rugosus</i> | ANSP 185102 | A5067 | MF595257 | MF489520 ^{†g} | MF595405 | MF595480 | MF595168 |
| <i>Pterobunocephalus depressus</i> | LBP 14063 | 58424 | MF595258 | – | – | MF595481 | MF595169 |
| Cetopsidae | | | | | | | |
| <i>Helogenes marmoratus</i> | MCP 46997 | – | MF595248 | MF595320 | DQ492421 ^{†b} | MF595506 | MF595157 |
| Diplomystidae | | | | | | | |
| <i>Diplomystes camposensis</i> | LBP 3106 | 19770 | MF595236 | – | – | MF595467 | MF595145 |
| <i>Diplomystes mesembrinus</i> | LBP 449 | 5813/581 | MF595237 | – | MF595389 | MF595468 | MF595146 |
| Doradidae | | | | | | | |
| <i>Acanthodoras cataphractus</i> | ANSP 182251 | 6060 | MF595208 | MF595281 | MF595362 | – | MF595112 |
| <i>Anadoras grypus</i> | ANSP 179473 | – | MF595221 | MF595291 | MF595372 | MF595451 | MF595124 |
| <i>Franciscodoras marmoratus</i> | LBP 272 | 4193 | MF595240 | MF595310 | – | MF595470 | MF595151 |
| <i>Megalodoras uranoscopus</i> | ANSP 78249 | 1685 | MF595250 | MF595322 | – | MF595475 | MF595159 |
| <i>Nemadoras humeralis</i> | ANSP 182596 | 6301 | MF595251 | MF595323 | MF595400 | MF595476 | MF595162 |
| <i>Oxydoras niger</i> | ANSP 181080 | 6056 | KC555672 ^{†a} | MF595324 | MF595401 | MF595477 | MF595163 |
| <i>Rhynchodoras woodsi</i> | ANSP 181042 | 6061 | MF595259 | MF595330 | MF595406 | MF595482 | MF595170 |
| <i>Trachydoras nattereri</i> | ANSP 182593 | 6313 | MF595279 | MF595353 | MF595430 | MF595497 | MF595196 |
| <i>Wertheimeria maculata</i> | MCP 43855 | – | KC555709 ^{†a} | – | – | – | KC555963 ^{†a} |
| Mochokidae | | | | | | | |
| <i>Atopochilus savorgnani</i> | CUMV 95141 | – | – | – | MF595440 | MF595510 | – |
| <i>Euchilichthys dybowskii</i> | CUMV 91375 | – | MF595204 | – | MF595438 | MF595507 | MF595150 |
| <i>Chiloglanis disneyi</i> | CUMV 93183 | – | – | MF595307 | MF595439 | MF595508 | MF595144 |
| <i>Mochokiella paynei</i> | CUMV 91904 | – | – | – | MF595437 | MF595505 | MF595160 |
| <i>Mochokus niloticus</i> | CUMV 91385/94765 | – | – | – | MF595436 | MF595504 | MF595161 |
| <i>Synodontis petricola</i> | MCP 48136 | V | MF595261 | – | MF595408 | MF595484 | MF595173 |
| Pimelodidae | | | | | | | |
| <i>Pimelodus tetramerus</i> | MCP 33091 | 678 | – | – | – | MF595503 | MF595164 |
| <i>Pimelodus maculatus</i> | MCP 28421 | – | GU701571 ^{†h} | – | JF898777 ^{†i} | – | – |

All sequences were generated in the present study, except those accession numbers in bold type and followed by an asterisk.

^{†a}Arce et al. (2013); ^{†b}Sullivan et al. (2006); ^{†c}Pereira et al. (2011); ^{†d}Betancur-R (2009); ^{†e}Ribeiro et al. (2012); ^{†f}Betancur-R & Armbruster (2009); ^{†g}Carvalho et al. (2018); ^{†h}Pereira et al. (2013); ^{†i}Lundberg et al. (2011).

the authors and/or collaborators or obtained from fish collections. In addition, all tissue samples have voucher specimens, which were identified by the first author, except for the Aspredinidae (identified by Tiago P. Carvalho). Specimens for which only molecular or morphological data were available were also included in the combined dataset matrix.

Morphological data

The osteological nomenclature follows [Lundberg & Baskin \(1969\)](#), including modifications by [Bockmann \(1998\)](#), [Britto \(2002\)](#) and [Birindelli \(2014\)](#). The taxonomic nomenclature used in this study follows the most current classification, summarized by [Ferraris \(2007\)](#), with the necessary updates. To examine characters involving bones and cartilage, the specimens were cleared and double-stained according to a modified protocol of [Taylor & van Dyke \(1985\)](#). When specimens were fragile, bones were stained with Alizarin Red dissolved in 98% ethanol. Skeletons (sk) of larger specimens were also prepared using dermestid beetles. Specimens not available for osteological preparations were submitted to radiography and high-resolution X-ray computed tomography (CT scan) whenever possible. In the morphological Character descriptions section, characters appear numbered from one to 264 (although in the combined data matrix they span from 3490 to 3753) to facilitate presentation and discussion. The numbers of the combined data matrix are also shown in square brackets in the character descriptions. All morphological material examined is listed in the [Supporting Information \(Appendix S1\)](#).

MARKER SELECTION

The molecular markers included in this study were chosen based on previous phylogenies of fishes, including [Sullivan *et al.* \(2000, 2006, 2008\)](#), [Lovejoy & Collette \(2001\)](#), [Hardman \(2002, 2004\)](#), [Lavoué & Sullivan \(2004\)](#), [López *et al.* \(2004\)](#), [Li *et al.* \(2007\)](#), [Cramer *et al.* \(2011\)](#) and [Arce *et al.* \(2013\)](#). Polymerase chain reaction (PCR) was used to obtain five fragments: two mitochondrial markers, the large subunit ribosomal RNA gene (16S) and cytochrome oxidase I (*coI*); and three nuclear markers, nuclear recombinae activating gene-2 (*rag2*), SH3 and PX3 domain containing three genes (*SH3PX3*) and myosin, heavy chain 6, cardiac muscle, alpha (*myh6*). A summary of the primers used and the corresponding authors is presented in [Table 3](#). A specific primer pair for the fragment of *rag2* gene was designed for auchenipterids in this study (*rag2-AucheF*, *rag2-AucheR*; by B.B.C.). Almost all molecular data used in this study are newly sequenced, with the exceptions shown in [Table 2](#).

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

Genomic DNA was extracted from muscle tissue and, less often, from fin rays. Tissues were preserved in 98–99.8% ethanol and stored in a freezer at -20°C . Total genomic DNA was isolated using the DNeasy Blood & Tissues Kit (Qiagen) or PureLink Genomic DNA Mini Kit (Invitrogen).

All PCRs were performed in 25 μL reactions using 1.25 μL of 10 μM of each primer, 12.5 μL of water, 8 μL of Master Mix Kit (Qiagen) or HotStarTaq Master Mix Kit (Qiagen; 3 μM MgCl_2 buffer and 400 μM of each dNTP) and 2 μL (10–50 ng) of DNA extract for mitochondrial genes; or 6 μL of water, 12.5 μL of Master Mix and 4 μL (10–50 ng) of DNA extract for nuclear genes. The first reaction of nested PCRs, used for *SH3PX3* and *myh6*, was performed in 12.5 μL reactions using half quantities of all reagents.

The first-choice primers used to amplify the ~614 bp fragment of *coI* were LCO1490 (forward) and HCO2198 (reverse; [Folmer *et al.*, 1994](#)) using the following PCR protocol: an initial denaturation step of 3 min at 95°C ; followed by a first cycle for ten times of denaturation at 95°C for 60 s, annealing at touchdown temperatures of 50, 48, 46, 44 and 42°C , for 5 s each, except at 50°C and 42°C for 20 s, and extension at 72°C for 180 s; and 25 repetitions of a second cycle of annealing at 42°C for 30 s and extension at 72°C for 180 s; followed by a final extension of 5 min at 72°C ; and storage at 4°C . Whenever amplifications failed, a second touchdown temperature protocol was used, as follows: initial denaturation at 95°C for 60 s; 40 repetitions of the cycle of 94°C for 30 s, 50°C for 20 s, 48°C for 5 s, 46°C for 5 s, 44°C for 5 s, 42°C for 5 s, 40°C for 20 s and 72°C for 180 s; and final extension at 72°C for 5 min. Additionally, the alternative primer cocktail used to amplify the 657 bp fragment of *coI* was COI-3, composed of FishF2_t1 and VF2_t1 (forward) and FishR2_t1 and FR1d_t1 (reverse; [Ivanova *et al.*, 2007](#)) using the following PCR conditions: 95°C for 3 min; 35 cycles of 94°C for 30 s, 52°C for 40 s, 72°C for 1 min; and a final extension at 72°C for 5 min.

The thermocycler conditions for 16S were an initial denaturation step of 3 min at 94°C ; 35 cycles of denaturation at 94°C for 60 s, annealing temperature at 48°C for 60 s and extension at 72°C for 180 s; followed by a final extension of 5 min at 72°C , and storage at 4°C . For those samples that were difficult to amplify, an annealing temperature of 40°C was used with the same protocol.

The thermocycler conditions for *rag2* primarily followed [Lovejoy \(2010\)](#): an initial denaturation for 1 min at 95°C ; two cycles of denaturation at 95°C for 30 s, touchdown annealing temperatures of 58°C for 20 s, 56°C for 5 s, 54°C for 5 s, 52°C for 20 s and extension at 72°C for 3 min; and 32 repetitions

Table 3. Loci examined with corresponding primer names and sequence, polymerase chain reaction (PCR) steps and author designer

| Marker/cocktail | Primer | Primer sequence 5'-3' | PCR steps | Reference |
|-----------------------|-----------|--|-----------|------------------------------|
| 16S | AR | CGCCTGTTTATCAAAAAACAT | 1st | Palumbi <i>et al.</i> (1991) |
| 16S | BR | CCGGTCTGAACTCAGATCACGT | 1st | Palumbi <i>et al.</i> (1991) |
| <i>col</i> | LCO1490 | GGTCAACAATCATAAAGATATTGG | 1st | Folmer <i>et al.</i> (1994) |
| <i>col</i> | HCO2198 | TAAACTTCAGGGTGACCAAAAAATCA | 1st | Folmer <i>et al.</i> (1994) |
| <i>col</i> /FishF1_t1 | VF2_t1_1 | TGTAAAACGACGGCCAGTCAACCAACCAAAAGACATTGGCAC | 1st | Ivanova <i>et al.</i> (2007) |
| <i>col</i> /FishF1_t1 | FishF2_t1 | TGTAAAACGACGGCCAGTCAACCAACCAAAAGATATCGGCAC | 1st | Ivanova <i>et al.</i> (2007) |
| <i>col</i> /FishR1_t1 | FishR2_t1 | CAGGAAACAGCTATGACACTTCAGGGTGACCGAAGAATCAGAA | 1st | Ivanova <i>et al.</i> (2007) |
| <i>col</i> /FishR1_t1 | FR1d_t1 | CAGGAAACAGCTATGACACCTCAGGGTGTCCGAAARAAYCARAA | 1st | Ivanova <i>et al.</i> (2007) |
| <i>rag2</i> | MGF1 | TGyTATCTCCCACTCTGCGyTACC | 1st | Hardman (2004) |
| <i>rag2</i> | MHR1 | TCATCCTCCTCATCKTCTCwTTGTA | 1st | Hardman (2004) |
| <i>rag2</i> | AucheF | GCCAGGAGAAAAGAKyTGG | 1st | This study |
| <i>rag2</i> | AucheR | ATTCTTGGCTGCAATGyCT | 1st | This study |
| <i>Myh6</i> | F459 | CATMTTyTCCATCTCAGATAATGC | 1st | Li <i>et al.</i> (2007) |
| <i>Myh6</i> | R1325 | ATTCTCACCCATCCAGTTGAA | 1st | Li <i>et al.</i> (2007) |
| <i>Myh6</i> | F507 | GGAGAATCARTckGTGCTCATCA | 2nd | Li <i>et al.</i> (2007) |
| <i>Myh6</i> | R1322 | CTCACCACTCCAGTTGAACAT | 2nd | Li <i>et al.</i> (2007) |
| <i>SH3PX3</i> | F461 | GTATGTSGGCAGGAACYTGAA | 1st | Li <i>et al.</i> (2007) |
| <i>SH3PX3</i> | R1303 | CAAAACAKCTCYCCGATGTTCTC | 1st | Li <i>et al.</i> (2007) |
| <i>SH3PX3</i> | F532 | GACGTTCCCATGATGGCWAAAAT | 2nd | Li <i>et al.</i> (2007) |
| <i>SH3PX3</i> | R1299 | CATCTCYCCGATGTTCTCGTA | 2nd | Li <i>et al.</i> (2007) |

of a second cycle with an annealing temperature at 50 °C for 20 s; followed by a final extension of 3 min at 72 °C; and storage at 4 °C. For those samples that were difficult to amplify, a specific primer was designed for the family (*rag2*-Auche), used with the following thermocycler conditions: initial denaturation step of 15 min at 95 °C; 40 cycles of denaturation at 95 °C for 30 s, annealing temperature at 54 °C for 30 s and extension at 72 °C for 90 s; followed by a final extension of 10 min at 72 °C, and storage at 4 °C. As an alternative, the same PCR protocol as that for the first *rag2* primers was used.

Amplification of *myh6* was performed in a two-stage, nested PCR using 1 µL of the first PCR product, following Li *et al.* (2007). The thermocycler conditions for the first PCR were an initial denaturation step of 15 min at 95 °C; 30 cycles of denaturation at 95 °C for 60 s, annealing temperature at 53 °C for 60 s and extension at 72 °C for 180 s; followed by a final extension of 10 min at 72 °C, and storage at 4 °C; for the second PCR, the same protocol was used but with an annealing temperature of 62 °C for 60 s.

Amplification of *SH3PX3* was also performed in a two-stage, nested PCR using 1 µL of the first PCR product, following Li *et al.* (2007). The thermocycler conditions for the first PCR were an initial denaturation of 15 min at 95 °C; 40 cycles of denaturation at 94 °C for 30 s, annealing temperature at 55 °C for 45 s and extension at 72 °C for 90 s; followed by a final extension of 10 min at 72 °C, and storage at 4 °C; for the second PCR, the same protocol was used but with an annealing temperature of 60 °C for 45 s, or for few samples at 62 °C for 45 s.

When the PCRs used the HotStarTaq Master Mix Kit (Qiagen), two steps of the protocols were modified following the Qiagen recommended protocol: the denaturation step was settled to 15 min, and the final extension was 10 min. After the PCR, the amplicons were stained with a mix of Blue Juice (diluted at 1:2 in milique-H₂O) plus gel red (1 µL diluted to 1 mL of the prepared Blue Juice mix), and then tested separated by horizontal gel electrophoresis on a 4% agarose gel.

Results of the amplicons were visualized and registered by photography with an ultraviolet camera. The PCR amplicons were purified and sequenced in both directions using three distinct sequencing services: Macrogen Inc., High Throughput Genomics Center (HTSeq) and Functional Biosciences, Inc.

MATRICES AND SEQUENCE ALIGNMENTS

The search for morphological characters was carried out based on previous phylogenies of Siluriformes, mainly those on Auchenipteridae (Brittski, 1972; Royero, 1987, 1999; Ferraris, 1988; Curran, 1989; Walsh, 1990; de Pinna, 1996, 1998; Soares-Porto, 1998;

Britto, 2002; Akama, 2004; Diogo, 2004; Vigliotta, 2008; Ribeiro, 2011; Marceniuk *et al.*, 2012; Birindelli, 2014). All characters were re-evaluated, and some were redefined based on the inclusion of greater morphological diversity among the ingroup members. The description and delineation of characters follow Sereno (2007), with modifications. Altogether, 264 morphological characters were coded and are presented in the Supporting Information (Appendix S2). A list of synapomorphy for each clade is presented in the Supporting Information (Appendix S3).

The morphological data matrix was organized and coded using Microsoft Excel and subsequently transposed to Mesquite v.3.31 (Maddison & Maddison, 2017). In the parsimony analyses, the inapplicable characters were coded as ‘-’, those where observation was not possible were considered missing and coded as ‘?’, and all possible states for polymorphic characters were noted with the symbol ‘&’. In the Bayesian analysis, inapplicable, missing and polymorphic data were coded as ‘?’ and not as a fifth state.

The chromatograms of molecular data were visualized and edited using Geneious R9 v.9.1.2 (<http://www.geneious.com>; Kearse *et al.*, 2012). The sequences were aligned in this same software using automatic assembly in the implemented MUSCLE with the default parameters, and each contig pair was visually checked and edited before consensus sequences were extracted. The alignment of 16S was completed using Simultaneous Alignment and Tree Estimation (SATÉ-Gui, Yu *et al.* v.2.2.7, 2013; Liu *et al.*, 2009); the loop region was alignable and, for this reason, was maintained in the sequences. The codon positions of the protein-coding genes were tested based on amino acid translation, and aligned sequences included in the analyses were open reading frames, starting in the first position. For species represented by more than one individual, if no differences were found between sequences, only one was kept in the analysis. Sequences disagreeing or highly incongruent with co-species were excluded from the dataset, and new sequences were generated in replacement.

For the combined dataset, morphological and molecular characters were concatenated into a single matrix (a total of 3754 characters), but the phylogenetic signal of each different partition and the integrity of sequences were tested separately according to the same nucleotide substitution models as the combined dataset.

PHYLOGENETIC ANALYSIS

Parsimony analysis

Hypotheses regarding relationships and monophyly were proposed according to the cladistic paradigm first proposed by Hennig (1950, 1966) and subsequently

developed, with relationship hypotheses being based exclusively on the possession of derived characters shared by the members of each hierarchical group. Maximum Parsimony (MP) was used as the optimality criterion because it provides synapomorphies to justify the diagnosis of each taxon. The MP analysis was implemented using TNT v1.5 (Goloboff *et al.*, 2003, 2008). In the parsimony analysis, the gaps were considered missing data. The indel/substitution cost ratio was set at 1:1 to establish the transformation cost matrix used to calculate the length of the tree (Arroyave & Stiassny, 2011). Heuristic searches were applied to find the optimal trees using the *Traditional Search* and *New Technologies Searches* methodologies. The analyses initially performed with *Traditional Search* were used to save trees in memory to advance in the search using *New Technologies*, including algorithms such as *sectorial searches* (default), *ratchet* (400 iterations), *tree-fusion* (six rounds) and *tree-drift* (30 rounds). Subsequently, the analyses were performed using the best previous trees saved in memory, increasing the number of iterations of *ratchet* to 600, 800, 1000, 1500, and above to stabilize the number of optimal trees. After all replicates (10 000 *ratchet*), a second round of searches, using the best trees saved in memory, was performed. The different topologies found in the most parsimonious fundamental cladograms were summarized in a strict consensus tree. Support values for the consensus tree were calculated using the Goodman–Bremer index (Bremer, 1988), which considers the numbers of extra steps necessary to collapse a branch. The reversals and convergences were considered as equally possible in the heuristic algorithm searches used (Swofford

& Maddison, 1987). The multistate characters were codified as unweighted and unordered, owing to the lack of information about the sequence of morphological features among the character states explicitly part of an ontogenetic series. A member of Diplomystidae was used as the rooting point, chosen based on previous phylogenies indicating this family to be the sister group to Siluroids (Arcila *et al.*, 2017; Betancur-R *et al.*, 2017).

Bayesian Inference analysis

The combined dataset was also subjected to phylogenetic analysis using Bayesian Inference (BI) (Guindon & Gascuel, 2003; Ronquist & Huelsenbeck, 2003). Analyses based on Bayesian methods were conducted using the software MrBayes v.3.2.6 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003; Altekar *et al.*, 2004). The morphological characters and the five molecular markers were treated as separate dataset partitions. The likelihood model Markov k (Mk), implemented in MrBayes v.3.1 (Lewis, 2001; Nylander *et al.*, 2004), was used for discrete morphological data, assuming equal rates of character change. Nucleotide substitution models were investigated and selected for each gene partition corresponding to a three-codon position using the Bayesian information criterion (BIC) implemented in PartitionFinder (v2.1.1.Gui; Lanfear *et al.*, 2012). The BIC parameters were assigned to all codon positions but not for 16S fragment (shown in Table 4) and morphology. Bayesian analyses were performed in MrBayes v.3.2.6 using the CIPRES supercomputing cluster (Miller *et al.*, 2010), and four chains were run. These chains were each programmed

Table 4. Summary statistics for each gene partition and best-fitting model

| Locus | Codon | Character number range in matrix | Length (bp) | Number of variable sites | Percentage of variable sites | Number of parsimony-informative sites | Best-fitting model (Bayesian information criterion) |
|---------------|-------|----------------------------------|-------------|--------------------------|------------------------------|---------------------------------------|---|
| <i>coI</i> | 1 | 1–657 | 219 | 60 | 27.4 | 44 | GTR+I+G |
| <i>coI</i> | 2 | | 219 | 6 | 2.7 | 3 | HKY+I+G |
| <i>coI</i> | 3 | | 219 | 218 | 99.5 | 214 | TRN+G |
| <i>myh6</i> | 1 | 658–1417 | 254 | 33 | 12.9 | 22 | GTR+I+G |
| <i>myh6</i> | 2 | | 254 | 13 | 5.1 | 9 | F81+I |
| <i>myh6</i> | 3 | | 254 | 188 | 74.0 | 134 | HKY+G |
| <i>rag2</i> | 1 | 1418–2221 | 268 | 109 | 40.6 | 67 | K80+G |
| <i>rag2</i> | 2 | | 268 | 67 | 25.0 | 32 | TIMEF+I+G |
| <i>rag2</i> | 3 | | 268 | 219 | 81.7 | 159 | HKY+G |
| <i>SH3PX3</i> | 1 | 2222–2900 | 227 | 48 | 21.1 | 33 | K81+I+G |
| <i>SH3PX3</i> | 2 | | 227 | 26 | 11.4 | 14 | TVM+I+G |
| <i>SH3PX3</i> | 3 | | 227 | 189 | 83.2 | 170 | TIM+G |
| 16S | – | 2901–3490 | 590 | 223 | 37.8 | 181 | GTR+I+G |
| Total | | 3490 | 3490 | 1399 | 40.1 | 1082 | |

to run for 100 000 000 generations, with sampling occurring every 1000 generations. To ensure sampling from a stationary posterior distribution, all analyses were examined for convergence by visualizing the plot of generation vs. the log-probability and by examining the values of estimated sample size (ESS) and potential scale reduction factor (PSRF) using Tracer v.1.6 (Rambaut *et al.*, 2014). Trees generated during the first 25% of the generations were discarded as burn-in.

RESULTS

CHARACTER DESCRIPTIONS

External morphology

- [3490] Orbit, margin: (0) free; (1) continuous (Vigliotta, 2008: char. 91).

In the plesiomorphic condition found in Diplomystidae, Ariidae, Pimelodidae (Arratia, 1987; Vigliotta, 2008) and the mochokids *Atopochilus* and *Euchilichthys*, the margin of the eye is surrounded by a groove that separates the eye from the skin, which is referred to as a free orbital margin. Among the taxa examined, Auchenipteridae, Aspredinidae, Doradidae, *Helogenes marmoratus* Günther, 1863 and Mochokidae have eyes covered by a continuous membrane that is conjoined to the skin, leaving no free zone between the eye and the skin.

- [3491] Eye, size: (0) relatively small, occupying up to half of head depth; (1) very large, occupying almost entire head depth.

Among Auchenipteridae, the eye can be relatively small, usually smaller than half head depth and restricted to the dorsal half of the head. In this condition, the eye does not reach the horizontal line through the pectoral-fin origin, except in *Ageneiosus* and *Tetranematichthys*, in which the eye is positioned more laterally, but still occupying up to half the head depth, and proportionally small relative to the head configuration. Furthermore, in the plesiomorphic condition the eye generally is not visible in ventral view, and when visible, such as in some species of *Tatia*, it is only slightly visible, much < 50% of the orbit. In *Auchenipterus*, *Centromochlus heckelii*, *Centromochlus existimatus*, *Centromochlus macracanthus*, *Centromochlus schultzi*, *Tatia carolae*, *Entomocorus*, *Epapterus*, *Pseudepapterus cucuhyensis* and *Tympanopleura*, the eye is large or extremely large in the case of some *Centromochlus* and *Tympanopleura*, lateroventrally oriented and

occupying almost the entire head depth, reaching to or surpassing the horizontal line through the pectoral-fin origin in lateral view (never reaching that point in *Tatia*).

- [3492] Mouth, mandibular arch, ventral surface, direction: (0) lateral margins of mandibulae diverging laterally; (1) lateral margins of mandibulae running approximately in parallel.

Most Auchenipteridae have large mouths; usually, the mandible is as wide as the premaxillary arch and participates in the anterolateral border of the head. In this condition, the posteroventral portion of the mandible forms a curve of semicircular shape, with the lateral margins broadening laterally, diverging from each other. In *Centromochlus existimatus*, *Centromochlus heckelii*, *Centromochlus schultzi*, *Tatia carolae* and *Centromochlus macracanthus*, the mandibular arch is narrower and digit-like, with the lateral margins of mandibulae parallel each other and always smaller than the premaxillary arch.

- [3493] Adipose fin: (0) present; (1) absent (Ferraris, 1988: char. O2; Akama, 2004: char. 186; Ribeiro, 2011: char. 234; Birindelli, 2014: char. 4).

The possession of an adipose fin is plesiomorphic within Ostariophysi (Fink & Fink, 1981). Among the taxa examined, the adipose fin is absent in the auchenipterids *Epapterus*, *Trachelyichthys*, *Trachelyopterichthys*, *Trachelyopterus coriaceus* and all members of the Aspredinidae.

- [3494] Adipose fin, pre-adipose ridge: (0) absent; (1) present (Birindelli, 2014: char. 5, modified).

Most auchenipterids have a short adipose fin lacking any ridge anteriorly, but the adipose fin of *Gelanoglanis nanonocticolus* and *Gelanoglanis varii* and the doradids *Rhinodoras* and *Megalodoras* is preceded by a thin, long skin ridge. Taxa without an adipose fin were coded as inapplicable for this character.

- [3495] Branchiostegal membranes, contact: (0) united to isthmus and close together; (1) separate from each other and free from isthmus; (2) united to isthmus and far apart; (3) united to each other and free from isthmus (Birindelli, 2014: char. 6).

In Diplomystidae, the branchiostegal membranes are united to the isthmus, but close together (state 0). Pimelodidae is the only catfish family examined where the branchiostegal membranes are separate from each other and free from the isthmus (state 1). The branchiostegal membranes of Auchenipteridae, Aspredinidae, Mochokidae

and Doradidae are united to the isthmus and far apart, positioned next to or at the lateral margin of head (state 2). In Ariidae and *Helogenes marmoratus*, the branchiostegal membranes are united to each other and free from the isthmus (state 3).

7. [3496] Head, surface, dermal tubercles in nuptial males: (0) absent; (1) present (Akama, 2004: char. 178; Birindelli, 2014: char. 26).

Nuptial males of catfishes usually do not possess any dermal tubercles, but *Auchenipterus*, *Entomocorus*, *Epapterus* and *Pseudepapterus* do develop soft tubercles on the dorsal surface of the head. Despite the presence of such breeding ornamentation, the shape of the tubercles could be informative and should be investigated further.

8. [3497] Tympanic area, long epidermal papillae: (0) absent; (1) present (Royero, 1999: char. 148; Akama, 2004: char. 183; Birindelli, 2014: char. 29).

Among taxa examined, epidermal papillae were absent on the tympanic area. Only species of *Pseudauchenipterus* and *Ageneiosus pardalis* have epidermal papillae along the tympanic area. In case of the former species, the epidermal papillae are probably related to the tolerance of the species to a higher salinity level (Akama, 2004).

9. [3498] Axillary slit: (0) present; (1) absent.

The axillary slit is present in most catfishes examined, except for Aspredinidae other than *Aspredo aspredo* (Linnaeus, 1758), the mochokid *Atopocheilus* and auchenipterids *Centromochlus meridionalis*, *Liosomadoras oncinus*, *Trachelyopterus teaguei*, *Trachelyopterus lucenai* and *Trachycorystes menezesi*. Most members of the Auchenipteridae have a tiny axillary slit that is very difficult to observe even under a stereomicroscope. The axillary slit is usually rounded and located between the last inner pectoral fin ray and the posterior process of the cleithrum. *Liosomadoras oncinus* has an axillary slit as a juvenile but lacks it as an adult.

Barbels

10. [3499] Maxillary barbel, length: (0) long, extending beyond anterior margin of orbit; (1) short, not surpassing anterior margin of orbit (Ferraris, 1988: char. J14; Royero, 1999: char. 117; Akama, 2004: char. 62; Birindelli, 2014: char. 10; modified).

The maxillary barbel in most Siluriformes is long, surpassing the anterior margin of the orbital. In *Ageneiosus*, *Tympanopleura* and *Tetranematichthys*, the maxillary barbel is extremely reduced and thin, and it is harboured and covered in a sulcus slightly below the posterior portion of the upper lip.

11. [3500] Maxillary barbel, fimbriae: (0) absent; (1) present.

Among all members of Siluriformes examined, only *Nemadoras humeralis* (Kner, 1855) and *Trachydoras nattereri* (Steindachner, 1881) share the presence of fimbriae on the ventral surface of the maxillary barbel.

12. [3501] Head, suborbital groove: (0) absent; (1) present (Ferraris, 1998: char. J16; Curran, 1989: char. 2; Royero, 1999: char. 116; Akama, 2004: char. 61; Birindelli, 2014: char. 14).

The suborbital groove for the maxillary barbel is usually absent. Auchenipterids have a deep suborbital groove, which lodges the maxillary bone and part of the maxillary barbel. Despite the presence of a groove to accommodate the maxillary barbel in *Ageneiosus* and *Tympanopleura*, the sulcus is located in the posterolateral region of lips, anterior to the orbit.

13. [3502] Maxillary barbel, soft papillae: (0) absent; (1) present.

In Siluriformes, the maxillary barbel is usually smooth, except in *Gelanoglanis*, which has conspicuous soft, rounded papillae along the entire length of the dorsal surface of the maxillary barbel (see Calegari *et al.*, 2014: fig. 5), in both juvenile and adult specimens. This character is not considered an ornamentation of mature males or coding in ossified barbel such as that found in *Tetranematichthys*, some *Auchenipterus* and *Entomocorus*. Although this structure was not observed in other members of Auchenipteridae, Ferraris & Vari (1999) identified and reported fleshy elaborations of the barbel in two specimens of *Pseudepapterus*. For this reason, the genus is considered to be polymorphic for this character.

14. [3503] Mental barbel: (0) absent; (1) present.

The mental barbel is absent in Diplomystidae and in the auchenipterids *Ageneiosus* and *Tympanopleura*. The mochokids *Atopochilus*, *Chiloglanis* and *Euchilichthys* also were considered to lack a distinct mental barbel, because they have the mental barbel incorporated into the

oral disc (see [Vigliotta, 2008](#): fig. 27C). Most other Siluriformes possess a mental barbel.

15. [3504] Mental barbel, number: (0) one pair; (1) two pairs ([Birindelli, 2014](#): char. 16; modified).

The auchenipterids *Gelanoglanis* and *Tetranematichthys* have one pair of inner mental barbels. In all other Siluriformes examined, there are two pairs of mental barbels. Species lacking mental barbels were coded as inapplicable for this character.

16. [3505] Mental barbel, fimbriae: (0) absent; (1) present ([Birindelli, 2014](#): char. 17).

Among most taxa examined, the mental barbel lacks any fimbriae, although the mochokids with lips not developed as an oral disc and the doradids *Nemadoras humeralis* and *Trachycodoras nattereri* have fimbriae in the mental barbels. [Birindelli \(2014\)](#) did not consider the fimbriae to be present in these taxa, but considered them to have delicate papillae and, thus, to have smooth mental barbels. However, *Nemadoras humeralis* and *Trachycodoras nattereri* have a barbel structure similar to that of the remaining members but with shorter fimbriae. For this reason, these taxa were coded with the derived condition. Species lacking mental barbels were coded as inapplicable for this character.

17. [3506] Mental barbel, fimbriae, arrangement: (0) one row; (1) two rows ([Birindelli, 2014](#): char. 18).

Among taxa with fimbriae on the mental barbels, *Nemadoras humeralis*, *Mochokus niloticus* Joannis, 1835 and *Mochokiella paynei* Howes, 1980 have the fimbriae distributed in one row, and *Synodontis* and *Trachycodoras nattereri* in two rows. All remaining catfishes examined with no fimbriae on the mental barbels or even the lack of these barbels were coded as inapplicable for this character.

18. [3507] Mental barbel, ornamentation: (0) absent; (1) present.

Siluriformes have smooth mental barbels, but a fleshy, digitiform and tridimensional elaborate process on the distal portion of the mental barbel is present in *Tetranematichthys wallacei*. Although *Tetranematichthys quadrifilis* was not examined in the present study, [Vari & Ferraris \(2006\)](#) reported that such an elaborate structure is also present in this species and suggested that it represents a possible synapomorphy for the genus. Taxa without mental barbels were coded as inapplicable for this character.

19. [3508] Mental barbel, relative length: (0) outer barbel longer than inner; (1) outer and inner barbels of approximately the same length ([Birindelli, 2014](#): char. 19).

In most Siluriformes, the outer pair of mental barbels is longer than the inner pair when extended ([Fig. 1C, D](#)). However, in *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, *Pseudauchenipterus* (except *Pseudauchenipterus jequitinhonhae*), *Centromochlus heckelii*, *Centromochlus existimatus*, *Centromochlus perugiae*, *Centromochlus romani*, the doradids *Nemadoras humeralis* and *Trachycodoras nattereri* and *Helogenes* the two pairs of mental barbels are of approximately the same length ([Fig. 1A, B](#)). Taxa without mental barbels were coded as inapplicable for this character.

20. [3509] Mental barbel, outer pair, length: (0) short, not reaching posterior margin of coracoid process; (1) long, surpassing posterior margin of coracoid process ([Curran, 1989](#): char. 6; [Akama, 2004](#): char. 64; [Birindelli, 2014](#): char. 20).

In most Siluriformes, the outer mental barbel is relatively short, never reaching the posterior margin of the coracoid process. In *Auchenipterus*, *Epapterus*, *Pseudepapterus*, *Pseudauchenipterus nodosus*, *Trachelyichthys*, *Trachelyopterus coriaceus*, *Trachelyopterus striatulus*, *Trachelyopterus porosus*, *Mochokus*, *Mochokiella*, *Helogenes* and Pimelodidae, the mental barbel is elongated and surpasses that process. [Birindelli \(2014\)](#) coded Ariidae as having a long mental barbel, although the two species of *Genidens* and *Cathoropsis spixii* examined herein have short mental barbels. Ariidae might be polymorphic for this character. Taxa without mental barbels were coded as inapplicable for this character.

21. [3510] Base of mental barbels, relative position: (0) base of inner mental barbels anterior to base of outer mental barbels; (1) base of both inner and outer barbels adjacent ([Ferraris, 1988](#): char. J18; [Curran, 1989](#): char. 13; [Walsh, 1990](#): char. 12; [Royero, 1999](#): char. 119; [Akama, 2004](#): char. 65; [Birindelli, 2014](#): char. 21).

In most catfishes, the insertion of the outer mental barbel is posterior to that of the inner mental barbel ([Fig. 1](#)). In the derived condition, however, inner and outer mental barbels are inserted along the same transverse line, more near to the lips. The derived condition is present in the auchenipterids *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus* and in the Ariidae, some species of Mochokidae, Pimelodidae, *Helogenes* and

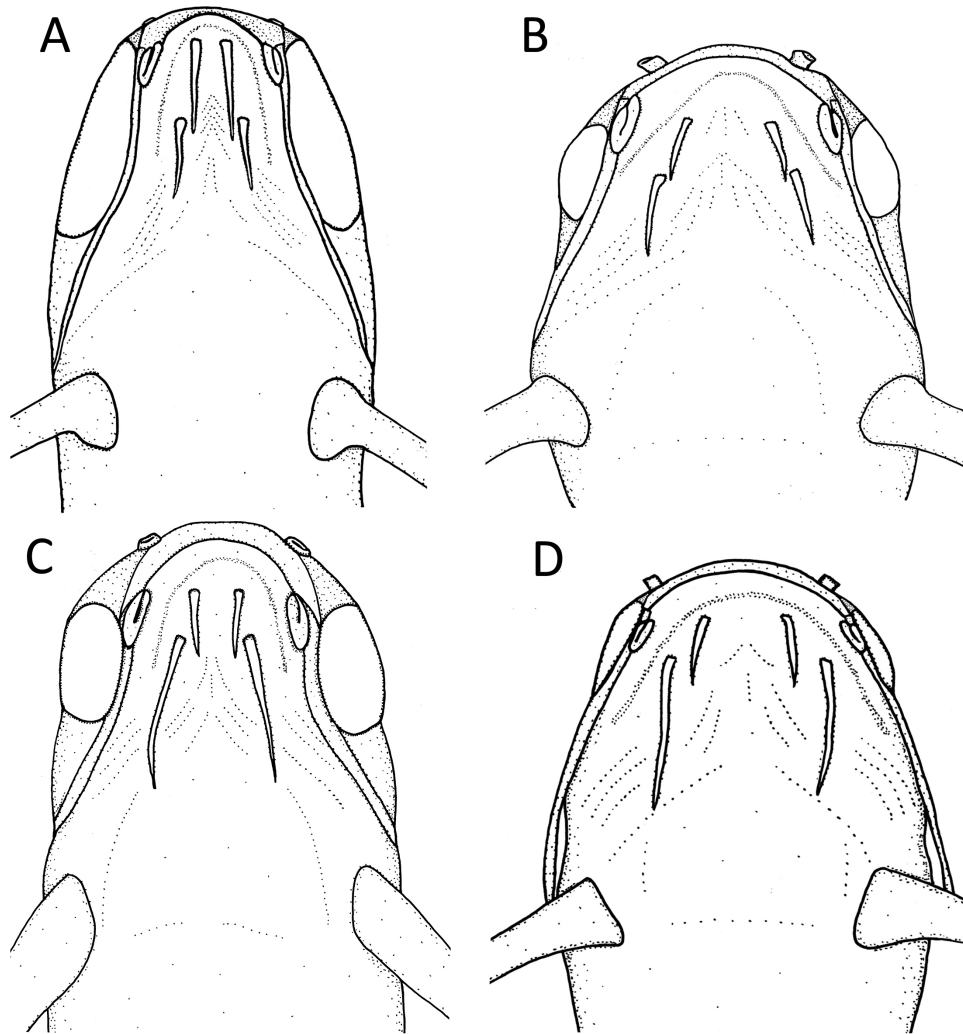


Figure 1. Ventral profile of head. A, *Centromochlus heckelii*, MCP 24171. B, *Doringlanis perugiae*, MCP 45749. C, *Balroglanis carolae*, ROM 62534. D, *Tatia strigata*, MCP 46595.

Doradidae examined here. Based on the figures of Birindelli (2014), which illustrate the states of the barbels, his interpretation of this character was distinct from the present observations. Taxa without mental barbels were coded as inapplicable for this character.

Lateral sensorial system

22. [3511] Nasal, ossification: (0) present; (1) absent.

The nasal bone is present in most Siluriformes (Arratia & Gayet, 1995). In *Pseudobunocephalus iheringi*, *Pseudobunocephalus rugosus* (Eigenmann & Kennedy, 1903), *Rhynchodoras woodsi* Glodek, 1976 and *Gelanoglanis*, the nasal bone is absent, but the supraorbital canal remains ossified, except in *Gelanoglanis*, in which it is unossified.

23. [3512] Nasal bone, shape: (0) tubular; (1) plate-like, laterally expanded (Soares-Porto, 1998: char. 5; Sousa, 2010: char. 20; Ribeiro, 2011: char. 50; Birindelli, 2014: char. 94).

In most auchenipterids, the nasal bone is tubular and anteroposteriorly oriented, whereas in some species of *Tatia*, *Trachelyopterus*, *Trachelyopterichthys*, *Trachycorystes* and *Spinipterus* sp. 'oncinha', the nasal bone is laterally expanded and shaped as a plate. *Tatia intermedia* has the tubular condition, although the nasal bone in adult specimens is not visible in dorsal view because the mesethmoid is strongly expanded laterally and covers the nasal.

24. [3513] Nasal, anterior portion, shape: (0) not bifurcated; (1) bifurcated (Ferraris, 1988:

char. N15; Walsh, 1990: char. 2; Royero, 1999: char. 107; Akama, 2004: char. 92; Ribeiro, 2011: char. 51).

Most Siluriformes have a tubular nasal bone (Arratia, 2003a) and carry an aperture for the lateral line ramus of the sensory canal system on the mid-portion of its lateral margin. However, *Ageneiosus*, *Tympanopleura*, *Tetranematichthys*, *Trachelyopterus insignis* and *Trachycorystes trachycorystes* have the derived state, in which this opening of the ramus of the lateral line is ossified and forms a long, anterolaterally oriented bifurcation. *Auchenipterus* also has a tubular nasal bone with the aperture of the lateral ramus slightly bifurcated, where the aperture forms an independent short, laterally oriented ramification that is less pronounced than in *Ageneiosus*, *Tympanopleura* and *Tetranematichthys*. In the last genus, the two ramifications are always separate from one another.

25. [3514] Antorbital, participation in orbital margin: (0) does not participate; (1) participates (Birindelli, 2014: char. 97).

The antorbital is usually termed the first infraorbital, lacrimal or lacrimal-antorbital (e.g. Bockmann, 1994: char. 769, fig. 4; Lundberg *et al.*, 1991: 843–845; Bockmann, 1998; Britto, 2002: char. 61). The antorbital is a complex structure that involves the first (or most anterior) ossified tubule of the infraorbital sensory canal series (i.e. the antorbital tubule) plus a strong laminar bony structure. Both structures have independent origins. Antorbital is used herein according to the homology proposed by Arratia & Huaquin (1995: 25, 26) based on evidence that the first ossified plate of the infraorbital series of Siluriformes is indeed the same as the antorbital of other Teleostei, i.e. the first infraorbital bone (= lacrimal) is absent in Siluriformes. Thus, antorbital is used herein only to indicate the ossification, without the antorbital tubule.

In the plesiomorphic condition present in some Siluriforms, the antorbital has a short ventral process or no process, and the bone is located anterior to and distant from the orbital margin. However, in most Auchenipteridae, the antorbital participates in the anterior margin of the orbit, and in most genera, the presence of a ventral projection surrounds the orbital margin, reaching approximately to the middle of its width.

26. [3515] Antorbital, dorsal projection: (0) present; (1) absent.

In Auchenipteridae, the dorsal portion of the antorbital bears a narrow, elongate projection that is dorsally extended or sometimes posterodorsally inclined. *Epapterus*, *Entomocorus*, *Pseudepapterus*, *Auchenipterus* and *Spinipterus* lack this process, and in those taxa, the dorsal margin of the bone is straight, not expanded.

27. [3516] Antorbital, ventral projection: (0) absent; (1) present (Ferraris, 1988: char. I2; Walsh, 1990: char. 13; Soares-Porto, 1998: char. 14; Akama, 2004: char. 29; Birindelli, 2014: char. 98; modified).

Gelanoglanis, *Asterophysus* and most siluriforms examined do not have the ventral process of the antorbital. However, members of the Auchenipteridae have a tubular projection on the antorbital that is sometimes elongated, ventrally straight and posteriorly curved and, in other cases, restricted to the ossified sensory canal. This projection is usually curved around the orbital margin. The extension of this projection occasionally reaches to the line through the middle of the orbital diameter along its ventral portion.

28. [3517] Antorbital and lateral ethmoid, articulation: (0) lateral ethmoid contacting only mesial portion of antorbital; (1) lateral ethmoid contacting posterior and mesial portions of antorbital; (2) lateral ethmoid contacting posterior portion of antorbital.

The position of the articulation between the antorbital and the lateral ethmoid is variable among the auchenipterids. In *Gelanoglanis*, *Pseudauchenipterus* and some *Ageneiosus*, the lateral ethmoid contacts the antorbital mesially. In most species examined, the lateral ethmoid contacts the posterior portion of the antorbital bone, which is anterolaterally positioned, whereas in remaining *Ageneiosus*, *Auchenipterus*, *Asterophysus*, *Epapterus*, *Pseudepapterus*, *Trachelyopterichthys*, *Trachelyichthys*, *Tympanopleura*, Mochokidae and *Wertheimeria*, the lateral ethmoid contacts the antorbital in its posterior and mesial portion.

29. [3518] Antorbital and lateral ethmoid, type of contact: (0) contact by ligament; (1) synchondral articulation; (2) sutural articulation to each other (Royero, 1999: char. 106; modified).

Within auchenipterids, in *Ageneiosus uranophthalmus*, *Gelanoglanis*, and some *Tympanopleura*, the antorbital and the lateral ethmoid are distant from each other, and the contact occurs through ligament. In *Pseudauchenipterus*, *Tetranematichthys* and most *Ageneiosus*, these bones contact each other through cartilage, whereas in most members

of Auchenipteridae, the antorbital and the lateral ethmoid contact each other directly through a suture. This condition is also present in *Centromochlus*, in which the articulation is between the anterolateral expansion of the lateral ethmoid and the mesial process of the antorbital, which is ventrally oriented.

30. [3519] Ossified suborbital tubules, numbers in adults: (0) six or more; (1) five; (2) four; (3) three; (4) two; (5) one; (6) none (Birindelli, 2014: char. 102; modified).

The infraorbital series is composed of bony plates that bear the ossified tubules of the infraorbital sensory canal (e.g. Arratia & Huaquin, 1995: char. 17, fig. 6; Fink & Fink, 1981: 315; Lundberg *et al.*, 1991: 850; Bockmann, 1998: 125–127). Thus, the ossified infraorbital canals are formed independently from the infraorbital bones during ontogeny. The infraorbital bones are integrally absent in Siluriformes and Gymnotiformes (except for Loricariidae and Callichthyidae, Britto, 2002: char. 63; and Sternopygidae, Lundberg & Mago-Lecia, 1986) when the homology is compared with the homonym elements in Ostariophysi (Bockmann, 1998). According to the terminology proposed by Bockmann (1998: 126), the ossified tubules of the infraorbital series comprise the antorbital tubule (= first ossified tubule) and the remaining subsequent suborbital tubules, which together compose the principal infraorbital canal. Accordingly, the homology of the present character is different from that considered by Birindelli (2014) owing to the exclusion in the present study of the antorbital tubule and of suborbital tubules that are genuinely unossified. The auchenipterids can have suborbital tubules that are not ossified (state 6), a condition found in *Gelanoglanis* and some small-sized *Tatia*, or that are distinctly ossified, as in the remaining members of the family. *Centromochlus perugiae* is polymorphic for this character, because the number of ossified suborbital tubules can be one or two; *Entomocorus gameroi* is also polymorphic, having more ossified suborbital tubules. Among catfishes, Diplomystidae have six ossified suborbital tubules, whereas Aspredinidae, some Mochokidae and Aspredinidae, most Doradidae and Pimelodidae have three.

31. [3520] Antorbital and ossified suborbital tubules, spines: (0) absent; (1) present (Royero, 1999: char. 102; Akama, 2004: char. 100; Sousa, 2010: char. 25; Birindelli, 2014: char. 106).

Most auchenipteridshavesmoothossifiedsuborbital tubules, without spines. In *Liosomadoras*, *Tatia caxiuanensis*, *Trachelyopterichthys*, *Trachycorystes*

trachycorystes and *Spinipterus*, the suborbital tubules, primarily the antorbital, bear short or enlarged spines.

32. [3521] Temporal canal, passageway: (0) passing from pterotic to posttemporal–supracleithrum; (1) passing from pterotic through epiotic to posttemporal–supracleithrum (Royero, 1999: char. 94; Akama, 2004: char. 104; Birindelli, 2014: char. 108).

In most auchenipterids, the temporal canal (otic canal plus postotic canal) generally passes via the pterotic, close to its margin, and runs directly to the posttemporal–supracleithrum. In some species, of *Auchenipterus*, *Entomocorus*, *Epapterus* and *Pseudepapterus*, but the temporal canal enters the pterotic, passing through the most elongated ventral portion of the epioccipital, and enters the posttemporal–supracleithrum.

33. [3522] Pterotic, temporal canal, position: (0) temporal canal positioned near lateral margin of the pterotic; (1) temporal canal positioned approximately in the middle of the pterotic.

In *Ageneiosus*, larger species of *Auchenipterus*, *Epapterus*, *Pseudepapterus*, *Tympanopleura* (except for *Tympanopleura brevis* and *Tympanopleura cryptica*) and *Trachelyopterus teaguei*, the temporal canal is positioned near the lateral margin of the pterotic. This condition is also found in Diplomystidae, Mochokidae and some Doradidae. However, in most auchenipterids, the temporal canal passes close to the middle of the pterotic.

34. [3523] Mandibular ramus: (0) present; (1) absent (Royero, 1999: char. 97; Akama, 2004: char. 102; Birindelli, 2014: char. 111).

Most examined taxa possess the mandibular ramus of the laterosensory canal system. In the derived condition, the preopercular canal terminates on the ventral portion of the preopercle near the end of the dentary and the anguloarticular, and the mandibular portion of the laterosensory canal system is absent. This condition is found in Aspredinidae (except in *Aspredo aspredo*), and according to de Pinna (1996) and Birindelli (2014) also in Chiloglanidinae mochokids, sisoroids and the erithistid *Conta*.

35. [3524] Mandibular ramus, passageway: (0) passing inside lower jaw; (1) passing outside lower jaw (Ferraris, 1988: char. I10; Birindelli, 2014: char. 112).

In most Siluriformes, the mandibular ramus of the laterosensory canal reaches the preopercle and passes inside the dentary. In *Gelanoglanis*, the

mandibular ramus is unossified and free from the dentary, passing outside and immediately below the dentary. In the aspredinid *Aspredo aspredo*, the mandibular ramus also passes outside the dentary, but in this case it is ossified in various tubules.

36. [3525] Lateral line, shape: (0) straight; (1) sinusoidal; (2) sinusoidal anteriorly and straight posteriorly (Ferraris, 1988: char. I12; Akama, 2004: char. 97; Birindelli, 2014: char. 115).

In most Auchenipteridae, the lateral line is straight or nearly straight, never forming conspicuous curves. In *Ageneiosus*, *Auchenipterichthys*, *Auchenipterus*, *Epapterus*, *Pseudauchenipterus*, *Pseudepapterus* and *Tympanopleura*, the lateral line is sinusoidal, forming long, divergent curves. Other auchenipterids, such as *Tocantinsia*, *Trachycorystes*, *Trachelyichthys* and *Trachelyopterichthys*, have a sinusoidal lateral line on the anterior half of the body and a straight line on the posterior half. Birindelli (2014) reported the following genera as having a sinusoidal lateral line: *Entomocorus*, *Liosomadoras*, *Tetranematichthys* and *Trachelyopterus*. However, the present results indicate that those taxa have lateral line tubules that are individually oriented and slightly perpendicular along the lateral line axis, sometimes bearing ventral ramifications that suggest a cracked shape, but the lateral line as a whole is visibly straight.

37. [3526] Lateral line, posterior extension, location of terminus: (0) surpassing beginning of caudal fin; (1) approaching end of caudal-fin peduncle; (2) ending well before caudal-fin peduncle, approximately at end of anal fin (Royero, 1999: char. 100; Akama, 2004: char. 87; modified).

In most Auchenipteridae, the terminus of the lateral line surpasses posteriorly the origin of the caudal-fin skeleton or the origin of caudal rays, and in most cases, it is extensive, reaching at least half the length of the caudal-fin rays. In some auchenipterid species of *Centromochlus perugiae*, *Centromochlus romani*, *Centromochlus reticulatus*, *Centromochlus simplex* and some species of *Tatia*, and the aspredinid *Aspredo* and *Pseudobunocephalus*, the lateral line nearly reaches or reaches to the caudal skeleton but never surpasses that point. Moreover, in *Gelanoglanis*, the lateral line is incomplete, and the terminus reaches only the end of the anal-fin rays.

38. [3527] Lateral line, posterior terminus, ramification: (0) unbranched; (1) branched into two divergent rami (Ferraris, 1988: char. I11; Royero,

1999: char. 101; Akama, 2004: char. 88; Birindelli, 2014: char. 116).

The branching pattern of the posterior end of the lateral line into two principal divergent rami is a common feature within Auchenipteridae, and the level of divergence and the orientation between the rami vary among genera. In the plesiomorphic condition, the posterior end of the lateral line is simple and unbranched. Within auchenipterids, the plesiomorphic condition is found in all members of Centromochlinae and in *Entomocorus*, *Liosomadoras*, *Pseudepapterus*, *Pseudotatia*, *Trachelyichthys* and *Trachelyopterichthys*. *Spinipterus acsi* was originally described with the posterior end of the lateral line simple (Akama & Ferraris, 2011), but further examination of the holotype and an additional non-type specimen (Calegari *et al.*, 2018) showed that the lateral line bifurcates after the caudal-fin origin, with the dorsal ramus more evident than the ventral one. The ventral ramus of the terminus of the lateral line is usually difficult to observe in specimens preserved in alcohol.

39. [3528] Midlateral scutes: (0) absent; (1) present (Birindelli, 2014: char. 118; modified).

In Auchenipteridae and the remaining catfishes examined here, the scutes are absent. In all doradids, the lateral line tubules are developed into a longitudinal mid-row of bony scutes. In addition, according to Birindelli (2014), among the doradids, *Doras micropoeus*, *Doraops*, *Hassar*, *Kalyptodoras*, *Nemadoras hemipeltis*, *Tenellus leporhinus* and *Wertheimeria* have weakly developed midlateral scutes.

40. [3529] Midlateral scutes, retrorse thorn: (0) absent; (1) present (Birindelli, 2014: char. 119).

All Doradidae examined have retrorse thorns on their midlateral scutes, except for *Wertheimeria*, which lacks thorns. *Wertheimeria maculata* Steindachner, 1877 generally has three scutes on the anterior portion of the body, and the remaining portion of the lateral line is tubule shaped and unossified, similar to those found in auchenipterids.

41. [3530] Midlateral scutes, orientation: (0) approximately perpendicular along body axis; (1) oblique along body axis (Birindelli, 2014: char. 120).

Most doradids have scutes oriented perpendicularly to the body axis. Among the Doradidae examined, only *Nemadoras* and *Trachydoras* have midlateral scutes that are oriented obliquely relative to the

body axis. According to [Birindelli \(2014\)](#), the derived condition is also present in *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Ossancora* and *Tenellus*, taxa not examined in the present study.

Neurocranium

42. [3531] Dorsal cranium surface, bones, structure: (0) compact; (1) trabeculate; (2) alveolate ([Britski, 1972](#): char. 12; [Royero, 1999](#): char. 30; [Ribeiro, 2011](#): char. 1; [Birindelli, 2014](#): char. 223; modified).

In most Auchenipteridae, the bones of the dorsal cranial surface are compact and structurally smooth, sometimes bearing strong superficial grooves, but never bearing unossified parts (*Liosomodoras oncinus*, *Tetranematichthys*, *Glanidium* and *Wertheimeria maculata*). In *Ageneiosus*, *Tympanopleura atronasus* and *Tympanopleura rondoni*, the bones of the cephalic shield are trabeculate and sponge-like, with deep longitudinal grooves and striae. In contrast, in *Pseudauchenipterus*, *Pseudepapterus*, *Epapterus*, four species of *Auchenipterus* (*Auchenipterus nigripinnis*, *Auchenipterus osteomystax*, *Auchenipterus nuchalis* and *Auchenipterus brachyurus*) and members of Aspredinidae, the bones of the cephalic shield are alveolate, not forming large grooves between the spaces, mostly on the anterior bones of the head. Previous authors codified *Tetranematichthys* as having trabeculate bones, the same condition found in *Ageneiosus*. However, the trabeculate bones of *Ageneiosus* seem not to be homologous with the strongly ossified and compact cranial bones, with grooves only under the surface of the bone found in *Tetranematichthys*. For this reason, in the present study *Tetranematichthys* was coded with the plesiomorphic condition.

43. [3532] Mesethmoid, shape in dorsal view: (0) expanded anterolaterally with notch on anterior and posterior portions; (1) expanded anterolaterally with notch only on posterior portion; (2) without anterolateral expansion, quadrate to rectangular; (3) elongate and narrow ([Royero, 1999](#): char. 9, 10; [Britto, 2002](#): char. 1; [Akama, 2004](#): char. 30; [Ribeiro, 2011](#): char. 4; [Birindelli, 2014](#): char. 52; modified).

In Auchenipteridae, the shape of the mesethmoid is highly variable among the genera because the shape of the head varies greatly in width, length and depth. In *Ageneiosus*, *Tetranematichthys* and *Tympanopleura*, the anterolateral portion of the mesethmoid is expanded, reaching to

near the anterolateral margin of the head, and the posterior portion of the bone is narrower and with anterior and posterior constrictions, with the latter forming the anterior portion of the anterior fontanel. Moreover, *Asterophysus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudotatia*, *Pseudepapterus*, *Pseudauchenipterus*, *Trachelyichthys* and *Trachelyopterichthys* have a mesethmoid similar to the plesiomorphic condition, but the middle and posterior portions of the bone are tightly compressed laterally and longer than wide, and only the posterior portion bears a constriction, similar to the plesiomorphic condition ([Fig. 2A, C](#)). In the genera *Auchenipterichthys*, *Tatia*, *Centromochlus*, *Glanidium* *Liosomadoras*, *Tocantinsia*, *Trachelyopterus*, *Spinipterus* and *Trachycorystes*, the mesethmoid has a quadrangular to rectangular shape, usually more restricted to the anterior portion of the head. In *Auchenipterichthys*, *Centromochlus existimatus* and *Centromochlus macracanthus*, the quadrangular mesethmoid also bears a constriction on its posterior portion, but the remaining species with the same shape lack the constriction ([Fig. 2D](#)). In *Gelanoglanis*, the mesethmoid is elongated and extremely narrow, longer than wide, and the anterior portion of the bone is approximately straight in the dorsal view.

44. [3533] Mesethmoid, length: (0) elongate, length of at least approximately twice its width; (1) short, length approximately equal to width ([Birindelli, 2014](#): char. 53).

Among auchenipterids, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, *Tetranematichthys* and *Gelanoglanis* have an elongated mesethmoid, with the length at least twice, sometimes three times, its width. However, in most Auchenipteridae, the mesethmoid is short, and its length is approximately equal to its width. [Birindelli \(2014\)](#) also considered two character states, short and elongate, but under different discretization.

45. [3534] Mesethmoid, anteroventral portion, contact with premaxilla: (0) contacting; (1) not contacting ([Ribeiro, 2011](#): char. 7)

The most common condition in Auchenipteridae is that where the mesethmoid ventrally contacts the premaxilla. In some cases, there is a gap between the mesethmoid and the premaxilla, as in *Ageneiosus* and *Tympanopleura* (except for *Tympanopleura cryptica*) and *Tetranematichthys*, where the premaxilla is oriented anteroventrally relative to the mesethmoid, and the premaxilla and mesethmoid do not contact each other mesially. Furthermore, *Gelanoglanis* has the premaxilla

laterally displaced, not contacting the mesethmoid anteromesially, and *Pseudepapterus* has the same condition, but the reduced premaxilla is located more posterolaterally to the mesethmoid.

46. [3535] Head, anterior region, composition: (0) formed by skin-covered mesethmoid and premaxillae; (1) possession of fleshy region anterior to mesethmoid and premaxillae.

Most Siluriformes and members of Auchenipteridae have a skin-covered mesethmoid, but no fleshy snout. In the case of *Ageneiosus*, *Pseudauchenipterus* and *Tympanopleura*, the lateral expansion of the mesethmoid reaches the posterior portion of the premaxillae, but the anteromedial portion of the snout does not contact the mesethmoid owing to recoil of the latter bone, leaving the anterior margin of the snout covered only by skin. *Gelanoglanis* alternatively has a highly modified morphology of the cranium, with an arched mesethmoid and lateral displacement of the premaxillae. In the derived condition, *Gelanoglanis* has a fleshy region anterior to the mesethmoid in the anterior portion of the head. The restructuring of the head is complemented by a thick layer of soft tissue over the anterior portion of the snout (see [Calegari et al., 2014](#)).

47. [3536] Premaxillae, position in dorsal view: (0) underneath mesethmoid; (1) in front of mesethmoid; (2) lateral to mesethmoid.

In most Auchenipteridae, the premaxilla is positioned under the mesethmoid. In *Ageneiosus*, *Asterophysus*, *Pseudauchenipterus*, *Tocantinsia*, *Tympanopleura*, *Tetranematichthys*, *Trachelyopterus*, *Trachelyopterichthys*, *Trachycorystes* and *Helogenes marmoratus*, most of the premaxillae is located in front of the mesethmoid and is completely visible in dorsal view. *Gelanoglanis* has the premaxillae positioned laterally to the mesethmoid, and the two bones do not contact each other.

48. [3537] Mesethmoid, anteroventral portion, process: (0) present, developed into laminar keel; (1) present, developed into uncinat process; (2) absent ([Birindelli, 2014](#): char. 55, modified).

In Auchenipteridae, except *Gelanoglanis*, the mesethmoid is flattened, without a process on its ventral portion. In most species, the mesethmoid is fused to, or ventrally covered by, the vomer and the premaxillae. In *Gelanoglanis*, the mesethmoid is elongated and bears a long, thin longitudinal laminar keel that is ventrally developed into a compressed process. In *Trachydoras*, *Atopocheilus*

and *Euchilichthys*, the mesethmoid is ventrally developed, and this expansion forms an uncinat process on the anterior portion. [Birindelli \(2014\)](#) coded the presence of this process also in *Oxydoras*; however, the present observations of *Oxydoras niger* (Valenciennes, 1821) revealed no process, and it was thus coded with the plesiomorphic condition.

49. [3538] Mesethmoid and nasal bones, union: (0) separated; (1) in contact with one another.

In most Auchenipteridae, the mesethmoid is distinctly separated from the nasal bone. The contralateral nasal bones are positioned laterally to the mesethmoid, but never contact it. Species of *Tatia* are variable for this character, and some species have the mesethmoid and nasal bones closely in contact with one another.

50. [3539] Anterior cranial fontanel: (0) present; (1) absent.

The anterior cranial fontanel is defined here as a fontanel between the frontals, either entering or not entering the mesethmoid anteriorly, and is sometimes divided into an anterior and a posterior portion by an epiphyseal bar. All Siluriformes examined have an anterior cranial fontanel, typically located at the point of contact between the mesethmoid and the frontals, except for *Gelanoglanis* (excluding *Gelanoglanis pan*), which lacks a cranial fontanel.

51. [3540] Anterior cranial fontanel, epiphyseal bar: (0) absent; (1) present ([Royero, 1999](#): char. 3; [Akama, 2004](#): char. 12, 13, 14; [Birindelli, 2014](#): char. 57; modified).

In most Siluriformes, the typical configuration of the anterior cranial fontanel is a large, singular opening. Within auchenipterids examined, the derived condition in which the aperture of the anterior cranial fontanel is divided by an epiphyseal bar is present in *Ageneiosus inermis*, *Auchenipterichthys thoracatus*, *Auchenipterus ambyiacus*, *Centromochlus heckelii*, *Centromochlus existimatus*, *Centromochlus meridionalis*, *Glanidium cesarpintoi*, *Liosomadoras*, *Tocantinsia*, *Trachelyopterichthys*, some *Trachelyopterus*, *Trachycorystes menezesi* and *Tympanopleura atronasus* ([Fig. 2B](#)). This division of the anterior fontanel is made by a bony bridge that is deeper than the superficial border of the frontals and is formed by contralateral extensions of the frontals.

52. [3541] Anterior cranial fontanel, location: (0) on mesethmoid and frontals; (1) restricted to frontals.

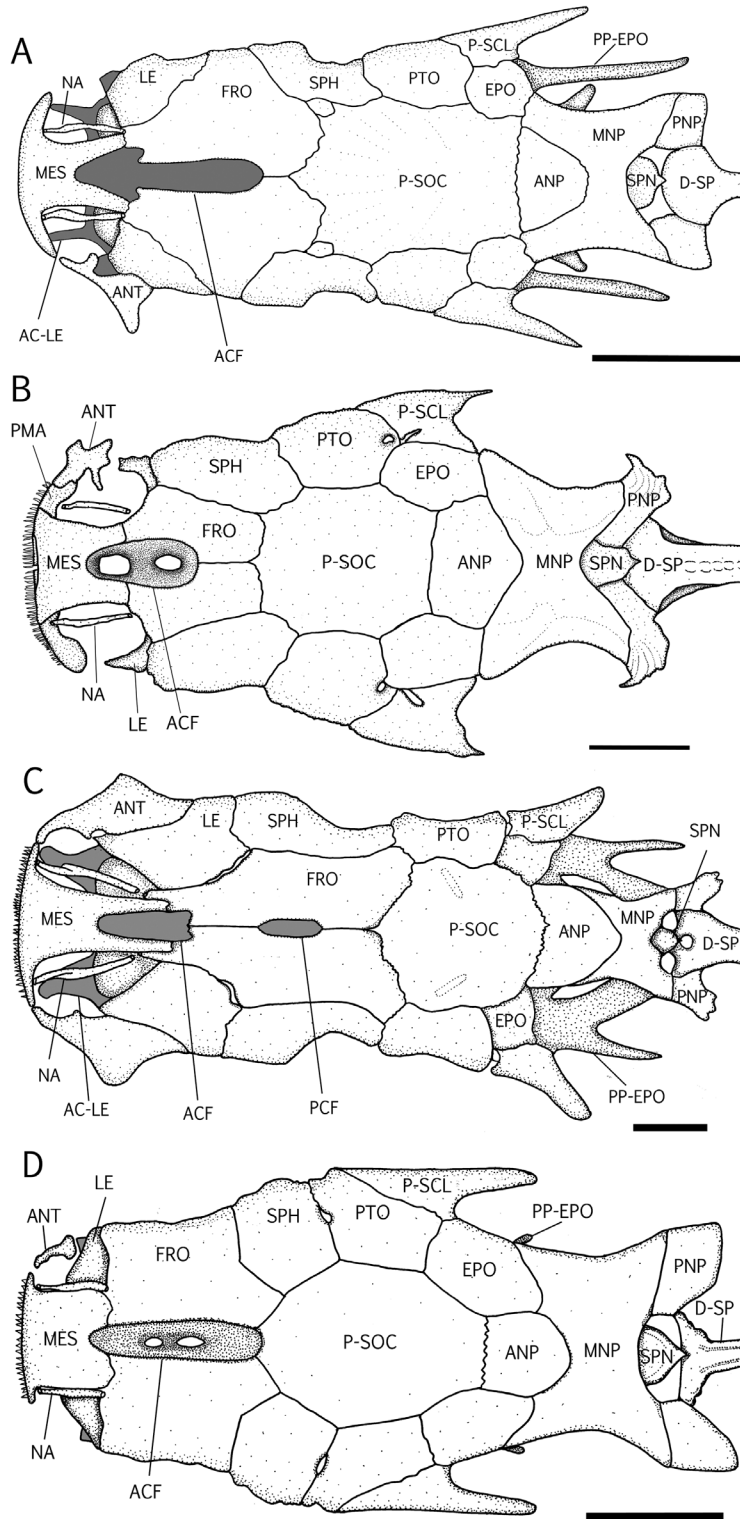


Figure 2. Dorsal view of head. A, *Entomocorus gameroi*, INHS 30016. B, *Liosomadoras oncinus*, MCP 46029. C, *Auchenipterus nuchalis*, MCP 19108. D, *Centromochlus existimatus*, MCP 29838. Abbreviations: ACF, anterior cranial fontanel; AC-LE, anterior cartilage of lateral ethmoid; ANP, anterior nuchal plate; ANT, antorbital; D-SP, dorsal-fin spinelet; EPO, epioccipital; FRO, frontal; LE, lateral ethmoid; MES, mesethmoid; MNP, middle-nuchal plate; NA, nasal; PCF, posterior cranial fontanel; PMA, premaxilla; PNP, posterior nuchal plate; PP-EPO, posterior process of epioccipital; P-SCL, posttemporal-supracleithrum; P-SOC, parieto-supraoccipital; PTO, pterotic; SPH, sphenotic; SPN, spinelet. Scale bars: 5 mm (A, B, D); C: 1 cm.

In Siluriformes, the anterior cranial fontanel is typically located between the mesethmoid and frontal bones (Fig. 2). A few species have the derived condition, in which the anterior cranial fontanel is restricted to the frontal, immediately after the posterior margin of the mesethmoid, as found in *Centromochlus heckelii*, *Centromochlus meridionalis*, *Centromochlus perugiae*, *Centromochlus simplex*, *Gelanoglanis pan* and *Spinipterus*.

53. [3542] Anterior cranial fontanel, shape: (0) elongated; (1) rounded; (2) elliptical (Royer, 1999: char. 4; Ferraris, 1988: char. N6; Birindelli, 2014: char. 56; modified).

In Auchenipteridae, the shape of the superficial aperture of the anterior cranial fontanel may be very elongated and narrow, beginning from the mesethmoid and extending up to the middle or almost to the end of the frontals. This condition is present in *Ageneiosus*, *Auchenipterus ambyiacus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, *Pseudauchenipterus* (except *Pseudauchenipterus nodosus*), *Tetranematichthys*, *Tympanopleura*, *Trachelyopterus insignis* and *Trachelyopterus teaguei*. The remaining species of auchenipterids have an elliptical anterior fontanel, except for a few species that have a rounded fontanel (*C. simplex*, *Gelanoglanis pan*, some species of *Tatia*, *Trachelyichthys* and *Spinipterus*).

54. [3543] Anterior cranial fontanel, anterior portion, cartilage: (0) absent; (1) present.

In the plesiomorphic condition, the anterior cranial fontanel is opened. In the derived condition, the anterior fontanel has an expanded cartilage on its anterior portion, which in part ventrally covers the aperture, which is present in *Ageneiosus vittatus*, *Ageneiosus dentatus*, *Asterophysus*, *Entomocorus*, *Epapterus*, *Auchenipterus nuchalis*, *Auchenipterus osteomystax*, *Auchenipterichthys longimanus*, *Auchenipterichthys punctatus*, *Pseudauchenipterus*, *Pseudepapterus*, *Tetranematichthys*, *Trachelyopterichthys* and *Tympanopleura cryptica*.

55. [3544] Cranial fontanel, posterior margin, longitudinal sulcus: (0) absent; (1) present (Royer, 1999: char. 5; Akama, 2004: char. 15; Ribeiro, 2011: char. 19; modified).

In most examined taxa, the posterior border of the cranial fontanel is delimited well by the contralateral frontals, which meet and form a flat cephalic shield. In *Ageneiosus*, *Tympanopleura rondoni* and *Pseudepapterus*, the end of the

posterior margin of the cranial fontanel is followed by a deep, elongated longitudinal sulcus, approaching the anterior margin of the parieto-supraoccipital or even surpassing this limit. Ariidae and some species of Doradidae also have the derived state.

56. [3545] Posterior cranial fontanel: (0) present; (1) absent (Marceniuk *et al.*, 2012: char. 27; Vigliotta, 2008: char. 6; Birindelli, 2014: char. 58; modified).

The posterior cranial fontanel is defined here as a fontanel between the frontals, either entering or not entering the parieto-supraoccipital, which is independent and posteriorly located relative to the anterior fontanel. The anterior and posterior cranial fontanelles are usually separated by a contact between the contralateral frontals. This connection of the frontals is not homologous with the epiphyseal bar that divides the anterior fontanel in two openings, and configures a deeper bony bridge located more ventrally than the surface of the anterior fontanel. In Auchenipteridae, the cranial morphology is highly diverse, with an unusual configuration where the parieto-supraoccipital rarely participates in the posterior cranial fontanel, which is usually restricted to the frontals. The posterior cranial fontanel is found in the auchenipterids *Auchenipterus*, *Epapterus* and *Pseudepapterus cucuhyensis*, most aspredinids examined, the doradid *Rhynchodoras woodsi*, *Helogenes* and Diplomystidae (Fig. 2C). The conceptualization of the anterior and posterior cranial fontanelles used herein is restricted to the catfishes examined, and a large-scale study is needed to establish the homology of this character in a broader context.

57. [3546] Lateral ethmoid, participation in dorsal region of cranium: (0) slightly exposed, equivalent to approximately one-third of frontal length; (1) greatly exposed, surpassing one-half length of frontal; (2) not exposed.

The lateral ethmoid contributes little to the formation of the surface of the cephalic shield in most catfish examined herein. Among auchenipterids, *Ageneiosus*, *Auchenipterichthys*, *Centromochlus macracanthus*, *Centromochlus shultzi*, *Entomocorus*, most species of *Glanidium*, *Spinipterus*, *Tocantinsia*, *Trachelyopterichthys*, *Trachelyopterus galeatus*, *Trachelyopterus lucenai*, *Trachycorystes* and *Tympanopleura* have the lateral ethmoid only slightly exposed (Fig. 2A). In contrast, in *Auchenipterus*, *Epapterus*, *Pseudepapterus*, some Mochokidae and Pimelodidae, the lateral ethmoid is greatly

exposed in the dorsal region of the cranium and anterodorsally expanded, contributing similarly to the frontal in the formation of the cephalic shield (Fig. 2C). Most of auchenipterids do not have the lateral ethmoid participating in the dorsal surface of the head.

58. [3547] Lateral ethmoid, anterior margin, anterior cartilage: (0) short, not extended; (1) long, extended.

In most Auchenipteridae, the anterior margin of the lateral ethmoid has a short cartilaginous extension that contacts the mesethmoid and vomer. In most species, the cartilage is approximately square or tapers anteriorly. In *Ageneiosus*, *Auchenipterus*, *Gelanoglanis pan*, *Gelanoglanis varii*, *Pseudepapterus*, *Pseudauchenipterus*, *Pseudotatia*, *Tympanopleura* and *Tetranematichthys*, the lateral ethmoid has a greater extension of cartilage along the entire anterior margin. Furthermore, in *Ageneiosus* and *Tympanopleura* the cartilage joins the lateral ethmoid with the mesethmoid and premaxillae, whereas in *Auchenipterus* the cartilage joins the above bones plus the vomer owing to the closer proximity between the lateral ethmoid and the premaxilla. This cartilage seems to serve as a protection for the olfactory lamellae, because the lamellae are situated immediately above the lateral ethmoid cartilage.

59. [3548] Lateral ethmoid, anterior expansion of cartilage, shape: (0) cylindrical; (1) conical; (2) square.

In *Ageneiosus*, *Gelanoglanis pan*, *Gelanoglanis varii*, *Pseudauchenipterus*, *Tetranematichthys* and *Tympanopleura*, the cartilage on the anterior margin of the lateral ethmoid is cylindrical, approximately the same width throughout its length (Fig. 3A). In contrast, in most *Auchenipterus* and *Pseudepapterus* the cartilage is approximately conical, tapering towards the snout tip and ending very thin at the opening of the anterior nostril (Fig. 3B). Yet, in *Asterophysus*, *Pseudotatia* and some Mochokids, this cartilage is square. For those species without an extended cartilage, the character was coded as inapplicable.

60. [3549] Lateral ethmoid, transverse keel in dorsal view: (0) absent; (1) present.

In most Auchenipteridae, the lateral ethmoid is straight, and its anterior portion is sloped anteroventrally and lacks any keel. In *Epapterus* and *Pseudepapterus*, this bone is almost straight along its length and bears a conspicuous transverse keel in dorsal view.

61. [3550] Lateral ethmoid and frontal, fenestra between bones: (0) present; (1) absent (de Pinna, 1993: char. 68; Britto, 2002: char. 6; Marceniuk *et al.*, 2012: char. 3; Birindelli, 2014: char. 60).

Among the catfish families examined, the fenestra between the lateral ethmoid and the frontal is present in Ariidae, Diplomystidae and *Helogenes*, and within Auchenipteridae, in *Pseudauchenipterus* and *Trachycorystes trachycorystes*. Although Birindelli (2014) coded Mochokidae and Pimelodidae as having the fenestra, in the present study both families were considered to lack the fenestra. In *Pseudauchenipterus*, the contact between lateral ethmoid and frontalis minor, in the lateral-most portion, at times, do not contact each other at all. The contact between those bones in Ariidae is by a distinct, narrow bone bridge.

62. [3551] Sphenotic, anterolateral process: (0) absent; (1) present (Royero, 1999: char. 12; Akama, 2004: char. 31; Birindelli, 2014: char. 62; modified).

In most auchenipterids, the sphenotic has approximately symmetric edges, without any projections. In *Ageneiosus*, *Tympanopleura* and *Tetranematichthys*, the sphenotic has an anterior projection that is greatly elongated and tubular, through which passes the sensory canal of the infraorbital series.

63. [3552] Sphenotic, posterolateral portion, shape: (0) straight; (1) slightly concave; (2) distinctly concave (Royero, 1999: char. 20; Akama, 2004: char. 34; Birindelli, 2014: char. 63; modified).

In some Auchenipteridae, the posterolateral margin of the sphenotic is almost straight, but never concave. In contrast, most *Ageneiosus* and *Centromochlus*, *Gelanoglanis*, *Pseudotatia*, *Liosomadoras morrowi*, some species of *Tatia*, *Trachelyichthys decaradiatus*, *Trachelyopterus lucenai*, *Trachelyopterus porosus* and *Trachycorystes*, the posterolateral margin of the sphenotic is slightly concave, concealing the articulation between the hyomandibula and the sphenotic. Conversely, in *Ageneiosus pardalis*, *Ageneiosus vittatus*, *Auchenipterus*, *Centromochlus reticulatus*, *Entomocorus*, *Epapterus*, *Pseudauchenipterus*, *Pseudepapterus*, *Tympanopleura*, *Tetranematichthys*, *Trachelyopterichthys* and *Spinipterus*, the margin of the sphenotic is strongly concave, usually exposing that articulation.

64. [3553] Frontal, lateral margin: (0) participating in orbital margin; (1) not participating in orbital margin (Ferraris, 1988: char. N8; Royero, 1999:

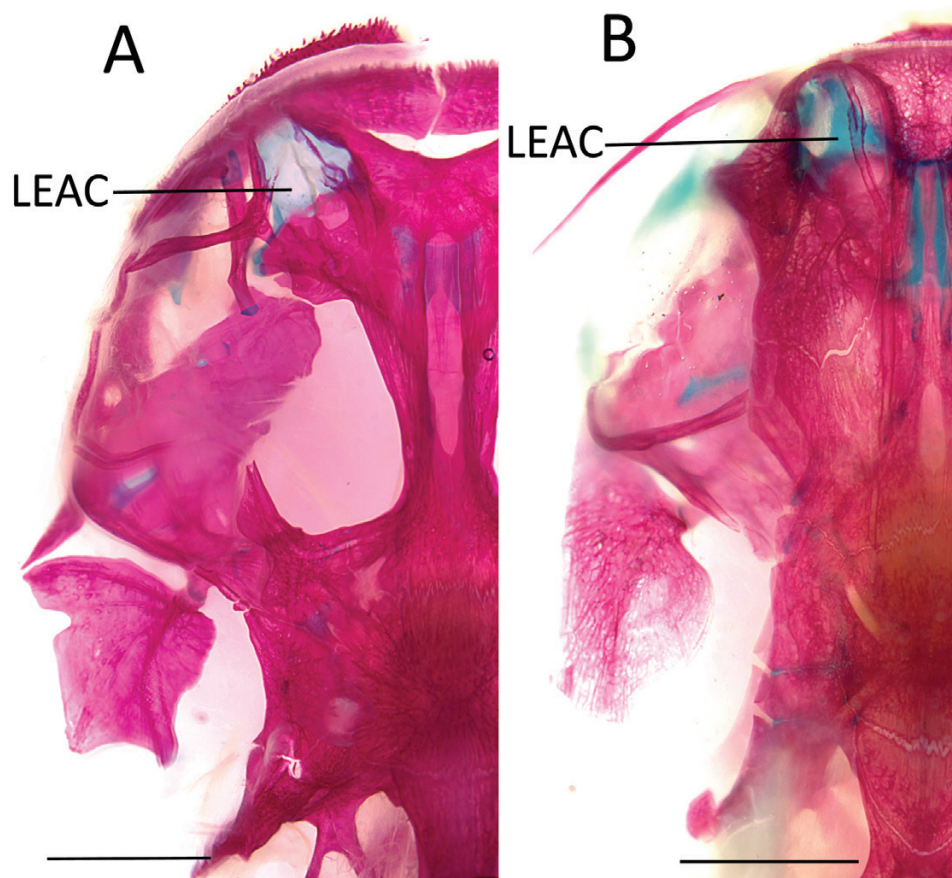


Figure 3. Dorsal view of cranium. A, *Tetranematichthys wallacei*, MCP 27174. B, *Auchenipterus nuchalis*, MCP 19708. Abbreviation: LEAC, lateral ethmoid anterior cartilage. Scale bars: 5 mm.

char. 1; Britto, 2002: char. 5; Akama, 2004: char. 17; Birindelli, 2014: char. 64).

In most catfish families, the frontal, lateral ethmoid and sphenotic compose the dorsal orbital rim, and the antorbital also participates in the margin anterodorsally (Fig. 2A, D). However, in *Auchenipterichthys*, *Auchenipterus*, *Epapterus*, *Liosomadoras*, *Pseudauchenipterus*, *Pseudepapterus*, *Tetranematichthys*, *Trachelyopterichthys*, *Trachelyopterus*, *Trachycorystes menezesi* and *Spinipterus*, the frontal does not participate in the orbital margin (Fig. 2B, C). The same condition is found in *Ageneiosus* and *Tympanopleura*, but the frontal is located dorsally from the orbital margin and far from the orbit, which is positioned laterally on the head.

65. [3554] Parieto-supraoccipital, pterotic and sphenotic, fenestra between bones: (0) absent; (1) present (Birindelli, 2014: char. 67).

In most auchenipterids, the bones of the cranium are well sutured to each other. In *Asterophysus*,

Trachelyopterus amblops and *Trachelyopterus coriaceus*, and in *Auchenipterus brevior*, *Auchenipterus fordicei* and *Auchenipterus dentatus*, there is a small fenestra between the parieto-supraoccipital, pterotic and sphenotic bones.

66. [3555] Epioccipital, exposition: (0) partly exposed, with only anterior portion participating in cephalic shield; (1) exposed, participating in cephalic shield; (2) not exposed, not participating in cephalic shield (Ribeiro, 2011: char. 35; Birindelli, 2014: char. 84; modified).

In the plesiomorphic condition, the epioccipital is exposed on the dorsal portion of the neurocranium and always contacts the pterotic and the posttemporal–supracleithrum. *Auchenipterus*, *Epapterus*, *Tetranematichthys*, Diplomystidae, Aspredinidae, *Cathorops spixii* (Agassiz, 1829) and *Helogenes marmoratus* have the epioccipital partly exposed, with only the anterior portion of the bone exposed and participating in the cephalic shield (Fig. 2C). In these cases, the

largest portion of the epioccipital is positioned more internally and covered by a thin skin. In most Auchenipteridae, however, the epioccipital is positioned posterodorsally or dorsolaterally to the posttemporal–supracleithrum, and entirely exposed on the cephalic shield (Fig. 2B, D). In *Tympanopleura*, which have the epioccipital exposed, the dorsal process of the posttemporal–supracleithrum covers up to the middle of the epioccipital, rendering the two bones difficult to distinguish in some cases. Moreover, in *Ageneiosus* and *Pseudepapterus*, some Ariidae and Mochokidae, and Pimelodidae, the epioccipital is not exposed or visible dorsolaterally as the remaining bones of the cephalic shield but is covered by skin and adipose tissue. In this condition, the epioccipital is located more posteriorly to the posttemporal–supracleithrum.

67. [3556] Temporal fossa: (0) absent; (1) present (de Pinna, 1996: char. 24; Marceniuk *et al.*, 2012; char. 36).

The temporal fossa is absent in most taxa examined. In some Siluriformes, such as the Aspredinidae, *Cathorops spixii*, *Synodontis petricola* Matthes, 1959 and *Nemadoras humeralis*, the temporal fossa is present and delimited by the parieto-supraoccipital, pterotic and posttemporal–supracleithrum. However, in some members of Auchenipteridae, the temporal fossa assumes the same position but is delimited by the parieto-supraoccipital, pterotic and epioccipital owing to the position of the last bone, which is completely exposed and occupies a most dorsal portion relative to the posttemporal–supracleithrum.

68. [3557] Parieto-supraoccipital, posterior process: (0) present; (1) absent (Royero, 1999: char. 22; Diogo, 2004: char. 131; Birindelli, 2014: char. 68).

Most Siluriformes have a posterior process on the parieto-supraoccipital, with an extension forming a tip on the posteromedial portion of that bone. In the Auchenipteridae, the parieto-supraoccipital lacks such a process, and the posterior portion of the bone is truncated. This posterior process is also absent in Mochokidae, the aspredinid *Pterobunocephalus*, and Doradidae. According to Diogo (2004), it is also absent in Malapteruridae.

69. [3558] Sphenotic and parieto-supraoccipital, contact: (0) present; (1) absent (Ferraris, 1988: char. N10; Royero, 1999: char. 2, 18; Britto, 2002: char. 7; Akama, 2004: char. 19, 26; Diogo, 2004: char. 97; de Pinna *et al.*, 2007: char. 37; Birindelli, 2014: char. 69).

In most Auchenipteridae, the sphenotic contacts the anterolateral border of parieto-supraoccipital (Fig. 2A). However, in *Auchenipterus* and *Pseudepapterus*, the sphenotic is separated from the parieto-supraoccipital by the frontal (Fig. 2C).

70. [3559] Frontal, sphenotic, and parieto-supraoccipital, accessory dermal ossification between these bones: (0) absent; (1) present (Ferraris, 1988: char. N13; Akama, 2004: char. 22; Birindelli, 2014: char. 70).

Most Auchenipteridae lack an accessory dermal ossification between the frontal, sphenotic and parieto-supraoccipital. However, Ferraris (1988) and Birindelli (2014) noted the presence of such accessory ossification in *Entomocorus*, corroborated herein.

71. [3560] Posttemporal–supracleithrum, dorsal portion, shape: (0) simple, not divided into two rami; (1) bifurcated, divided into two rami (Ribeiro, 2011: char. 21).

In most species of Auchenipteridae, the posttemporal–supracleithrum is slightly oblique, and its dorsal margin is straight and not divided into two rami. In the derived condition presented in *Ageneiosus*, *Tympanopleura* and *Trachelyopterus insignis*, the dorsal portion of the posttemporal–supracleithrum is strongly bifurcated.

72. [3561] Posttemporal–supracleithrum, posterior process, orientation: (0) ventrally oriented; (1) posteroventrally oriented (Ribeiro, 2011: char. 23).

In the plesiomorphic condition, the posttemporal–supracleithrum is more ventrally oriented or fairly vertical to the body axis, as found in a few representatives of *Ageneiosus*, *Auchenipterus*, some *Glanidium*, *Liosomadoras*, *Pseudauchenipterus* (except *Pseudauchenipterus nodosus*), *Pseudepapterus*, *Tetranematichthys*, *Trachycorystes*, *Tocantinsia*, *Tympanopleura* and most *Trachelyopterus*. However, in most Auchenipteridae the posterior portion of the posttemporal–supracleithrum is posteroventrally oriented.

73. [3562] Epioccipital, posterior process: (0) absent; (1) present (Ferraris, 1988: char. N4; de Pinna, 1993: char. 85; de Pinna, 1996: char. 29; Royero, 1999: char. 50; Britto, 2002: char. 50; Akama, 2004: char. 7; Marceniuk *et al.*, 2012: char. 40; Birindelli, 2014: char. 85; modified).

Some taxa examined lack the posterior process of the epioccipital, including *Franciscodoras marmoratus* (Lütken, 1874), *Wertheimeria*

maculata, Mochokidae and Diplomystidae. Notwithstanding, the epioccipital of most Siluriformes has a posterior process, usually visible in lateral view. However, in some cases this process can be difficult to detect because the process is covered by nuchal plates, as in case of some doradids and the auchenipterids *Centromochlus* and *Spinipterus*.

74. [3563] Epioccipital, posterior process, shape: (0) forming simple spine; (1) bifurcated; (2) laminar; (3) pointed.

The posterior process of the epioccipital can vary in shape among Auchenipteridae. In *Asterophysus*, *Auchenipterichthys*, *Entomocorus*, *Gelanoglanis*, *Centromochlus macracanthus*, *Centromochlus schultzi* and *Trachelyopterichthys*, the process forms a long, thin spine (Fig. 2A). In *Auchenipterus*, *Epapterus*, *Pseudoauchenipterus*, *Tetranematichthys*, *Trachelyichthys* and *Trachelyopterus*, the long process is bifurcated, ending in a thin, pointed shape (Fig. 2C); these groups are distinguished from *Ageneiosus*, *Pseudepapterus* and *Tympanopleura* because the latter have a very elongated laminar bone, but the medial branch is wider and sutured to the compound vertebrae. In contrast, in most species of *Centromochlus*, *Glanidium*, *Liosomadoras*, *Spinipterus*, *Tatia*, *Pseudotatia*, *Trachycorystes* and *Tocantinsia*, the posterior process of the epioccipital is pointed and very short, with a wide base formed by the lateral border of the epioccipital (Fig. 2D). Especially in *Centromochlus romani* and *Centromochlus simplex*, the process is greatly reduced and covered by the nuchal plate. Those taxa lacking a posterior process on the epioccipital were coded as inapplicable.

75. [3564] Epioccipital, posterior process, size: (0) elongated, surpassing at least half the length of the middle nuchal plate; (1) short, not reaching to that point.

The posterior process of the epioccipital varies in size independently of its shape, which is most clearly observable in species with a spine-shaped process. Most auchenipterids have an elongated process that surpasses half the length of the middle nuchal plate, usually reaching to the origin of the dorsal fin. Within Auchenipteridae, *Centromochlus*, *Glanidium*, *Tatia*, *Pseudotatia*, *Liosomadoras*, *Tocantinsia*, *Trachycorystes* and *Spinipterus* have a short process, not reaching to half the length of the middle nuchal plate. Taxa lacking the posterior process of the epioccipital were coded as inapplicable.

76. [3565] Epioccipital, posterior process, composition: (0) mainly ligamentous, more than half the length formed by ligament; (1) mainly ossified, more than half the length formed by bone (Ferraris, 1988: char. N4; de Pinna, 1993: char. 85; de Pinna, 1996: char. 29; Royero, 1999: char. 50; Britto, 2002: char. 50; Akama, 2004: char. 7; Sousa, 2010: char. 19; Marceniuk *et al.*, 2012: char. 40; Birindelli, 2014: char. 85; modified).

The posterior process of epioccipital is mainly ligamentous in *Centromochlinae*, *Pseudotatia*, *Liosomadoras*, *Tocantinsia*, *Trachycorystes* and *Spinipterus*. The remaining auchenipterids have this process mainly ossified. Taxa lacking the posterior process on the epioccipital were coded as inapplicable.

77. [3566] Epioccipital, connection between posterior process and parapophyses of compound centrum: (0) not connected; (1) connected by suture (Ferraris, 1988: char. N5, 7, V10; Curran, 1989: char. 3; Walsh, 1990: char. 19; Royero, 1999: char. 51, 52, 53, 54; Akama, 2004: char. 8, 9, 10, 11; Birindelli, 2014: char. 87).

In the plesiomorphic condition, the posterior process of the epioccipital is thinner and does not reach to the lateral portion of the fifth and sixth vertebrae, and its extension does not contact the parapophyses. In contrast, *Ageneiosus*, *Auchenipterus*, *Epapterus*, *Pseudepapterus*, *Tetranematichthys*, *Tympanopleura*, *Trachelyichthys*, *Trachelyopterus coriaceus*, Ariidae, *Helogenes* and *Trachydoras nattereri* have this process enlarged, and it contact the parapophyses of the fifth and sixth vertebrae in a strong suture. Taxa lacking the posterior process were coded as inapplicable.

78. [3567] Extrascapular: (0) present; (1) absent (Arratia, 1992: char. 43; Britto, 2002: char. 51; Birindelli, 2014: char. 88).

The extrascapular is a small ossification located dorsally to the posttemporal–supracleithrum and ventrally to the parieto-supraoccipital. In species with a temporal fossa, the extrascapular is positioned immediately after the fossa. This bone is present in Diplomystidae, Ariidae, *Helogenes marmoratus*, Pimelodidae and Aspredinidae. In Aspredinidae, the extrascapular is tiny and difficult to observe. According to an extensive study by Pastana (2014) of the anatomy and homology of the canals and pores of the lateral sensorial system in Characiformes, the extrascapular was the only bony plate associated with the presence of the temporal and supratemporal canals.

However, Siluriformes lack a supratemporal canal (Arratia & Gayet, 1995), and the postotic canal in this group is located on the pterotic and posttemporal–supracleithrum. Pastana's (2014) notes are relevant to the controversy regarding the homology of the extrascapular, which definitely needs further investigation in Siluriformes.

79. [3568] Cranium and posttemporal–supracleithrum, connection: (0) via ligament; (1) via bony suture (de Pinna, 1993: char. 26; Royero, 1999: char. 16; Britto, 2002: char. 38; Arratia, 2003a: char. 130; Diogo, 2004: char. 155; Birindelli, 2014: char. 89).

In Diplomystidae and Aspredinidae, the posttemporal–supracleithrum is connected to the cranium via a ligament. In all remaining taxa examined, the posttemporal–supracleithrum is strongly sutured to the neurocranium. In Ariidae, the connection condition is slightly different, because only the tip of the dorsal portion of the posttemporal–supracleithrum is connected to the cranium.

80. [3569] Posterior portion of posttemporal–supracleithrum and lamina formed by parapophysis of Weberian complex, suture: (0) absent, or slightly contacting; (1) present, connected by long bony suture (de Pinna, 1996: char. 27; Britto, 2002: char. 44; Birindelli, 2014: char. 90).

The posttemporal–supracleithrum is a tridimensional, complex structure and probably involves many evolutionary processes. According to de Pinna (1996), the plesiomorphic condition for the posttemporal–supracleithrum in the Siluriformes is difficult to surmise because this structure includes a number of independent characters. The posttemporal–supracleithrum can vary in position and orientation on the neurocranium in Siluriformes. However, in the supposed derived condition, the posttemporal–supracleithrum assumes a more dorsal and posterior position relative to the parieto-supraoccipital. This condition, present only in Aspredinidae, caused the posterior process of the posttemporal–supracleithrum to occupy the dorsal portion of the parapophyses lamina of the Weberian complex, more specifically the fourth and fifth vertebrae, with the posterior process strongly sutured to the parapophyses. In the other condition, the posterior process is anterior to the parapophyses lamina of the Weberian complex and does not contact or only slightly contacts the anterior portion of the complex, and is never sutured.

81. [3570] Transcapular process, direction: (0) transverse to body axis; (1) at angle of $\sim 45^\circ$ relative

to body axis (Royero, 1999: char. 47; Akama, 2004: char. 44; Birindelli, 2014: char. 92).

The transcapular process is usually transverse to the body axis in most Siluriformes. Alternatively, *Ageneiosus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Liosomadoras morrowi*, *Pseudepapterus*, *Spinipterus*, *Tatia intermedia*, *Tetranematichtys*, most *Trachelyichthys*, *Trachelyopterus galeatus*, *Trachelyopterus lucenai*, *Trachycorystes trachycorystes* and *Tympanopleura* have the derived condition, in which the transcapular process is at an angle of $\sim 45^\circ$ relative to the body axis.

82. [3571] Transcapular process, shape: (0) blunt, not extended ventrally; (1) ventrally extended into bony lamina (Eigenmann, 1925: char. 287; Higuchi, 1992: char. 29, 30, 41; Birindelli, 2014: char. 93).

Most Siluriformes lack any ventral extension on the transcapular process, but some Doradidae (*Nemadoras*, *Oxydoras*, *Rhynchodoras*, *Trachydoras* and *Franciscodoras*) have a large transcapular process with a ventral, elongated laminar projection in its lateral portion. Birindelli (2014) considered *Rhynchodoras* and *Franciscodoras* to lack the ventral extension, but the derived condition was observed in both taxa.

83. [3572] Vomer, configuration: (0) present as independent bone; (1) present, but fused to mesethmoid; (2) absent (Ferraris, 1988: char. N11; Birindelli, 2014: char. 72).

The vomer is present in most Siluriformes on the anterior portion of the ventral surface of the neurocranium (Fig. 4A, C). Although Ferraris (1988), Soares-Porto *et al.* (1999), Rengifo *et al.* (2008) and Birindelli (2014) asserted the absence of the vomer as a synapomorphy for *Gelanoglanis*, a different condition is observed; the vomer is present but fused to the mesethmoid in all species of *Gelanoglanis*. The fusion of the vomer to the mesethmoid can probably be explained as a consequence of the different cranial morphology in *Gelanoglanis*, which is very laterally compressed compared with the remaining auchenipterids (Fig. 4B). This head shape configuration is a result of the arched and narrow mesethmoid, which is easily visible in dorsal view because it is positioned dorsally to the vomer instead of slightly anteriorly, as in the remaining members of the family. The mesethmoid of *Gelanoglanis* is similar to that of *Pseudepapterus* in dorsal view, with a ventral laminar keel oriented along the axis of the head that is strongly fused to the anterior portion of the vomer. In ventral view, the vomer is

the anteriormost structure of the neurocranium because the premaxillae are markedly displaced laterally. The vomer fused to the mesethmoid in *Gelanoglanis* has a very short posterior portion where it is articulated to the parasphenoid and has the same shape as in the centromochlines, with an anterolateral projection. The vomer almost completely forms the roof of the oral cavity because the snout is narrow, and the vomer occupies the anterior region. This distinct condition found in *Gelanoglanis* is different from that in Aspredinidae, in which the vomer was completely lost. For this reason, the character coding for the presence of the vomer was modified to include the distinct condition present in *Gelanoglanis*. However, a more comprehensive study with an ontogenetic series should be completed. Among catfishes examined, only Aspredinidae lack the vomer.

84. [3573] Vomer, anterior portion, shape: (0) anteriorly enlarged, without projections; (1) with distinct anterolateral projections (Ferraris, 1988: char. N18; Arratia, 1992: char. 50; Higuchi, 1992: char. 14; Soares-Porto, 1998: char. 11; Walsh, 1990: char. 3; Akama, 2004: char. 24; Birindelli, 2014: char. 73; modified).

Among Auchenipteridae, *Ageneiosus*, *Tetranematichthys* and *Tympanopleura* (except *Tympanopleura brevis* and *Tympanopleura piperata*) have the anterior portion of the vomer enlarged and rounded, and it never bears lateral projections (Fig. 4A). In Auchenipteridae, the vomer is positioned very anteriorly in the head

and ventrally to the mesethmoid and usually also to the premaxilla. In this configuration, the vomer is strongly sutured to the premaxilla, and it is sometimes difficult to distinguish the lateral limits of the anterior portion of the vomer. In most Auchenipteridae, the anterior portion of the vomer bears lateral projections with rounded tips, somewhat T-shaped (Fig. 4C).

85. [3574] Vomer, teeth: (0) present; (1) absent (de Pinna, 1993: char. 60; Royero, 1999: char. 32; Britto, 2002: char. 31; de Pinna *et al.*, 2007: char. 37; Marceniuk *et al.*, 2012: char. 53; Birindelli, 2014: char. 74).

Among the taxa examined, only Diplomystidae possess vomerine teeth. All Auchenipteridae lack teeth on the vomer.

86. [3575] Vomer, accessory tooth plate: (0) absent; (1) present (de Pinna, 1993: char. 72; Royero, 1999: char. 32; Britto, 2002: char. 32; Akama, 2004: char. 52; Marceniuk *et al.*, 2012: char. 56; Birindelli, 2014: char. 75).

Most Siluriformes and all members of Auchenipteridae lack the dentigerous plate on the vomer. In Ariidae, *Helogenes marmoratus* and, according to the above authors, also in Claroteidae, Pangasiidae and Schilbeidae, an accessory tooth plate is attached to the vomer.

87. [3576] Parasphenoid, anterior half, ventral keel: (0) absent; (1) present (Ferraris, 1988: char. N17; Akama, 2004: char. 23; Birindelli, 2014: char. 78; modified).

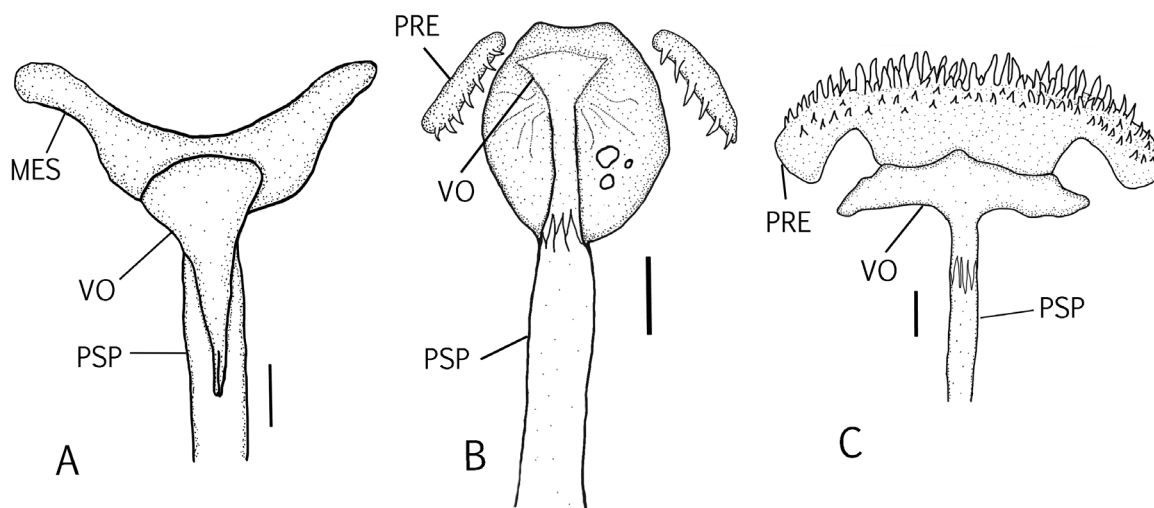


Figure 4. Ventral view of vomer. A, *Tetranematichthys wallacei*, MCP 27174; scale bar: 2 mm. B, *Gelanoglanis pan*, MZUSP 96032; scale bar: 1 mm. C, *Tatia nigra*, MCP 46028; scale bar: 1 mm. Abbreviations: MES, mesethmoid; PRE, premaxilla; PSP, parasphenoid; VO, vomer.

Among taxa examined, the parasphenoid is enlarged in the posterior half and narrow in the anterior half. Most taxa examined have the narrower portion of the parasphenoid like a flat cylinder or digit-like, but never laterally compressed forming a deep, ventral keel. In the derived state, found in *Centromochlus heckelii* and *Centromochlus existimatus*, the parasphenoid forms a prominent deep keel composed by the compressed lateral walls. [Birindelli \(2014\)](#) described this character as the presence/absence of a cranial keel.

88. [3577] Parasphenoid, narrow anterior portion, length: (0) short, < 50% of bone; (1) elongate, > 50% of bone.

The parasphenoid usually has a configuration where the posterior portion of the bone is enlarged and wide, and the anterior portion narrows in a long, rod-like bone. In most Auchenipteridae, the parasphenoid is relatively enlarged and flat along its length, and the anterior half of the bone is short. In this condition, < 50% of the parasphenoid is formed by the anterior, narrow portion, generally not reaching to the vertical through the prootic. In the derived state, found in *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, *Centromochlus* (except *Centromochlus meridionalis*), *Tatia* (except *Tatia creutzbergi* and *Tatia gyrina*), some mochokid species and *Pimelodus*, the parasphenoid forms an elongate and narrow anterior, rod-like portion, occupying > 50% of the bone length.

89. [3578] Basioccipital, lateral expansion: (0) absent; (1) present ([Royero, 1999](#): char. 46; [Vigliotta, 2008](#): char. 13; [Marceniuk et al., 2012](#): char. 75; [Birindelli, 2014](#): char. 80; modified).

In the plesiomorphic condition, the basioccipital has no expansion on its lateral margin; its width is approximately the same along the length. In the derived condition, shared by Auchenipteridae, Ariidae, some Mochokidae and Doradidae, the basioccipital is laterally expanded, forming arms, distinctively wider than its lateral margins. [Lundberg \(1993\)](#) suggested this distinct lateral expansion of the basioccipital as synapomorphic for the arioids, which includes the above families plus the fossil *Titanoglanis* (see also comments by [Vigliotta, 2008](#); [Birindelli, 2014](#)). In some taxa with the plesiomorphic condition, the basioccipital can be slightly wider in the posterior portion, but far from having a distinctive arm or process. Although [Birindelli \(2014\)](#) coded this derived condition also for Aspredinidae, in the present study no lateral

expansion was observed among the aspredinids; instead, the basioccipital was laterally straight as in remaining catfishes.

90. [3579] Exoccipital and neural arch of complex vertebra, connection: (0) connected by cartilage; (1) connected by bony suture ([Ferraris, 1988](#): char. V1; [Akama, 2004](#): char. 45; [Birindelli, 2014](#): char. 82).

In most Siluriformes, the neural arch of the complex centrum barely contacts the posterior margin of the exoccipital, except for its anteromesial portion, which contacts by means of cartilage. In Doradoidea, the exoccipital is strongly sutured to the neural arch along its entire length. This character is visible only in lateral view.

91. [3580] Trigemino-facial and optic foramina, aperture: (0) united; (1) separated ([Mo, 1991](#): char. 19; [Britto, 2002](#): char. 52; [Birindelli, 2014](#): char. 79).

The plesiomorphic condition, found in Diplomystidae, is the union of the trigemino-facial and optic foramina into a single aperture. However, in most Auchenipteridae, the border between the prootic and the pterosphenotic holds the trigemino-facial foramen, with the aperture oriented transversely to the lateral portion of the head owing to the lowering of the sphenotic to a different level relative to the remaining bones of the neurocranium. Auchenipterids have a separate optic foramen that is smaller and anterior to the trigemino-facial foramen, and usually located on the border between the pterosphenoid, orbitosphenoid and frontal. Based on the condition observed in *Epapterus blohmi* (one cleared and double-stained, USNM 260638) and probably representative of the other members of Auchenipteridae, the trigemino-facial nerve has three large nerves that pass through the foramen and run towards the mandibular arch. Of the two trigemino-facial nerves that run to the mandibular arch, one overtakes the hyomandibula, where it ramifies into two rami, which run to the preopercle and then quadrate and pass through the articulation with the angulo-articular, passing to the posterior portion of the dentary and reaching the anterior tip. The second nerve is the largest and runs through the dorsal portion of the dentary to its anterior portion, where it divides into two rami to innervate the outer and inner mandibular barbels. The third nerve runs directly to the anterior portion of the maxilla and innervates the maxillary barbel. One specimen examined of *Tatia brunnea* has both conditions in the same individual, a single fenestra on one

side and a double fenestra with the bones sutured, nearly separating the apertures. This individual is possibly a sub-adult, with the suture remaining open owing to incomplete ontogeny.

92. [3581] Foramen trigeminofacial, exposure: (0) exposed; (1) not exposed, covered by parasphenoid.

In the plesiomorphic condition, the trigeminofacial foramen is visible in ventral view owing to the configuration of the bones on the cranial roof. In auchenipterids, *Ageneiosus*, *Auchenipterichthys*, *Auchenipterus ambyiacus* and *Auchenipterus brachyurus*, *Glanidium*, *Liosomadoras*, *Tetranematichthys*, *Tympanopleura* (except *Tympanopleura cryptica* and *Tympanopleura brevis*), *Tocantinsia*, *Trachelyichthys* (except *Trachelyichthys decaradiatus*), *Trachelyopterus* (except *Trachelyopterus amblops*) and *Spinipterus* have the bones of the neurocranium with a different configuration, where the posterolateral portion of the parasphenoid and the posteroventral process of the sphenotic cover the aperture of the trigeminofacial foramen in ventral view, partly occluding it.

Mandibular arch

93. [3582] Premaxilla, size: (0) well developed; (1) reduced.

In most taxa examined, the premaxilla is well developed and clearly visible in ventral view. In *Pseudepapterus*, the premaxilla is almost undetectable to the eye and extremely reduced to a tiny and very slender bone, which is located not on the border of the mesethmoid but slightly below the lateral mesethmoid wing.

94. [3583] Premaxilla, shape: (0) plate-like, width distinctly greater than depth; (1) conical with dorsal apex, depth distinctly greater than width; (2) shaped like block, depth and width approximately equal; (3) vertically laminar (Ferraris, 1988: char. J9, 20; Royero, 1999: char. 57; Akama, 2004: char. 51; Birindelli, 2014: char. 125; modified).

The plesiomorphic condition in Siluriformes is that the premaxilla is plate-like and flattened. The doradids, *Nemadoras*, *Oxydoras*, *Trachydoras* and *Rhincodoras*, have a narrow premaxilla, cone shaped with a dorsal apex and its depth greater than width. In contrast, in most Mochokidae the premaxilla is block shaped, with the depth and width approximately equal and without a dorsal projection. Furthermore, *Helogenes* and *Gelanoglanis* have a very thin

laminar premaxilla that is oriented vertically to the head.

95. [3584] Premaxilla, curvature: (0) almost straight; (1) curved.

In most of the outgroup and some species of Auchenipteridae, including *Auchenipterichthys*, *Entomocorus*, *Gelanoglanis*, *Glanidium catharinensis* and *Glanidium cesarpinto*, the premaxilla is straight, with the bone positioned at the anteriormost portion of the head. In the remaining taxa, the premaxilla is curved, forming a conspicuous angle and consequently occupying an anterolateral position on the head.

96. [3585] Premaxilla, posteromedial portion, bony expansion: (0) absent; (1) present (Ribeiro, 2011: char. 71).

In most Siluriformes, the posteromedial portion of the premaxilla has approximately the same length throughout its width. In most *Ageneiosus*, *Auchenipterus fordicei*, *Tympanopleura brevis*, *Tympanopleura cryptica* and *Trachycorystes*, the posteromedial face of the premaxilla has a long, laminar expansion that sometimes forms a distinct pointed process.

97. [3586] Premaxilla, distal portion, extension: (0) absent; (1) present (Ferraris, 1988: char. J21; Akama, 2004: char. 54; Birindelli, 2014: char. 127; modified).

In the plesiomorphic condition, the premaxilla has a mostly consistent width along its length, with no projections on the distal portion of the premaxilla. In the auchenipterids *Ageneiosus*, *Auchenipterus*, *Epapterus*, *Pseudepapterus cucuhyensis*, *Gelanoglanis*, *Tympanopleura* and *Tetranematichthys*, the distal portion of the premaxilla has a thin, elongate extension.

98. [3587] Premaxilla, posteromesial portion, process: (0) absent; (1) present (Ribeiro, 2011: char. 74).

In most Siluriformes, the posterior portion of the premaxilla is straight, with the same depth throughout its length. Within auchenipterids, *Ageneiosus*, *Centromochlus existimatus*, *Centromochlus perugiae*, *Tympanopleura*, *Tetranematichthys* and *Trachelyopterichthys* have the posteromesial portion of the premaxilla with a large, somewhat pointed process, which sustains the posterior portion of the antorbital.

99. [3588] Premaxilla, teeth: (0) present; (1) absent (Ferraris, 1988: char. J8; Higuchi, 1992: char. 42; Sabaj, 2002: char. 13; Birindelli, 2014: char. 128).

In all examined taxa, except the auchenipterids *Epapterus* and *Pseudepapterus* and the doradids *Nemadoras*, *Oxydoras* and *Trachydoras*, the premaxilla has teeth.

100. [3589] Premaxilla, tooth, shape: (0) curved; (1) straight; (2) sinuous, S-shaped (Vigliotta, 2008: char. 37; Birindelli, 2014: char. 129; modified).

Most examined taxa have the premaxillary tooth curved in the distal portion. Among the auchenipterids examined, the teeth are straight only in *Entomocorus*, *Gelanoglanis*, *Glanidium cesarpintoi*, *Liosomadoras*, some species of *Tatia*, *Trachelyopterichthys*, *Tocantinsia*, *Trachycorystes trachycorystes* and *Spinipterus*. Mochokidae (except *Mochokus* and *Mochokiella*) is the only family with the derived condition of S-shaped teeth. Taxa without premaxillary teeth were coded as inapplicable for this character.

101. [3590] Maxilla, size: (0) short; (1) elongate, rod-like (Ferraris, 1988: char. J11; Vigliotta, 2008: char. 33; Ribeiro, 2011: char. 81; Birindelli, 2014: char. 131).

In most examined taxa, the maxilla is short, always shorter than the autopalatine. In *Auchenipterus*, *Epapterus*, *Entomocorus*, *Gelanoglanis*, *Pseudepapterus*, *Pseudotatia*, *Centromochlus* (except *Centromochlus reticulatus*, *Centromochlus simplex* and *Centromochlus perugiae*), *Tatia carolae*, *Trachelyopterus amblops*, *Trachelyopterus insignis* and *Tympanopleura brevis*, the maxilla is elongate in adults. In those species with the derived condition, the rod-shaped maxilla is larger than the autopalatine, sometimes reaching to the anterior margin of the orbit. Nuptial males, which have an altered condition of an enlarged, ossified maxillary barbel, were excluded from the evaluation of the present feature.

102. [3591] Maxilla, dorsal articulation, expansion: (0) present; (1) absent.

Among siluriforms with double maxillary condyles for articulation to the cranium, both articulations commonly have the same length. Alternatively, in *Auchenipterus*, *Epapterus*, *Pseudepapterus* and Diplomystidae, the dorsal condyle is expanded in a laminar ossification, which is approximately twice as large as the ventral condyle.

103. [3592] Maxilla, teeth: (0) present; (0) absent (Arratia, 1992: char. 1; de Pinna, 1993: char. 53; Britto, 2002: char. 148; Diogo, 2004: char. 259; de Pinna *et al.*, 2007: char. 3, Birindelli, 2014: char. 133; modified).

Among the examined taxa, only Diplomystidae have teeth along the maxilla.

104. [3593] Maxilla, size in mature males: (0) similar to females and non-nuptial males; (1) elongate, distinctly longer than in females and non-nuptial males (Ferraris, 1988: char. J13; Akama, 2004: char. 171; Ribeiro, 2011: char. 82; Birindelli, 2014: char. 134; modified).

The maxilla of males is usually of the same size as in females, even in the reproductive season. However, the elongation of the maxillary bone in nuptial males is a distinctive feature of some Auchenipteridae (Akama, 2004). Among them, in nuptial males of *Ageneiosus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, *Tympanopleura*, *Tetranematichthys*, *Trachelyopterus teaguei*, *Trachelyopterus insignis* and *Trachelyopterus amblops*, the maxilla is much longer than that of females and non-nuptial males.

105. [3594] Maxilla, tubercles in nuptial males: (0) absent; (1) present (Ferraris, 1988: char. J15; Walsh, 1990: char. 22; Royero, 1999: char. 129, 130; Akama, 2004: char. 172; Birindelli, 2014: char. 135).

Among the species examined, strongly ossified tubercles on the maxilla of nuptial males occur in *Ageneiosus*, *Tympanopleura*, *Tetranematichthys* and *Trachelyopterus insignis*. The number, distribution and shape of the tubercles vary among those taxa.

106. [3595] Coronomeckelian bone: (0) present; (1) absent (Arratia, 1992: char. 47; de Pinna, 1993: char. 23; Diogo, 2004: char. 424; Vigliotta, 2008: char. 26; Birindelli, 2014: char. 136).

The coronomeckelian bone is a small, ossified element present mesially on the medial portion of the mandibular arch (see Vigliotta, 2008: fig. 7a). The coronomeckelian is positioned anteriorly to the anguloarticular and is block-like, bearing a tiny ossified process on its dorsal portion. Among the taxa examined, the coronomeckelian bone is absent in some species of Aspredinidae (according to Birindelli, 2014) and Mochokidae. However, all species of Aspredinidae observed herein, except for *Pterobunocephalus*, have a coronomeckelian bone. Furthermore, this bone is also absent in Hoplomizontinae and *Xylophius* (Friel, 1994). Previous authors (Mo, 1991; de Pinna, 1993; Diogo, 2004; Birindelli, 2014) have also observed the absence of this bone in Astroblepidae, Callichthyidae, Loricariidae, Malapteruridae

and Scoloplacidae. However, contrary to the above authors, [Vigliotta \(2008\)](#) observed a reduced coronomeckelian bone in mochokid species of *Synodontis* but coded the reduction of this bone as an absence. In the present study, *Synodontis ornatipinnis* Boulenger, 1899, *Synodontis petricola*, *Mochokus*, *Mochokiella* and *Chiloglanis* lack the coronomeckelian bone. Furthermore, *Helogenes* has a greatly reduced coronomeckelian bone that is very distinctive relative to other Siluriformes.

107. [3596] Coronomeckelian bone, position: (0) horizontal; (1) oblique.

The coronomeckelian bone in most Siluriformes is located anterior to the anguloarticular and is positioned horizontally and slightly above the mandibular ramus, in the same direction as the horizontal Meckel's cartilage. In the Centromochlinae (except *Centromochlus existimatus*, *Centromochlus heckelii*, *Centromochlus perugiae*, *Centromochlus meridionalis*, *Centromochlus schultzi*, *Tatia intermedia*, *Tatia* sp. 4 and *Glanidium*),

Liosomadoras and the outgroup Pimelodidae, *Atopocheilus* and *Euchilichthys*, the coronomeckelian bone is obliquely positioned, beside the ascending process, and is located more dorsally relative to the anguloarticular lamina. Taxa without a coronomeckelian bone were coded as inapplicable for this character.

108. [3597] Coronomeckelian bone, configuration: (0) conspicuously separated from anguloarticular; (1) strongly sutured and continuous with anguloarticular.

The coronomeckelian in most Siluriformes is a bony element that is conspicuously separated from the laminar anguloarticular bone ([Fig. 5C](#)). Auchenipteridae and Doradidae are variable for this character and, in some taxa, the coronomeckelian bone is continuous with the bony lamina of the anguloarticular, which are sutured to each other ([Fig. 5A, B, D, E](#)). Taxa lacking the coronomeckelian bone were coded as inapplicable for this character.

109. [3598] Meckel's cartilage, ascending process: (0) present; (1) absent ([Mo, 1991](#): char. 35; [de Pinna](#),

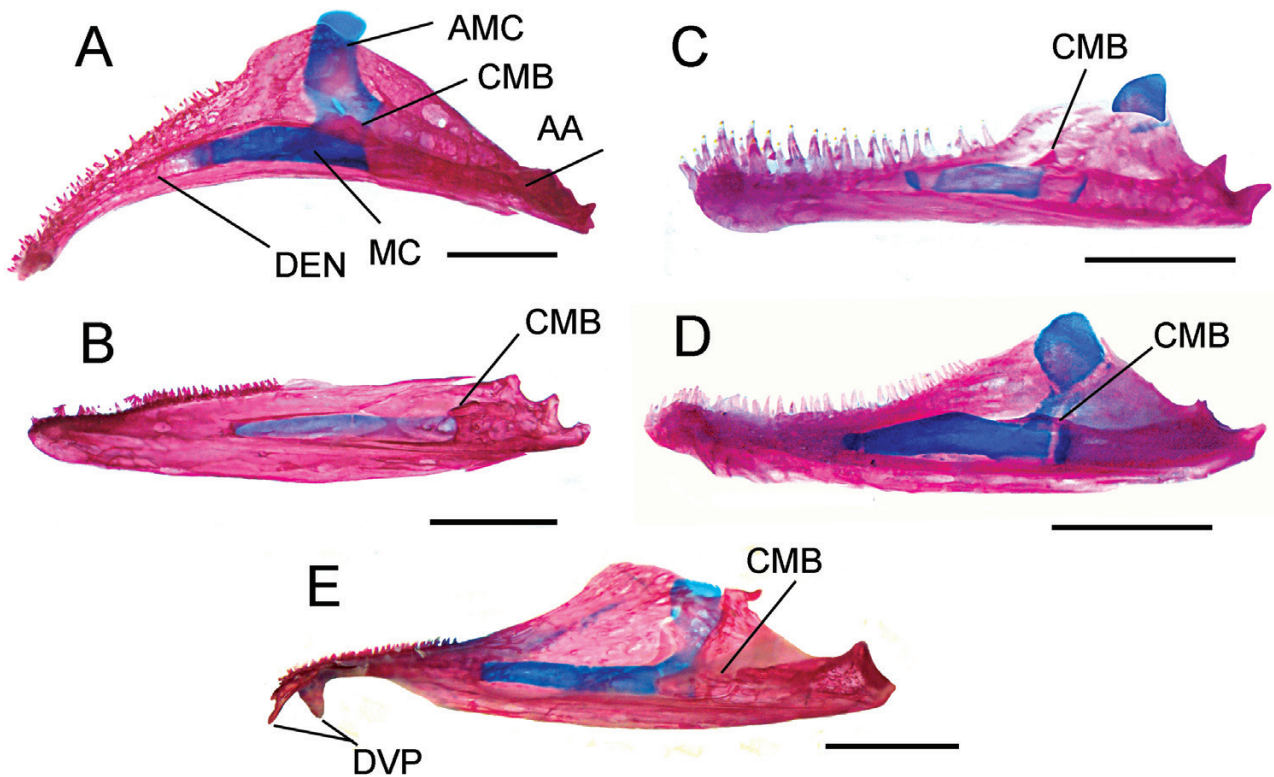


Figure 5. Medial view of the lower jaw. A, *Tympanopleura brevis*, MCP 30617. B, *Centromochlus existimatus*, MCP 29838. C, *Tatia strigata*, MCP 46595. D, *Pseudauchenipterus affinis*, MZUSP 51720. E, *Auchenipterus nuchalis*, MCP 19708. Abbreviations: AA, anguloarticular; AMC, ascending process of Meckel's cartilage; CMB, coronomeckelian bone; DEN, dentary; DVP, dentary ventral process; MC, Meckel's cartilage. Scale bars: 5 mm.

1993: char. 22; Britto, 2002: char. 155; Diogo, 2004: char. 419; Vigliotta, 2008: char. 244; Birindelli, 2014: char. 138).

In the plesiomorphic condition of catfishes, Meckel's cartilage is composed of two rami: a branch running horizontally in the middle of the dentary (horizontal Meckel's cartilage) and a branch running vertically on the posterodorsal portion of the dentary (i.e. ascending Meckel's cartilage), which is near the articulation with the coronoid process and lateral to the coronomeckelian bone. Among the taxa examined, only Mochokidae, *Helogenes marmoratus* and the auchenipterids *Asterophysus*, *Centromochlus existimatus* and *Centromochlus heckelii* lack the ascending process of Meckel's cartilage, a derived condition within Siluriformes (Fig. 5B).

110. [3599] Meckel's cartilage, ascending process, extension: (0) absent; (1) present, greatly surpassing dorsal margin of dentary.

In the plesiomorphic condition, the ascending process lacks an extension. Among the taxa examined, *Entomocorus* and some species of *Ageneiosus*, *Auchenipterichthys*, *Tympanopleura* and *Trachycorystes menezesi* have an elongate dorsal projection on the ascending process of Meckel's cartilage, starting from the middle of the dentary and greatly surpassing its dorsal margin. Taxa without an ascending process of Meckel's cartilage were coded as inapplicable for this character.

111. [3600] Mandible, coronoid process: (0) present; (1) absent (de Pinna, 1993: char. 50; Britto, 2002: char. 151; Diogo, 2004: char. 400; Vigliotta, 2008: char. 27; Birindelli, 2014: char. 139).

The coronoid process is a bony elevation formed by the confluence of the dentary and the anguloarticular (retroanguloarticular in remaining Otophysi) that holds innumerable tendons and muscles of the adductor mandibulae complex in its dorsomedial surface connecting the mandible to the palatoquadrate, suspensorium and opercular bony structures. Additionally, the coronoid process is involved in the connection of the mandible to the neurocranium through the attachment of the dorsal extension of the muscle malaris onto the neurocranium, which is considered a synapomorphy to the Siluriphysi (Datovo & Vari, 2014). In Auchenipteridae, the coronoid process is well developed in most species. Among the taxa examined, the coronoid process is absent in Mochokidae and in the auchenipterids *Asterophysus*, *Centromochlus existimatus* and *Centromochlus heckelii* (Fig. 5B).

112. [3601] Mandible, anguloarticular, coronoid process, size: (0) approximately same size as posterior portion of dentary; (1) deeper than posterior portion of dentary; (2) shallower than posterior portion of dentary.

In most catfishes, the anguloarticular portion that participates of the conformation of the coronoid process is approximately the same size as the dentary portion of the process, with the dorsal border of both bones ending approximately at the same line (Fig. 5C). In some taxa with the derived condition, the anguloarticular portion of the coronoid process is deeper or surpasses the dorsal margin of the posterior portion of the dentary (dentary portion of the coronoid process), as in Ariidae, Pimelodidae, some species of Aspredinidae, *Trachelyopterus*, *Spinipterus* and *Auchenipterus* (Fig. 5E). In contrast, in *Entomocorus*, *Epapterus*, *Gelanoglanis* and most species of *Ageneiosus*, *Tympanopleura piperata*, *Tympanopleura cryptica* and Doradidae, the anguloarticular portion of the coronoid process is smaller than the posterior portion of the dentary.

113. [3602] Mandible, anguloarticular, coronoid process, shape: (0) developed as a thin, conspicuous process; (1) developed as a large, laminar process (Britto, 2002: char. 153; modified).

Some taxa have a very conspicuous coronoid process in the anguloarticular portion, developed as a deep, thin, dorsal projection of bone configuring the plesiomorphic condition. In some species of Centromochlinae with the plesiomorphic condition, the coronoid process is not much elongated but still forms a distinct point. In the derived condition, the coronoid process is developed into a large lamina that is somewhat elevated and curved but never pointed, and found in Centromochlinae (except *Glanidium*, a few species of *Tatia* and *Centromochlus meridionalis*), *Ageneiosus* (except *Ageneiosus dentatus*), *Auchenipterichthys*, *Pseudauchenipterus*, *Trachelyichthys*, *Tympanopleura atronatus* and *Tympanopleura rondoni*.

114. [3603] Dentary, posterodorsal portion, shape: (0) elevated; (1) straight.

In most catfishes, the posterodorsal portion of the dentary is elevated, forming a dorsal apex. In *Asterophysus*, *Centromochlus existimatus*, *Centromochlus heckelii*, Mochokidae and most Aspredinidae, the dorsal margin of the dentary is entirely straight, without any distinctive elevation along its length.

115. [3604] Dentary, pair of ventral processes: (0) absent; (1) present (Ferraris, 1988: char. J17; Akama, 2004: char. 53; Marceniuk *et al.*, 2012: char. 108; Birindelli, 2014: char. 142).

In the plesiomorphic condition, the ventral margin of dentary lacks any process. A conspicuous ventral process on the ventral margin of the anterior portion of the dentary is present in some Auchenipteridae (*Auchenipterus*, *Epapterus*, *Pseudepapterus* and *Spinipterus acsi*) and may be associated with the mental barbels (Ferraris, 1988; Akama, 2004; Birindelli, 2014). In contrast to the observations of Birindelli (2014), no ventral process linked to the mental barbels was found in the species of *Entomocorus* or *Genidens* examined here.

116. [3605] Dentary, teeth: (0) present; (1) absent (Sabaj, 2002: char. 14; Birindelli, 2014: char. 143; modified).

The plesiomorphic condition within Siluriformes is the possession of teeth on the dentary. The auchenipterids *Epapterus* and *Pseudepapterus* and the doradids *Oxydoras* and *Trachydoras* lack dentary teeth.

117. [3606] Dentary, symphysis, ventral process: (0) absent; (1) present (Britto, 2002: char. 162; Birindelli, 2014: char. 145).

Among the taxa examined, the Ariidae, *Helogenes*, some Doradidae, and the auchenipterids *Asterophysus*, *Auchenipterus*, *Pseudauchenipterus* (except *Pseudauchenipterus flavescens*), *Tympanopleura brevis*, *Tympanopleura rondoni*, *Ageneiosus lineatus*, *Ageneiosus dentatus* and *Trachycorystes trachycorystes* have an anteroventral process on the dentary symphysis (Fig. 5E).

118. [3607] Dentary, symphysis, orientation: (0) straight; (1) dorsally projected.

Most catfishes have straight contralateral dentaries on the symphysis. Among the taxa examined, only *Asterophysus* and *Tocantinsia* have the medial portion of the dentary dorsally arched on the symphysis, forming a curved elevation on its anterior portion and rendering the mandible prognathous relative to the premaxilla.

Suspensorium and opercular series

119. [3608] Autopalatine, anterior portion, condyle, number: (0) two; (1) one (Arratia, 1992: char. 9; Britto, 2002: char. 171; Birindelli, 2014: char. 146).

In the plesiomorphic condition of Diplomystidae, the anterior portion of the autopalatine is bifurcated and developed into two large condyles.

The anterior portion of the autopalatine bears a unique condyle covered with cartilage in most taxa examined, configuring the derived condition.

120. [3609] Autopalatine, posterior condyle, cartilage: (0) large; (1) small (de Pinna, 1993: char. 21; Diogo, 2004: char. 283; Vigliotta, 2008: char. 41; Birindelli, 2014: char. 152; modified).

In most Siluriformes, the autopalatine has an anterior and a posterior condyle, each covered by a cartilage. In most catfishes, the cartilages of both condyles are large and approximately of the same size. *Ageneiosus*, *Tympanopleura*, *Auchenipterus*, *Entomocorus*, some species of *Tatia* and Mochokidae have a reduced cartilage on the posterior condyle, which is almost completely restricted to the mesial portion of the condylar facet and not conspicuously expanded to the lateral surface.

121. [3610] Autopalatine, mesial portion, expansion: (0) absent; (1) present.

Within auchenipterids, in *Ageneiosus* and *Tympanopleura*, and in *Helogenes*, the mesial portion of the autopalatine is distinctly expanded to articulate with the lateral ethmoid anterolateral cartilage. In remaining taxa, the autopalatine and the lateral ethmoid are also in contact, but the autopalatine is not expanded and is positioned more ventrally.

122. [3611] Autopalatine, posterior portion, shape: (0) mesially curved; (1) straight.

In *Diplomystes*, *Ageneiosus* (except *Ageneiosus intrusus* and *Ageneiosus dentatus*) and *Tympanopleura* (except *Tympanopleura atronatus* and *Tympanopleura cryptica*), the posterior portion of the autopalatine is curved mesially. In most catfishes, the autopalatine is approximately straight throughout its length.

123. [3612] Autopalatine and premaxilla, relative position: (0) distant from each other; (1) autopalatine close to posterior portion of premaxilla; (2) autopalatine close to medial portion of premaxilla.

Among Auchenipteridae, *Entomocorus*, *Epapterus*, *Gelanoglanis stroudi*, *Gelanoglanis travieso*, *Pseudepapterus* and some species of *Auchenipterus*, the autopalatine is distantly positioned relative to the premaxilla, and the anterior cartilage of the condyle is positioned laterally to the premaxilla. In most Siluriformes, the autopalatine is positioned close to the posterior portion of the premaxilla, and the

anterior portion of the autopalatine overlaps the premaxilla. In *Ageneiosus*, *Tympanopleura* and *Tetranematichthys*, the autopalatine is close to the middle of the premaxilla.

124. [3613] Hyomandibula, posterodorsal process: (0) absent; (1) present, weakly developed; (2) present, well developed (Royer, 1999: char. 61; Akama, 2004: char. 56; Birindelli, 2014: char. 159).

The dorsal portion of the hyomandibula can have two distinct processes, the anterior and the posterior. The presence of an anterior process on the hyomandibula is a plesiomorphy, being the common condition in most catfishes. The posterodorsal process of the hyomandibula helps its articulation to the neurocranium, and it is usually similar in shape to the anterior process, but smaller in size. In Auchenipteridae, most *Auchenipterus*, *Entomocorus*, *Epapterus*, *Gelanoglanis*, *Pseudauchenipterus flavescens*, *Pseudepapterus* and *Spinipterus* lack the posterodorsal process of hyomandibula. This process is present and weakly developed in *Auchenipterichthys punctatus*, some *Auchenipterus*, *Tetranematichthys*, *Tocantinsia*, *Trachelyopterichthys*, *Trachycorystes menezesi*, *Tympanopleura atronatus* and most species of the genera *Centromochlus*, *Pseudauchenipterus* and *Tatia*, whereas it is well developed in *Ageneiosus* (except *Ageneiosus inermis*), most *Auchenipterichthys*, *Glanidium*, *Liosomadoras*, *Pseudotatia*, *Trachelyopterus*, *Trachycorystes trachycorystes* and a few *Centromochlus* and *Tatia*.

125. [3614] Hyomandibula, posterodorsal process, shape: (0) wide, length equal to depth; (1) thin, length shorter than depth.

The hyomandibular posterodorsal process is relatively wide, with the distal portion rounded in most catfishes examined. This process is longer and thinner, somewhat spine shaped in *Ageneiosus militaris*, *Ageneiosus pardalis*, *Auchenipterichthys* (except *Auchenipterichthys punctatus*), *Glanidium*, *Liosomadoras*, *Tympanopleura atronatus*, most *Trachelyopterus* and some *Centromochlus* and *Tatia*. Those taxa lacking the hyomandibular posterodorsal process were coded as inapplicable for this character.

126. [3615] Hyomandibula, adductor crest: (0) absent or indistinguishable; (1) present (Lundberg, 1970: char. 61; modified).

The adductor crest in Siluriformes is a bony ridge present on the posterior portion of the

lateral face of the hyomandibular, a vertical bony ridge where the pars epistegalis of the adductor mandibulae muscle is inserted (Datovo & Vari, 2014; e.g. CA3 of Lundberg, 1970: fig. 68). The shape of the hyomandibula and the configuration of the suspensorium complex are variable among the Siluriformes, rendering it difficult at times to distinguish the adductor crest from the levator crest, especially when both form a continuous prominent curve along the hyomandibula. Certain catfishes, such as Diplomystidae, Ariidae, some species of Mochokidae, Pimelodidae and Doradidae, lack a distinct adductor crest.

127. [3616] Hyomandibula, adductor crest, development: (0) weakly developed; (1) well developed.

The adductor crest of the hyomandibula in most catfishes is poorly developed, visible as a strong scar on the bone, but rarely forming a laminar elevated crest. Conversely, in some taxa, the adductor crest is developed into a vertical bony keel, distinctively large. Taxa without an adductor crest were coded as inapplicable for this character.

128. [3617] Hyomandibular, levator operculi crest: (0) absent; (1) present (Lundberg, 1970: char. 64; Birindelli, 2014: char. 157; modified).

Dorsal to the hyomandibular condyle, a distinctive large bony crest can be present on the posterodorsal portion of the hyomandibula, where the muscle levator operculi is inserted. The presence of such a crest is variable among the auchenipterids.

129. [3618] Hyomandibula, opercular condyle, size: (0) short, with no distinct base; (1) elongate, with distinct base (Royer, 1999: char. 63; Akama, 2004: char. 58; Birindelli, 2014: char. 160; modified).

In most taxa examined, the hyomandibular opercular condyle is short and lacks a distinct base, with the base length smaller than its width. The posterior margin of the hyomandibula bears a condyle that articulates with the opercle. This condyle is more evident in the aspredinids, *Helogenes*, and the auchenipterids *Auchenipterus* and *Epapterus*, which have a relatively elongate and distinct base to the condyle, surpassing the posterior margin of the suspensorium. Birindelli (2014) coded *Entomocorus* and *Pseudepapterus* as bearing an elongate condyle, but this condition was not observed in the present study.

130. [3619] Hyomandibula, articulation to neurocranium: (0) via sphenotic, pterotic and

prootic; (1) via sphenotic and pterotic; (2) via prootic and sphenotic, (3) via sphenotic only (Mo, 1991: char. 21; Arratia, 1992: char. 35; Royero, 1999: char. 56; Britto, 2002: char. 181; Vigliotta, 2008: char. 10; Birindelli, 2014: char. 162; modified).

The bones involved in the articulation of the hyomandibula to the neurocranium vary among Auchenipteridae. The plesiomorphic condition is present only in the outgroup. Among auchenipterids, the hyomandibula can be articulated to the neurocranium via the sphenotic and pterotic, a condition found in *Ageneiosus*, *Auchenipterichthys*, *Liosomadoras*, *Pseudauchenipterus*, *Pseudotatia*, *Spinipterus acsi*, a few *Tatia*, *Tetranematichthys*, *Trachelyichthys* (except *Trachelyichthys exilis*), *Trachelyopterichthys*, *Trachycorystes menezesi*, *Tympanopleura* and most species of the genera *Centromochlus*, *Glanidium* and *Trachelyopterus*. Only *Asterophysus* has the hyomandibula articulated via the prootic and sphenotic, whereas

in most of the family this articulation occurs via the sphenotic only.

131. [3620] Hyomandibula and metapterygoid, contact: (0) in contact with each other; (1) separated (Arratia, 1992: char. 25; Britto, 2002: char. 189; Birindelli, 2014: char. 164).

In almost all catfishes, the hyomandibula articulates to the metapterygoid anteriorly (Fig. 6B). However, the dorsal or posterodorsal expansion of the quadrate in some cases, in addition to the elongation of the hyomandibula in others, may cause the hyomandibula and metapterygoid to lose contact. This derived condition is found in the auchenipterids *Ageneiosus*, *Tatia* (except *Tatia carolae*), *Tympanopleura*, *Tetranematichthys* and *Centromochlus existimatus*, *Centromochlus heckelii*, *Centromochlus reticulatus*, *Centromochlus simplex*, the doradids *Nemadoras*, *Oxydoras*, *Rhynchodoras* and *Trachydoras* and the aspredinid *Pseudobunocephalus* (Fig. 6A). Birindelli (2014) coded Aspredinidae as

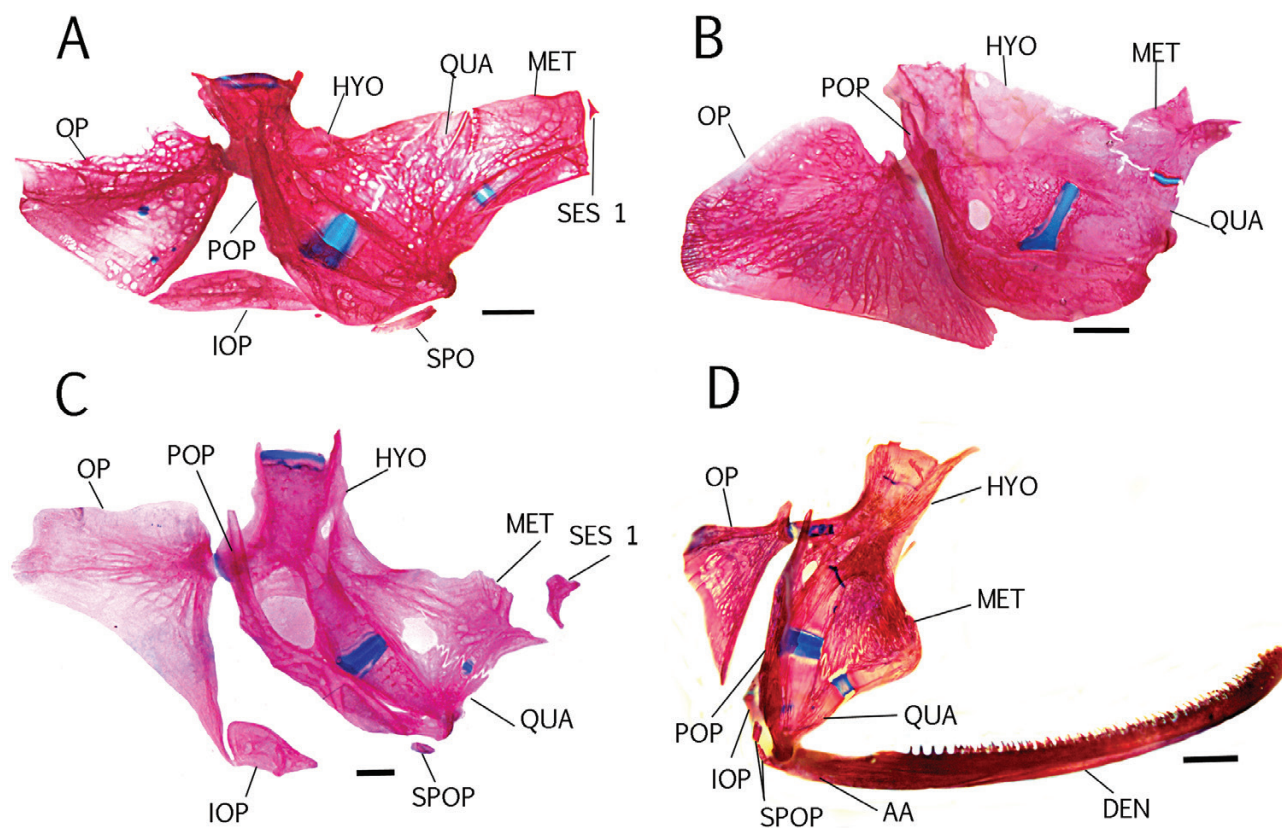


Figure 6. Lateral view of suspensorium. A, *Tympanopleura brevis*, MCP 30617. B, *Auchenipterus nuchalis*, MCP 19708. C, *Pseudauchenipterus affinis*, MZUSP 51720. D, *Asterophysus batrachus*, ANSP 158294. Abbreviations: AA, anguloarticular; DEN, dentary; HYO, hyomandibula; IOP, interopercle; MET, metapterygoid; OP, opercle; POP, preopercle; QUA, quadrate; SES 1, sesamoid 1; SPOP, subpreopercle. Scale bars: 1 mm (A–C); 2 mm (D).

having no contact between the hyomandibula and the metapterygoid. Although Birindelli observed different species of *Bunocephalus* and *Pseudobunocephalus*, the contact between these elements was confirmed in *Bunocephalus doriae* Boulenger, 1902. However, according to Friel (2008: fig. 1), *Pseudobunocephalus lundbergi* also lacks contact between the hyomandibula and the metapterygoid, with the latter element extremely reduced in size. Thus, Aspredinidae seem to be highly variable for this feature, even at the intrageneric level. Furthermore, *Aspredo aspredo* was coded as inapplicable for this character because it lacks the metapterygoid, and *Pterobunocephalus depressus* (Haseman, 1911) was coded as polymorphic.

132. [3621] Sesamoid bone 1 (= entopterygoid; anterior pterygoid element), shape: (0) very elongated and flattened; (1) curved and irregular in shape; (2) large, plate-like; (3) extremely reduced, spherical to ovoid (Vigliotta, 2008: char. 44; modified).

The homology of pterygoid elements among catfishes remains unclear relative to the remaining members of Teleostei. The homology of these elements has been extensively discussed, as has the origin attributed to these structures in Siluriformes: whether they originated from a dermal bone, chondro-bone or tendon-bone. The anterior displacement of the metapterygoid in Siluriformes relative to other Teleostei, and the laminar expansion of the hyomandibula, might explain the existence of so many different hypotheses regarding the homology of the suspensorium elements in catfishes (for more details, see Britto, 2002: char. 186). In this context, according to Regan (1911), Kindred (1919), Alexander (1965), Gosline (1975), Arratia (1990, 1992) and Arratia & Schultze (1991), and corroborated by Britto (2002), the endopterygoid (= entopterygoid of Arratia, 1992 and Birindelli, 2014; sesamoid 1 of Diogo *et al.*, 2001 and Britto, 2002; and anterior pterygoid element of Vigliotta, 2008) and the ectopterygoid (sesamoid bone 2 of Diogo *et al.*, 2001) would be in the equivalent position of the metapterygoid in other Teleostei, which could cause misinterpretation of their homology. Another homology hypothesis is the fusion of the endopterygoid and ectopterygoid to the metapterygoid (Howes & Teugels, 1989). However, the origin of both pterygoid elements in catfishes is a common assertion among most of the above authors, in which these structures are ossifications derived from the mineralization of the ligament between the metapterygoid and the neurocranium (Britto, 2002; Vigliotta, 2008) and positioned in the

ventromedial portion of the palate, rather than derived from the dermal membrane.

In most Auchenipteridae, the sesamoid bone 1 is relatively small compared with the metapterygoid and has an irregular shape, curved, with the medial portion rounded or truncated, in some cases bearing one or two small processes, and with the lateral portion tapering to a tip. However, especially in *Gelanoglanis*, the mochokid *Synodontis* and the aspredinid *Pseudobunocephalus*, sesamoid bone 1 is extremely reduced and rounded to ovoid. Furthermore, in *Ageneiosus*, *Tympanopleura*, *Tetranematichthys*, *Helogenes marmoratus*, the Doradidae and some species of Aspredinidae, sesamoid 1 is approximately rectangular to plate-like, and is positioned near to or in contact with the metapterygoid in *Ageneiosus* and *Tympanopleura*. A more extreme condition can be found in *Auchenipterus*, *Epapterus*, *Pseudepapterus*, some Mochokidae and Diplomystidae, in which sesamoid 1 is very elongate, thin and flattened and positioned transversely to the body axis. According to Arratia (1990, 1992), sesamoid bone 1 is occasionally present in *Diplomystes*. Notwithstanding, Arratia (1990, 1992) noted that the presence of the tendon-bone entopterygoid is a synapomorphy for the siluriforms (the condition is reversed in the loricarioids). *Mochokiella paynei* was coded as inapplicable because sesamoid bone 1 is absent.

133. [3622] Sesamoid bone 2 (= ectopterygoid): (0) present; (1) absent (Ferraris, 1988: char. J4; Arratia, 1992: char. 18; Britto, 2002: char. 188; Birindelli, 2014: char. 166).

The sesamoid bone 2 or ectopterygoid is an ossicle derived from the mineralization of a ligament (tendon-bone) and is positioned between sesamoid 1 (= entopterygoid) and the autopalatine. The anterior end of sesamoid bone 2 is in contact with the posterior autopalatine cartilage. In some species of *Diplomystes*, this articulation is very strong, and sesamoid bone 2 is plate-like, fused to the ventral portion of the autopalatine. Among the taxa examined, Pimelodidae, Ariidae, Diplomystidae, *Pseudobunocephalus rugosus* and *Oxydoras niger* have a sesamoid bone 2.

134. [3623] Suprapreopercle: (0) present; (1) absent (Lundberg, 1970: char. 70; Britski, 1972: char. 21; Britto, 2002: char. 196; Birindelli, 2014: char. 167).

The suprapreopercle is an ossicle located dorsally to the preopercle and ventrally to the pterotic. Sometimes, the suprapreopercle is restricted to a

tubular ossification that involves the preopercle–mandibular ramus of the sensorial canal. The suprapreopercle and the preopercle–mandibular ramus seem to have independent origins, because the features of the suprapreopercle are independent of the presence of a preopercle canal in the temporal region (Pastana, 2014). The suprapreopercle is present in all auchenipterids, except *Centromochlus perugiae*, *Gelanoglanis stroudi*, *Gelanoglanis travieso*, and *Spinipterus acsi*, and in all outgroup families except Diplomystidae, *Helogenes* and *Wertheimeria*. In *Gelanoglanis*, the tubular preopercle–mandibular ramus of the sensorial canal is present, but the ossification is not.

135. [3624] Suprapreopercle, size: (0) short, its length never surpassing twice width; (1) elongate, much longer than wide.

The suprapreopercle can vary in size from elongate to short. In the plesiomorphic condition, the suprapreopercle is short, usually rectangular in shape, and its length never exceeds twice its width. In the derived condition, the suprapreopercle is elongate and tubular, and its length is three times or more its width, as found in *Ageneiosus*, *Asterophysus*, most *Auchenipterus*, *Centromochlus meridionalis*, *Centromochlus reticulatus*, *Entomocorus*, *Epapterus*, *Gelanoglanis pan*, *Gelanoglanis varii*, *Glanidium cesarpintoii*, *Liosomadoras*, *Pseudauchenipterus flavescens*, *Pseudotatia*, some *Tatia*, *Tetranematichthys*, *Trachelyichthys*, *Tympanopleura*, some *Trachelyopterus* and *Trachycorystes menezesi*.

136. [3625] Subpreopercle: (0) present; (1) absent (Britto, 2002: char. 197; Birindelli, 2014: char. 168).

The subpreopercle is a tiny ossification of the sensorial canal located between the preopercle and the mandibular complex. All auchenipterids have the subpreopercle, located below the hyomandibula and mesially to the preopercle. Among the taxa examined, the subpreopercle is absent in Mochokidae and Ariidae.

137. [3626] Interopercle, shape: (0) large, ovoid, surpassing half of quadrate length; (1) large, elongated; (2) small ovoid, never reaching half of quadrate length.

The opercular series of Siluriformes comprises the opercle, preopercle and interopercle, with the subopercle absent (Fink & Fink, 1981). The interopercle is located anteriorly to the opercle and is attached to it by connective tissue (Britto,

2002). In Siluriformes, the interopercle has a wide variation in size and shape. The interopercle is located ventromedially in the suspensorium complex and between the opercle and the mandibula, and in the auchenipterids, it is anterior to the subpreopercle ossicle and usually medially overlapping a portion of the preopercle plus the hyomandibula. In *Auchenipterichthys*, *Gelanoglanis*, *Trachelyopterichthys*, Diplomystidae, Ariidae (except *Cathorops spixii*), Pimelodidae, Aspredinidae (except *Aspredo*), Doradidae (except *Trachydoras*) and *Mochokiella*, the interopercle is a large, flat bone, with approximately the same width as the quadrate or at least surpassing half its length. In Auchenipteridae, the shape of the interopercle is highly variable; it can be elongated (Fig. 6A), as in most Auchenipterini species, or it may be small and ovoid, with its length never surpassing half the quadrate length. The latter condition is found in some species of *Centromochlus* and *Tatia*, *Glanidium*, *Pseudauchenipterus* and *Liosomadoras* (Fig. 6C).

Hyoid arch

138. [3627] Urohyal, ventral surface, lateral laminar wings: (0) present; (1) absent (Mo, 1991: char. 39; de Pinna, 1993: char. 239; Royero, 1999: char. 146; Britto, 2002: char. 81; Vigliotta, 2008: char. 46; Diogo, 2004: char. 388; Birindelli, 2014: char. 169).

The anterior portion of the urohyal is articulated to the ventral hypohyal, with the lateral margins of the posteroventral portion expanded into laminar flanges forming large wings in most catfishes. In Diplomystidae, these laminar expansions are very conspicuous. In Auchenipteridae, Doradidae, and the aspredinids *Aspredo aspredo* and *Pseudobunocephalus*, the laminar expansions are absent. This character should be examined in ventral view, because dorsally the urohyal has a cylindrical projection, somewhat elongate and, in auchenipterids, can also bear small wings that could be confused with the ventral ones.

139. [3628] Urohyal, ventral surface, posterior portion, length: (0) elongate, at least twice the length of the main body of the urohyal; (1) short, approximately the same length as the main body of the urohyal; (2) absent.

The urohyal is a short bony element and generally bears a very conspicuous posterior projection developed in a vertical bony lamina, visible only in ventral view in cleared and stained specimens. Among Siluriformes, the size of this

posterior projection is variable, and in most catfishes, it is short, equivalent in length to the urohyal or, in most cases, never surpassing half the length of the anterior ceratohyal. However, in the auchenipterids *Ageneiosus*, *Auchenipterus*, *Auchenipterichthys longimanus*, *Centromochlus heckelii*, *Centromochlus existimatus*, *Epapterus*, *Pseudepapterus*, *Tympanopleura*, *Tetranematichthys*, Diplomystidae, Ariidae and some species of Doradidae, the posterior projection is very elongated, surpassing at least

half the length of the anterior ceratohyal and reaching approximately three times the size of the urohyal (Fig. 7A–C).

140. [3629] Urohyal, ventral surface, posterior portion, width: (0) compact; (1) laminar.

The posterior portion of the ventral surface of the urohyal in most catfishes is relatively large, usually a robust, somewhat cylindrical bony structure, or laterally expanded (Fig. 7B). However, in *Epapterus*, *Pseudepapterus*

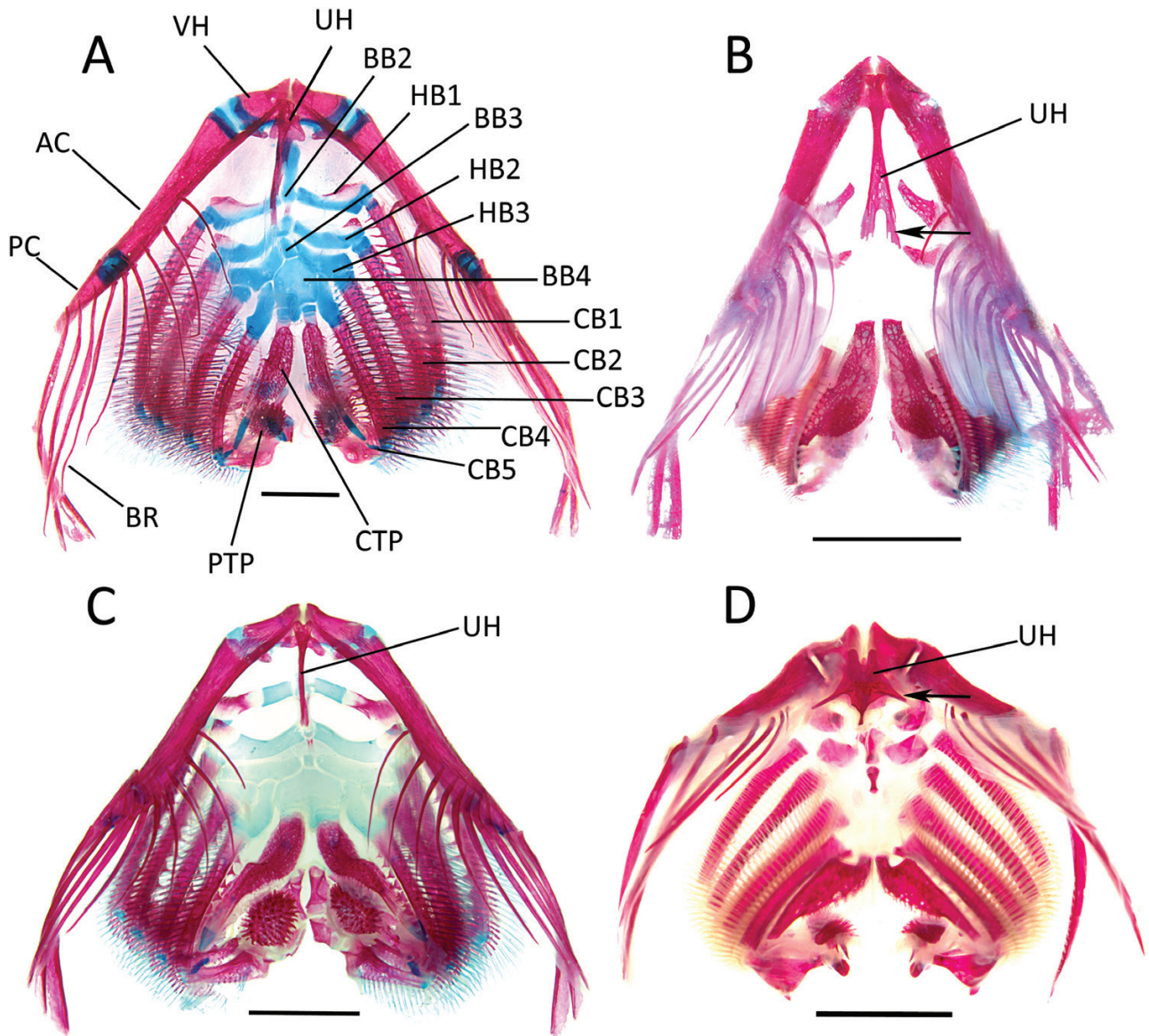


Figure 7. Ventral view of hyoid arches. A, *Tympanopleura brevis*, MCP 30617. B, *Ageneiosus uranophthalmus*, MCP 35507; arrow, bifurcation of urohyal. C, *Tetranematichthys wallacei*, MCP 27174. D, *Genidens genidens*, MCP 8317; arrow, lateral process of urohyal. Abbreviations: AC, anterior ceratohyal; BB, basibranchial; BR, branchiostegal rays; CB, ceratobranchial; CTP, ceratobranchial tooth plate; HB, hypobranchial; PC, posterior ceratohyal; PTP, pharyngobranchial tooth plate; UH, urohyal; VH, ventral hypohyal. Scale bars: 2 mm (A, C); 10 mm (B); 5 mm (D).

cucuhyensis, *Tetranematichthys*, *Tympanopleura brevis*, and *Tympanopleura cryptica*, the posterior portion is narrow and laminar dorsoventrally, not developed laterally (Fig. 7A, C).

141. [3630] Urohyal, ventral surface, posterior portion, shape: (0) simple; (1) bifurcated.

The posterior portion of the ventral surface of the urohyal can be restricted to a simple bone, not bifurcated (Fig. 7A, C) or, as found in most catfishes, bifurcated distally in species of *Ageneiosus*, *Tympanopleura* (except

Tympanopleura brevis and *Tympanopleura cryptica*) and *Tetranematichthys* (Fig. 7B).

142. [3631] Urohyal, dorsal surface, lateral projections: (0) absent; (1) present.

In most catfishes, the urohyal dorsal surface is slightly expanded posteriorly, becoming somewhat triangular to spearhead shaped, having no conspicuous lateral projections (Fig. 8A–C). In *Tetranematichthys*, there are conspicuous projections on the lateral margins of the urohyal, forming wings (Fig. 8B).

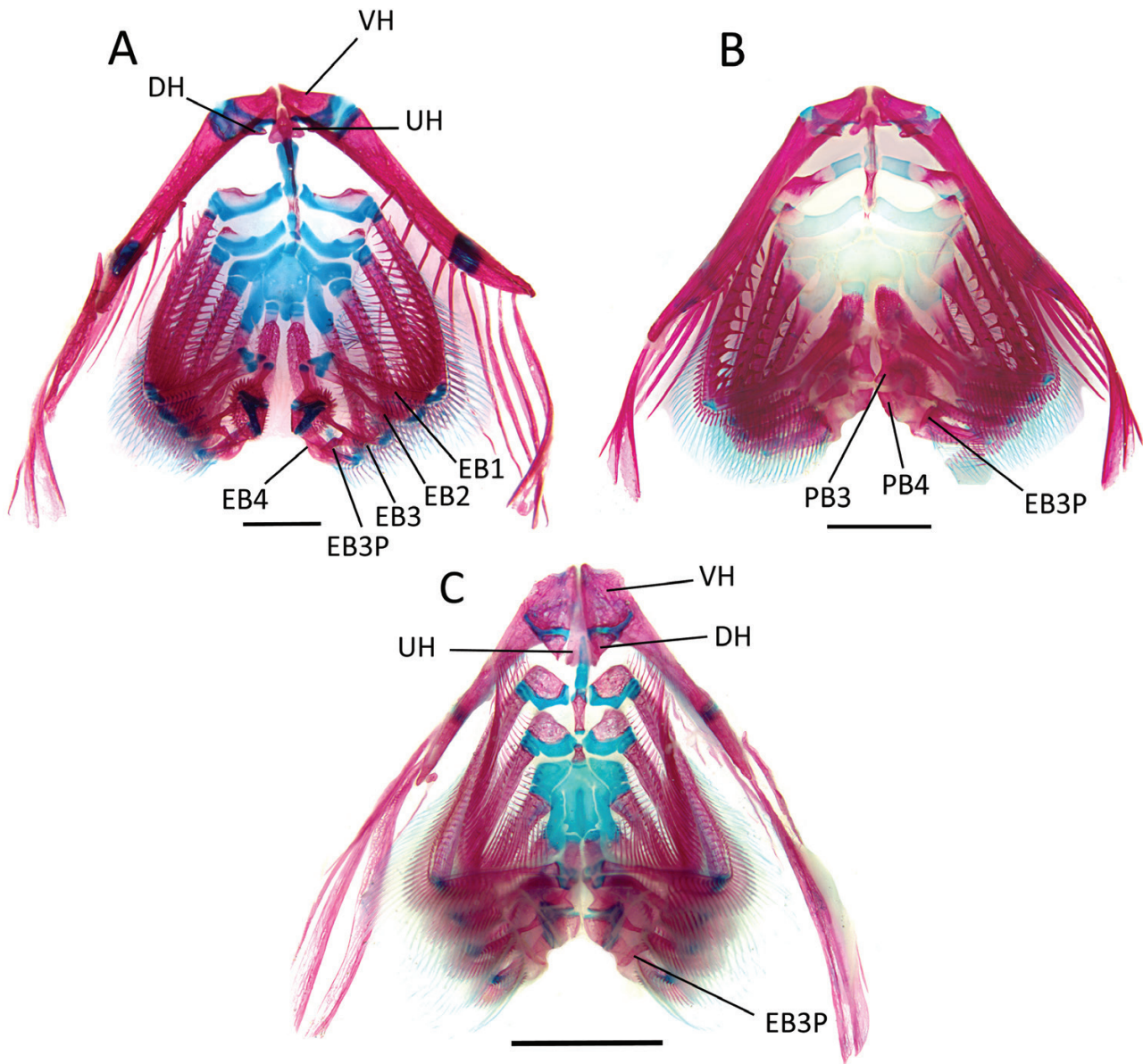


Figure 8. Dorsal view of hyoid arches. A, *Tympanopleura brevis*, MCP 30617. B, *Tetranematichthys wallacei*, MCP 27174. C, *Auchenipterus nuchalis*, MCP 19708. Abbreviations: DH, dorsal hypohyal; EB, epibranchial; EB3P, epibranchial 3 process; PB, pharyngobranchial; UH, urohyal; VH, ventral hypohyal. Scale bars: 2 mm (A, B); 5 mm (C).

143. [3632] Urohyal, ventral surface, lateral projections: (0) absent; (1) present.

In most siluriforms, the ventral surface of the urohyal is devoid of lateral processes (Fig. 7A–C). In Ariidae, the urohyal has a large lateral process on its ventral surface, forming a tripod (Fig. 7D).

144. [3633] Dorsal hypohyal: (0) present; (1) absent (Mo, 1991: char. 43; Britto, 2002: char. 75; Birindelli, 2014: char. 171).

The dorsal hypohyal is present in all taxa examined except the Aspredinidae, which lack this element.

145. [3634] Ventral hypohyal and anterior ceratohyal, ventral connection: (0) synchondral; (1) bony suture (Ferraris, 1988: char. G8; Walsh 1990: char. 10; Akama, 2004: char. 83; Birindelli, 2014: char. 175).

In most catfishes, the posterior portion of the ventral hypohyal and the anterior ceratohyal are synchondrally articulated (Fig. 7D). In *Ageneiosus*, *Tympanopleura* and *Tetranematichthys*, these bones are connected by means of a strong bony suture, visible in ventral view (Fig. 7A–C).

Branchial arches

146. [3635] First two branchial arches, gill rakers, number of rows: (0) two; (1) one; (2) none (Britski, 1972: char. 24; de Pinna, 1993: char. 176; Royero, 1999: char. 113; Britto, 2002: char. 129; Akama, 2004: char. 85; modified; Birindelli, 2014: char. 181).

The branchial arches of the Otophysi usually bear two rows of gill rakers (Britto, 2002). Notwithstanding, certain catfish families have only one row of gill rakers in the first two branchial arches. Furthermore, in *Gelanoglanis* and *Pseudobunocephalus*, the gill rakers are entirely absent from those arches. In *Trachelyichthys*, *Trachelyopterichthys* and in some species of Aspredinidae, the gill rakers are extremely reduced in size and barely ossified, almost imperceptible even under a stereomicroscope, but they are present.

147. [3636] Third and fourth branchial arches, gill rakers, number of rows: (0) two; (1) one; (2) none (Britski, 1972: char. 24; de Pinna, 1993: char. 176; Royero, 1999: char. 113; Britto, 2002: char. 129; Akama, 2004: char. 85; Birindelli, 2014: char. 182).

In most catfishes, the third and fourth branchial arches have the same number of gill-raker rows as

in the first two arches. However, *Synodontis* and most species of *Centromochlus* have only one row of gill rakers on the third and fourth branchial arches. *Gelanoglanis* and *Pseudobunocephalus* lack gill rakers on those arches. In *Trachelyichthys* and *Trachelyopterichthys*, the third and fourth gill rakers are present in two rows and are reduced in size, as described for the previous character.

148. [3637] Gill rakers, size across branchial arches: (0) gill rakers of all branchial arches of same size; (1) gill rakers of first branchial arch distinctly longer than those in remaining arches.

The gill rakers are approximately the same size across all branchial arches in most catfishes. However, in *Ageneiosus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, *Pseudauchenipterus*, *Tympanopleura* and the outgroup, except for Diplomystidae, Aspredinidae and some Mochokidae, the first branchial arch bears very elongate gill rakers, distinctly longer than those in the remaining branchial arches, with the gill rakers in arches 2–4 decreasing slightly in size.

149. [3638] Upper gill rakers, size: (0) moderate, length approximately half of gill filaments; (1) reduced, length less than one-fifth of gill filaments; (2) long, length two-thirds of gill filaments (Britski, 1972: char. 24; Ferraris, 1988: char. G4; Walsh, 1990: char. 27; Royero, 1999: char. 111; Akama, 2004: char. 84, 86; Birindelli, 2014: char. 181, modified).

The gill rakers in most catfishes are of moderate size, reaching to but not surpassing half the length of the gill filaments. However, the gill rakers of most auchenipterids are reduced in size, less than one-fifth the length of the gill filaments. Conversely, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus* and *Tympanopleura cryptica* have elongate gill rakers, approximately two-thirds the length of the gill filaments. This character was modified and the size restricted to only the gill rakers located on the upper portion of the branchial arch because the size of the gill rakers can vary in some species.

150. [3639] Upper gill rakers, shape: (0) conical; (1) base greatly wide, thin tip; (2) filamentous.

The gill rakers of auchenipterids are variable in shape and seem to be related to the diet. In most auchenipterids, the upper gill rakers are conical, similar to a short tooth (Fig. 9A). However, in *Ageneiosus*, *Pseudauchenipterus* and *Tetranematichthys*, the gill rakers are shaped somewhat like shark teeth, with a wide base

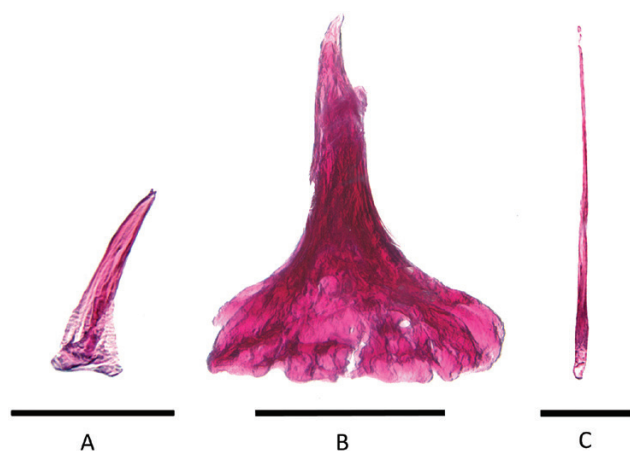


Figure 9. Shape of gill rakers. A, *Tympanopleura atronasus*, MCP 36338. B, *Tetranematichthys wallacei*, MCP 27174. C, *Epapterus dispilurus*, MCP 40991. Scale bars: 200 μ m (A); 500 μ m (B, C).

(but not serrated) and with the distal portion being thinner and pointed, sometimes slightly curved (Fig. 9B). Furthermore, the gill rakers of *Auchenipterus*, *Entomocorus*, *Epapterus* and *Pseudepapterus* are very elongate and filamentous, although ossified (Fig. 9C).

151. [3640] Gill rakers, spines: (0) absent; (1) present (Royer, 1999: char. 112; Birindelli, 2014: char. 184).

Siluriformes usually have smooth gill rakers, but some species of *Ageneiosus* and *Tympanopleura*, and *Tetranematichthys* have hard, spine-shaped processes on the gill rakers. Although in *Ageneiosus* the spiny processes are present on different sides of the gill rakers, in *Tetranematichthys* the spines are found on the dorsal and ventral surfaces (Fig. 9A, B). In the latter case, the spines give the impression of bifurcated gill rakers, as already noted by Royer (1999). In addition, the present observations corroborate those of Royer (1999), who coded the presence of spines also to *Ageneiosus* through *Ageneiosus magoi*, which was not examined here. In contrast, Birindelli (2014) considered the spines to be absent in *Ageneiosus* based on the taxa he observed.

152. [3641] Gill filaments, ossification: (0) not ossified; (1) ossified (Britto, 2002: char. 126).

In the plesiomorphic condition, as in the auchenipterids *Asterophysus*, *Auchenipterus brevior*, some species of *Centromochlus* and *Gelanoglanis*, the gill filaments are unossified (Britto, 2002; fig. 66B). In most catfishes examined,

the gill filaments are partly ossified (Britto, 2002; fig. 66A). The level of ossification is variable, sometimes restricted to the proximal portion and very subtle, as in most *Centromochlinae*, or the ossification may extend almost to the mid-length of the filament.

153. [3642] Second and third basibranchials, size: (0) moderate to large; (1) reduced (Ferraris, 1988: char. G6; Akama, 2004: char. 81; Birindelli, 2014: char. 187).

Most catfishes have the second and third basibranchials large and normally developed. Particularly in *Asterophysus*, *Ageneiosus*, *Gelanoglanis* and *Tympanopleura*, these bones are much reduced in size.

154. [3643] Fourth basibranchial, posterior process: (0) absent; (1) present (Birindelli, 2014: char. 188).

Among the taxa examined, only the Doradidae and *Euchilichthys* have a distinctly thin, elongated process on the posterior portion of the fourth basibranchial. Birindelli (2014) mentioned this process as ventral in the character title, but in the discussion and in the figure legend it is referred to as the posterior process, an anatomical description more in line with the position of this element, a term adopted herein.

155. [3644] Third and fourth basibranchial, accessory cartilage: (0) absent; (1) present (Ferraris, 1988: char. G2; de Pinna, 1993: char. 184; de Pinna, 1996: char. 41; Britto, 2002: char. 90; Akama, 2004: char. 79; Birindelli, 2014: char. 190).

In Auchenipteridae, a relatively extensive, rounded accessory cartilage is present between the third and the fourth basibranchials in some species of *Ageneiosus*, *Auchenipterichthys*, *Auchenipterus fordicei*, *Centromochlus perugiae*, *Pseudauchenipterus flavescens*, *Pseudepapterus hasemani*, *Tetranematichthys*, *Trachelyichthys* and *Trachelyopterichthys*. This cartilage is also present in Mochokidae, but absent in the remaining species examined.

156. [3645] First hypobranchial, shape: (0) discoid; (1) funnel shaped, with constriction at mid-portion and medial margin narrower than lateral margin; (2) both distal portions of approximately same width, rectangular to hourglass shaped; (3) elongated, cylindrical (Higuchi, 1992: char. A46; Birindelli, 2014: char. 191, modified).

Most catfishes have the first hypobranchial discoid or somewhat ovoid, usually bearing an anterior pointed process (state 0; Fig. 8C). The

first hypobranchial in the auchenipterids varies in shape. In some groups, it is funnel shaped, with the lateral margin more than twice the width of the medial one (state 1; Fig. 8A). In the second derived condition, the first hypobranchial is rectangular to hourglass shaped, usually with a conspicuous constriction on the medial portion of both anterior and posterior margins, but in some cases curved on the posterior margin and somewhat straight on the anterior. In this condition, both tips, medial and lateral, are large and of approximately the same width (state 2; Fig. 8B). *Asterophysus* and *Gelanoglanis* are the only taxa in Auchenipteridae having the first hypobranchial very long and cylindrical (state 3). This character was distinctly coded as compared with Birindelli (2014), because the inclusion of many taxa introduced a greater variation of shapes.

157. [3646] Second hypobranchial: (0) ossified; (1) cartilaginous (de Pinna, 1996: char. 38; Britto, 2002: char. 92; de Pinna et al., 2007: char. 38; Birindelli, 2014: char. 192).

In Siluriformes, the second hypobranchial is partly or totally ossified. Among taxa examined, the second hypobranchial is entirely cartilaginous in *Gelanoglanis stroudi*, *Gelanoglanis travieso*, *Trachelyichthys*, some Aspredinidae and *Helogenes marmoratus*.

158. [3647] First epibranchial, shape: (0) medial portion enlarged, wider than lateral portion; (1) uniformly cylindrical (Ferraris, 1988: char. G3; Walsh, 1990: char. 8; Royero, 1999: char. 109; Akama, 2004: char. 7; Birindelli, 2014: char. 195).

The epibranchials are located on the dorsal portion of the branchial arch and contact the pharyngobranchial elements medially. In Diplomystidae and the auchenipterids *Ageneiosus*, *Tympanopleura* (except *Tympanopleura brevis* and *Tympanopleura cryptica*) and *Tetranematichthys*, the medial portion of the first epibranchial, which contacts the third pharyngobranchial, is larger than its lateral portion. In most Siluriformes, the first epibranchial is usually cylindrical, with approximately the same width throughout its length.

159. [3648] Third epibranchial, posterior process, size: (0) short, shorter than epibranchial portion mesial to the process bifurcation point; (1) long, approximately of the same length as the epibranchial portion mesial to the bifurcation point.

The third epibranchial of catfishes bears a distinct process on the posterior portion that causes this element to appear bifurcated. Some taxa have a short posterior process, shorter than the epibranchial portion mesial to the bifurcation point (Fig. 8B). However, the process is usually approximately the same length as the third epibranchial portion mesial to the process bifurcation point, which is not covered by gill filaments in *Ageneiosus vitattus*, *Auchenipterus*, *Auchenipterichthys longimanus*, *Auchenipterichthys thoracatus*, *Epapterus*, *Gelanoglanis*, *Pseudauchenipterus* (except *Pseudauchenipterus affinis*), *Pseudepapterus*, *Pseudotatia*, *Spinipterus acsi*, *Trachycorystes trachycorystes*, *Tympanopleura atronatus* and most *Trachelyopterus* and *Trachelyichthys* (Fig. 8C). *Pseudobunocephalus* was coded as inapplicable because it lacks a posterior process.

160. [3649] Third epibranchial, posterior process, distal portion, shape: (0) rounded to square; (1) pointed.

The distal portion of the posterior process of the third epibranchial is usually rounded to square, and its base is wide (Fig. 8C). In *Ageneiosus* (except *Ageneiosus inermis* and *Ageneiosus militaris*), *Auchenipterus ambyiacus*, *Auchenipterus brachyurus*, *Centromochlus* (except *Centromochlus macracanthus* and *Centromochlus meridionalis*), *Gelanoglanis Entomocorus*, *Pseudauchenipterus*, *Pseudepapterus*, *Pseudotatia* and some species of the genera *Tatia*, *Trachelyichthys*, *Trachelyopterus* and *Tympanopleura brevis*, the process tapers and ends in a sharp point, and its base is relatively thin (Fig. 8A).

161. [3650] First pharyngobranchial: (0) present; (1) absent (Mo, 1991: char. 47; de Pinna, 1993: char. 140; Britto, 2002: char. 116; de Pinna et al., 2007: char. 75; Marceniuk et al., 2012: char. 182; Birindelli, 2014: char. 197).

Among Siluriformes, only Ariidae and Diplomystidae possess the first pharyngobranchial.

162. [3651] Second pharyngobranchial: (0) present; (1) absent (de Pinna, 1993: char. 185; Britto, 2002: char. 118; de Pinna et al., 2007: char. 65; Birindelli, 2014: char. 198).

Among Siluriformes, only Diplomystidae have the second pharyngobranchial.

163. [3652] Upper pharyngobranchial tooth plate, shape: (0) rounded to ovoid, slightly longer than wider; (1) elongate, length at least three times its width (Britski, 1972: char. 25; Ferraris, 1988: char. G5; Akama, 2004: char. 80; Birindelli, 2014: char. 199; modified).

In most auchenipterids, the upper pharyngobranchial tooth plate is rounded to ovoid. It is attached to the fourth pharyngobranchial and also contacts the third pharyngobranchial. In the auchenipterids *Asterophysus*, *Auchenipterus ambyiacus*, *Auchenipterus brachyurus*, *Epapterus*, *Gelanoglanis*, *Liosomadoras*, *Pseudepapterus* and some species of *Trachelyopterus*, the upper pharyngobranchial tooth plate is elongated, and its length is approximately three times its width.

164. [3653] Upper pharyngobranchial tooth plate, anterior process: (0) present; (1) absent.

Among catfishes, a pointed anterior process on the upper pharyngobranchial tooth plate is variably present. Among outgroups examined, the Aspredinidae, the Doradidae (except for *Anadoras grypus* (Cope, 1872)), *Helogenes* and *Mochokiella* lack the anterior process. Among the auchenipterids, this process is absent in *Ageneiosus*, *Asterophysus*, *Epapterus*, *Pseudepapterus*, *Pseudotatia*, *Trachycorystes trachycorystes*, *Tatia* sp. 1, *Tympanopleura* and some species of the genera *Auchenipterichthys*, *Auchenipterus* and *Centromochlus*.

Vertebrae, Weberian apparatus and associated structures

165. [3654] Transformator process of tripus, posterior portion, shape: (0) straight; (1) ventromedially folded; (2) ventrally curved (Britski, 1972: char. 19; Ferraris, 1988: char. V2; Royero, 1999: char. 73; Akama, 2004: char. 69; Birindelli, 2014: char. 203; modified).

The parapophysis of the third vertebra and its corresponding rib are hypothesized to be the origin of the tripus (Rosen & Greenwood, 1970; Arratia, 1987; Britto, 2002). In most Otophysi, the tripus has a posterior process modified into a hook (Britto, 2002), which is termed the transformator process of the tripus. In most Siluriformes, it is usually straight to slightly concave ventrally and, according to the above authors, weakly attached to the gas bladder. However, in Auchenipteridae and Doradidae, the posterior margin of the transformator process is ventromedially folded and strongly attached to the gas bladder. In

most mochokids, the transformator process is semicircular, hood-like and ventrally curved. Conversely, the mochokid *Synodontis* have the transformator process straight or very slightly curved ventrally, but visibly do not configure the folded condition.

166. [3655] Os suspensorium, size: (0) moderate; (1) reduced (Ferraris, 1988: char. V4; Royero, 1999: char. 70; Britto, 2002: char. 213; Akama, 2004: char. 70; Birindelli, 2014: char. 204).

The ventral margin of the os suspensorium is composed of a narrow nodule that usually has a strong connection to the compound vertebral centrum. In most Siluriformes, the os suspensorium is of moderate size and firmly attached to the compound centrum (Fig. 10B). Conversely, in most Doradoidea, *Pseudobunocephalus* and *Euchilichthys*, the os suspensorium is also connected to the compound centrum but is much smaller (Fig. 10A).

167. [3656] Os suspensorium, shape: (0) flat and rectangular; (1) round or angled (Vigliotta, 2008: char. 83; modified).

The os suspensorium is variable in shape among the siluriforms, sometimes elongated and forming a rectangular, flattened bone that is not articulated to or in contact with the vertebra, or in other cases with the ventral region rounded to angled and sometimes attached to the vertebra.

168. [3657] Compound centrum, anterior parapophysis and transcapular process, connection: (0) sutured together; (1) free from each other (Birindelli, 2014: char. 205; modified).

The parapophysis of the compound centrum usually has two rami. The anterior ramus is large and elongated and sutured to the posterolateral portion of the transcapular process in all Siluriformes examined except the Auchenipteridae, Doradidae, Mochokidae (except *Chiloglanis*) and Ariidae. In these taxa, there is no contact between the anterior parapophysis of the compound centrum and the transcapular process.

169. [3658] Compound centrum, anterior parapophysis, shape: (0) laminar bone, not developed into a modified process; (1) developed into a modified process called the Müllerian ramus (Vigliotta, 2008: char. 76; Birindelli, 2014: char. 205; modified).

The anterior ramus of the parapophyses of the compound centrum in most catfishes is a large

laminar bone, which is usually attached to the ventrolateral portion of the transcapular process. However, the Ariidae bear a laminar anterior parapophysis that is not sutured to the transcapular process. In contrast, Auchenipteridae, Doradidae and Mochokidae have a distinct parapophysis of the compound centrum, where the distal portion is modified into a flexible structure with a rod-like base bearing a discoid bony element (the Müllerian ramus) on its lateral portion (Fig. 10). The Müllerian ramus in combination with its protractor muscle forms the elastic spring apparatus (Müller, 1842a, b) capable of producing sound via the contraction and retraction of the muscle responsible for distending and vibrating the gas bladder. This very elaborate structure seems to represent a complex evolutionary process that probably involves many events within the evolutionary history.

170. [3659] Müllerian ramus, depth: (0) deep discoid; (1) shallow disc.

In Auchenipteridae and Doradidae, the anterior parapophysis of the compound centrum is modified into a Müllerian ramus, with the distal process as a deep or thick discoid element

(Fig. 10). However, the Mochokidae also have the Müllerian ramus enlarged, but as a shallow discoid, laminar bone. The taxa in which the anterior parapophysis of the compound centrum is not modified into a Müllerian ramus were coded as inapplicable for this character (see character 169).

171. [3660] Müllerian ramus, distal portion, shape: (0) flattened disc; (1) protruded posteriorly (Ferraris, 1988: char. V8; Soares-Porto, 1998: char. 16; Royero, 1999: char. 67; Akama, 2004: char. 68; Birindelli, 2014: char. 206).

Among taxa with a Müllerian ramus, the distal portion is a flattened disc that contacts the anterior surface of the swimbladder (Ferraris, 1988: char. V8). Only *Centromochlus heckelii* and *Centromochlus existimatus* have the Müllerian ramus protruded posteriorly, forming a deep and hollow bag, which inwardly contacts the anterior surface of the swimbladder.

172. [3661] Müllerian ramus, size: (0) large; (1) reduced.

Among taxa examined, the lateral discoid process is large, much larger compared with the tripus. However, a rare condition of a reduced

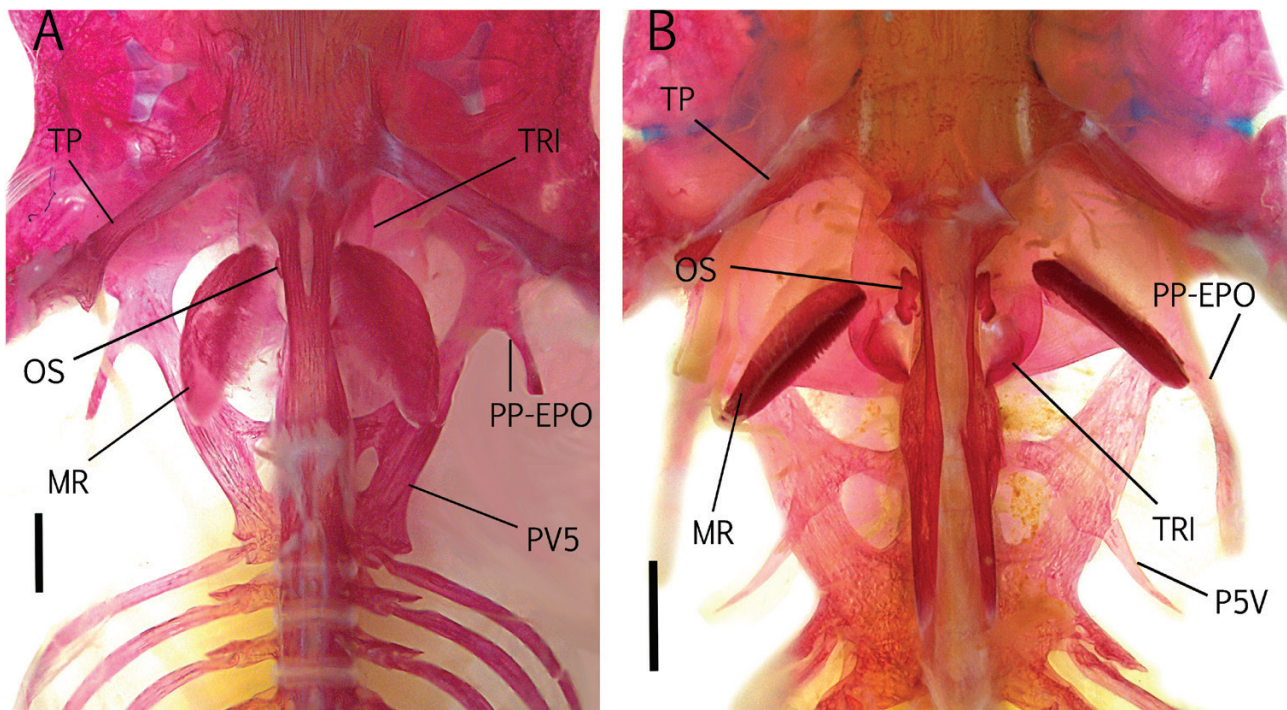


Figure 10. Compound centrum and associated structures. A, *Tetranematichthys wallacei*, MCP 27174. B, *Auchenipterus nuchalis*, MCP 19708. Abbreviations: MR, Müllerian ramus; OS, os suspensorium; PP-EPO, posterior process of epioccipital; P5V, parapophysis of fifth vertebra; TP, transcapular process; TRI, tripus. Scale bars: 2 mm.

discoïd process, smaller compared with the tripus, is present in *Ageneiosus*, *Gelanoglanis*, *Pseudepapterus* and *Atopocheilus*. Although the discoïd process of *Gelanoglanis* is relatively long, it is much reduced in size, smaller than the tripus. The taxa in which the anterior parapophysis of the compound centrum was not modified into a Müllerian ramus were coded as inapplicable for this character (see character 167).

173. [3662] Müllerian ramus, orientation: (0) horizontally oriented; (1) vertically oriented.

Orientation of the discoïd Müllerian ramus is variable among Siluriformes that possess it. In the Doradidae, except *Franciscodoras* and *Trachydoras*, the flat side of the disc is oriented horizontally and facing ventrally. In auchenipterids, the disc is oriented vertically, with the flat surfaces contacting the gas bladder facing posteromesially. The taxa in which the anterior parapophysis of the compound centrum is not modified into a Müllerian ramus were coded as inapplicable for this character (see character 169).

174. [3663] Gas bladder, wall: (0) not ossified; (1) ossified (Ribeiro, 2011: char. 204; modified).

The lateral and ventral walls of the gas bladder in most catfishes are non-ossified, or not encapsulated in adults. In *Ageneiosus* (except for *Ageneiosus lineatus*), *Tympanopleura piperata* and *Tympanopleura cryptica*, the gas bladder wall is strongly ossified (encapsulated), with its anterior portion firmly attached to the posterior face of the Müllerian ramus. This observation corroborates the classification of Ribeiro (2011) for this character, except for *Ageneiosus lineatus*, in which no ossification was observed.

175. [3664] Compound centrum, posterior parapophysis: (0) present; (1) absent (Vigliotta, 2008: char. 79; Birindelli, 2014: char. 210).

The parapophysis of the compound centrum has large anterior and posterior rami. Almost all catfishes have the posterior ramus (posterior parapophysis), which is usually laminar and large but at times similar in shape to the parapophysis of the fifth vertebra. However, in Auchenipteridae and Doradidae, the posterior ramus is absent.

176. [3665] Fifth vertebra, parapophysis, size: (0) large, distinctly larger than parapophysis of sixth vertebra; (1) moderate, approximately same size as parapophysis of sixth vertebra; (2) small, distinctly smaller than parapophysis of sixth vertebra; (3) absent (de Pinna, 1996:

char. 57, 62; Britto, 2002: char. 233; Diogo, 2004: char. 138; Vigliotta, 2008: char. 80; Birindelli, 2014: char. 211; modified).

In the plesiomorphic condition, present in the auchenipterids *Ageneiosus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, *Tympanopleura*, *Tetranematichthys*, *Trachelyichthys* (except *Trachelyichthys* sp. 1), *Tatia carolae*, *Tatia creutzbergi* and *Trachelyopterus coriaceus*, the parapophysis of the fifth vertebra is very large, distinctly larger than the next one. However, in most auchenipterids, the parapophysis of the fifth vertebra is moderate in size, similar to the parapophysis of the subsequent vertebra. Notwithstanding, *Asterophysus*, *Auchenipterichthys*, *Pseudauchenipterus*, *Gelanoglanis*, *Trachelyopterichthys*, *Centromochlus existimatus*, *Centromochlus heckelii*, *Auchenipterus osteomystax*, *Tatia intermedia*, some species of *Glanidium* and some species of *Trachelyopterus* have a small parapophysis on the fifth vertebra. Among the auchenipterids examined, the parapophysis of the fifth vertebra is absent in *Trachelyopterus amblops*, *Trachelyopterus lucenai*, *Trachelyopterus teaguei*, *Trachelyopterus striatulus* and *Trachelyopterus porosus*. Birindelli (2014) did not report an expanded parapophysis on the fifth vertebra for Auchenipteridae. The present character was coded by comparing the parapophysis of the fifth vertebra with the sixth vertebra only, owing to variation in size between the sixth and the subsequent vertebrae. Commonly in siluriforms, the parapophysis of the sixth vertebra is larger than the subsequent ones, which usually decrease slightly in size towards the caudal peduncle.

177. [3666] Compound centrum, postzygapophysis, extension: (0) absent; (1) extending to end of fifth vertebra; (2) extending to end of sixth vertebra; (3) extending to end of seventh vertebra; (4) extending to end of eighth vertebra (Britto, 2002: char. 222, modified).

The vertebral centra of the Weberian apparatus in Siluriformes are fused to each other, forming a compound centrum, which is sutured to the fifth vertebra. The opposite condition can be found in the remaining Otophysi, in which the vertebral centra are separated by cartilage and not sutured to each other (Britto, 2002). The compound centrum of catfishes bears a pair of processes on the posterior end of the centrum, the postzygapophysis, which joins the neural prezygapophysis (processes on the anterior

portion of the centrum) of the subsequent posterior vertebra. This feature is variable in auchenipterids, and the ventral postzygapophysis of the compound centrum extends to the suture with the prezygapophysis of the sixth (Britto, 2002: fig. 100b), seventh (Britto, 2002: fig. 101) or eighth vertebral centrum. In addition, the postzygapophysis can be much smaller, reaching to the prezygapophysis of the fifth vertebra, as found in Aspredinidae and the doradids *Franciscodoras* and *Wertheimeria*, or they can be absent, as in Diplomystidae, *Cathorops* and *Helogenes*.

178. [3667] Compound centrum, composition: (0) including up to fourth vertebra; (1) including up to fifth vertebra; (2) including up to sixth vertebra; (3) including up to seventh vertebra; (4) including up to eighth vertebra (Arratia, 1992: char. 40; de Pinna, 1993: char. 208; Marceniuk *et al.*, 2012: char. 204; Vigliotta, 2008: char. 82; Birindelli, 2014: char. 217).

The compound centrum is composed of vertebral centra articulated to each other by a deep suture or fused. In the plesiomorphic condition, found in Diplomystidae and Cetopsidae, the compound centrum is composed of the second to fourth vertebrae, with the fifth vertebra free from the complex. In Diplomystidae, the first vertebral centrum is present and separated from the compound centrum; Arratia (1987) hypothesized this to be the primitive condition within the siluriforms. However, the number of vertebrae included in the compound centrum is variable in Siluriformes, especially in Auchenipteridae. Thus, in the present study, this variation was accounted for by coding the last vertebra included in the compound centrum. In most auchenipterids, the compound centrum includes the seventh vertebra, but the composition is variable within the family and can include the fifth, sixth, seventh or eighth vertebra. Birindelli (2014) coded *Ageneiosus*, *Asterophysus*, *Liosomadoras* and *Tetranemichthys* as including up to the seventh vertebra in the compound centrum, but in the present analysis only up to the sixth vertebra are included in those taxa. Additionally, disagreement with the codification of Birindelli (2014) occurred in the doradids *Acanthodoras*, *Oxydoras* and *Megalodoras*. The Doradoidea have a conspicuous ventral lamina usually covering or, in some cases, enclosing a portion of the compound centrum. Nevertheless, the expansion of this ventral laminar bone is independent from the fusion of the compound centrum, and the latter cannot be evaluated because the expansion

of the end of this ventral laminar bone in some species sometimes makes it either shorter or longer than the compound centrum.

179. [3668] Anterior ribs and parapophyses, articulation: (0) articulated to ventral surface of parapophysis; (1) articulated to posterodorsal surface of parapophysis; (2) articulated to posteroventral surface of parapophysis (Ferraris, 1988: char. V12; Vigliotta, 2008: char. 84; Birindelli, 2014: char. 219; modified).

The ribs on the anterior portion of the trunk are articulated to the distal portion of the parapophysis of the corresponding vertebral centra. The articulation can be to the ventral surface of the parapophysis, as found in the outgroup, except doradids, or through the posterodorsal surface of the parapophysis, as found in some *Ageneiosus*, *Auchenipterichthys*, *Auchenipterus nigripinnis*, some *Centromochlus*, *Gelanoglanis stroudi*, *Gelanoglanis pan*, *Glanidium ribeiroi*, *Liosomadoras*, *Tatia* (except *Tatia boemia*, *Tatia caxiuanaensis* and *Tatia intermedia*), some species of *Trachelyopterus*, *Tympanopleura brevis* and *Spinipterus*. Nonetheless, most auchenipterids have the anterior ribs articulated to the posteroventral surface of the parapophysis.

180. [3669] Ribs, proximal extremity, shape: (0) straight; (1) twisted (Ferraris, 1988: char. V12; de Pinna, 1993: char. 198; Britto, 2002: char. 239; Vigliotta, 2008: char. 84; Birindelli, 2014: char. 220).

The proximal portion of the anterior ribs, which are articulated to the vertebral parapophyses, is usually rounded but varies in shape between straight, as in *Diplomystes*, *Asterophysus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Gelanoglanis*, *Tocantinsia*, *Trachelyichthys*, *Trachelyopterichthys*, some *Tatia*, *Trachelyopterus teaguei*, *Trachycorystes menezesi* and *Tympanopleura brevis*, and twisted, as in most catfishes, with the proximal portion recurved to follow the articular surface on the parapophysis.

Dorsal fin and associated elements

181. [3670] Anterior nuchal plate: (0) present; (1) absent (Britski, 1972: char. 27; Ferraris, 1988: char. D1; Walsh, 1990: char. 4; Soares-Porto, 1998: char. 9; Royero, 1999: char. 26; Akama, 2004: char. 32, 40; Vigliotta, 2008: char. 19; Birindelli, 2014: char. 228).

The anterior nuchal plate is a dorsal expansion of the supraneural, and its presence varies among catfishes. The absence of the anterior nuchal plate was previously discussed by Birindelli (2014) and can involve two different events. In some groups, the anterior nuchal plate is fused to the middle nuchal plate or, according to Birindelli *et al.* (2007), it can reduce and disappear during ontogeny. The anterior nuchal plate is absent in the auchenipterids *Ageneiosus*, most *Centromochlus* (except *Centromochlus existimatus*, *Centromochlus heckelii* and *Centromochlus perugiae*), *Gelanoglanis*, *Pseudepapterus*, *Tatia carolae*, *Tatia musaica*, *Tatia meesi*, *Tympanopleura* and *Tetranematichthys*. Additionally, Ariidae, *Helogenes marmoratus*, Aspredinidae, *Euchilichthys*, *Chiloglanis*, *Nemadoras* and *Rhincodoras*, among the outgroups, were coded as missing the anterior nuchal plate. Contrary to the present study, Birindelli (2014) coded *Epapterus* and *Glanidium cesarpinto* with the derived condition. In *Epapterus*, the anterior nuchal plate is much reduced in size and circular in shape, surrounded by the middle nuchal plate. In *Glanidium cesarpinto*, the anterior nuchal plate is clearly evident and large, as in the remaining Auchenipteridae.

182. [3671] Anterior nuchal plate and parieto-supraoccipital, contact: (0) separated, not in contact; (1) in contact, sutured (Chardon, 1968: char. 229; Mo, 1991: char. 90; Royero, 1999: char. 25, 27; Britto, 2002: char. 282; Akama, 2004: char. 40; Birindelli, 2014: char. 229, modified).

In Diplomystidae, the anterior nuchal plate is located far from and not contacting the parieto-supraoccipital. However, the anterior nuchal plate in some Siluriformes contacts the parieto-supraoccipital through a strong suture. In the Auchenipteridae, Doradidae, Mochokidae and Pimelodidae examined herein, the anterior nuchal plate is strongly sutured along the entire posterior border of the parieto-supraoccipital. Those taxa where the anterior nuchal plate is absent were coded as inapplicable for this character.

183. [3672] Middle nuchal plate and parieto-supraoccipital, contact: (0) separated, not in contact; (1) in contact, sutured (Britski, 1972: char. 27; Ferraris, 1988: char. D3; Walsh, 1990: char. 4; Royero, 1999: char. 23; Vigliotta, 2008: char. 20; Akama, 2004: char. 35, 126; Birindelli, 2014: char. 231).

Most auchenipterids have a large anterior nuchal plate, which consequently, precludes the

middle nuchal plate from contacting the parieto-supraoccipital. The contact occurs in a few taxa in which the anterior nuchal plate is absent or reduced in size and a concomitant anterolateral expansion of the middle nuchal plate has occurred, which forms a configuration that allows such contact. This latter configuration of the derived condition is found in *Asterophysus batrachus*, *Entomocorus*, *Epapterus*, *Glanidium ribeiroi*, *Pseudotatia parva* and *Synodontis*. Contrary to the present study, Birindelli (2014) considered *Pseudotatia* to have no contact between the middle nuchal plate and the parieto-supraoccipital. Additionally, *Ageneiosus*, most *Centromochlus*, *Gelanoglanis*, *G. ribeiroi*, *Pseudepapterus*, *Tatia carolae*, *Tatia musaica*, *Tatia meesi*, *Tympanopleura*, *Tetranematichthys*, the Ariidae, Mochokidae, Pimelodidae and Doradidae also have contact between the middle nuchal plate and the parieto-supraoccipital. *Helogenes marmoratus* was coded as inapplicable for this character because the middle nuchal plate is absent.

184. [3673] Posterior nuchal plate, width: (0) narrow, narrower than base of dorsal-fin spine; (1) broad, approximately as wide as or wider than base of dorsal-fin spine.

The width of the posterior nuchal plate varies among the auchenipterids. The posterior nuchal plate can be narrower than the base of the dorsal-fin spine. Alternatively, the posterior nuchal plate can be wide, having approximately the same width or wider than the base of the dorsal-fin spine. *Helogenes marmoratus* was coded as inapplicable for this character because the posterior nuchal plate is absent.

185. [3674] First and second dorsal-fin pterygiophores and their corresponding neural spines, contact: (0) not sutured; (1) sutured (Britski, 1972: char. 26; Royero, 1999: char. 75; Britto, 2002: char. 286; Akama, 2004: char. 125; Birindelli, 2014: char. 234).

Diplomystidae, Aspredinidae and *Helogenes* have the first and second dorsal-fin pterygiophores not sutured to the neural spines, with those structures usually in contact via a ligament instead (Birindelli, 2014). In most catfishes examined, the first and second dorsal-fin pterygiophores are sutured to their corresponding neural spines.

186. [3675] Dorsal fin, free pterygiophores, number: (0) seven; (1) six; (2) five; (3) four; (4) three; (5) two (Ribeiro, 2011: char. 159, modified).

The plesiomorphic condition in catfishes is to have seven (Diplomystidae) or usually a higher

number (Ariidae, Pimelodidae, most Mochokidae) of pterygiophores supporting the soft dorsal-fin rays. However, among auchenipterids, this characteristic is variable and informative. Most species of Auchenipteridae and the Doradidae have five pterygiophores supporting the soft dorsal-fin rays. Notwithstanding, *Gelanoglanis*, *Spinipterus*, *Glanidium cesarpintoi*, *Trachelyopterichthys anduzei* and most species of *Tatia* and some of *Trachelyopterus* have four pterygiophores supporting the soft dorsal-fin rays. Exceptionally, in the auchenipterid *Trachelyopterichthys taeniatus*, *Trachelyichthys exilis*, *Pseudepapterus cucuhyensis* and Aspredinidae (except *Pseudobunocephalus iheringii* (Boulenger, 1891), there are three pterygiophores; and uniquely, in *Epapterus* there are only two, and six in *Pseudotatia*.

187. [3676] Dorsal fin, proximal radials, joined: (0) second and remaining proximal radials separated from first radial; (1) second and third proximal radials joined to first radial; (2) only second proximal radial joined to first radial.

The proximal radials in siluriforms are fused to medial ones (Schaefer, 1987) and herein referred to as the proximal radial. Nevertheless, the first proximal radial is considered to be fused to the supraneural of the dorsal fin (Schaefer, 1987) and to support the spinelet and the first unbranched dorsal-fin ray (usually modified into a spine). The configuration of the dorsal-fin skeleton in the plesiomorphic condition present in Diplomystidae, Pimelodidae and Cetopsidae is that all pterygiophores support branched rays (i.e. second proximal radial and thereafter) free from the first proximal radial complex. In some species of Mochokidae, the second and third proximal radials are fused to the first one. Notwithstanding, Auchenipteridae, Ariidae, Aspredinidae, Doradidae and remaining Mochokidae have the second proximal radial sutured to the first one.

188. [3677] Dorsal fin, posteriormost pterygiophore: (0) supporting ray; (1) not supporting ray.

Most Siluriformes have the posteriormost pterygiophore of the dorsal fin supporting one ray, or less commonly two rays, in which the last one is smaller and unbranched (see next character). A rarest condition of not supporting any rays is present in *Centromochlus* (except *Centromochlus meridionalis*), *Entomocorus*, some *Glanidium*, some *Tatia*, *Pseudotatia*, *Trachelyichthys* sp. 1, *Trachelyopterus coriaceus* and the Mochokid

Euchilichthys dybowskii (Vaillant, 1892). The complexity of the configuration of the dorsal-fin skeleton makes it difficult to trace the evolutionary scenario of distinct events, whether the posteriormost pterygiophore only lacks its corresponding ray (state 0) rather than the last pterygiophore being fused to the penultimate, when a ray is present (alternative hypothesis to state 0), or the last pterygiophore and its corresponding ray are, in fact, both absent (state 1). To understand properly the homology of the pterygiophores assuming any condition of loss, presence or fusion, an ontogenetic study is necessary.

189. [3678] Dorsal fin, number of soft rays: (0) seven; (1) six; (2) five; (3) four; (4) three.

The number of soft rays, i.e. not considering the first unbranched ray, which can be modified into a spine, is variable among Siluriformes, but considerably consistent within the groups, demonstrating this to be evolutionarily informative. The plesiomorphic condition is seven soft rays, a condition found in members of Diplomystidae, Ariidae and some Mochokidae. Pimelodidae, Doradidae and Auchenipterinae have six soft dorsal-fin rays (except some species of *Trachelyopterus* and *Trachelyichthys*), whereas members of Centromochlinae usually have five, except for some species of *Tatia*, mostly those of small body size with four, and *Glanidium ribeiroi* with six. Exceptionally, *Auchenipterus* has seven soft rays and *Epapterus*, three.

190. [3679] Dorsal fin, last pterygiophore, ventral bony projection: (0) present; (1) absent (Ribeiro, 2011: char. 160).

The last dorsal-fin pterygiophore in auchenipterids is usually similar to the more anterior ones, somewhat quadrangular but smaller in size. In the auchenipterids *Pseudoauchenipterus*, *Pseudepapterus cucuhyensis* and *Tetranematichthys* and in Diplomystidae, Ariidae, Pimelodidae and the doradids *Anadoras grypus* and *Megalodoras uranoscopus* (Eigenmann & Eigenmann, 1888), the last pterygiophore has a ventral bony projection that is more slender than the remaining portion of the structure. Ribeiro (2011) coded *Epapterus dispilurus* as having the ventral projection, which was not observed in the individuals examined herein.

191. [3680] Dorsal fin, last pterygiophore, posterior bony projection: (0) absent; (1) present.

Among catfishes, the last dorsal-fin pterygiophore has approximately the same depth throughout its length. However, the last dorsal-fin pterygiophore can bear a posterior bony projection, usually surpassing the origin of the last ray. This posterior projection is thinner than the remaining portion of the element. The latter condition is found in the auchenipterids *Ageneiosus*, *Auchenipterus*, *Auchenipterichthys* (except for *Auchenipterichthys punctatus*), *Epapterus*, most species of *Centromochlus* and *Tatia*, *Pseudepapterus*, *Pseudauchenipterus*, *Spinipeterus* sp. 'oncinha', *Tetranematichthys*, *Tocantinsia*, *Trachelyopterus* and *Tympanopleura*, and in *Pimelodus*, *Atopochilus* and *Nemadoras*.

192. [3681] Dorsal fin, spinelet: (0) present; (1) absent (Britto, 2002: char. 288; Birindelli, 2014: char. 235).

The spinelet is the first dorsal-fin ray, which in most catfishes is modified into a small element and, in some groups, serves as a locking mechanism for the second dorsal-fin ray, which is usually modified into a spine. Among the taxa examined, the dorsal-fin spinelet is absent in the Aspredinidae, *Helogenes*, *Gelanoglanis nanonotocolus* and *Gelanoglanis varii*.

193. [3682] Dorsal fin, spinelet, ventral process, size: (0) short, reaching ventrally to 20% of pterygiophore height; (1) long, reaching ventrally to middle of pterygiophore (Ferraris, 1988: char. D7; de Pinna, 1993: char. 233; de Pinna, 1996: char. 88; Britto, 2002: char. 289; Royero, 1999: char. 76; Birindelli, 2014: char. 236).

Among the taxa examined, Ariidae, Diplomystidae, Pimelodidae and, exceptionally, the auchenipterids *Pseudepapterus* and *Entomocorus gameroi* have a short ventral process on the spinelet. Those taxa without the dorsal-fin spinelet were coded as inapplicable for this character.

194. [3683] Dorsal fin, spinelet, ventral process, shape: (0) straight; (1) posteriorly curved.

The auchenipterids *Liosomadoras oncinus*, *Pseudauchenipterus affinis*, *Pseudauchenipterus jequitinhonhae*, *Tocantinsia*, *Trachycorystes*, *Trachelyopterichthys* and the Diplomystidae, Pimelodidae, Ariidae and some Mochokidae have a straight ventral process in the dorsal-fin spinelet. However, in most catfishes examined, the ventral process is curved posteriorly, forming a semicircle. Those taxa without the dorsal-fin spinelet were coded as inapplicable for this character.

195. [3684] Dorsal fin, spine: (0) present; (1) absent.

Among the taxa examined, only in *Gelanoglanis nanonotocolus*, *Gelanoglanis varii*, *Helogenes* and the Aspredinidae, the second dorsal-fin ray is not modified into a spine.

196. [3685] Dorsal fin, spine, size: (0) moderate, less than one-third of SL; (1) short, less than one-sixth of SL; (2) long, greater than one-third of SL (Britski, 1972: char. 27; Ferraris, 1988: char. D13; Curran, 1989: char. 14; Soares-Porto, 1998: char. 23; Akama, 2004: char. 127; Birindelli, 2014: char. 238; modified).

The dorsal-fin spine of most Auchenipteridae is of moderate length, never reaching one-third of the SL. Among the species examined, *Asterophysus*, *Epapterus*, *Pseudepapterus* and *Spinipeterus* have a very short spine. In contrast, *Centromochlus heckelii*, *Centromochlus existimatus*, *Tatia intermedia*, the mochokid *Synodontis ornatipinnis* and the doradids *Nemadoras humeralis* and *Trachydoras nattereri* have a long spine, surpassing one-third of the SL. Those taxa without a dorsal-fin spine were coded as inapplicable for this character.

197. [3686] Dorsal fin, spine of nuptial males, size: (0) same size as females and non-nuptial males; (1) longer than females and non-nuptial males (Royero, 1999: char. 126; Akama, 2004: char. 162; Birindelli, 2014: char. 239).

Nuptial males of Siluriformes have the dorsal-fin spine of the same size as females, except *Ageneiosus*, *Auchenipterus*, *Auchenipterichthys*, *Entomocorus*, *Epapterus*, *Liosomadoras*, *Pseudauchenipterus nodosus*, *Pseudepapterus*, *Tetranematichthys*, *Tympanopleura*, *Trachelyichthys*, *Trachelyopterichthys* and *Trachelyopterus*, which are modified in size and longer than in non-nuptial males and females. Those species for which a nuptial male was unavailable or for which there was no literature information were coded as unknown. Additionally, those taxa without a dorsal-fin spine were coded as inapplicable for this character.

198. [3687] Dorsal fin, spine of nuptial males, curvature: (0) straight; (1) strongly arched (Akama, 2004: char. 165; Birindelli, 2014: char. 240).

The plesiomorphic condition and common shape for nuptial male Siluriformes is a straight dorsal-fin spine. In the auchenipterids *Ageneiosus*, *Tetranematichthys*, *Tympanopleura*, *Trachelyopterus insignis*, *Trachelyopterus amblops* and *Trachelyopterus teaguei*, the

dorsal-fin spine is noticeably arched during the reproductive season. The changes in shape, size and ornamentation of the dorsal-fin spine of males seem to be linked directly to the amplexus behaviour during spawning. Those species for which a nuptial male was unavailable or for which there was no literature information were coded as unknown. Those taxa without a dorsal-fin spine were coded as inapplicable for this character.

199. [3688] Dorsal fin, spine of nuptial males, displacement when erect: (0) not sloping anteriorly, forming angle of $\sim 90^\circ$ relative to body axis; (1) sloping anteriorly, forming angle $> 90^\circ$ relative to body axis (Ferraris, 1988: char. D12; Royero, 1999: char. 127; Akama, 2004: char. 167; Birindelli, 2014: char. 241; modified).

Most nuptial males of achenipterids lack the ability to angle the dorsal-fin spine anteriorly. However, nuptial males of *Ageneiosus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, *Tetranematichthys*, *Tympanopleura* and *Trachelyopterus* have a strongly modified dorsal-fin spine during the reproductive season. In those taxa, the dorsal-fin spine is angled anteriorly, with the distal tip pointing anteriorly. Those species for which a nuptial male was unavailable or for which there was no literature information were coded as unknown. Those taxa without a dorsal-fin spine were coded as inapplicable for this character.

200. [3689] Dorsal fin, spine, anterior margin, serration: (0) absent; (1) present (Royero, 1999: char. 80; Akama, 2004: char. 129; Vigliotta, 2008: char. 62; Birindelli, 2014: char. 242; modified).

In the plesiomorphic condition, the anterior margin of the dorsal-fin spine is smooth, without serrae. However, most Achenipteridae have conspicuous serrae along the anterior margin of the spine. The achenipterids *Auchenipterus*, *Centromochlus existimatus*, *Centromochlus meridionalis*, *Entomocorus*, *Epapterus*, *Gelanoglanis*, some *Pseudauchenipterus*, *Pseudepapterus*, *Trachelyichthys decaradiatus*, *Trachelyichthys* sp. 1, and the outgroups *Diplomystidae*, *Mochokidae* (except *Mochokus*), *Pimelodus maculatus* Lacepède, 1803, *Anadoras grypus* and *Megalodoras uranoscopus* have a smooth anterior margin of the dorsal-fin spine, without any serrae. This character was coded distinctly from Akama (2004), Vigliotta (2008) and Birindelli (2014), who considered rudimentary serration as absent, and it was assumed as present even if weakly developed, such as in

Trachelyopterus coriaceus, *Trachelyopterus galeatus* and *C. romani*. Those taxa without a dorsal-fin spine were coded as inapplicable for this character.

201. [3690] Dorsal-fin spine, anterior margin, serration, number of rows: (0) one; (1) two; (2) three.

Achenipterids usually have one mid-row of serrae along the entire anterior margin of the dorsal-fin spine. Although the serrae on the distal portion of the spine are always arranged in one row, serrae on the proximal portion are arranged in two anterolateral rows in *Trachelyoptericthys*, *Trachycorystes trachycorystes* and *Cathorops spixii*, or three rows in *Spinipterus* and *Liosomadoras*, in which one row is located at the mid-line and two rows are positioned at the lateral margins. This character was coded disregarding nuptial males, which may develop serrae arranged in one or two rows centrally on the anterior margin of the spine (e.g. *Ageneiosus* and *Trachelyopterus*). Those taxa without a dorsal-fin spine or without serrae on the spine were coded as inapplicable for this character.

202. [3691] Dorsal-fin spine, anterior margin, proximal portion, irregular serration: (0) absent; (1) present.

Among taxa with serrae on the anterior margin of the dorsal-fin spine, only *Asterophysus*, *Aucheniptericthys*, and *Trachelyichthys* have a patch of round serrae irregularly arranged in the proximal portion of the spine, not forming a distinctive row. This character was coded disregarding nuptial males, which may develop serrae arranged in one or two rows centrally on the anterior margin of the spine (e.g. *Ageneiosus* and *Trachelyopterus*). Those taxa without a dorsal-fin spine or without serrae on the spine were coded as inapplicable for this character.

203. [3692] Dorsal fin, spine, anterior margin, serration, shape: (0) rounded, (1) pointed.

In the taxa with serrae on the anterior margin of the dorsal-fin spine, the serrae are generally short and distally blunt. However, among the achenipterids, *Asterophysus batrachus*, *Centromochlus romani*, *Centromochlus perugiae*, *Centromochlus reticulatus*, *Liosomadoras*, some *Tatia*, *Trachelyichthys exilis*, *Trachelyopterus amblops* and *Trachelyopterus teaguei*, and the *Doradidae* and *Mochokus* have larger, stronger, pointed serrae. Those taxa without a dorsal-fin spine or without serrae on the spine were coded as inapplicable for this character.

204. [3693] Dorsal fin, spine, posterior margin, serration: (0) present; (1) absent (Royero, 1999: char. 79; Akama, 2004: char. 130; Sousa, 2010: char. 57; Birindelli, 2014: char. 245).

Among the Auchenipteridae, *Ageneiosus* (except for *Ageneiosus vittatus* and *Ageneiosus dentatus*), *Asterophysus*, *Centromochlus perugiae*, *Centromochlus reticulatus*, *Centromochlus* aff. *C. simplex*, *Epapterus*, *Gelanoglanis travieso*, *Glanidium cesarpintoi*, *Pseudepapterus*, *Pseudotatia*, *Tatia* (except *Tatia carolae* and *Tatia intermedia*), *Tocantinsia*, *Trachelyopterichthys*, *Trachelyopterus amblops*, *Trachelyopterus insignis*, *Trachycorystes trachycorystes* and *Spinipterus* lack serrae along the posterior margin of the dorsal-fin spine. Those taxa without a dorsal-fin spine were coded as inapplicable for this character.

Pectoral girdle

205. [3694] Pectoral girdle, anterior margin, shape: (0) arched; (1) truncated; (2) acute tip (Soares-Porto, 1998: char. 18; Birindelli, 2014: char. 249; modified).

In most catfishes, the anterior margin of the pectoral girdle is arched in ventral aspect, with the anterior border somewhat rounded. In auchenipterids, *Ageneiosus* (except *Ageneiosus vittatus* and *Ageneiosus lineatus*) and *Tympanopleura rondoni* have the anterior margin of the pectoral girdle truncated. In *Asterophysus*, *Auchenipterus*, *Centromochlus* (except *Centromochlus simplex*), *Entomocorus*, *Gelanoglanis*, *Glanidium* (except *Glanidium catharinensis*), *Pseudauchenipterus*, *Pseudotatia*, *Tatia* (except *Tatia intermedia* and *Tatia* sp. 4), *Trachelyopterus insignis*, *Trachycorystes menezesi*, *Spinipterus acsi* and *Trachelyichthys decaradiatus*, the margin of the pectoral girdle is anteriorly pointed, giving the girdle a triangular shape.

206. [3695] Pectoral girdle, symphysis, length: (0) moderate, less than half its width; (1) very short, mesial tip of pectoral girdle barely in contact; (2) long, at least equivalent to half the width of the pectoral girdle.

The length of the ventral symphysis between contralateral bones of the pectoral girdle is usually shorter than half its width. Among Auchenipteridae, this plesiomorphic condition is found in *Ageneiosus*, *Auchenipterus*, *Epapterus*, *Glanidium catharinensis*, *Pseudauchenipterus*,

Pseudepapterus, *Tympanopleura*, *Tetranematichthys*, *Tocantinsia*, *Trachelyichthys*, *Trachelyopterichthys*, *Trachycorystes trachycorystes* and *Trachelyopterus striatulus*. A very distinct condition is found in *Asterophysus batrachus*, where the cleithrum and the coracoid are very thin and barely in contact at the ventral midline. In most Auchenipteridae, and in the Ariidae, Pimelodidae and Doradidae (except *Megalodoras uranoscopus* and *Wertheimeria maculata*), the pectoral girdle symphysis is long, with its length being at least twice its width.

207. [3696] Pectoral girdle, contralateral bones, contact: (0) strongly in contact; (1) barely in contact.

In the plesiomorphic condition, the contralateral bones of pectoral girdle are articulated in an elongate, strong symphysis ventromedially. In the derived condition, found in *Asterophysus batrachus*, the pectoral girdle is barely joined through weak contact only by the tip of both bones, and without a posteriorly laminar expansion.

208. [3697] Mesocoracoid: (0) separated from main body of scapulo-coracoid, forming conspicuous arch; (1) totally fused and nearly indistinguishable from main body of scapulo-coracoid (Ferraris, 1988: char. P1; Royero, 1999: char. 82; Britto, 2002: char. 247; Akama, 2004: char. 105; Diogo, 2004: char. 185; Vigliotta, 2008: char. 55; Marceniuk et al., 2012: char. 219; Birindelli, 2014: char. 250; modified).

The mesocoracoid is plesiomorphically present in catfishes and more easily observed in dorsal view. The mesocoracoid is a thin arch located on the posterodorsal portion of the pectoral girdle that joins the dorsolateral portion of the cleithrum and the scapulo-coracoid. In the plesiomorphic condition, found in Diplomystidae, Mochokidae, Pimelodidae and *Helogenes marmoratus*, the anterior portion of the mesocoracoid arch is usually near the proximal radials, and the posterior end is attached to the mesial margin of the posterior process of the scapulo-coracoid. In contrast, the condition found in most Auchenipteridae is the mesocoracoid totally fused to the dorsolateral laminar portion of the scapulo-coracoid, and almost indistinguishable from the scapulo-coracoid in some taxa. However, in *Auchenipterus* and *Pseudepapterus*, the mesocoracoid is observable as a tenuous line along the border of the mesocoracoid. It connects the lateral portion of the cleithrum to the scapulo-coracoid as a continuous laminar bone that runs lateromedially to the posterior

process of the scapulo-coracoid and is fused laterally to its transverse lamina. The very distinct configuration of the pectoral girdle in dorsal view, which supports a very elongated and wide laminar crest fused to the mesocoracoid, renders it very difficult to observe. Nevertheless, in *Ageneiosus lineatus*, *Ageneiosus dentatus* and *Tympanopleura atronatus*, the mesocoracoid is a separate arch from the main body of the scapulo-coracoid. This plesiomorphic condition provides strong evidence for the hypothesis of the fusion of the mesocoracoid in Auchenipteridae and the remaining taxa. Birindelli (2014) and other previous authors, in contrast to Diogo (2004), assumed the absence of the mesocoracoid in Auchenipteridae, Doradoidea and Aspredinidae. In the present study, the mesocoracoid was considered not as a separate bone structure but totally fused to the scapulo-coracoid in the auchenipterids (except for *Tympanopleura atronatus*, *Ageneiosus lineatus* and *Ageneiosus dentatus*). Given that a distinct, arch-shaped mesocoracoid was not observed in the Ariidae, Aspredinidae or Doradidae, the derived condition was considered to include both conditions, the lack of the mesocoracoid and the total fusion, for these groups. The absence of the mesocoracoid was considered as a non-exclusive synapomorphy for Doradoidea by Birindelli (2014).

209. [3698] Pectoral fin, third proximal radial: (0) present; (1) absent (Ferraris, 1988: char. P10; Akama, 2004: char. 114).

Among the taxa examined, the third proximal radial is absent in *Gelanoglanis* and *Pseudobunocephalus*.

210. [3699] Pectoral fin, third proximal radial, size: (0) narrow; (1) wide, expanded laterally (Ferraris, 1988: char. P9; Walsh, 1990: char. 6; Royero, 1999: char. 90; Akama, 2004: char. 115; Ribeiro, 2011: char. 134; Birindelli, 2014: char. 255, modified).

The third proximal radial of the pectoral fin in most catfishes is narrow, with approximately the same width throughout its length, and it is also similar in size to the second proximal radial and somewhat rod shaped to rectangular. However, in *Ageneiosus* and *Tympanopleura* (except for *Tympanopleura atronatus* and *Tympanopleura piperata*), the distal portion of the third proximal radial is very large, approximately twice the size of the second. Previous authors assumed that this condition was present in *Tetranematichthys*, but in the present observations the third proximal radial is slightly larger than the second, but with the distal expansion very distinct from that

found in *Ageneiosus*. Furthermore, Birindelli (2014) described this character as variation in the size of the second proximal radial, contrary to previous authors and the present observations that the variation in size is indeed in the third proximal radial.

211. [3700] Pectoral fin, first unbranched ray: (0) rigid, sharp spine; (1) somewhat rigid, not sharp; (2) soft (Walsh, 1990: char. 33; Ribeiro, 2011: char. 119, modified).

In many catfishes, the first element of the pectoral fin is modified into a strong, sharp spine. In *Ageneiosus inermis*, *Ageneiosus militaris*, *Ageneiosus ucayalensis*, *Ageneiosus uranophthalmus* and *Helogenes marmoratus*, the first unbranched ray is somewhat rigid, but not modified into a sharp spine. Notwithstanding, in *Gelanoglanis nanonotocolus* and *Gelanoglanis varii*, the first unbranched pectoral-fin ray is soft (see more details by Calegari *et al.*, 2014; Calegari & Reis, 2016).

212. [3701] Pectoral fin, first unbranched ray, base, dorsal process, development: (0) small, simple; (1) large, discoid (Royero, 1999: char. 86; Akama, 2004: char. 117; Birindelli, 2014: char. 256).

In the outgroup taxa (except Doradidae), *Ageneiosus pardalis* and *Tympanopleura piperata*, the dorsal process of the base of the pectoral-fin spine is small and simple. In contrast, most Auchenipteridae and all Doradidae have the dorsal process of the first unbranched ray of the pectoral fin large and discoid.

213. [3702] Pectoral-fin spine, anterior margin, serrations: (0) absent; (1) present (Ferraris, 1988: char. P7; Walsh, 1990: char. 34; Soares-Porto, 1998: char. 20; Royero, 1999: char. 88; Akama, 2004: char. 107; Britto, 2002: char. 255; Vigliotta, 2008: char. 59; Birindelli, 2014: char. 257).

In Diplomystidae, some Mochokidae and the auchenipterids *Ageneiosus inermis*, *Ageneiosus vittatus*, *Ageneiosus dentatus*, *Ageneiosus militaris*, *Auchenipterus* (except for *Auchenipterus fordicei*), *Centromochlus existimatus*, *Centromochlus heckelii*, *Epapterus*, *Gelanoglanis*, *Pseudepapterus* and *Pseudauchenipterus*, the pectoral-fin spine is smooth along its anterior margin or bears a few tiny blunt granules only on the proximalmost portion, but not serrae. Ribeiro (2011) considered *Ageneiosus inermis* to have reduced granular serrae on the anterior margin of the spine; however, the tiny blunt granules were coded as serrae absent. However, most examined catfishes that have the

first element of the pectoral fin modified into a spine also have serrae on its anterior margin. Those taxa in which the first unbranched ray of the pectoral fin is not modified into a spine were coded as inapplicable for this character.

214. [3703] Pectoral-fin spine, anterior margin, serrations, orientation: (0) antrorse; (1) retrorse; (2) perpendicular (Ferraris, 1988: char. P5; Birindelli, 2014: char. 258).

Within auchenipterids, *Centromochlus meridionalis*, *Tatia carolae*, *Pseudotatia* and *Asterophysus batrachus* have antrorse, or anteriorly oriented, serrae on the pectoral-fin spine. However, in *Entomocorus*, *Auchenipterichthys*, *Trachelyichthys* (except *Trachelyichthys* sp. 1), *Trachelyopterus* (except *Trachelyopterus amblops* and *Trachelyopterus coriaceus*) and *Trachycorystes menezesi*, the serrae are retrorse or posteriorly oriented. In most Auchenipteridae that have serrae on the anterior margin of the pectoral-fin spine, the serrae are perpendicular to the spine axis. Those taxa in which the first unbranched ray of the pectoral fin is not modified into a spine and those without serrae on the anterior margin were coded as inapplicable for this character.

215. [3704] Pectoral-fin spine, anterior margin, serrations, shape: (0) sharp, pointed; (1) blunt or truncated.

Among the taxa examined, *Pimelodus maculatus*, Ariidae, *Ageneiosus*, *Auchenipterus fordicei*, *Glanidium ribeiroi*, *Tatia intermedia*, *Tetranematichthys*, *Tympanopleura*, *Tocantinsia* and *Trachelyopterus coriaceus* have serrae on the anterior margin of the pectoral-fin spine that are blunt or truncated, not ending as a sharp point. In *Ageneiosus*, the serrae are very small and somewhat globular. Those taxa in which the first unbranched ray of the pectoral fin is not modified into a spine and those without serrae on the anterior margin were coded as inapplicable for this character.

216. [3705] Pectoral-fin spine, dorsal surface, serrations: (0) absent; (1) present (Akama, 2004: char. 110; Birindelli, 2014: char. 260).

Among the catfishes examined, *Spinipterus* and *Acanthodoras cataphractus* (Linnaeus, 1758) have serrae along the entire dorsal surface of the pectoral-fin spine. Birindelli (2014) also coded the presence of those serrae in *Trachelyopterichthys taeniatus*, *Trachelyopterus porosus* and *Trachelyopterus striatulus*, but in the present study serrae in those taxa were not

observed. The serrae observed by Birindelli are possibly associated with a sexually dimorphic feature of mature males during the reproductive season, because those species usually present remarkable sexual modifications on the fin spines. The derived condition observed in *Spinipterus* and *Acanthodoras* is permanent and not limited to the reproductive season. Those taxa in which the first unbranched ray of the pectoral fin is not modified into a spine were coded as inapplicable for this character.

217. [3706] Pectoral-fin spine, length: (0) moderate, less than one-third of SL; (1) elongate, greater than one-third of SL (Ferraris, 1988: char. P2; Royero, 1999: char. 91; Akama, 2004: char. 106; Birindelli, 2014: char. 261).

Most catfishes examined have a moderate-sized pectoral-fin spine. Among the taxa examined, *Centromochlus heckelii*, *Centromochlus existimatus*, *Centromochlus macracanthus* and the doradids *Trachycodoras nattereri* and *Franciscodoras marmoratus* have a very long pectoral-fin spine, which reaches to or surpasses one-third of SL. Those taxa in which the first unbranched ray of the pectoral fin is not modified into a spine were coded as inapplicable for this character.

218. [3707] Cleithrum and coracoid, fenestra: (0) present; (1) absent.

Among the catfishes examined, Auchenipteridae, Diplomystidae, Ariidae, Aspredinidae, most Mochokidae and *Helogenes marmoratus* have a fenestra in the suture that articulates the cleithrum and coracoid ventrally. Although the fenestra in most Mochokidae is present, it is restricted to the lateral portion and is ventrally covered by the scapulo-coracoid. *Pimelodus* and most Doradidae (except *Trachydoras*, *Franciscodoras* and *Wertheimeria*) lack the cleithrum–coracoid fenestra.

219. [3708] Cleithrum, dorsal process, size: (0) moderate, shorter than pectoral-fin spine; (1) distinctively large, approximately the same length as the pectoral-fin spine.

The dorsal process of the cleithrum is usually of moderate size, shorter than the pectoral-fin spine. Among all taxa examined, only *Gelanoglanis* has the derived condition, a huge dorsal process on the cleithrum, approximately the same length as the pectoral-fin spine or the first unbranched ray when the spine is absent (Fig. 11). Although the dorsal process in *Asterophysus batrachus* is approximately



Figure 11. Lateral view of pectoral girdle of *Gelanoglanis pan*, paratype, MZUSP 96032. Abbreviations: DP-CLE, dorsal process of cleithrum; PP-CLE, posterior process of cleithrum. Scale bar: 2 mm.

the same size as the pectoral-fin spine, it was coded as being of moderate size because the relative size in this taxon is an artefact of the reduction of the pectoral-fin spine. Additionally, to assert the homology of this state in this taxon compared with the remaining auchenipterids, the posterior process was considered moderate in size.

220. [3709] Cleithrum, posterodorsal process: (0) present; (1) absent.

Most catfishes have a conspicuous pointy process between the dorsal and the posterior process of the cleithrum. Among the taxa examined, the auchenipterids *Centromochlus existimatus*, *Centromochlus perugiae*, *Centromochlus heckelii*, *Centromochlus reticulatus*, *Gelanoglanis*, *Tatia brunnea*, *Tatia carolae*, *Tatia creutzbergi*, *Tatia jacaratia*, *Tatia meesi*, *Tatia* sp. 1 and sp. 2 and the outgroup *Nemadoras humeralis*, *Oxydoras niger*, *Rhynchodoras woodsi*, *Trachydoras nattereri*, *Aspredinidae*, *Helogenes marmoratus* and *Synodontis ornatipinnis* lack the posterodorsal process.

221. [3710] Cleithrum, posterior process: (0) present; (1) absent (Ferraris, 1988: char. P8; Walsh, 1990: char. 5; Royero, 1999: char. 84; Akama, 2004: char. 112; Britto, 2002: char. 246; Vigliotta, 2008: char. 53; Birindelli, 2014: char. 265; modified).

The posterior process of the cleithrum forms an extension of the lateral margin of the pectoral girdle dorsal to the pectoral-fin insertion. In most catfishes, the posterior process is present, elongated and pointed. Among the taxa examined, *Ageneiosus*, *Tympanopleura* (except

Tympanopleura brevis and *Tympanopleura rondoni*) and *Helogenes marmoratus* lack the posterior process of the cleithrum.

222. [3711] Cleithrum, posterior process, size: (0) small, not surpassing base of branched pectoral-fin rays; (1) moderate, approximately half the length of the pectoral-fin spine; (2) long, approximately two-thirds the length of the pectoral-fin spine (Ferraris, 1988: char. P8; Royero, 1999: char. 84; Walsh, 1990: char. 5; Akama, 2004: char. 112; Britto, 2002: char. 246; Vigliotta, 2008: char. 53; Birindelli, 2014: char. 265; modified).

The size of the cleithrum posterior process is variable among catfishes. Within the auchenipterids, *Asterophysus batrachus*, *Pseudepapterus*, *Tetranematichthys*, *Tympanopleura brevis* and *Tympanopleura rondoni* have a small posterior process, not surpassing the base of the branched pectoral-fin rays. *Auchenipterichthys*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Gelanoglanis*, *Pseudauchenipterus*, *Tocantinsia*, *Trachelyopterus* and *Spinipterus* sp. 'oncinha' have a moderate posterior process on the cleithrum, approximately half the length of the pectoral-fin spine. Finally, *Centromochlus*, *Glanidium*, *Liosomadoras*, *Tatia*, *Pseudotatia*, *Trachelyichthys*, *Trachelyopterichthys*, *Spinipterus acsi* and *Trachycorystes* have an elongated posterior process, reaching to at least two-thirds of the pectoral-fin spine, but usually surpassing that point. Those taxa lacking the posterior process of cleithrum were coded as inapplicable for this character.

223. [3712] Cleithrum, posterior process, ornamentation: (0) absent; (1) present (Curran, 1989: char. 11; Akama, 2004: char. 113; Birindelli, 2014: char. 267).

Most auchenipterids have small, bony, rounded protuberances on the posterior process of cleithrum, more numerous along the lateral margin. Among the auchenipterids examined, *Tympanopleura brevis*, *Tympanopleura rondoni*, *Asterophysus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Gelanoglanis*, *Glanidium* (except *Glanidium cesarpintoii*), *Pseudepapterus jequitinhonhae*, *Pseudepapterus nodosus*, *Tetranematichthys* and *Trachycorystes menezesi* have the posterior process smooth, without any ornamentation. Those taxa lacking the posterior process of cleithrum were coded as inapplicable for this character.

224. [3713] Cleithrum, posterior process, ornamentation, arrangement: (0) scattered; (1)

arranged in single row; (2) arranged in two rows (Curran, 1989: char. 11; Akama, 2004: char. 113; Birindelli, 2014: char. 267; modified).

In most taxa that have ornamentation on the posterior process of cleithrum, the ornamentation is scattered and homogeneously spread. *Tatia brunnea*, *Tatia carolae*, *Tatia creutzbergi*, *Tatia strigata*, *Tatia* sp. 2 and the doradids *Oxydoras niger*, *Rhynchodoras woodsi* and *Trachydoras nattereri* have ornamentation on the posterior process distributed in only one row. Furthermore, *Liosomadoras*, *Spinipterus acsi*, *Anadoras grypus*, *Megalodoras uranoscopus* and *Nemadoras humeralis* have two rows of ornamentation. Those taxa that lack the cleithrum posterior process were coded as inapplicable for this character.

225. [3714] Scapulo-coracoids, articulation at symphysis, shape: (0) straight; (1) entirely interdigitate; (2) interdigitated in posterior portion only (Mo, 1991; de Pinna *et al.*, 2007: char. 103; Birindelli, 2014: char. 269).

The plesiomorphic condition of the symphysis articulation between the contralateral scapulo-coracoids is straight, as found in Diplomystidae and *Helogenes marmoratus*. Most catfishes have an interdigitated suture along the entire length of the symphysis. Nevertheless, in the auchenipterids *Asterophysus*, some *Centromochlus*, *Gelanoglanis*, *Pseudepapterus*, some *Tatia*, the aspredinid *Pterobunocephalus* and the mochokid *Euchilichthys*, the interdigitated suture is only in the posterior portion of the length of the scapulo-coracoids.

226. [3715] Scapulo-coracoid, posterior process: (0) absent; (1) present (de Pinna, 1996: char. 79).

The absence of the scapulo-coracoid posterior process is a plesiomorphic condition found only in Diplomystidae.

227. [3716] Scapulo-coracoid, posterior process, size: (0) short, extending up to base of branched pectoral-fin rays; (1) elongate, greatly surpassing base of branched pectoral-fin rays (Britto, 2002: char. 250; Birindelli, 2014: char. 270).

The plesiomorphic and most common condition in Auchenipteridae is the possession of a short scapulo-coracoid posterior process, reaching to approximately the base of the branched pectoral-fin rays. In *Auchenipterichthys coracoideus*, *Auchenipterichthys thoracatus*, *Auchenipterus*, *Epapterus*, *Trachelyichthys exilis* and the outgroups Aspredinidae (except *Pterobunocephalus*) and doradid *Trachydoras nattereri*, the posterior

process is elongated, surpassing the base of the branched pectoral-fin rays and usually reaching to half the length of the rays. Birindelli (2014) coded *Pseudepapterus* as bearing a long posterior process, but in the specimens analysed herein, a short posterior process was observed, as in the remaining auchenipterids. Those taxa that lack the scapulo-coracoid posterior process were coded as inapplicable for this character.

228. [3717] Scapulo-coracoid, posterior process: (0) straight; (1) twisted, forming deep concavity.

The scapulo-coracoid posterior process of most catfishes is a relatively straight projection of the lateral portion, never forming a concavity. However, *Entomocorus*, *Pseudauchenipterus affinis*, *Pseudauchenipterus flavescens* and *Pseudepapterus* have a condition in which a transverse, twisted laminar bony crest forms the posterior process. This configuration causes a strong concavity similar to a tunnel.

229. [3718] Scapulo-coracoid, posterior process, distal margin, shape: (0) rounded and wide; (1) pointed and thin.

In most catfishes, the distal portion of the scapulo-coracoid posterior process is rounded and relatively wide and wing shaped. The derived condition, shared by *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudauchenipterus affinis* and *Pseudauchenipterus flavescens*, *Pseudepapterus*, the Aspredinidae (except *Aspredo aspredo*) and the Doradidae, is a pointed and thin posterior process.

230. [3719] Scapulo-coracoid, bony crest: (0) absent; (1) present (Birindelli *et al.*, 2007: char. 673; Birindelli, 2014: char. 273).

A transverse laminar bony crest is present dorsally on the scapulo-coracoid, between the adductor superficialis and the arrector ventralis muscles in most auchenipterids, except *Gelanoglanis*, which shares the plesiomorphic condition with Diplomystidae. Birindelli (2014) considered that crest to be absent in *Auchenipterus*, *Epapterus*, *Pseudepapterus*, Doradidae and Mochokidae. That laminar crest was indeed observed in those taxa; however, it is located more posteriorly, near to or at the posterior border, along the end of the scapulo-coracoid suture.

Pelvic girdle

231. [3720] Pelvic fin, position: (0) at approximately middle of SL; (1) within anterior half of SL (Birindelli, 2014: char. 275).

In the outgroups (except *Aspredo aspredo*, *Helogenes* and *Pterobunocephalus*) and other auchenipterids, the pelvic fin originates approximately at the midbody, differing from the auchenipterids *Asterophysus*, *Auchenipterus*, *Epapterus*, *Pseudepapterus*, *Trachelyichthys* and *Trachelyopterichthys*, where the pelvic fin originates within the anterior half of the SL. Contrary to [Birindelli \(2014\)](#), the derived condition was recognized in members of Auchenipteridae.

232. [3721] Pelvic fin, first unbranched ray in nuptial males, length: (0) same size as in females and non-nuptial males; (1) longer than in females and non-nuptial males ([Ferraris, 1988](#): char. PV2; [Royer, 1999](#): char. 133; [Akama, 2004](#): char. 170; [Birindelli, 2014](#): char. 279).

A highly specialized feature within Siluriformes is the modified size of the first unbranched pelvic-fin ray of nuptial males, with an elongated soft ray that differs from that of females or non-nuptial males. This derived condition is found only in *Entomocorus*, and the modified pelvic-fin ray reaches nearly to the end of the anal-fin base.

233. [3722] Pelvic fins, innermost rays, union: (0) separate; (1) united by skin ([Ferraris, 1988](#): char. PV6; [Ferraris & Vari, 1999](#): 393 pp.; [Akama, 2004](#): char. 123; [Birindelli, 2014](#): char. 281).

Most catfishes have the pelvic fins separated from each other. *Auchenipterus*, *Epapterus* and *Pseudepapterus* share a derived condition of a consistent skin membrane joining the proximal half of the contralateral last pelvic-fin rays.

234. [3723] Basipterygium, anteromedial processes, union: (0) separated from each other; (1) sutured together along their entire length; (2) sutured together only anteriorly.

In most catfishes, the anteromedial process of the basipterygium is separated from the main portion of the bone, forming an elongate, rod-like extension ([Fig. 12A, C–E](#)). In *Auchenipterus*, *Epapterus*, *Pseudepapterus* and *Pseudotatia*, the anteromedial process is entirely incorporated into the anterior portion of the basipterygium through a bony lamina. In such cases, the anteromesial portion of the basipterygium seems to increase in size during ontogeny ([Fig. 12B](#)). Furthermore, a similar condition is found in *Centromochlus heckelii*, *Centromochlus existimatus*, *Entomocorus*, *Gelanoglanis stroudi* and *Gelanoglanis travieso*, *Tatia* (except for *Tatia musaica* and *Tatia meesi*), *Trachelyopterichthys*, *Trachelyopterus insignis*,

Trachelyopterus albicrux, *Trachelyopterus striatulus* and *Trachelyopterus teaguei*, in which the anteromedial process is united to its contralateral pair by the anterior portion only, leaving the most posterior portion of the process separate.

235. [3724] Basipterygium, anterolateral and anteromedial processes, distance: (0) widely separated, with distance greater than the width of the anterolateral processes; (1) close, with distance approximately the same width as the anterolateral processes.

Most catfishes have the processes on the anterior margin of the basipterygium widely separated from each other by a distance at least twice the width of the anterolateral processes ([Fig. 12B, D, E](#)). In *Ageneiosus*, *Centromochlus perugiae*, *Centromochlus meridionalis*, *Centromochlus simplex*, *Centromochlus* aff. *C. simplex* and *Tympanopleura*, the anterior processes are close together, separated from each other by a distance similar to the width of the anterolateral process ([Fig. 12A, C](#)).

236. [3725] Basipterygium, anterolateral and anteromedial processes, relative length: (0) anterolateral and anteromedial processes approximately of the same length; (1) anterolateral process much longer than anteromedial.

In the plesiomorphic condition found in *Ageneiosus*, *Auchenipterus*, *Epapterus*, *Centromochlus meridionalis*, *Glanidium*, *Pseudauchenipterus*, *Pseudepapterus*, *Tetranematichthys*, *Tympanopleura*, *Trachelyopterus amblops*, *Trachelyopterus coriaceus* and *Trachycorystes menesezi*, the processes on the anterior margin of the basipterygium are similar in length ([Fig. 12A, B, D, E](#)). However, in most catfishes, both processes are of different lengths relative to each other ([Fig. 12C](#)).

237. [3726] Basipterygium, anterolateral process, dorsal portion, bony crest: (0) absent; (1) present.

In the very distinctive derived condition found in *Auchenipterus*, *Epapterus* and *Pseudepapterus*, the dorsal surface of the anterolateral process of the basipterygium bears a large, elongate and transversely positioned bony crest. This bony crest runs approximately along the same orientation as the anterolateral process.

238. [3727] Basipterygium, lateral process, cartilage, extension: (0) short; (1) long, anteriorly expanded ([Birindelli, 2014](#): char. 285; modified).

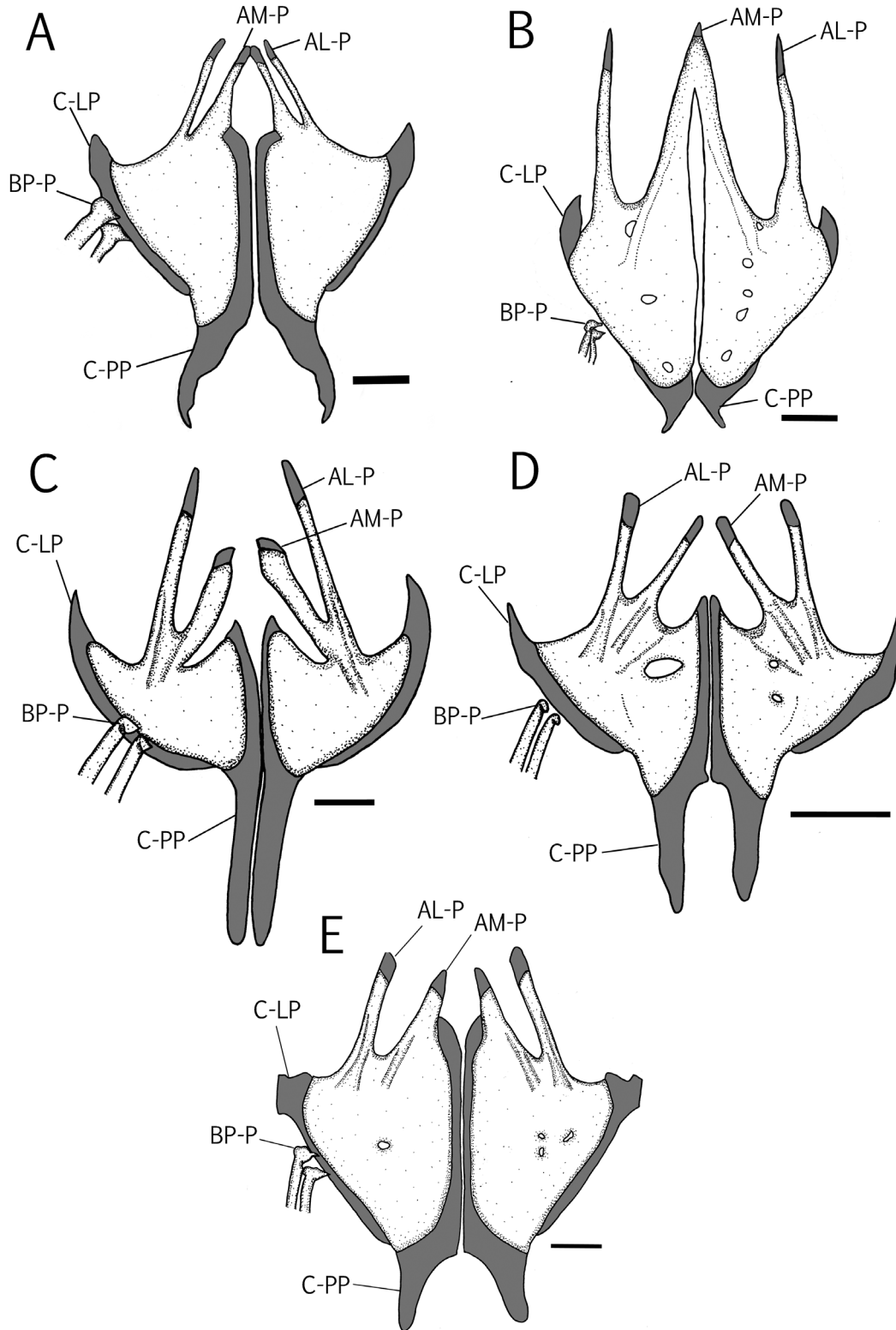


Figure 12. Dorsal view of pelvic girdles. A, *Tympanopleura brevis*, MCP 30617. B, *Auchenipterus brevior*, CAS 52135. C, *Centromochlus meridionalis*, MZUSP 96595. D, *Pseudoauchenipterus affinis*, MZUSP 51720. E, *Tetranematichthys wallacei*, MCP 27174. Abbreviations: AL-P, anterolateral process; AM-P, anteromedial process; BP-P, basal process of the pterygophore; C-LP, cartilage of the lateral process; C-PP, cartilage of the posterior process. Scale bars: 1 mm (A, B, D); 0.5 mm (C); 2 mm (E).

The cartilage of the lateral process of the basipterygium is robust, hard and covers the lateral and anterior portions of the process in all catfishes examined (but not Diplomystidae, Ariidae, Aspredinidae and *Helogenes marmoratus*, which lack the process itself). In most catfishes, the lateral process has a short extension of rounded cartilage on its distal tip, approximately the same size as the lateral process. Within the Auchenipteridae, this condition is found in *Entomocorus*, *Epapterus*, *Glanidium*, *Tetranematchthys*, *Trachelyichthys* sp. 1, *Trachelyopterichthys* and the outgroups Mochokidae, Pimelodidae and Doradidae (Fig. 12E). However, a long anterior extension of cartilage on the lateral margin of the basipterygium is found in most Auchenipteridae (Fig. 12A–D). Those taxa without the lateral process were coded as inapplicable for this character.

239. [3728] Basipterygium, lateral process, cartilage, union with basipterygium: (0) separated from basipterygium; (1) fused to basipterygium.

The cartilage on the lateral process of the basipterygium is commonly separated from the lateral margin of the basipterygium. In *Pseudepapterus*, the anteriorly expanded lateral process is fused to the lateral wall of the basipterygium. Those taxa with an absence of the lateral process of the basipterygium were coded as inapplicable for this character.

240. [3729] Basipterygium, posterior portion, shape: (0) short, without conspicuous process; (1) long, with process developed as wing; (2) long, with thin, pointed process (Akama, 2004: char. 121; Birindelli, 2014: char. 286; modified).

In most catfishes examined, the posterior portion of the basipterygium is short, without a conspicuous or elongate posterior process. In some taxa, the basipterygium is longer and wider, forming a wing on its posterior portion, as in *Ageneiosus*, *Asterophysus*, *Centromochlus existimatus*, *Centromochlus heckelii*, *Trachelyopterus*, *Tympanopleura*, *Trachycorystes*, Ariidae, Pimelodidae, *Chiloglanis disneyi* Trewavas, 1974 and *Aspredo aspredo*. A less common condition is the posterior process developed as a long, pointed extension with a thin posterior tip; this latter condition is found in *Auchenipterichthys*, *Liosomadoras* and Aspredinidae.

241. [3730] Basipterygium, posterior margin, cartilage, size: (0) short, half length of basipterygium; (1) long, approximately same length as basipterygium.

The basipterygium of the catfishes examined has an extension of hard cartilage attached to the posterior border. This cartilage is difficult to observe in specimens where the cartilage was not stained and is usually lost in dry skeletons. In Auchenipteridae, the cartilage assists with the attachment of the pelvic girdle to the skin by means of a ligament originating at the tip of the cartilage and running horizontally along the length of the ventral portion of the basipterygium. Most catfishes examined have a relatively short posterior cartilage, approximately half the length of the basipterygium or, usually, one-third the length of the first unbranched pelvic-fin ray. *Auchenipterichthys punctatus*, *Auchenipterichthys longimanus*, *Trachelyichthys*, *Trachelyopterichthys* and all the centromochlines (except for some species of *Glanidium* where this character was not possible to observe) have an elongate posterior process; its length is similar to the length of the basipterygium (Fig. 12C).

242. [3731] Basipterygium, posterior portion, cartilage in ventral view, direction: (0) posteriorly projected; (1) ventrally directly.

The posterior cartilage of the basipterygium is straight and posteriorly directed in most catfishes examined. A distinct derived condition is found in *Entomocorus*, *Auchenipterus*, *Epapterus* and *Pseudepapterus*, where the posterior cartilage is ventrally folded, forming a curve. This elaboration on the posterior cartilage seems functionally to improve the attachment of the pelvic girdle to the skin, because the posterior and the anterior portions of the basipterygium are connected by strong ligaments to the skin.

243. [3732] Pelvic-fin ray, dorsal surface, basal process, orientation: (0) oriented posteromedially; (1) oriented dorsally.

The basal process of the pelvic-fin rays is oriented posteromedially, facing the next ray in most catfishes. In *Auchenipterichthys*, *Centromochlus*, *Entomocorus*, *Liosomadoras*, *Pseudotatia*, *Tatia*, *Tocantinsia*, *Trachelyichthys*, *Trachelyopterus insignis*, *Spinipterus* and the outgroups *Rhynchodoras woodsi*, *Megalodoras uranoscopus*, *Bunocephalus doriae* and *Aspredo aspredo*, the process is oriented dorsally.

Anal fin

244. [3733] Urogenital pore, female, modification: (0) unmodified, ending as developed papilla; (1)

modified, with enlarged pore ending in internal cavity for insemination (Royero, 1999: char. 124; Akama, 2004: char. 144).

In most catfishes, the female urogenital pore has a developed papilla. In Auchenipteridae, however, the urogenital aperture of females is internally enlarged, ending in a cavity developed to retain spermatozooids transferred by males during insemination.

245. [3734] Urogenital organ, male, modification: (0) absent; (1) present, modified as intromittent organ (Ferraris, 1988: char. A1; Akama, 2004: char. 146; modified).

Auchenipteridae are inseminating fishes with an intromittent organ (i.e. gonopodium) on the modified anal fin of adult males, which is used to transfer spermatozooids to females. The primary function of the modifications of the anal fin (enlargement, elongation and fusion of the proximal radials) is, possibly, to help in sustaining the intromittent organ during the reproductive act. Although inseminating behaviour is also known in Scoloplacidae (Spadella *et al.*, 2006) and Astroblepidae (Spadella *et al.*, 2012), this character seems to have evolved independently in those groups.

246. [3735] Intromittent organ, genital tube, position: (0) at base of anal fin and united by skin to anterior anal-fin rays; (1) anterior to anal fin and apart from anal-fin rays (Birindelli, 2014: char. 46; modified).

The genital tube in Auchenipteridae varies in its position relative to the anal fin. In most Auchenipteridae, the genital tube is joined to the anal-fin base and attached to the first anal-fin rays by skin. In Centromochlinae and *Entomocorus*, the genital tube is positioned anteriorly to the anal fin and separated from the first rays. Although examination of the type series of *Pseudotatia parva* allowed codification as state 1, Mees (1974: 107) stated that the urogenital opening of presumed males is at the end of a tube along the anterior edge of the anal fin, and Ferraris (1988: 95 p.) reported that the urogenital tube extends nearly the entire length of the anterior margin of the anal fin. For this reason and because of the rarity of this species, collection of new specimens is highly desirable. This character requires further investigation because additional traits could be involved in the configuration of the intromittent organ. Those taxa without an intromittent organ were coded as inapplicable for this character.

247. [3736] Urogenital papilla, male, hood-like flap of skin covering urogenital base: (0) absent; (1) present (Ferraris, 1988: char. A4).

Among Siluriformes, the Auchenipteridae is the only family with the urogenital organ tubular and slender, modified into an intromittent organ in adult males. Members of Centromochlinae (except *Gelanoglanis*) have the genital tube emerging from a hood-like flap of skin that covers the base of the urogenital tube (Ferraris, 1988: char. A4), as in *Centromochlus* and *Tatia*, or sometimes that covers almost the entire urogenital tube, as in *Glanidium*.

248. [3737] Anal fin, dimorphic shape: (0) absent, males and females with similar anal fins; (1) present, males and females with distinct anal fins.

Auchenipteridae are inseminating fishes with conspicuous sexual dimorphism. Differences in shape and, to a lesser extent, size and orientation represent important modifications of the anal fin. In centromochlines, the anal fin of both nuptial and non-nuptial males is very distinct from that of females, thus representing secondary sexual dimorphism. In Auchenipterinae and outgroups, the shape of the anal fin of males and females has no conspicuous differences.

249. [3738] Anal fin, proximal radials, fusion in nuptial males: (0) separated, not fused; (1) partly or totally fused (Ferraris, 1988: char. A5, A6; Soares-Porto, 1998: char. 28; Royero, 1999: char. 132; Akama, 2004: char. 133, 152; Birindelli, 2014: char. 288, 289, 291; modified).

The orientation of the anal-fin rays of mature males of Auchenipteridae is variable depending on the modification of the proximal radials. During the reproductive season, mature males undergo enlargement and fusion of the proximal radials and sometimes also of the anal-fin rays. The thickening of the proximal radials and genital tube results in a curvature of the anal-fin pterigophores, in which they assume a backward orientation rather than the typical ventral orientation. This fusing configuration of the anal-fin proximal radials is a common modification in the centromochlines. Akama (2004) considered the orientation and the modification of the proximal radials to be separate characters, and Birindelli (2014) interpreted them as three separate characters: the orientation of the anal fin, the orientation of the proximal radials, and the fusion of the radials. However, the orientation

of the anal fin is herein considered to be dependent on the modification of the proximal radials, and all taxa with modified proximal radials also have a posteriorly oriented anal fin. Therefore, in the present study, the features that represent this transformation series were included as a single event.

250. [3739] Anal fin, proximal radials, fusion in nuptial males, degree: (0) partly fused; (1) totally fused.

In centromochlines, nuptial males have different degrees of fusion of the anal-fin proximal radials. In *Centromochlus*, *Tatia* and *Glanidium*, the radials are partly fused, whereas in *Gelanoglanis*, all proximal radials are entirely fused to each other. In *Centromochlus* and *Tatia*, the anteriormost portions of the proximal radials are separated from each other. Conversely, in *Glanidium*, the fusion is restricted to the anteriormost portions of the proximal radials, which are separated from each other distally. Those taxa with free proximal radials were coded as inapplicable for this character.

251. [3740] Anal fin, size: (0) moderate, roughly one-third of SL; (1) short, not surpassing one-eighth of SL; (2) long, at least half of SL.

Three different size patterns exist among the anal fins of auchenipterids. In the plesiomorphic condition, the anal fin is moderate in size, approximately one-third of the SL. Although *Diplomystes* appears to have a short anal fin relative to its body length, when compared with species having a truly short anal fin, *Diplomystes* fits in the condition of moderate anal fin. Some taxa, such as the centromochlines, have a very short anal fin, which is less than one-eighth of the SL. On the contrary, *Ageneiosus*, *Auchenipterus*, *Epapterus*, *Pseudepapterus*, *Tetranematichthys*, *Tympanopleura*, *Trachelyichthys* and *Trachelyopterichthys* have a very long anal fin, never shorter than approximately half the SL.

252. [3741] Anal fin, last proximal radial, shape: (0) rod-like; (1) laminar (Ferraris, 1988: char. A8; Akama, 2004: char. 134; Birindelli, 2014: char. 292).

Most examined taxa have the last proximal radial of the anal fin rod-like in shape. Among auchenipterids, in most species of *Ageneiosus*, *Auchenipterus*, *Auchenipterichthys*, *Tocantinsia*, *Tympanopleura rondoni* and *Tympanopleura cryptica*, the posteriormost proximal radial of the anal fin is laminar and laterally expanded, with

its length being approximately twice the length of the anterior proximal radial.

253. [3742] Anal fin, unbranched rays, distal portion, ornamentation in nuptial males: (0) absent; (1) present (Akama, 2004: char. 158; Birindelli, 2014: char. 295).

Among nuptial males of the auchenipterids examined, all species of *Auchenipterus* have blunt hooks on the distal portion of the fused unbranched anal-fin rays.

254. [3743] Anal fin, anterior rays, size in nuptial males: (0) equal to non-nuptial males; (1) larger than non-nuptial males (Royero, 1999: char. 131; Akama, 2004: char. 148; Birindelli, 2014: char. 299).

Males of Siluriformes have the anterior anal-fin rays equal in size to those of females. In nuptial males of all auchenipterids examined, the anterior anal-fin rays are enlarged relative to the remaining rays when compared with non-nuptial males. According to previous authors, this condition should be absent in centromochlines, *Entomocorus*, *Pseudauchenipterus*, *Asterophysus* and *Tocantinsia*. However, an enlargement to different degrees of the first anal-fin rays (usually the three first rays) was observed in nuptial males of all the auchenipterids.

255. [3744] Anterior anal-fin rays of nuptial males, distal portion, spermatic vesicle: (0) absent; (1) present (Akama, 2004: char. 149; Birindelli, 2014: char. 48).

Nuptial males of *Pseudauchenipterus nodosus*, *Pseudauchenipterus affinis*, *Pseudepapterus*, *Asterophysus batrachus* and *Trachelyichthys* possess a vesicle in the distal portion of the anteriormost anal-fin ray. This vesicle supposedly stores sperm in the reproductive season and might, potentially, occur in other members of the Auchenipterinae, although not observed here. Given that the level of maturation of nuptial males involves different stages of development of the vesicle, this trait requires further investigation. The shape of this vesicle is variable between these taxa. In *Trachelyichthys*, the vesicle is a distal compressed skin fold, expanded ventrally to the ray. *Pseudauchenipterus* have a large rounded vesicle also in the distal portion of the ray, whereas *Pseudepapterus* bears an elongated vesicle in the posterior half portion of the ray, which is laterally expanded with conspicuous transverse lamellae. *Asterophysus* has a thickened skin fold on the distal portion of the ray.

256. [3745] Anal-fin rays, space between modified anterior rays and remaining rays of nuptial males: (0) absent; (1) present (Birindelli, 2014: char. 49).

In the plesiomorphic condition, catfishes lack gaps between contiguous anal-fin rays. However, *Epapterus* has a derived condition, in which the first anal-fin rays are distally separated from the remaining rays. This gap is caused by the presence of two very short subsequent rays that brake the continuity of the anal fin, giving the impression of a space between the anteriormost and the remaining rays.

Caudal fin

257. [3746] Caudal fin, shape: (0) bifurcated; (1) truncated; (2) rounded (Ferraris, 1988: char. C1; Walsh, 1990: char. 26; Royero, 1999: char. 142; Akama, 2004: char. 135; Birindelli, 2014: char. 300).

Among catfishes examined, a bifurcated caudal fin seems to be the plesiomorphic condition. Among the auchenipterids, *Ageneiosus inermis*, *Ageneiosus vittatus*, *Auchenipterichthys*, *Epapterus*, *Liosomadoras*, *Tetranematichthys*, *Tympanopleura*, *Trachelyichthys*, *Trachelyopterichthys*, *Trachelyopterus*, *Trachycorystes* and *Spinipterus* have a truncated caudal fin. *Auchenipterus nuchalis* was considered polymorphic for this character. Furthermore, Aspredinidae (except *Aspredo aspredo*), the Doradid *Acanthodoras cataphractus*, and the Mochokids *Chiloglanis disneyi* and *Atopochilus savorgnani* Sauvage, 1879 have a rounded caudal-fin shape.

258. [3747] Hypurapophysis, type: (0) type A; (1) type B; (2) type C; (3) type D (Lundberg & Baskin, 1969; Ferraris, 1988: char. C7; Akama, 2004: char. 141; Birindelli, 2014: char. 303).

Among catfishes examined, the hypurapophysis may be arranged in four different shapes, according to the description of Lundberg & Baskin (1969). Type A is when the hypurapophysis is on the parahypural arch, and the second hypurapophysis is on the base of the hypural (Lundberg & Baskin, 1969: fig. 3A), a condition found only in Diplomystidae and *Megalodoras uranoscopus* within examined taxa. Type B is when the hypurapophysis and the secondary hypurapophysis are laterally continuous, with the secondary hypurapophysis on the hypural 1 (Lundberg & Baskin, 1969: fig. 3B), as found in *Tympanopleura brevis*, *Tympanopleura piperata*,

Asterophysus batrachus, *Auchenipterichthys punctatus*, *Auchenipterichthys longimanus*, *Centromochlus reticulatus*, *Epapterus*, some species of *Glanidium*, *Tatia musaica*, *Tatia caxiuanensis*, *Tatia* sp. 1, *Pseudepapterus*, *Trachycorystes trachycorystes*, *Trachelyichthys*, *Trachelyopterichthys*, *Tetranematichthys* and most Doradidae. Type C is similar to type B, but the secondary hypurapophysis is on hypurals 1 and 2 (Lundberg & Baskin, 1969: fig. 3C), and is found in most catfishes examined. Type D is when the hypurapophysis is on the parahypural, and the secondary hypurapophysis is on hypurals 1 and 2 (Lundberg & Baskin, 1969: fig. 3D), as found in *Gelanoglanis*, *Trachelyopterus teaguei*, *Trachelyopterus albicrux*, *Trachelyopterus lucenai*, *Trachelyopterus coriaceus*, some Mochokidae, *Helogenes* and Aspredinidae; this is in contrast with the observations of Birindelli (2014), who coded *Gelanoglanis* as type C.

259. [3748] Hypurapophysis, ventral process: (0) absent; (1) present (Ferraris, 1988: char. C5; Akama, 2004: char. 139; Birindelli, 2014: char. 304).

The hypurapophysis in the derived condition bears a conspicuous, rod-like ventral process oriented longitudinally to the body axis. Among the taxa examined, *Asterophysus*, *Auchenipterus*, *Centromochlus*, *Glanidium*, *Entomocorus*, *Epapterus*, *Liosomadoras*, most species of *Tatia*, *Pseudauchenipterus*, *Pseudepapterus*, *Tetranematichthys* and the outgroups Mochokidae (except *Chiloglanis*) and *Genidens barbatus* (Lacépède, 1803) have a ventral process on the hypurapophysis. In *Epapterus* and *Pseudepapterus*, it is more extremely developed, with a ventral process that is highly elongated and somewhat curved anteriorly.

260. [3749] Caudal fin, ventral lobe, principal rays, first unbranched ray, site of articulation: (0) on parahypural; (1) on last haemal spine; (2) on penultimate haemal spine; (3) on antepenultimate haemal spine; (4) on last fourth haemal spine (Ferraris, 1988: char. C3; Akama, 2004: char. 137; Birindelli, 2014: char. 307; modified).

In the plesiomorphic condition, the principal unbranched ray on the ventral lobe of the caudal fin is attached to the parahypural. In most catfishes, the first unbranched principal ray is attached to the last haemal spine. However, *Auchenipterichthys*, *Trachelyichthys*, *Trachelyopterichthys*, *Trachelyopterus amblops*, *Trachelyopterus galeatus*, *Trachelyopterus lucenai*, *Trachelyopterus teaguei* and *Spinipterus* have the unbranched

ray articulating to the penultimate haemal spine. Additionally, *Tetranematichthys*, *Trachelyopterus striatulus* and *Trachelyopterus porosus* have the unbranched ray articulating to the antepenultimate haemal spine, whereas *Trachelyopterus coriaceus* and *Trachelyopterus albicrux* have it attached to the last fourth haemal spine.

261. [3750] Caudal-fin skeleton, dorsal elements, fusion: (0) all hypurals separated; (1) hypurals 3 and 4 fused, and 5 distinct; (2) hypurals 3, 4 and 5 fused (Vigliotta, 2008: char. 72; Birindelli, 2014: char. 309).

In the plesiomorphic condition, the dorsal elements of the caudal fin skeleton are separated from each other. Most catfishes examined have the third and fourth hypurals fused and the fifth separated. Furthermore, *Tatia strigata*, *Pseudauchenipterus jequitinhonhae* and the outgroups Aspredinidae, most Mochokidae and the doradids *Acanthodoras cataphractus* and *Trachycodoras nattereri* have all dorsal elements fused.

262. [3751] Caudal-fin skeleton, ventral elements, fusion: (0) all hypurals separated; (1) hypurals 1 and 2 fused, and parahypural distinct; (2) hypurals 1, 2 and parahypural fused (Vigliotta, 2008: char. 71; Birindelli, 2014: char. 310).

The plesiomorphic condition, in which all ventral elements are separated from each other, is present in Diplomystidae and *Helogenes marmoratus*, among the taxa examined. All members of Auchenipteridae and the remaining outgroups have the opposite condition, in which all ventral elements are fused, except for the doradid *Oxydoras niger* and Mochokids *Atopochilus*, *Euchilichthys* and *Mochokiella*, which have the parahypural free from the first and second hypurals.

263. [3752] Fifth hypural, proximal portion, contact with confluence between third and fourth hypurals and epineural: (0) contacting; (1) not contacting.

The plesiomorphic condition found in Diplomystidae, in which the base of the fifth hypural contacts the confluence between the fourth hypural and the epineural, is shared with *Centromochlus* (except for *Centromochlus heckelii*, *Centromochlus meridionalis* and *Centromochlus existimatus*), *Entomocorus*, *Glanidium* (except for *Glanidium catharinensis*), *Liosomadoras oncinus*, *Pseudotatia parva*, some *Tatia* and the doradid *Rhynchodoras woodsi*. All remaining auchenipterids lack such contact.

264. [3753] Caudal skeleton, orientation: (0) posteriorly oriented; (1) posteroventrally oriented.

The caudal fin is oriented posteriorly in most catfishes. However, *Tetranematichthys*, *Trachelyichthys*, *Trachelyopterichthys* and *Trachycorystes trachycorystes* have a somewhat posteroventrally directed caudal fin. Interestingly, the dorsal profile of the caudal fin forms a slope, probably caused by the high number of procurrent rays that situate the caudal fin into a more ventral position.

SPECIES CLASSIFICATION AND TAXONOMIC ARRANGEMENT

As the first large-scale phylogeny of Auchenipteridae, a new classification for the family is inferred based on the MP reconstruction and is presented herein to bring the taxonomy more in line with our new phylogenetic hypothesis. This classification follows the sequencing convention (Wiley, 1981), which exactly reflects the tree without the necessity of naming every node, avoiding the creation of unnecessary new rank categories.

The strict consensus tree corroborates the monophyly of the superfamily Doradoidea, the family Auchenipteridae and its two subfamilies, Centromochlinae and Auchenipterinae. The classification increases the number of tribes in Auchenipteridae from two to nine, based on evidence of major groups in Auchenipterinae (Liosomadoradini, Trachelyopterini, Asterophysini, Auchenipterini and Ageneiosini) and in Centromochlinae (Gelanoglanini, Pseudotatiini, Centromochlini and Glanidiini). In contrast, *Centromochlus*, *Glanidium* and *Tatia* were recovered as paraphyletic. To maintain the classification monophyletic, previously proposed subgeneric names are being recognized as genera, with a nomenclatural reorganization of the species of *Tatia* and *Centromochlus*. In addition, *Glanidium leopardum* is regarded as a separate genus, resurrecting the available name *Gephyromochlus*. Finally, the phylogenetic position of the intriguing monotypic genus *Spinipterus* was tested with a complete codification for the first time, including osteological characters through a CT scan analysis and molecular data, revealing its closest relationship with *Trachelyopterus*.

PHYLOGENETIC RECONSTRUCTION AND DIAGNOSES OF CLADES

The phylogenetic relationships are inferred based on the strict consensus tree from 146 taxa obtained by the MP analysis of 264 morphological characters and 1082 molecular informative sites of a total of 3490 bp. The morphology data matrix is shown in the Supporting Information (Appendix S2). Owing to an artefact of TNT software, the character count

starts from zero, in which 0–3489 refer to molecular data and 3490–3753 to morphological data, which are presented in this way in the synapomorphy list ([Supporting Information, Appendix S3](#)) and diagnoses. The consensus tree is generated from 211 maximally parsimonious primary trees of 9025 steps, consistency index 0.27 and retention index 0.66 ([Figs 13, 14](#); clade numbers appear above branches and Goodman–Bremer index below). The diagnoses of the clades herein presented correspond to the results of the phylogenetics hypothesis, and the character number and state transformation is given in parenthesis after each synapomorphy. Convergences and reversions within each clade are also reported. Synapomorphies are distinguished as exclusive and non-exclusive, in which the more inclusive clades (e.g. superfamily, families and subfamilies) consider the exclusivity in the scope of all taxa included, and those less inclusive within Auchenipteridae (e.g. tribes, subtribes, genera) consider the exclusivity in the family. The phylogenetic diagnosis is followed by additional synapomorphies previously proposed by other studies, in the case of those characters that were not included in the present analysis. After the phylogenetic diagnosis, a complementary taxonomic diagnosis, mostly including features not covered in the phylogenetic analysis, is presented as a comparison section seeking to facilitate the recognition/identification of the taxon. An asterisk preceding the taxon name indicates that it was not included in the present study but is also part of the phylogenetic group proposed, even provisionally.

CLASSIFICATION

- Family Auchenipteridae Bleeker, 1862
 Subfamily Centromochlinae Bleeker, 1862
 Tribe Gelanoglanini, trib. nov.
 Genus *Ferrarissoaresia* Grant, 2015, stat. nov.
 Genus *Gelanoglanis* Böhlke, 1980
 Tribe Pseudotatiini, trib. nov.
 Genus *Pseudotatia* Mees, 1974
 Tribe Centromochlini Bleeker, 1862
 Genus *Gephyromochlus* Hoedman, 1961, stat. nov.
 Genus *Centromochlus* Kner, 1857
 Genus *Duringlanis* Grant, 2015, stat. nov.
 Tribe Glanidiini, trib. nov.
 Genus *Balroglanis* Grant, 2015, stat. nov.
 Genus *Glanidium* Lütken, 1874
 Genus *Tatia* Miranda Ribeiro, 1911
 Subfamily Auchenipterinae Bleeker, 1862
 Tribe Liosomadoradini, trib. nov.
 Genus *Liosomadoras* Fowler, 1940
 Tribe Trachelyopterini Bleeker, 1858

- Subtribe Trachycorystina Miranda Ribeiro, 1911
 Genus *Tocantinsia* Mees, 1974
 Genus *Trachycorystes* Bleeker, 1858
 Subtribe Auchenipterichthyina, subtrib. nov.
 Genus *Auchenipterichthys* Bleeker, 1862
 Genus *Trachelyopterichthys* Bleeker, 1862
 Genus *Trachelyichthys* Mees, 1974
 Subtribe Trachelyopterina Bleeker, 1858
 Genus *Spinipterus* Akama & Ferraris, 2011
 Genus *Trachelyopterus* Valenciennes, 1840
 Tribe Asterophysini Bleeker, 1862
 Genus *Asterophysus* Kner, 1857
 Tribe Auchenipterini Bleeker, 1862
 Genus *Pseudauchenipterus* Bleeker, 1862
 Genus *Entomocorus* Eigenmann, 1917
 Genus *Pseudepapterus* Steindachner, 1915
 Genus *Epapterus* Cope, 1878
 Genus *Auchenipterus* Valenciennes, 1840
 Tribe Ageiosini Bleeker, 1862
 Genus *Tetranematichthys* Bleeker, 1858
 Genus *Tympanopleura* Eigenmann, 1912
 Genus *Ageiosus* La Cépède, 1803

SUPERFAMILY DORADOIDEA BLEEKER, 1858 (CLADE 20)

Doradini [Bleeker, 1858a](#): 39 (type family: Doradidae Bleeker, 1858; also in [Bleeker, 1858b](#): 48, 52).
Included families: Auchenipteridae Bleeker, 1862 and Doradidae Bleeker, 1858.

Diagnosis: Doradoidea is diagnosed by 17 molecular and 12 morphological synapomorphies. **Exclusive**: (1) antorbital directly articulated to lateral ethmoid (char. 3518: 0 → 2), reversed in *Gelanoglanis*, *Pseudauchenipterus*, Ageiosini, *Megalodoras uranoscopus* and *Oxydoras niger*; (2) exoccipital and neural arch of complex vertebra connected by bony suture (char. 3579: 0 → 1); (3) posterior portion of transformator process of tripus ventromedially folded (char. 3654: 0 → 1); (4) posterior parapophysis of compound centrum absent (char. 3664: 0 → 1); (5) base of dorsal process of first pectoral-fin unbranched ray large, discoid (char. 3701: 0 → 1); (6) premaxillary teeth curved (char. 3589: 1 → 0); reversed in some Doradoidea. **Non-exclusive**: (7) coronoid process of anguloarticular of same size as coronoid process of dentary (char. 3601: 1 → 0), convergent in Diplomystidae and *Bunocephalus*, reversed in some *Ageiosus*, *Tympanopleura*, and in *Auchenipterus*, *Epapterus*, *Entomocorus*, *Trachelyopterus*, *Spinipterus* and doradids Clade 25; (8) bony contact of autopalatine on posterior portion of premaxilla (char. 3612: 0 → 1), convergent in *Synodontis petricola* and Pimelodidae, and reversed in Ageiosini, *Asterophysus*, *Epapterus*, *Pseudepapterus*, *Entomocorus* and some *Auchenipterus*

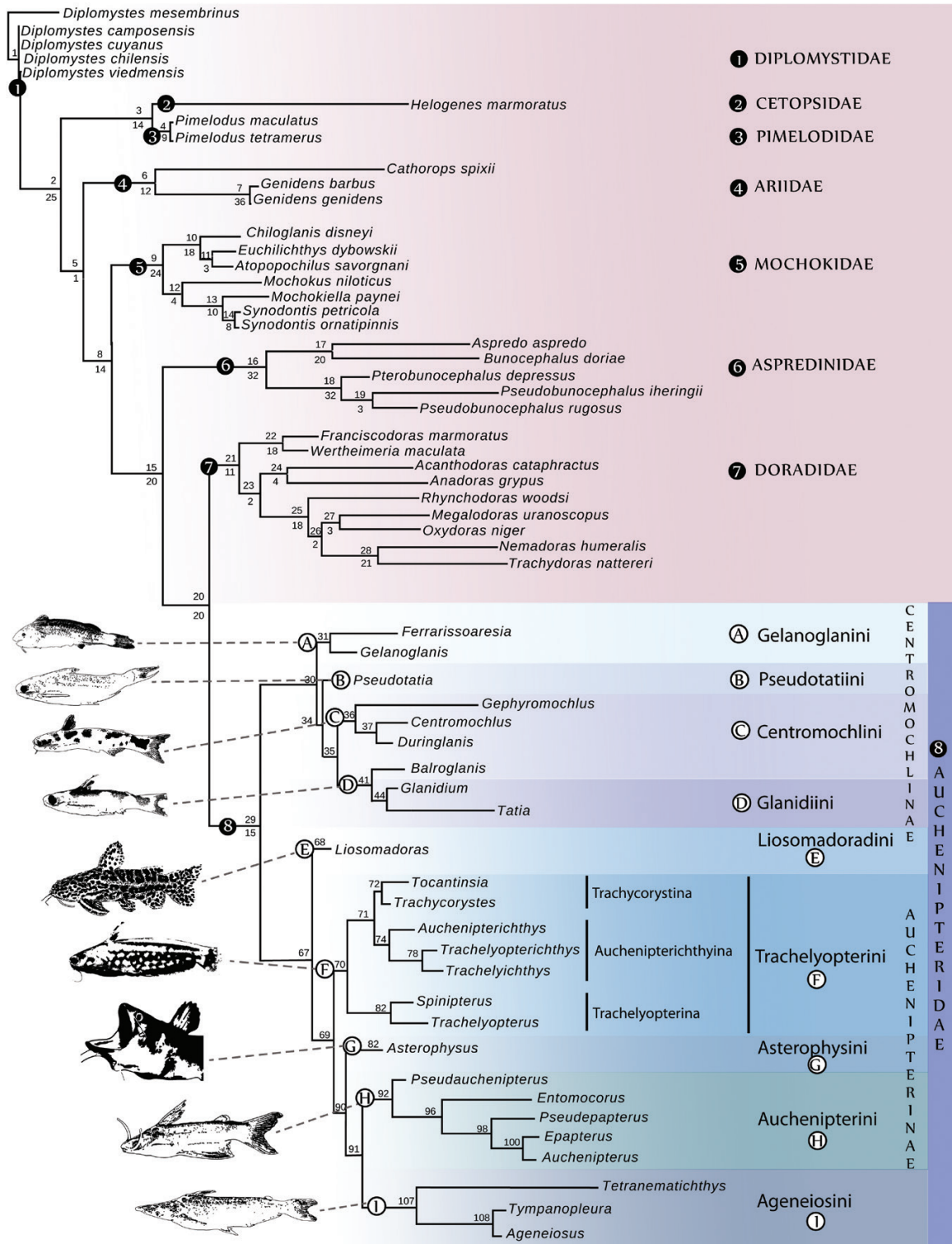
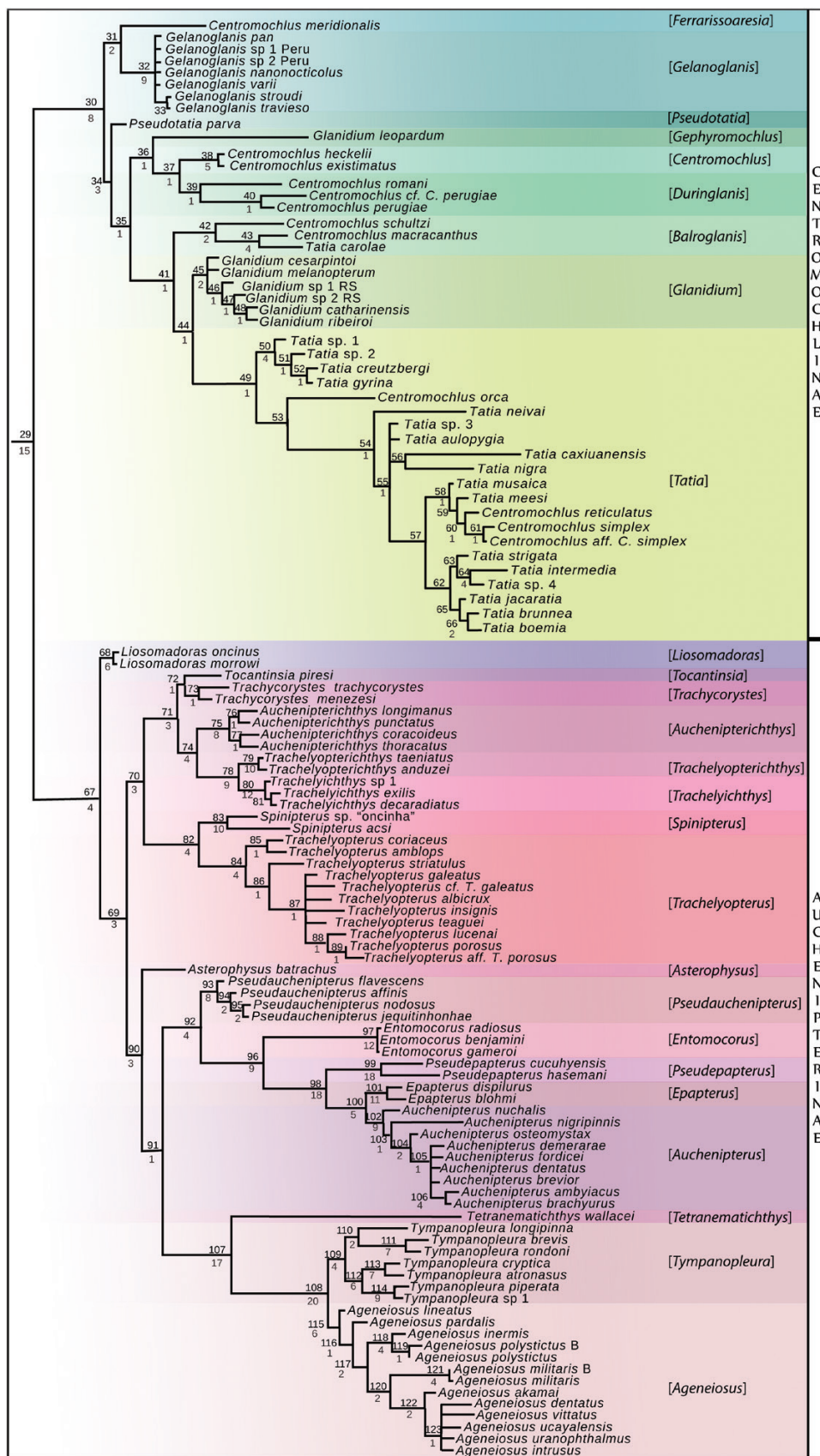


Figure 13. Parsimony analysis of combined data from morphology (264 characters) and five genes (*coI*, 16S, *rag2*, *myh6* and *SH3PX3*). Strict consensus of 211 maximally parsimonious trees (consistency index = 0.27; retention index = 0.66) with 9025 steps, showing the relationships of Auchenipteridae genera and a new proposed classification. Tree branches were truncated at genus level. Clade numbers appear above branches and Goodman–Bremer index below.



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and *Gelanoglanis*; (9) gill filaments ossified (char. 3641: 0 → 1), convergent in some species of Mochokidae; reversed in *Asterophysus*, *Gelanoglanis* and some species of *Centromochlus*; (10) pectoral girdle elongated (char. 3695: 0 → 2), convergent in *Pimelodus* and some mochokids; reversed in Trachycorystina, Auchenipterichthyina (except *Auchenipterichthys*), Auchenipterini (except *Entomocorus*), *Asterophysus*, *Ageneiosini* and *Glanidium catharinensis*; (11) posterior process of cleithrum elongated, approximately two-thirds to same length as pectoral-fin spine (char. 3711: 1 → 2), convergent in *Aspredo aspredo*, reversed in *Ageneiosini*, Auchenipterini, *Asterophysus*, Trachelyopterina and *Gelanoglanis*; and (12) posterior process of cleithrum ornamented (char. 3712: 0 → 1), convergent in some species of Mochokidae, reversed in Auchenipterina (except *Pseudauchenipterus jequitinhonhae* and *Pseudauchenipterus nodosus*) and *Ageneiosini*.

Additional synapomorphies: dorsal surface of epiotic participating in cephalic shield (char. 83: 0 → 1, exclusive); and seven to nine branchiostegal rays (char. 177: 0 → 1) (Birindelli, 2014).

Comparisons: Doradoidea species differ from Pimelodidae, Ariidae, Diplomystidae Pseudopimelodidae, Heptapteridae, Cetopsidae and Trichomycteridae by the continuous orbital margin, i.e. eye covered by a continuous membrane that is conjoint to the skin (vs. free orbital margin); they differ from Pimelodidae, Diplomystidae, Ariidae and Cetopsidae by having the gill-opening membranes united with the isthmus across a large extension (vs. separate from each other and free from the isthmus, or united with the isthmus at one single location, or united to each other and free from the isthmus).

FAMILY DORADIDAE BLEEKER, 1858 (CLADE 21)

Doradini Bleeker, 1858a: 39 (type genus: *Doras* La Cèpe, 1803; also in Bleeker, 1858b: 48, 52).

Included taxa: *Acanthodoras* Bleeker, 1862, **Agamyxis* Cope, 1878, *Franciscodoras* Eigenmann, 1925, Astrodoradinae Higuchi *et al.*, 2007, Doradinae Bleeker, 1858 and Wertheimerinae Birindelli, 2014.

Diagnosis: Doradidae is diagnosed by 13 molecular and seven morphological synapomorphies. **Exclusive:** (1) midlateral scutes present (char. 3528: 0 → 1); and (2) ventral process on fourth basibranchial present

(char. 3643: 0 → 1). **Non-exclusive:** (3) gill rakers of first branchial arch distinctly longer than those in remaining arches (char. 3637: 0 → 1), convergent in Ariidae, some mochokids, *Pimelodus*, Auchenipterini, *Ageneiosus* and *Tympanopleura*; (4) posterior process of third epibranchial of approximately the same length as its mesial portion (char. 3648: 0 → 1), convergent in several siluriforms; (5) distal portion of posterior process of third epibranchial pointed (char. 3649: 0 → 1); convergent in several auchenipterids; (6) posterior nuchal plate broad (char. 3673: 0 → 1), convergent in some auchenipterids; and (7) hypurapophysis of type B (Lundberg & Baskin, 1969) (char. 3747: 2 → 1), convergent in some auchenipterids, reversed in *Megalodoras uranoscopus*.

Additional synapomorphies: Ligament present between Müllerian ramus and lateral line (char. 212: 0 → 1, exclusive); infranuchal ligament between posterior nuchal plate and first rib ossified (char. 213: 1 → 2, exclusive); pectoral-fin spine locking foramen absent (char. 253: 0 → 1); and six or seven branched rays in ventral lobe of caudal fin (char. 306: 1 → 0). In addition, the coronomeckelian bone connected to dentary (char. 137: 0 → 1) was also proposed by Birindelli (2014) as diagnostic for the family, but in the present observations, the coronomeckelian bone of auchenipterids contacts the dentary in the same way as in doradids, with the shape and size of the coronomeckelian bone being variable between both families (Birindelli, 2014).

Comparisons: Doradids are distinguished from all Siluriformes by having one longitudinal row of bony scutes on each side of the midlateral portion of body, in which each midlateral scute bears a backward-directed thorn (except *Wertheimeria*, although sometimes, large individuals possess such scutes in the caudal peduncle; vs. bony scutes absent in Siluriformes, except Loricariidae and Callichthyidae, in diverse configurations); it differs from Auchenipteridae by the subterminal or ventral mouth, except Astrodoradinae (vs. terminal mouth, except *Ageneiosini*), lack of suborbital groove (vs. suborbital groove present), and intromittent organ absent in anal fin of males (vs. intromittent organ present, anterior to or attached at anterior rays, in anal fin of males).

FAMILY AUCHENIPTERIDAE BLEEKER, 1862 (CLADE 29)

Euanemini Bleeker, 1858a: 39 (type genus: *Euanemus* Müller & Troschel, 1842; also in Bleeker, 1858b: 49).

Figure 14. Parsimony analysis of combined data from morphology (264 characters) and five genes (*coI*, 16S, *rag2*, *myh6* and *SH3PX3*). Strict consensus of 211 maximally parsimonious trees (consistency index = 0.27; retention index = 0.66) with 9025 steps, showing the relationships of Centromochlinae and Auchenipterinae, including all species examined, and the new proposed classification. Clade numbers appear above branches and Goodman–Bremer index below.

Auchenipterini Bleeker, 1862 (in [Bleeker, 1862–63](#)): 14 (type genus: *Auchenipterus* Valenciennes, in [Cuvier & Valenciennes, 1840](#); name in prevailing recent practice, ICZN Article 35.5).

Type genus: *Auchenipterus* Valenciennes, 1840.

Included subfamilies: Auchenipterinae Bleeker, 1862 and Centromochlinae Bleeker, 1862.

Diagnosis: Auchenipteridae is diagnosed by 20 molecular and 14 morphological synapomorphies. **Exclusive**: (1) suborbital groove to lodge maxillary bone present (char. 3501: 0 → 1); (2) urogenital pore of female enlarged, ending in internal cavity for insemination (char. 3733: 0 → 1); (3) anal fin of male with intromittent organ (char. 3734: 0 → 1); (4) anterior rays of anal fin of nuptial males larger than in non-nuptial males (char. 3743: 0 → 1); (5) first hypobranchial funnel shaped, with constriction on mid-portion and medial margin narrower than lateral (char. 3645: 0 → 1), reversed in several auchenipterids; and (6) cartilage on lateral process of basipterygium anteriorly elongated (char. 3727: 0 → 1), reversed in *Entomocorus*, *Epapterus*, *Glanidium*, *Tetranematichthys*, *Trachelyopterichthys* and *Trachelyichthys* sp. 1. **Non-exclusive**: (7) antorbital participating in orbital margin (char. 3514: 0 → 1), convergent in *Helogenes*, reversed in *Ageneiosini*, *Gelanoglanis* and *Trachelyopterus insignis*; (8) ventral projection on antorbital present (char. 3516: 0 → 1), convergent in *Anadoras grypus*, *Bunocephalus doriae* and *Pimelodus maculatus*; (9) premaxillary curved (char. 3584: 0 → 1), reversed in *Auchenipterichthys*, *Entomocorus*, *Gelanoglanis*, *Glanidium catharinensis* and *Glanidium cesarpintoi*, convergent in *Pseudobunocephalus* and *Helogenes*; (10) levator operculi crest on hyomandibula present (char. 3617: 0 → 1), convergent in *Helogenes* and most mochokids, reversed in several auchenipterids; (11) interopercle short, ovoid (char. 3626: 0 → 2), reversed in several auchenipterids, convergent in *Helogenes* and *Aspredo aspredo*; (12) os suspensorium reduced (char. 3655: 0 → 1), reversed in several auchenipterids, convergent in some doradids, *Pseudobunocephalus* and *Euchilichthys dybowskii*; (13) basal process of pelvic-fin rays dorsally oriented (char. 3732: 0 → 1), reversed in *Ageneiosini*, *Asterophysus*, *Gelanoglanis*, Auchenipterini (except *Entomocorus*), *Trachelyopterus*, *Trachelyopterichthys* and *Trachycorystes*, convergent in *Aspredo aspredo*, *Bunocephalus doriae*, *Megalodoras uranoscopus* and *Rhynchodoras woodsi*; and (14) ventral process on hypurapophysis present (char. 3748: 0 → 1), reversed in *Ageneiosus*, *Tympanopleura*, *Gelanoglanis* and

Trachelyopterini, convergent in *Genidens barbatus* and most mochokids.

Additional synapomorphies: maxillary barbel moving vertically (char. 13: 0 > 1, exclusive); posterior testicular lobes modified into hypertrophied storage bags (char. 44: 0 > 1); and vertical rows of neuromasts dorsal to lateral line present (char. 117: 0 > 1) ([Birindelli, 2014](#)).

Comparisons: Auchenipterids differ from other Siluriformes by having a suborbital groove (vs. suborbital region without depression), secondary sexual dimorphism present in anal fin of males; genital tube present attached to anteriormost ray or anterior to anal fin (vs. lack of intromittent organ, except *Astroblepidae* and *Scoloplacidae*), anal fin of nuptial males larger than non-nuptial males (vs. anal fin of nuptial males and non-nuptial males of same size).

SUBFAMILY CENTROMOCHLINA BLEEKER, 1862 (CLADE 30)

Centromochli Bleeker, 1862 (in [Bleeker, 1862–63](#)): 7 (type genus: *Centromochlus* Kner, 1857).

Included tribes: Centromochlini, Gelanoglanini, Glanidiini and Pseudotatiini.

Diagnosis: Centromochlinae is diagnosed by 28 molecular and eight morphological synapomorphies. **Exclusive**: (1) secondary sexual dimorphism in anal fin present, male and female with distinct anal-fin shape (char. 3737: 0 → 1); and (2) proximal radials of anal fin partly or totally fused in nuptial males (char. 3738: 0 → 1); **Non-exclusive**: (3) posterior process of posttemporal-supracleithrum anteroventrally oriented (char. 3561: 0 → 1), reversed in *Glanidium catharinensis* and *Glanidium* sp. 1 RS, and *Glanidium* sp. 2 RS, convergent in several auchenipterids; (4) lateroposterior portion of sphenotic slightly concave (char. 3552: 0 → 1), reversed in *Glanidium*, *Centromochlus heckelii*, some species of *Tatia*, convergent in *Liosomadoras morrowi*, *Trachelyichthys decaradiatus*, *Trachelyichthys* sp. 1, *Trachelyopterus lucenai*, *Trachelyopterus porosus*, some mochokids and doradids and *Pimelodus tetramerus* Ribeiro & Lucena, 2006; (5) maxilla elongated, rod-like (char. 3590: 0 → 1), reversed in *Glanidium* and *Tatia*, convergent in *Auchenipterichthys*, *Pseudepapterus*, *Trachelyopterus amblops*, *Trachelyopterus insignis* and some mochokids; (6) middle nuchal plate and parieto-supraoccipital in contact (char. 3672: 0 → 1), reversed in *Centromochlus*, *Duringlanis perugiae*, *Glanidium* and some species of *Tatia*, convergent in *Ageneiosini*, *Asterophysus*, *Entomocorus*,

Epapterus, *Pseudepapterus*, some mochokids, Ariidae, *Nemadoras humeralis* and *Rhynchodoras woodsi*; (7) anterior margin of pectoral girdle anteriorly pointed (char. 3694: 0 → 2), reversed in *Tatia simplex*, *Glanidium catharinensis*, *Tatia intermedia*, *Tatia* sp. 4, convergent in *Asterophysus*, *Auchenipterus*, *Entomocorus*, *Pseudauchenipterus*, *Trachelyichthys decaradiatus*, *Trachelyopterus insignis*, *Trachycorystes menezesi*, *Spinipterus acsi*, *Pimelodus*, *Helogenes*, *Pterobunocephalus depressus* and *Trachycodoras nattereri*; and (8) cartilage on posterior margin of basipterygium elongated, approximately same length as basipterygium (char. 3730: 0 → 1), convergent in *Auchenipterichthys longimanus*, *Auchenipterichthys punctatus* and *Trachelyopterichthys*.

Additional synapomorphies: four to six branchiostegal rays (char. 177: 1 → 0); and five branched dorsal-fin rays (char. 237: 0 → 1) (Birindelli, 2014).

Comparisons: Centromochlines are distinguished from auchenipterines by several characteristics related to modifications of the anal fin for copulation, such as: short anal-fin base (males and females); presence of secondary sexual dimorphism in the anal fin, where males have a drop-shaped anal fin (vs. lack of sexual dimorphism in the shape of the anal fin in the non-reproductive season); genital tube of adult males located anterior to the anal-fin rays and apart from anal-fin base (vs. genital tube of adult males attached to the base of anal-fin origin and united by skin anteriorly to the anal-fin rays); proximal radials of the anal fin fused in nuptial males, transforming the fin into a strong, functional structure (vs. proximal radials of anal fin not fused to each other); and, except for *Gelanoglanis*, the genital papilla of adult males with a hood-like flap of skin covering urogenital base (vs. genital papilla of adult males not covered by a hood-like flap of skin). Additionally, this subfamily is distinguished from the remaining auchenipterids by the very elongate cartilage on the posterior margin of the basipterygium, with approximately the same length as the basipterygium (vs. cartilage short).

TRIBE GELANOGLANINI CALEGARI, VARI & REIS
TRIB. NOV. (CLADE 31)

Type genus: *Gelanoglanis* Böhlke, 1980.
lsid: zoobank.org:act:E5676982-D0D0-4EE7-8BE2-DC9285AE2752

Included genera: *Gelanoglanis* Böhlke, 1980 and *Ferrarissoaresia* Grant, 2015.

Diagnosis: *Gelanoglanini* is diagnosed by five molecular and five morphological synapomorphies.

Non-exclusive: (1) gill filaments not ossified (char. 3641: 0 → 1), convergent in *Balroglanis schultzi*, *Balroglanis macracanthus* and *Duringlanis romani*; (2) anterior nuchal plate absent (char. 3670: 0 → 1), convergent in Ageneiosini, *Duringlanis romani*, *Pseudepapterus* and Clade 58 in *Tatia*; (3) four pterygiophores supporting soft dorsal-fin ray (char. 3675: 2 → 3), convergent in *Glanidium cesarpintoii*, most species of *Tatia*, *Pseudepapterus*, *Trachelyichthys*, *Trachelyopterichthys anduzei*, some species of *Trachelyopterus* and *Spinipterus*; (4) serration on anterior margin of dorsal-fin spine absent (char. 3689: 1 → 0), convergent in *Centromochlus existimatus*, *Auchenipterini* and *Trachelyichthys*; and (5) suture between scapulo-coracoids conspicuously interdigitated up to middle of coracoids, or only near posterior border (char. 3714: 1 → 2), convergent in *Asterophysus*, *Gephyromochlus*, *Pseudepapterus* and some species of *Tatia*.

GENUS GELANOGLANIS BÖHLKE, 1980 (CLADE 32)

Gelanoglanis Böhlke, 1980: 150 (type species: *Gelanoglanis stroudi* Böhlke, 1980; type by original designation. Gender masculine).

Included species: *Gelanoglanis nanonoticolus* Soares-Porto, Walsh, Nico & Netto, 1999, *Gelanoglanis pan* Calegari, Reis & Vari, 2014, *Gelanoglanis stroudi* Böhlke, 1980, *Gelanoglanis travieso* Rengifo, Lujan, Taphorn & Petry, 2008, *Gelanoglanis varii* Calegari & Reis, 2016, *Gelanoglanis* sp. 1 Peru Sabaj-Pérez *et al.*, undescribed, and *Gelanoglanis* sp. 2 Peru Sabaj-Pérez *et al.*, undescribed.

Diagnosis: *Gelanoglanis* is diagnosed by 37 molecular and 50 morphological synapomorphies. **Exclusive:** (1) soft papillae on maxillary barbel (char. 3502: 0 → 1); (2) nasal unossified (char. 3511: 0 → 1); (3) passageway of mandibular ramus outside to lower jaw (char. 3524: 0 → 1); (4) lateral line ending well before caudal-fin peduncle, approximately at end of anal fin (char. 3526: 0 → 2); (5) mesethmoid, elongate and narrow in dorsal view (char. 3532: 2 → 3); (6) anterior region of head with fleshy region anterior to mesethmoid and premaxillae (char. 3535: 0 → 1); (7) premaxillae positioned laterally to mesethmoid in dorsal view (char. 3536: 0 → 2); (8) anteroventral portion of mesethmoid with process developed into laminar keel (char. 3537: 2 → 0); (9) anterior cranial fontanel absent (char. 3539: 0 → 1); (10) vomer fused to mesethmoid (char. 3572: 0 → 1); (11) premaxilla vertically laminar (char. 3583: 0 → 3); (12) sesamoid 1 extremely reduced, spherical to ovoid shaped (char. 3621: 1 → 3); (13) first two branchial arches without gill rakers (char. 3635: 1 → 2); (14) third and fourth branchial arches without gill rakers (char. 3636: 0 → 2); (15) third proximal radial of pectoral

fin absent (char. 3698: 0 → 1); (16) dorsal process of cleithrum distinctively large, approximately the same length as the pectoral-fin spine (char. 3708: 0 → 1); (17) scapulo-coracoid without bony crest (char. 3719: 1 → 0); (18) proximal radials of anal-fin totally fused to each other in mature males (char. 3739: 0 → 1); and (19) first unbranched ray of ventral lobe of caudal fin articulated on parahypural (char. 3749: 1 → 0). **Non-exclusive:** (20) one pair of mental barbels (char. 3504: 1 → 0), convergent in *Ageneiosini*; (21) antorbital not participating on orbital margin (char. 3514: 1 → 0), convergent in *Trachelyopterus insignis* and *Ageneiosini*; (22) ventral projection on antorbital absent (char. 3516: 1 → 0), convergent in *Asterophysus*; (23) lateral ethmoid contacting only mesial portion of antorbital (char. 3517: 2 → 0), convergent in some species of *Ageneiosus* and *Tympanopleura*, *Entomocorus*, *Liosomadoras* and *Pseudauchenipterus*; (24) contact between antorbital and lateral ethmoid by ligament (char. 3518: 2 → 0), convergent in *Tympanopleura brevis* and *Ageneiosus uranophthalmus*; (25) infraorbitals not ossified (char. 3519: 3 → 6), convergent in small body-sized *Tatia* of clade 50 (except *Tatia creutzbergi*); (26) mesethmoid elongated, with length at least twice its width (char. 3533: 1 → 0), convergent in *Auchenipterini* (except *Pseudauchenipterus*) and *Tetranematichthys*; (27) anteromedial portion of mesethmoid not contacting premaxilla (char. 3534: 0 → 1), convergent in *Ageneiosini* and *Pseudepapterus*; (28) posterior process of epioccipital forming simple spine (char. 3563: 3 → 0), convergent in *Asterophysus*, *Auchenipterichthys*, *Balroglanis macracanthus*, *Balroglanis schultzi*, *Entomocorus* and *Trachelyopterichthys*; (29) premaxilla straight (char. 3584: 0 → 1), convergent in *Auchenipterichthys*, *Entomocorus*, *Glanidium catharinensis* and *Glanidium cesarpintoi*; (30) distal portion of premaxilla extended (char. 3586: 0 → 1); convergent in *Ageneiosini*, *Auchenipterus* and *Pseudepapterus cucuhyensis*; (31) premaxillary teeth straight (char. 3589: 0 → 1), convergent in several *Auchenipterids*; (32) coronomeckelian bone positioned oblique (char. 3596: 0 → 1), convergent in most species of *Tatia*, *Duringlanis romani*, *Balroglanis macracanthus* and *Liosomadoras*; (33) coronoid process on mandible smaller than posterior portion of dentary (char. 3601: 0 → 2), convergent in some species of *Ageneiosus* and *Tympanopleura*, *Entomocorus* and *Epapterus*; (34) hyomandibula articulated only to sphenotic (char. 3619: 1 → 3), convergent in several *Auchenipterids*; (35) hyomandibula separated from metapterygoid (char. 3620: 0 → 1), convergent in *Ageneiosini*, *Centromochlus*, *Tatia*, *Tetranematichthys*, *Pseudobunocephalus* and several *doradids*; (36) interopercle large, plate shaped (char. 3626: 2 → 0), convergent in *Auchenipterichthys* and *Trachelyopterichthys*; (37) third and fourth branchial arches without gill rakers (char. 3642: 0 → 2), convergent in *Ageneiosus* and *Tympanopleura*; (38) first hypobranchial elongate, cylindrical (char. 3645: 1 → 3),

convergent in *Asterophysus*; (39) posterior process of third epibranchial approximately of same length as its mesial portion (char. 3648: 0 → 1), convergent in several *Auchenipterids*; (40) distal portion of posterior process of third epibranchial pointed (char. 3649: 0 → 1), convergent in several *Auchenipterids*; (41) Müllerian ramus reduced, not surpassing one-half the length of the transcapular process (char. 3661: 0 → 1), convergent in *Ageneiosus* and *Pseudepapterus*; (42) proximal extremity of ribs straight (char. 3649: 1 → 0), convergent in several *Auchenipterids*; (43) serration on lateral margin of pectoral-fin spine absent (char. 3702: 1 → 0), convergent in some species of *Ageneiosus*, *Centromochlus* and *Auchenipterini* (except *Auchenipterus fordicei* and *Entomocorus*); (44) posterodorsal process of cleithrum absent (char. 3709: 0 → 1), convergent in some species of *Tatia* and *Duringlanis perugiae*; (45) posterior process of cleithrum moderated in size, approximately half the length of the pectoral-fin spine (char. 3711: 2 → 1), convergent in *Auchenipterini* (except *Pseudepapterus*), *Tocantinsia*, *Trachelyopterus* and *Spinipterus* sp. 'oncinha'; (46) posterior process of cleithrum smooth, without ornamentation (char. 3712: 1 → 0), convergent in *Tympanopleura brevis*, *Tympanopleura rondoni*, *Asterophysus*, *Auchenipterini* (except *Pseudauchenipterus flavescens* and *Pseudauchenipterus affinis*) and *Tetranematichthys*; (47) contralateral anteromedial processes of basipterygium sutured to each other only on anterior portion (char. 3723: 0 → 2), convergent in *Centromochlus*, *Entomocorus*, *Gephyromochlus*, *Tatia* (except *Tatia musaica* and *Tatia meesi*), *Trachelyopterichthys* and some species of *Trachelyopterus*; (48) basal process of pelvic-fin rays posteromedially oriented (char. 3732: 1 → 0), convergent in several *Auchenipterids*; (49) hypurapophysis of type D (Lundberg & Baskin, 1969) (char. 3747: 2 → 3), convergent in some species of *Trachelyopterus*; and (50) ventral process of hypurapophysis absent (char. 3748: 1 → 0), convergent in several *Auchenipterids*.

Additional diagnosis: posterior naris long, narrow and located immediately anterior to eye (Calegari *et al.*, 2014: char. 2); and mouth oblique and sinuous, with free fleshy flange around angle of mouth opening (Calegari *et al.*, 2014: char. 5). The only synapomorphy proposed by Soares-Porto *et al.* (1999) not included in the present analysis is the short base in all fins (except caudal fin), including relatively few fin rays (Calegari *et al.*, 2014: char. 6). However, the present results indicate that *Gelanoglanis* is similar to the remaining *Centromochlinae* with respect to the number of fin rays and the size of the fin base, not representing a diagnostic feature (Böhlke, 1980; Soares-Porto *et al.*, 1999; Calegari *et al.*, 2014).

Comparisons: *Gelanoglanis* is the only miniature group of species in the family, thus easily distinguished

by the smaller body size. It differs from other auchenipterid genera by the laterally compressed head (vs. rounded head, slightly or deeply depressed), sinuous shape of the mouth in lateral view (vs. mouth straight), anterior portion of snout with a fleshy region, not supported by skeleton (vs. anterior portion of snout structured by premaxilla and mesethmoid bones), premaxillae positioned laterally to the mesethmoid (vs. premaxilla positioned anterior or anterolaterally), premaxilla laminar and oriented vertically to the head (vs. premaxilla horizontally oriented), passageway of mandibular ramus of lateral line system running outside to the lower jaw (vs. mandibular ramus running inside dentary), lateral line ending well before caudal-fin peduncle, approximately at the end of the anal fin (vs. reaching near or surpassing the caudal fin). Furthermore, it differs from all auchenipterids, except Ageneiosini, by having one pair of mental barbels (vs. two pairs of mental barbels).

GENUS *FERRARISSOARESIA* GRANT, 2015 STAT. NOV.

Centromochlus (*Ferrarissoaresia*) Grant, 2015: 3 (type species: *Centromochlus meridionalis* Sarmiento-Soares, Cabeceira, Carvalho, Zuanon & Akama, 2013, by original designation and monotypy. Gender feminine). lsid: zoobank.org:act:9F4414A7-126A-4DE0-8010-41B11730AC6E

Included species: **Ferrarissoaresia ferrarisi* (Birindelli, Sarmiento-Soares & Lima, 2015) and *Ferrarissoaresia meridionalis* (Sarmiento-Soares, Cabeceira, Carvalho, Zuanon & Akama, 2013).

Diagnosis: *Ferrarissoaresia* is diagnosed by 43 molecular and five morphological autapomorphies: **Exclusive:** (1) axillary slit absent in adults (char. 3498: 0 → 1), exclusive within Centromochlinae, convergent in *Liosomadoras morrowi*, *Trachelyopterus lucenai*, *Trachelyopterus teaguei* and *Trachycorystes menezesi*. **Non-exclusive:** (2) epiphyseal bar present in anterior cranial fontanel (char. 3540: 0 → 1), convergent in *Centromochlus*, *Glanidium cesarpintoi*, *Tympanopleura atronassus*, *Ageneiosus inermis*, *Auchenipterichthys longimanus*, *Auchenipterichthys thoracatus*, *Auchenipterus ambyiacus*, *Liosomadoras*, *Tocantinsia*, *Trachelyopterichthys*, some species of *Trachelyopterus* and *Trachycorystes menezesi*; (3) coronoid process of anguloarticular developed into a thin and conspicuous process (char. 3602: 1 → 0), convergent in clade 90 in Auchenipterini, *Glanidium*, *Liosomadoras*, some species of *Tatia*, *Tetranematichthys*, *Trachelyopterina*, *Trachycorystina* and *Trachelyopterichthys*; (4) posterior bony projection on last pterygiophore of dorsal fin (char. 3680: 0 → 1), convergent in *Centromochlus*, *Balroglanis macracanthus*, *Balroglanis schultzi*,

some species of *Tatia* and several auchenipterines; and (5) anterolateral and anteromedial processes of basipterygium approximately of same length (char. 3725: 1 → 0), convergent in Ageneiosini, Auchenipterini (except *Entomocorus*), *Glanidium*, *Trachycorystes menezesi*, *Trachelyopterus amblops* and *Trachelyopterus coriaceus*.

Comparisons: *Ferrarissoaria* is distinguished from all Centromochlinae by the relatively long outer mental barbel, surpassing the pectoral-fin base (vs. outer mental barbel short, similar to the size of the inner barbel, ending much anterior to the pectoral-fin origin); from all Centromochlinae (except *Gelanoglanis*) by the small eye, approximately one-third of head depth, not surpassing the mouth gap or the line of upper lip (vs. eye relatively large, occupying half of head depth or more), and except *Tatia*, *Glanidium* and *Pseudotatia*, by having the eye positioned dorsolaterally (vs. eye positioned laterally). *Ferrarissoaresia* differs from *Gephyromochlus*, *Centromochlus*, *Duringlanis* and *Balroglanis* by the eye not being visible in ventral view (vs. visible in ventral view). It is further distinguished from *Centromochlus*, *Tatia* and *Gelanoglanis* by having the hyomandibular and metapterygoid contacting each other (vs. not contacting each other), and from *Centromochlus*, *Tatia* (except *Tatia musaica*, *Tatia meesi*, *Tatia reticulata* and *Tatia simplex*) and *Glanidium* by the lack of an anterior nuchal plate (vs. anterior nuchal plate present).

Remarks: *Ferrarissoaresia*, with the single species *Ferrarissoaresia meridionalis*, has a distinctive body shape and a splotchy colour pattern consisting of median brown speckles with darker large spots concentrated in the dorsolateral surface of body. Although *Centromochlus ferrarisi* was not included in the present study, it is provisionally transferred to the genus *Ferrarissoaresia* based on the sharing of several diagnostic characters. The lack of an anterior nuchal plate, the hyomandibular contacting the metapterygoid, the small-sized eye positioned dorsolaterally, the short body length, and the outer mental barbel elongated, characteristics not found in *Tatia* and *Centromochlus*, support the allocation in *Ferrarissoaresia*. In spite of that, the inclusion of *Ferrarissoaresia ferrarisi* in a phylogenetic context is necessary to confirm its generic position.

TRIBE PSEUDOTATIINI CALEGARI, VARI & REIS TRIB. NOV.

Type genus: *Pseudotatia* Mees, 1974.
lsid: zoobank.org:act:C6BC3B58-2803-4A6F-A0F6-E41203A34DFB

Included genus: *Pseudotatia* Mees, 1974.

Diagnosis: Pseudotatiini is diagnosed by seven morphological autapomorphies. **Exclusive:** (1) mesethmoid expanded anterolaterally, with notch only on posterior portion (char. 3532: 0 → 1), exclusive within Centromochlinae, convergent in Auchenipterini, *Trachelyichthys* and *Trachelyopterichthys*; (2) six free pterygiophores on dorsal fin (char. 3675: 2 → 1); and (3) contralateral anteromedial processes of basipterygium sutured to each other along entire length (char. 3723: 0 → 1), convergent in *Auchenipterus*, *Epapterus* and *Pseudepapterus* (clade 92). **Non-exclusive:** (4) anterior cartilage of lateral ethmoid extended (char. 3547: 0 → 1), convergent in *Gelanoglanis varii*, *Gelanoglanis pan*, Auchenipterini and Ageneiosini; (5) posterior process of third epibranchial elongated, approximately the same length as its mesial portion (char. 3648: 0 → 1), convergent in *Trachelyichthys* (except *Tatia* sp. 1), Auchenipterini (except *Pseudauchenipterus affinis* and *Entomocorus*), *Gelanoglanis*, *Auchenipterichthys longimanus*, *Auchenipterichthys thoracatus*, *Ageneiosus vittatus*, *Tympanopleura atronasmus*, some species of *Trachelyopterus* and *Spinipterus*; (6) posterior process of third epibranchial pointed (char. 3649: 0 → 1), convergent in several auchenipterids; and (7) serration absent on posterior margin of dorsal-fin spine (char. 3693: 0 → 1), convergent in most of *Ageneiosus*, *Asterophysus*, *Epapterus*, *Duringlanis perugiae*, *Gelanoglanis travieso*, *Glanidium cesarpinto*, *Pseudepapterus*, *Tatia* (except *Tatia intermedia*), *Tocantinsia*, *Trachelyopterichthys*, *Trachelyopterus amblops*, *Trachelyopterus insignis*, *Trachycorystes trachycorystes* and *Spinipterus*.

GENUS *PSEUDOTATIA* MEES, 1974

Pseudotatia Mees, 1974: 105 (type species: *Pseudotatia parva* Mees, 1974; type by original designation. Gender feminine).

Included species: *Pseudotatia parva* Mees, 1974.

Diagnosis: Same as for tribe Pseudotatiini.

Comparisons: *Pseudotatia* differs from all centromochlines by having more numerous rays on the anal fin, a total of 15–17 rays (vs. 7–14 total anal-fin rays) and, except for *Glanidium ribeiroi*, by having more numerous rays on the dorsal fin, six branched rays (vs. five in remaining genera, except *Tatia creutzbergi* and *Tatia gyrina* with four rays). It differs from *Centromochlus*, *Balroglanis*, *Glanidium* (except *Glanidium cesarpinto*) and *Duringlanis romani* by the lack of serration on the posterior margin of the dorsal-fin spine. It differs from *Ferrarissoaresia* by the shorter outer mental barbel, not reaching the pectoral-fin

spine (vs. long outer mental barbel surpassing the pectoral-fin base); and from *Tatia*, *Gelanoglanis* and *Centromochlus* by having the hyomandibula and metapterygoid in contact to each other (vs. such bones not in contact).

TRIBE CENTROMOCHLINI BLEEKER, 1862 (CLADE 36)
Centromochlini Bleeker, 1862 (in Bleeker, 1862–63): 7
(type genus: *Centromochlus* Kner, 1857).

Included genera: *Centromochlus* Kner, 1857, *Duringlanis* Grant, 2015 and *Gephyromochlus* Hoedmann, 1961.

Diagnosis: Centromochlini is diagnosed by 11 molecular synapomorphies.

GENUS *GEPHYROMOCHLUS* (HOEDMAN, 1961) STAT. NOV.

Centromochlus (*Gephyromochlus*) Hoedman, 1961: 135 (type species: *Centromochlus* (*Gephyromochlus*) *leopardus* Hoedman, 1961; type by monotypy. Gender masculine).

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Included species: *Gephyromochlus leopardus* (Hoedman, 1961).

Diagnosis: *Gephyromochlus* is diagnosed by 71 molecular autapomorphies.

Comparisons: *Gephyromochlus* differs from all centromochlines, except *Centromochlus* and *Gelanoglanis*, by having the anterior margin of the pectoral-fin spine smooth, without serration (vs. pectoral-fin spine serrated). It differs from *Duringlanis* by having the lateral border of the median nuchal plate arched, curved mesially (vs. lateral border of median nuchal plate straight), and elongated anterior fontanel, surpassing the line of the posterior naris (vs. small, not surpassing the line of the posterior naris); from *Centromochlus* by the possession of an anterior nuchal plate (vs. anterior nuchal plate absent); from *Balroglanis* by having the anterior margin of the dorsal-fin spine smooth, not serrated (vs. anterior margin of dorsal-fin spine serrated); from *Ferrarissoaresia* by the outer mental barbel being short, ending much anterior to the pectoral-fin origin (vs. relatively long outer mental barbel, surpassing the pectoral-fin base); from *Tatia* by having more branched anal-fin rays, nine or 10 (vs. six to eight); and from *Gelanoglanis* by having a rounded and slightly depressed head (vs. laterally compressed head), possession of two pairs of

mental barbels (vs. one pair of mental barbels) and other features that can be seen in the *Gelanoglanis* diagnosis.

GENUS *CENTROMOCHLUS* KNER, 1857 (CLADE 38)

Centromochlus Kner, 1857: 430 (type species: *Centromochlus megalops* Kner, 1857; type by subsequent designation by Bleeker, 1862 (in Bleeker, 1862–63): 7. Gender masculine. Species considered as junior synonym of *Centromochlus heckelii* by Mees, 1974).

Included species: *Centromochlus existimatus* Mees, 1974 and *Centromochlus heckelii* (De Filippi, 1853).

Diagnosis: *Centromochlus* is diagnosed by 20 morphological synapomorphies. **Exclusive:** (1) ventral keel on parasphenoid present (char. 3576: 0 → 1), exclusive within Auchenipteridae; and (2) distal portion of Müllerian ramus protruded posteriorly (char. 3660: 0 → 1). **Non-exclusive:** (3) eye extremely large, occupying almost entire head depth (char. 3491: 0 → 1), convergent in *Tympanopleura*, *Auchenipterus*, *Balroglanis macracanthus*, *Balroglanis schultzi*, *Entomocorus* and *Epapterus*; (4) contralateral mandibulae running approximately in parallel (char. 3492: 0 → 1), convergent in *Balroglanis*; (5) epiphyseal bar on anterior cranial fontanel present (char. 3540: 0 → 1), convergent in *Tympanopleura atronasus*, *Ageneiosus inermis*, *Auchenipterichthys longimanus*, *Auchenipterichthys thoracatus*, *Auchenipterus ambyiacus*, *Ferrarissoaresia*, *Liosomadoras*, *Trachelyopterichthys*, *Trachycorystes menezesi* and some species of *Trachelyopterus*; (6) coronomeckelian bone strongly sutured, continuous to anguloarticular (char. 3597: 0 → 1), convergent in Ageneiosini, Trachelyopterini (except *Trachelyichthys*), Auchenipterini (except *Pseudepapterus*, *Pseudauchenipterus jequitinhonhae* and *Pseudauchenipterus nodosus*), *Glanidium cesarpinto* and *Gephyromochlus*; (7) ascending process of Meckel's cartilage absent (char. 3598: 0 → 1), exclusive within Centromochlinae, convergent in *Asterophysus* within Auchenipteridae; (8) coronoid process of mandible absent (char. 3600: 0 → 1), exclusive within Centromochlinae, convergent in *Asterophysus* within Auchenipteridae; (9) posterodorsal portion of dentary straight (char. 3603: 0 → 1), exclusive within Centromochlinae, convergent in *Asterophysus* within Auchenipteridae; (10) metapterygoid and hyomandibula separated (char. 3620: 0 → 1), convergent in Ageneiosini, *Gelanoglanis* and *Tatia*; (11) posterior projection on urohyal in ventral view elongated, at least twice the length of the main body of the urohyal (char. 3628: 1 → 0), convergent

in Ageneiosini, *Auchenipterichthys longimanus*, *Auchenipterus*, *Epapterus* and *Pseudepapterus*; (12) distal tips of first hypobranchial approximately with same width, in hourglass shape (char. 3645: 1 → 2), convergent in Trachelyopterini, *Tetranematichthys*, *Balroglanis*, *Tatia meesi* and *Tatia intermedia*; (13) parapophysis of fifth vertebra small, smaller than subsequent vertebra (3665: 1 → 2), convergent in *Asterophysus*, *Auchenipterichthys*, *Auchenipterus osteomystax*, *Gelanoglanis*, *Glanidium catharinensis*, *Glanidium ribeiroi*, *Pseudauchenipterus*, *Trachelyopterichthys*, *Trachycorystes* and some species of *Trachelyopterus*; (14) compound centrum including up to eighth vertebra (char. 3667: 3 → 4), exclusive within Centromochlinae, convergent in Trachelyopterini (except *Trachelyichthys*, *Trachelyopterus albicrux* and *Trachelyopterus teaguei*); (15) posterior bony projection on last dorsal-fin pterygiophore present (char. 3680: 0 → 1), convergent in Ageneiosini, *Auchenipterichthys* (except *Auchenipterichthys punctatus*), Auchenipterini, some species of *Tatia*, *Tocantinsia* and Trachelyopterina (except *Spinipterus acsi*); (16) dorsal-fin spine elongated, greater than one-third of SL (char. 3685: 0 → 2), convergent in *Tatia intermedia*; (17) anterior margin of pectoral-fin spine smooth, without serration (char. 3702: 1 → 0), some species of *Ageneiosus*, Auchenipterini (except *Entomocorus* and *Auchenipterus fordicei*), *Gelanoglanis* and *Gephyromochlus*; (18) pectoral-fin spine elongated, greater than one-third of SL (char. 3706: 0 → 1), convergent in *Balroglanis macracanthus*; (19) posterior portion of basipterygium long, with process developed as wing (char. 3729: 0 → 1), convergent in Ageneiosini, Auchenipterina, Trachycorystina and *Asterophysus*; and (20) anterior portion of fifth hypural contacting point of convergence between third and fourth hypurals and epineural (char. 3752: 0 → 1), convergent in Auchenipterinae (except *Liosomadoras morrowi* and *Entomocorus*), *Gelanoglanis* and some species of *Tatia*.

Comparisons: *Centromochlus* differs from all Centromochlinae by having a ventral keel on the anterior half of the parasphenoid (vs. ventral keel absent); except for *Balroglanis* by having the proximal portion of the maxillary barbel ventrally positioned, in such a way that it is visible ventrally (vs. proximal portion of maxillary barbel laterally positioned, not visible ventrally); and lateral margins of the mandibulae running approximately in parallel (vs. lateral margins of mandibulae diverging laterally). *Centromochlus* differs from all centromochlines, except *Gelanoglanis* and *Gephyromochlus*, by having the anterior margin of the pectoral-fin spine smooth, without serration (vs. anterior margin of pectoral-fin spine serrated); from all centromochlines, except

Balroglanis and *Duringlanis*, by having the eye ventrally displaced, in such a way that that almost the entire eye is visible in ventral view (vs. eye not visible, or little visible in ventral view) and, except *Balroglanis*, by having the origin of the outer mental barbel aligned near to the vertical line of the inner one (Fig. 1A) (vs. origin of outer mental barbel positioned further laterally relative to the inner, spaced from each other by more than the barbel-base size; Fig. 1D); from *Ferrarissoaresia*, *Duringlanis*, *Balroglanis* and *Gephyromochlus* by having the posterior process of the urohyal dorsally curved, concave (vs. straight), and by the longer pectoral-fin spine, greater than one-third of SL (vs. less than one-third of SL). It differs from *Balroglanis* by having subequal outer and inner barbels (Fig. 1A) (vs. outer mental barbel distinctly longest than inner; Fig. 1C). It differs from *Glanidium* and *Tatia* (except *Tatia boemia* and *Tatia jacaratia*) by the posterior process of the cleithrum being positioned posteriorly (vs. posterior process of cleithrum dorsally inclined).

Remarks: *Centromochlus* was described by Kner (1857) to include two species: *Centromochlus megalops*, whose holotype was not designated, and *Centromochlus aulopygius* (currently *Tatia*). In his description of *Centromochlus*, Kner did not designate a type species for the genus. Additionally, Kner (1857) reported the type locality for *Centromochlus heckelii* as Bogotá, without any additional information about a particular river or basin. Given that Bogotá is a town high in the Andes, as already noted by Mees (1974), and there is no records of this species in that region, it indicates that the type locality is not precise and likely to be wrong. Thereafter, Bleeker (1862–63; volume II: 7), by describing a new ‘Phalanx’ *Centromochli*, proposed by subsequent designation *Centromochlus megalops* as the type species of *Centromochlus*, but without any further discussion about the decision. Notwithstanding, in the study addressing the Auchenipteridae and Pimelodidae diversity of fishes from Suriname, Mees (1974) proposed *Centromochlus megalops* Kner, 1857 as a junior synonym of *Centromochlus heckelii*. Controversially, Royero (1999: 257), in his PhD dissertation, analysed populations of *Centromochlus heckelii* from the Orinoco basin and opted for the revalidation of *Centromochlus megalops*. His decision was mostly based on a lot (ICN-MHN 1927) of *Centromochlus* from the Meta River in Colombia, which he considered to be a representative of *Centromochlus megalops* under a unique distinction of the absence of pigmentation on the caudal peduncle base (vs. pigmentation present in *Centromochlus heckelii*). The syntypes of *Centromochlus megalops* analysed herein (see Supporting Information, Appendix S1, Material

examined), indeed have the caudal peduncle base with such pigmentation (see Fig. 15, syntype photographs), thus not matching the unique diagnostic feature proposed to distinguish *Centromochlus megalops* from *Centromochlus heckelii*. Perhaps, this condition of a hyaline caudal-fin base is present only in populations from the Orinoco River other than that in the Meta River, and possibly represent a third species (specimens of that population were not analysed in detail in the present study). Yet, reinforcing that the population in the Meta River is *Centromochlus heckelii*, the anterior cranial fontanel does not reach the parieto-supraoccipital, a feature observed in specimens analysed from this locality (ANSP 131675). Consequently, the analysis of photographs and X-rays of the syntypes of *Centromochlus megalops* (NMW 47359, one specimen; NMW 47360; one specimen), allowed us to identify these specimens clearly and maintain this species herein as a junior synonym of *Centromochlus heckelii*, based on the anterior fontanel not reaching to the parieto-supraoccipital (Fig. 15) and fewer pectoral-fin rays.

GENUS *DURINGLANIS* GRANT, 2015
(CLADE 39) STAT. NOV.

Centromochlus (*Duringlanis*) Grant, 2015: 1 (type species: *Centromochlus perugiae* Steindachner, 1882; type by original designation. Gender masculine).
lsid: zoobank.org:act:C0379B54-EE63-48BF-AA81-A13862C6AE20

Included species: **Duringlanis altae* (Fowler, 1945), *Duringlanis perugiae* (Steindachner, 1882) and *Duringlanis romani* (Mees, 1988).

Diagnosis: *Duringlanis* is diagnosed by eight molecular and three morphological synapomorphies. **Non-exclusive:** (1) terminus of lateral line approaching end of caudal-fin peduncle (char. 3526: 0 → 1), convergent in the small body-sized *Tatia* of clades 50 and 58; (2) one row of gill rakers on third and fourth branchial arches (char. 3636: 0 → 1), convergent in *Balroglanis* (except *Balroglanis carolae*), *Tatia simplex* and *Tatia* aff. *Tatia simplex*; and (3) serration on anterior margin of dorsal-fin spine, spine shaped (char. 3692: 0 → 1); convergent in *Asterophysus*, *Liosomadoras* and some species of *Tatia* (*Tatia reticulata*, *Tatia boemia*, *Tatia brunnea*, *Tatia caxiuanensis*, *Tatia nigra*, *Tatia strigata*, *Tatia* sp. 2, *Tatia* sp. 3 and *Tatia* sp. 4).

Comparisons: *Duringlanis* differs from *Gephyromochlus*, *Balroglanis* and *Centromochlus* by having a small, rounded anterior fontanel, not surpassing the line of the posterior naris (vs. ellipsoid



Figure 15. Ventral and dorsal view of *Centromochlus megalops*, syntype, NMW 47359. Photography credits to Naturhistorisches Museum, Vienna.

anterior fontanel, elongated, surpassing the line of the posterior naris); from *Balroglanis* by having the posterior nuchal plate rounded and lacking lateroposterior projection (Fig. 16A) (vs. posterior nuchal plate forming an arch owing to the presence of lateral and posterior projections; Fig. 16B); spiny posterior process of epioccipital not exposed, covered by the median nuchal plate (Fig. 16A) (vs. posterior process of epioccipital exposed beyond the lateral border of median nuchal plate; Fig. 16B); lateral border of median nuchal plate straight (Fig. 16A) (vs. lateral border of median nuchal plate arched, curved mesially; Fig. 16B); from *Centromochlus* by having a shorter pectoral-fin spine, less than one-third of SL (vs. long pectoral-fin spine, greater than one-third of SL); and from *Ferrarissoaresia* by having the dorsal-fin spine serrated, serration particularly tiny and restricted to the tip of the spine in *Duringlanis romani* (vs. smooth anterior margin of dorsal-fin spine), and shorter outer mental barbel, distant from pectoral-fin origin (vs. outer mental barbel long, surpassing the pectoral-fin origin). It differs from *Tatia*, *Gephyromochlus* and *Glanidium* by having subequal outer and inner mental barbels (Fig. 1B) (vs. outer mental barbel distinctly longest than inner; Fig. 1C, D); from *Tatia*, *Centromochlus* and *Gelanoglanis* by having the hyomandibula and metapterygoid in contact with each other (vs. hyomandibula and metapterygoid separate from each other); and from *Glanidium* by the lateral line ending

near to the caudal peduncle (vs. terminus of lateral line surpassing the caudal-fin origin).

**TRIBE GLANIDIINI CALEGARI, VARI & REIS TRIB.
NOV. (CLADE 41)**

Type genus: *Glanidium* Lütken, 1874.

lsid: zoobank.org:act:C20A6ACA-BCA1-445E-98E1-A9556FA43EC2

Included genera: *Balroglanis* Grant, 2015, *Glanidium* Lütken, 1874 and *Tatia* Miranda Ribeiro, 1911.

Diagnosis: Glanidiini is diagnosed by 22 molecular synapomorphies.

**GENUS BALROGLANIS (GRANT, 2015)
(CLADE 42) STAT. NOV.**

Centromochlus (Balroglanis) Grant, 2015: 2 (type species: *Centromochlus schultzi* Rössel, 1962; by original designation. Gender masculine).

lsid: zoobank.org:act:A6E7310F-02A5-4CB5-9537-5D73D126D1BF

Included species: *Balroglanis carolae* (Vari & Ferraris, 2013), *Balroglanis macracanthus* (Soares-Porto, 2000) and *Balroglanis schultzi* (Rössel, 1962).

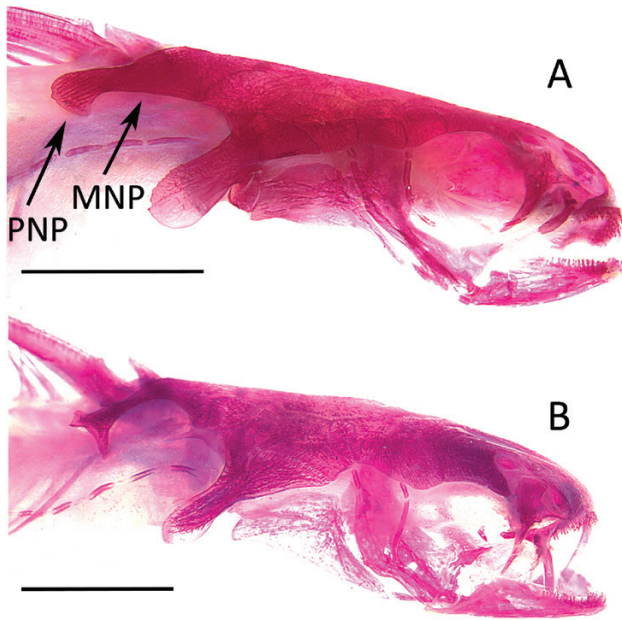


Figure 16. Lateral profile of head. A, *Duringlanis romani*, AMNH 91382, right side. B, *Balroglanis schultzi*, MZUSP 94138, left side. Abbreviations: MNP, middle nuchal plate; PNP, posterior nuchal plate. Scale bars: 5 mm.

Diagnosis: *Balroglanis* is diagnosed by 19 molecular and three morphological synapomorphies. **Non-exclusive:** (1) contralateral mandibulae running approximately in parallel (char. 3492: 0 → 1), convergent in *Centromochlus*; (2) distal tips of first hypobranchial approximately of the same width, hourglass shaped (char. 3645: 1 → 2), convergent in Trachelyopterini, *Tetranematichthys*, *Centromochlus*, *Tatia meesi* and *Tatia intermedia*; and (3) anterior nuchal plate absent (char. 3670: 0 → 1), convergent in Ageneiosini, Gelanoglanini, *Duringlanis romani*, *Pseudepapterus* and clade 58 in *Tatia*.

Comparisons: *Balroglanis* differs from all centromochlines, except *Centromochlus* and *Duringlanis*, by having the eye ventrally displaced, in a way such that almost the entire eye is visible in ventral view (vs. eye not visible, or little visible in ventral view); and except *Centromochlus* by the outer mental barbel being aligned near to the vertical line of the inner one (Fig. 1C) (vs. origin of outer mental barbel positioned further laterally relative to the inner, spaced from each other by more than the barbel-base size; Fig. 1D). It further differs from *Centromochlus*, *Gephyromochlus* and *Glanidium* by the lack of an anterior nuchal plate (vs. anterior nuchal plate present); from *Tatia* (except *Tatia intermedia* and *Tatia simplex*) and *Pseudotatia* by having the

dorsal-fin spine serrated on the posterior border (vs. serrations absent on posterior border of dorsal-fin spine); from *Glanidium* and *Tatia* (except *Tatia boemia* and *Tatia jacaratia*) by having the posterior process of cleithrum positioned posteriorly (vs. posterior process of cleithrum dorsally inclined); and from *Duringlanis* by having the lateral border of the median nuchal plate arched, curved mesially (Fig. 16B) (vs. lateral border of the median nuchal plate straight; Fig. 16A), ellipsoid anterior fontanel, elongated, surpassing the line of the posterior naris (vs. small, rounded anterior fontanel, not surpassing the line of the posterior naris), the posterior nuchal plate forming an arch in the lateral portion owing to the presence of lateral and posterior projections (Fig. 16B) (vs. posterior nuchal plate rounded and lacking lateral projection; Fig. 16A), posterior process of epioccipital exposed beyond the lateral border of the median nuchal plate (Fig. 16B) (vs. spiny posterior process of epioccipital not exposed, covered by the median nuchal plate; Fig. 16A); from *Centromochlus* by having smaller pectoral-fin spine, less than one-third of SL (vs. pectoral-fin spine long, greater than one-third of SL); from *Gelanoglanis* by having rounded head, slightly depressed (vs. head laterally compressed); and from *Pseudotatia* by having fewer anal-fin rays, seven to nine (vs. 15–17 total anal-fin rays).

GENUS *GLANIDIUM* LÜTKEN, 1874 (CLADE 45)

Glanidium Lütken, 1874: 31 (type species: *Glanidium albescens* Lütken, 1874; type by monotypy. Gender neuter).

Included species: **Glanidium albescens* Reinhardt, 1874, **Glanidium botocudo* Sarmiento-Soares & Martins-Pinheiro, 2013, *Glanidium catharinensis* Miranda Ribeiro, 1962, *Glanidium cesarpinto* Ihering, 1928, *Glanidium melanopterum* Miranda Ribeiro, 1918, *Glanidium ribeiroi* (Haseman, 1911), *Glanidium* sp. RS 1 Sarmiento-Soares, Calegari, Martins-Pinheiro & Malabarba, undescribed, *Glanidium* sp. RS 2 Sarmiento-Soares, Calegari, Martins-Pinheiro & Malabarba, undescribed.

Diagnosis: *Glanidium* is diagnosed by three molecular and six morphological synapomorphies. **Non-exclusive:** (1) parasphenoid short, ≥ 50% of its length composed by wide base of bone (char. 3577: 1 → 0), convergent in Ageneiosini, Gelanoglanini, *Pseudotatia*, *Tatia gyrina*, *Tatia creutzbergi*, *Pseudauchenipterus*, Trachelyopterini, Liosomadoradini and Asterophysini; (2) trigeminofacial foramen not exposed, covered by parasphenoid (char. 3581: 0 → 1), exclusive within Centromochlinae, convergent in Ageneiosini (*Tympanopleura piperata* and *Tympanopleura cryptica*),

Liosomadoras, *Auchenipterichthys*, *Auchenipterus brachyurus*, *Auchenipterus ambyiacus*, *Trachelyopterina* (except *Trachelyopterus amblops*), *Trachycorystina* and *Trachelyichthys* (except *Trachelyichthys decaradiatus*); (3) coronoid process of anguloarticular developed into thin and conspicuous process (char. 3602: 1 → 0), convergent in *Auchenipterus*, *Ferrarissoaresia*, *Pseudepapterus*, *Liosomadoras*, *Tatia boemia*, *Tatia* sp. 4, *Tatia jacaratia*, *Tatia nigra*, *Trachelyopterichthys*, *Trachelyopterina*, *Trachycorystina* and *Tetranematichthys*; (4) anterolateral and anteromedial processes of basipterygium of approximately same length (char. 3725: 1 → 0), exclusive within *Centromochlinae*, convergent in *Ageneiosini*, *Auchenipterini* (except *Entomocorus*), *Trachelyopterus amblops* and *Trachelyopterus coriaceus*; (5) cartilage of lateral process of basipterygium short (char. 3727: 1 → 0), exclusive within *Centromochlinae*, convergent in *Entomocorus*, *Epapterus*, *Trachelyopterichthys*, *Tetranematichthys* and *Trachelyichthys* sp. 1; and (6) basal process of pelvic-fin rays oriented posteromedially in dorsal view (char. 3732: 1 → 0), convergent in *Gelanoglanis*, *Ageneiosini*, *Auchenipterini* (except *Entomocorus*), *Trachelyopterichthys*, *Trachelyopterus* and *Trachycorystes*.

Comparisons: *Glanidium* differs from remaining centromochlines by having the trigeminofacial foramen not exposed, covered by the parasphenoid (vs. trigeminofacial foramen exposed in ventral view) and anterolateral and anteromedial processes of the basipterygium of approximately the same length (vs. anterolateral process longer than anteromedial process). It differs from *Tatia*, *Centromochlus* and *Gelanoglanis* by having the hyomandibula and metapterygoid in contact with each other (vs. hyomandibula and metapterygoid separated from each other); from *Balroglanis* and *Gelanoglanis* by the possession of an anterior nuchal plate (vs. anterior nuchal plate absent); from *Centromochlus*, *Duringlanis* and *Balroglanis* by having the eye not or little visible in ventral view (vs. eye ventrally displaced, in such a way that almost the entire eye is visible in ventral view). It differs from *Pseudotatia* by having fewer anal-fin rays, 12–14 total rays (vs. 15–17 total rays); from *Ferrarissoaresia* by having the outer and inner mental barbels of similar length, ending much anterior to the pectoral-fin origin (vs. long outer mental barbel, surpassing the pectoral-fin origin); from *Centromochlus* by having the maxillary barbel laterally positioned, not visible ventrally (vs. proximal portion of maxillary barbel ventrally positioned, in such a way that it is visible ventrally); and from *Duringlanis* by having the terminus of the lateral line surpassing the caudal-fin origin (vs. lateral line ending near to the caudal peduncle).

GENUS *TATIA* MIRANDA RIBEIRO, 1911 (CLADE 49)

Tatia Miranda Ribeiro, 1911: 360 (type species: *Centromochlus intermedius* Steindachner, 1877; type by subsequent designation by Jordan, 1920: 545. Gender feminine).

Included species: *Tatia aulopygia* Kner, 1857, *Tatia boemia* Koch & Reis, 1996, *Tatia bockmanni* (Sarmiento-Soares & Buckup, 2005), **Tatia britskii* (Sarmiento-Soares & Birindelli, 2015), *Tatia brunnea* Mees, 1974, *Tatia caudosignata* DoNascimento, Albornoz-Garzón & García-Melo 2019, *Tatia caxiuanensis* Sarmiento-Soares & Martins-Pinheiro, 2008, *Tatia concolor* Mees, 1974, *Tatia creutzbergi* (Boeseman, 1953), **Tatia dunni* (Fowler, 1945), **Tatia galaxias* Mees, 1974, *Tatia gyrina* (Eigenmann & Allen, 1942), *Tatia jacaratia* Pavanelli & Bifi, 2009, *Tatia intermedia* (Steindachner, 1877), **Tatia marthae* Vari & Ferraris, 2013, *Tatia meesi* Sarmiento-Soares & Martins Pinheiro, 2008, **Tatia melanoleuca* Vari & Calegari, 2014, *Tatia musaica* Royero, 1992, *Tatia neivai* (Ihering, 1930), *Tatia nigra* Sarmiento-Soares & Martins-Pinheiro 2008, *Tatia orca* (Sarmiento-Soares, Lazzarotto, Rapp Py-Daniel & Leitão, 2017), **Tatia punctata* Mees, 1974, *Tatia reticulata* Mees, 1974, *Tatia simplex* Mees, 1974, *Tatia* aff. *Tatia simplex* Mees, 1974, *Tatia strigata* Soares-Porto, 1995, *Tatia* sp. 1 Calegari & Reis, undescribed, *Tatia* sp. 2 Calegari & Reis, undescribed, *Tatia* sp. 3 Calegari & Reis, undescribed and *Tatia* sp. 4 Calegari & Reis, undescribed.

Diagnosis: *Tatia* is diagnosed by 13 molecular and three morphological synapomorphies. **Non-exclusive:** (1) coronomeckelian bone obliquely positioned (char. 3596: 0 → 1), reversed in *Tatia intermedia* and *Tatia* sp. 4, convergent in *Duringlanis romani*, *Balroglanis macracanthus*, *Gelanoglanis* and *Liosomadoras*; (2) hyomandibula and metapterygoid separated from each other (char. 3620: 0 → 1), convergent in *Ageneiosini*, *Gelanoglanis* and *Centromochlus*; and (3) contralateral anteromedial processes of basipterygium sutured to each other on anterior portion only (char. 3723: 0 → 2), reversed in *Tatia musaica* and *Tatia meesi*, convergent in *Gelanoglanis*, *Centromochlus*, *Entomocorus*, *Gephyromochlus*, *Trachelyopterichthys*, *Trachelyopterus albicrux*, *Trachelyopterus insignis*, *Trachelyopterus striatulus* and *Trachelyopterus teaguei*.

Comparisons: *Tatia* differs from remaining centromochlines, except *Gelanoglanis* and *Centromochlus*, by having the hyomandibula and metapterygoid separated from each other (vs. hyomandibula and metapterygoid contacting each

other). *Tatia* (but not *Tatia intermedia* and *Tatia simplex*) is distinguished from *Glanidium*, except *Glanidium cesarpintoi*, *Balroglanis*, *Ferrarissoaresia* and *Centromochlus*, by the lack of serration on the posterior border of the dorsal-fin spine (vs. dorsal-fin spine serrated on posterior border). It differs from *Duringlanis* and *Centromochlus* by having the outer mental barbel longer than inner (vs. outer and inner mental barbels of approximately the same length); from *Centromochlus* and *Balroglanis* by having the maxillary barbel laterally positioned, not visible ventrally (vs. proximal portion of maxillary barbel ventrally positioned, in such a way that it is visible ventrally), and eye not visible, or little visible in ventral view (vs. eye ventrally displaced, in such a way that almost the entire eye is visible in ventral view); and from *Gelanoglanis* by the rounded and depressed head (vs. laterally compressed head) and mouth straight (vs. mouth sinuous in lateral view). *Tatia*, except *Tatia meesi*, *Tatia musaica*, *Tatia reticulata* and *Tatia simplex*, is further distinguished from *Gephyromochlus*, *Ferrarissoaresia*, *Balroglanis* and *Gelanoglanis* by the possession of an anterior nuchal plate (vs. anterior nuchal plate absent).

SUBFAMILY AUCHENIPTERINAE BLEEKER, 1862
(CLADE 67)

Auchenipterini Bleeker, 1862 (in [Bleeker, 1862–63](#)): 14 (type genus: *Auchenipterus* Valenciennes, 1840).

Included tribes: Asterophysini, Ageneiosini, Auchenipterini, Liosomadoradini and Trachelyopterini.

Diagnosis: Auchenipterinae are diagnosed by 21 molecular and three morphological synapomorphies. **Exclusive:** (1) lateral margin of frontal not participating in orbital margin (char. 3553: 0 → 1), reversed in *Entomocorus*, *Tocantinsia*, *Trachycorystes trachycorystes* and *Trachelyichthys*. **Non-exclusive:** (2) coronoid process of anguloarticular developed as a large and laminar process (char. 3602: 0 → 1), reversed in *Ageneiosus* (except *Ageneiosus dentatus*), *Auchenipterichthys*, *Pseudoauchenipterus* and *Trachelyichthys*, convergent in *Tatia boemia*, *Tatia nigra*, *Tatia jacaratia*, *Tatia* sp. 4, *Glanidium* and *Ferrarissoaresia*; and (3) compound centrum including up to sixth vertebra (char. 3667: 1 → 2), reversed in Auchenipterini and Trachelyopterini (except *Pseudepapterus*), *Tympanopleura cryptica*, *Tympanopleura brevis* and *Ageneiosus militaris*, convergent in *Glanidium catharinensis* and *Glanidium cesarpintoi*.

Comparisons: Auchenipterinae is mostly represented by members of large body size, except *Epapterus*, *Pseudepapterus* and *Spinipterus*, and differs from all

centromochlines by having a medium to long anal fin (vs. short anal fin), genital tube of adult males attached to the base of the anal-fin origin and united by skin to the anal-fin rays (vs. genital tube of adult males located anterior to the anal-fin rays and apart from anal-fin base), lack of sexual dimorphism in the shape of the anal fin (vs. secondary sexual dimorphism present in the anal fin, where the male and female have distinct anal-fin shapes), and by the genital papilla of adult males not being covered by a hood-like flap of skin (vs. adult males with a hood-like flap of skin covering the urogenital base, except *Gelanoglanis*).

LIOSOMADORADINI CALEGARI, VARI & REIS TRIB.
NOV. (CLADE 68)

Type genus: *Liosomadoras* Fowler, 1940.
lsid: zoobank.org:act:993091D9-5BA7-4322-8D53-6AC3CADBF67E

Included genus: *Liosomadoras* Fowler, 1940.

Diagnosis: Liosomadoradini is diagnosed by seven morphological synapomorphies. **Exclusive:** (1) coronomeckelian bone obliquely positioned (char. 3596: 0 → 1), exclusive within Auchenipterinae, convergent in *Duringlanis romani*, *Balroglanis macracanthus*, *Gelanoglanis* and *Tatia* (except *Tatia intermedia* and *Tatia* sp. 4). **Non-exclusive:** (2) lateral ethmoid contacting only mesial portion of antorbital (char. 3517: 2 → 0), convergent in *Entomocorus*, *Gelanoglanis*, *Pseudoauchenipterus*, *Ageneiosus intrusus*, *Ageneiosus uranophthalmus*, *Ageneiosus militaris*, *Ageneiosus dentatus* and *Ageneiosus inermis*; (3) spines present on antorbital and suborbital ossified tubules (char. 3520: 0 → 1), convergent in *Tatia caxiuanensis*, *Trachelyopterichthys*, *Trachycorystes trachycorystes* and *Spinipterus*; (4) posterodorsal process of hyomandibula present, well developed (char. 3613: 0 → 2), convergent in some species of *Ageneiosus* and *Tympanopleura*, *Glanidium*, some species of *Tatia*, *Balroglanis schultzi*, *Pseudotatia*, *Auchenipterichthys* (except *Auchenipterichthys punctatus*), *Trachelyopterichthys* and *Trachycorystes trachycorystes*; (5) posterodorsal process of hyomandibula thin, shorter than its depth (char. 3614: 0 → 1), convergent in *Ageneiosus militaris*, *Ageneiosus pardalis*, *Tympanopleura atronasus*, *Glanidium*, some species of *Tatia*, *Balroglanis schultzi*, *Auchenipterichthys* (except *Auchenipterichthys punctatus*), most species of *Trachelyopterichthys* and *Trachycorystes trachycorystes*; (6) three rows of serration on anterior margin of dorsal-fin spine (char. 3690: 0 → 2), convergent in *Spinipterus*; and (7) ornamentation on posterior process of cleithrum

arranged in two rows (char. 3713: 0 → 2), convergent only in *Spinipterus acsi*.

GENUS *LIOSOMADORAS* FOWLER, 1940 (CLADE 68)

Liosomadoras Fowler, 1940: 226 (type species: *Liosomadoras morrowi* Fowler, 1940; type by original designation. Gender masculine).

Included species: *Liosomadoras morrowi* Fowler, 1940 and *Liosomadoras oncinus* (Jardine in Schomburgk, 1841).

Diagnosis: Same as for tribe Liosomadoradini.

Comparisons: *Liosomadoras* is easily distinguished from all members of Auchenipteridae by its colour pattern, reminiscent of the jaguar, which gives to the genus its popular name of jaguar catfish (vs. several distinct colour patterns, including bold spotted, white narrow stripes, black thick stripes, diffused blotches, or with unique background colour); and except for *Spinipterus*, by having three vertical rows of serration along the anterior margin of the dorsal-fin spine (vs. one row, or two in *Trachycorystes trachycorystes* and *Trachelyopterichthys*) and, except for *Spinipterus acsi*, by having two rows of ornamentation on the posterior process of the cleithrum. It differs from all auchenipterids except *Trachelyopterichthys*, *Trachycorystes trachycorystes* and *Spinipterus* by having spines on the antorbital and infraorbitals bones (vs. such bones smooth, without any spines), and from Ageneiosini, Auchenipterini (except *Entomocorus*), *Trachelyopterichthys* and *Trachelyichthys* by having a moderate-sized anal fin, approximately one-third of SL (vs. anal fin long, at least half SL). *Liosomadoras* is further distinguished from *Spinipterus* by the lack of serration on the dorsal margin of the pectoral-fin spine (vs. dorsal margin of pectoral-fin spine serrated), posterior margin of dorsal-fin spine smooth, without serration (vs. posterior margin of dorsal-fin spine serrated) and anterior fontanel rounded (vs. anterior fontanel elliptic).

TRIBE TRACHELYOPTERINI BLEEKER, 1858 (CLADE 70)

Trachelyopterini [Trachelyopterini] Bleeker, 1858a: 40 (type genus: *Trachelyopterus Valenciennes*, 1840. Also in Bleeker, 1858b: 49, 250, 257).

Included subtribes: Auchenipterichthyina, Trachelyopterina and Trachycorystina.

Diagnosis: Trachelyopterini is diagnosed by six molecular and three morphological synapomorphies.

Non-exclusive: (1) postzygapophysis of compound centrum extended up to eighth vertebra (char. 3666: 2 → 4), reversed in *Trachelyichthys* and *Trachelyopterus teaguei*, convergent in *Epapterus dispilurus*; (2) compound centrum including up to eighth vertebra (char. 3667: 2 → 4), reversed in *Trachelyichthys*, *Trachelyopterus teaguei* and *Trachelyopterus albricrux*, exclusive within Auchenipterinae, convergent in *Centromochlus*; and (3) ventral process of hypurapophysis absent (char. 3748: 1 → 0), convergent in *Ageneiosus*, *Tympanopleura* and *Gelanoglanis*.

SUBTRIBE TRACHYCORYSTINA MIRANDA RIBEIRO, 1911 (CLADE 72)

Trachycorystina Miranda Ribeiro, 1911: 25, 352 (type genus: *Trachycorystes* Bleeker, 1858).

Included genera: *Tocantinsia* Mees, 1974 and *Trachycorystes* Bleeker, 1858.

Diagnosis: Trachycorystina is diagnosed by four molecular and one morphological synapomorphy. **Non-exclusive:** (1) ventral processes of dorsal-fin spinelet straight (char. 3683: 1 → 0), convergent in *Trachelyopterichthys*, *Pseudauchenipterus jequitinhonhae*, *Pseudauchenipterus affinis* and *Liosomadoras oncinus*.

GENUS *TOCANTINSIA* MEES, 1974

Tocantinsia Mees, 1974: 108 (type species: *Tocantinsia depressa* Mees, 1974; type by original designation. Gender feminine. Subsequent to the description of the genus, Mees (1984) proposed the synonymization of its type species with *Glanidium piresi* Miranda Ribeiro, 1920, still recognizing the genus *Tocantinsia* as valid).

Included species: *Tocantinsia piresi* (Miranda Ribeiro, 1920).

Diagnosis: *Tocantinsia* is diagnosed by 13 molecular and five morphological synapomorphies. **Non-exclusive:** (1) Medial portion of dentary dorsally arched on symphysis (char. 3607: 0 → 1), convergent in *Asterophysus*; (2) upper gill rakers moderate in size, approximately half length of gill filaments (char. 3638: 1 → 0), convergent in Ageneiosini (except *Tympanopleura cryptica*), *Glanidium* (except *Glanidium cesarpintoi*), *Gephyromochlus* and *Pseudauchenipterus*; (3) serration on anterior margin of pectoral-fin spine truncated (char. 3704: 0 → 1), convergent in Ageneiosini, *Auchenipterus fordicei*, *Glanidium ribeiroi*, *Tatia intermedia* and *Trachelyopterus coriaceus*; (4) last proximal radial of anal fin laminar (char. 3741: 0 → 1), convergent in

Ageneiosus (except *Ageneiosus inermis*, *Ageneiosus militaris* and *Ageneiosus lineatus*), *Tympanopleura rondoni*, *Tympanopleura cryptica*, *Auchenipterus* and *Auchenipterichthys*; and (5) caudal fin bifurcated (char. 3746: 1 → 0), convergent in Centromochlinae, Auchenipterini (except *Epapterus*), *Tympanopleura*, *Ageneiosus* (except *Ageneiosus inermis*, *Ageneiosus vittatus*).

Comparisons: *Tocantinsia* is a predator species comprising individuals of relatively large size, robust, frequently serving as a source of food in local communities along the Tocantins drainage. It is easily distinguished from remaining auchenipterids, except *Asterophysus*, by having the medial portion of the dentary dorsally arched on the symphysis (vs. dentary straight); and from auchenipterines, except Auchenipterini (apart from *Epapterus*), *Asterophysus*, *Tympanopleura* and *Ageneiosus* (apart from *Ageneiosus inermis* and *Ageneiosus vittatus*), by having the caudal fin bifurcated (vs. caudal fin truncated). It differs from auchenipterines, except *Trachycorystes*, *Spinipterus* and *Liosomadoras*, by the posterior process of the epioccipital being pointed and very short, with a wide base formed by the lateral border of the epioccipital (vs. epioccipital forming a simple spine, bifurcated or laminar) and, except for *Asterophysus*, by having the dorsal profile of the head posteriorly to the eye flat and straight (vs. head posteriorly arched or with some level of curvature). It is further distinguished from *Asterophysus* by having the dorsal-fin origin posteriorly displaced relative to the pectoral-fin origin, at a distance approximately equivalent to the length of the dorsal-fin spine (vs. dorsal-fin origin approximately at a vertical line from the pectoral-fin origin), posterior process of post-temporal supracleithrum surpassing the vertical line from the dorsal-fin origin (vs. posterior process of post-temporal supracleithrum not reaching the vertical line from the dorsal-fin origin), and the mouth gape reaching the eye, but never surpassing it (vs. end of mouth gape far surpassing the eye).

GENUS *TRACHYCORYSTES* BLEEKER, 1858 (CLADE 73)

Trachycorystes Bleeker, 1858b: 200 (type species: *Auchenipterus trachycorystes* Valenciennes, 1840; type by absolute tautonymy. Gender masculine).

Included species: *Trachycorystes menezesi* Britski & Akama, 2011 and *Trachycorystes trachycorystes* (Valenciennes, 1840).

Diagnosis: *Trachycorystes* is diagnosed by six morphological synapomorphies. **Non-exclusive:** (1) nasal bone plate-like, laterally expanded (char. 3512: 0 → 1), convergent in *Tatia boemia*,

Tatia brunnea, *Tatia jacaratia*, *Tatia caxiuanensis*, *Tatia nigra*, *Trachelyopterichthys*, *Trachelyopterus* and *Spinipterus* sp. 'oncinha'; (2) lateroposterior portion of sphenotic slightly concave (char. 3552: 0 → 1), convergent in *Ageneiosus* (except *Ageneiosus pardalis* and *Ageneiosus vittatus*), *Liosomadoras morrowi*, *Trachelyichthys*, *Trachelyopterus lucenai*, *Trachelyopterus porosus* and several centromochlines; (3) bony expansion in posteromedial portion of premaxilla (char. 3585: 0 → 1), convergent in *Ageneiosus* (except *Ageneiosus intrusus* and *Ageneiosus uranophthalmus*) and *Auchenipterus fordicei*; (4) posterior bony projection on last dorsal-fin pterygiophore absent (char. 3680: 0 → 1), convergent in *Auchenipterichthys punctatus*, *Liosomadoras*, *Entomocorus*, *Gelanoglanis*, *Glanidium*, *Duringlanis perugiae*, *Tatia simplex*, *Pseudotatia*, *Tatia nigra*, *Tatia intermedia*, *Tatia caxiuanensis*, *Tatia* sp. 2, *Balroglanis carolae*, *Trachelyichthys*, *Trachelyopterichthys* and *Spinipterus acsi*; (5) posterior portion of basipterygium long, with process developed as wing (char. 3729: 0 → 1), convergent in *Ageneiosus*, *Tympanopleura*, *Asterophysus*, *Centromochlus* and *Trachelyopterus*; and (6) basal process of pelvic-fin rays posteromedially oriented (char. 3732: 1 → 0), convergent in *Epapterus*, *Pseudepapterus*, *Pseudoauchenipterus*, *Glanidium*, *Gelanoglanis*, *Ageneiosini*, *Asterophysus*, *Trachelyopterichthys* and *Trachelyopterus* (except *Trachelyopterus insignis*).

Comparisons: *Trachycorystes* are medium-sized predator species with the cephalic shield well exposed on the surface of the head, and distinguished from all auchenipterines, except *Asterophysus*, by the uniform dark brown or greyish to black coloration of the body, lacking any colour marks (vs. distinctly marked colour patterns present, or light background with darker dorsal profile); from all auchenipterines, except *Asterophysus* and *Trachelyopterus*, by having the lower jaw prognate, slightly outward in comparison to the premaxilla (less evident in *Trachycorystes menezesi*) (vs. lower and upper jaws ending in the same vertical line); and except for *Trachycorystes menezesi*, distinguishes from *Tocantinsia*, *Asterophysus*, *Pseudepapterus*, *Pseudoauchenipterus*, *Entomocorus*, *Auchenipterus*, *Ageneiosus* (except *Ageneiosus vittatus* and *Ageneiosus inermis*) and *Tympanopleura* by having truncated caudal fin (vs. bifurcated caudal fin). It is distinguished from auchenipterines, except *Ageneiosini*, *Auchenipterichthys*, *Pseudoauchenipterus*, *Liosomadoras*, *Tocantinsia* and some species of *Trachelyopterus* (*Trachelyopterus insignis*, *Trachelyopterus galeatus*, *Trachelyopterus amblops* and *Trachelyopterus albicrux*) by

having six branched dorsal-fin rays (vs. five, four, three or seven branched dorsal-fin rays); and, except for *Auchenipterichthys*, *Asterophysus* and *Pseudepapterus*, by the number of branched pelvic-fin rays, eight or nine (vs. *Entomocorus*, *Trachelyopterus* and *Spinipterus* with five rays, *Pseudauchenipterus* with seven rays, *Trachelyichthys* with ten or 11 rays, *Auchenipterus* and *Trachelyopterichthys* with 10–14 rays, and *Epapterus* with 14–16 rays). It differs from all auchenipterines, except *Trachelyichthys*, *Trachelyopterichthys* and *Spinipterus acsi*, by having a long posterior process of the cleithrum, approximately two-thirds or the same length as the pectoral-fin spine (vs. posterior process of cleithrum small, not surpassing the base of branched pectoral-fin rays, or moderate, approximately half of pectoral-fin spine length).

SUBTRIBE **AUCHENIPTERICHTHYINA** CALEGARI, VARI & REIS SUBTRIB. NOV. (CLADE 74)

Type genus: *Auchenipterichthys* Bleeker, 1862.

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Included genera: *Auchenipterichthys* Bleeker, 1862, *Trachelyichthys* Mees, 1974 and *Trachelyopterichthys* Bleeker, 1862.

Diagnosis: Auchenipterichthyina is diagnosed by six molecular and four morphological synapomorphies. **Non-exclusive:** (1) posterior process of posttemporal-supracleithrum dorsoventrally oriented (char. 3561: 1 → 0), convergent in *Entomocorus*, *Epapterus*, *Pseudauchenipterus nodosus*, *Trachelyopterus amblops*, *Trachelyopterus* cf. *Trachelyopterus galeatus*, *Trachelyopterus insignis*, *Spinipterus*, most species of *Ageneiosus* and *Tympanopleura* and Centromochlinae (except *Glanidium catharinensis*, *Glanidium* sp. 1 RS and *Glanidium* sp. 2 RS); (2) posterior process of epioccipital forming simple spine (char. 3563: 3 → 0), reversed in *Trachelyichthys*, convergent in *Asterophysus*, *Entomocorus*, *Gelanoglanis* and *Balroglanis* (except *Balroglanis carolae*); (3) accessory cartilage between third and fourth basibranchials present (char. 3644: 0 → 1), convergent in *Ageneiosus* (except *Ageneiosus lineatus*), *Auchenipterus fordicei*, *Duringlanis*, *Pseudauchenipterus flavescens*, *Pseudepapterus hasemani* and *Tetranematichthys*; and (4) os suspensorium moderate in size (char. 3655: 1 → 0), convergent in *Auchenipterus ambyacus*, *Auchenipterus nuchalis*, *Balroglanis*, *Duringlanis romani*, *Centromochlus*, *Glanidium*, *Entomocorus*,

Epapterus, *Pseudauchenipterus*, *Gephyromochlus*, most species of *Tatia*, *Trachelyopterus* (except *Trachelyopterus* aff. *Trachelyopterus porosus*) and *Trachycorystes menezesi*.

GENUS **AUCHENIPTERICHTHYS** BLEEKER, 1862
(CLADE 75)

Auchenipterichthys Bleeker, 1862 (in Bleeker, 1862–63): 7 (type species: *Auchenipterus thoracatus* Kner, 1857; type by original designation. Gender masculine).

Included species: *Auchenipterichthys coracoideus* (Eigenmann & Allen, 1942), *Auchenipterichthys longimanus* (Günther, 1864), *Auchenipterichthys punctatus* (Valenciennes, 1840) and *Auchenipterichthys thoracatus* (Kner, 1857).

Diagnosis: *Auchenipterichthys* is diagnosed by 12 molecular and five morphological synapomorphies. **Non-exclusive:** (1) lateral line sinusoidal (char. 3525: 2 → 1), convergent in *Ageneiosus*, *Tympanopleura* and Auchenipterini (except *Entomocorus*); (2) laminar expansion on posteromedial portion of premaxilla absent (char. 3584: 1 → 0), convergent in *Entomocorus*, *Gelanoglanis*, *Glanidium catharinensis* and *Glanidium cesarpintoi*; (3) serrations on anterior margin of pectoral-fin spine retrorse (char. 3703: 2 → 1), convergent in *Entomocorus*, *Trachelyichthys* (except *Trachelyichthys* sp. 1), *Trachelyopterus* (except *Trachelyopterus amblops* and *Trachelyopterus coriaceus*) and *Trachycorystes menezesi*; (4) posterior portion of basipterygium long, with thin and pointed process (char. 3729: 0 → 2), convergent in *Liosomadoras*; and (5) last proximal radial of anal fin laminar (char. 3741: 0 → 1), convergent in *Ageneiosus* (except *Ageneiosus lineatus*), *Tympanopleura cryptica*, *Auchenipterus* and *Tocantinsia*.

Comparisons: *Auchenipterichthys* is distinguished from all auchenipterines, except *Ageneiosus*, *Tympanopleura*, *Auchenipterus*, *Pseudauchenipterus*, *Epapterus* and *Pseudepapterus*, by having the lateral line sinusoidal along its entire length (vs. lateral line straight, or sinusoidal in the anterior portion and straight in the posterior half); and except for *Trachycorystes*, *Asterophysus* and *Pseudepapterus*, by the number of branched pelvic-fin rays, eight or nine (one specimen with ten) (vs. six in *Liosomadoras*, *Tocantinsia*, *Ageneiosus*, *Tympanopleura* and *Tetranematichthys*, five in *Entomocorus*, *Trachelyopterus* and *Spinipterus*; seven in *Pseudauchenipterus*, ten or 11 in *Trachelyichthys*, 10–14 in *Auchenipterus* and *Trachelyopterichthys*, and 14–16 in *Epapterus*). Yet, it differs from

Pseudepapterus by having a robust dorsal-fin spine, moderate in size, approximately one-third of SL (vs. rudimentary dorsal-fin spine, less than one-sixth of SL), with six branched dorsal-fin rays (vs. three to five rays), and anterior margin of dorsal-fin spine serrated (vs. anterior margin of dorsal-fin spine smooth, lacking serration).

GENUS *TRACHELYOPTERICHTHYS* BLEEKER, 1862
(CLADE 79)

Trachelyopterichthys Bleeker, 1862 (in Bleeker, 1862–63): 16 (type species: *Trachelyopterus taeniatus* Kner, 1857; type by original designation and monotypy. Gender masculine).

Included species: *Trachelyopterichthys anduzei* Ferraris & Fernandez, 1987 and *Trachelyopterichthys taeniatus* (Kner, 1857).

Diagnosis: *Trachelyopterichthys* is diagnosed by ten morphological synapomorphies. **Non-exclusive:** (1) nasal bone plate-like, laterally expanded (char. 3512: 0 → 1), convergent in *Tatia boemia*, *Tatia brunnea*, *Tatia jacaratia*, *Tatia caxiuanensis*, *Tatia nigra*, *Trachelyopterus* and *Spinipeterus* sp. ‘oncinha’; (2) antorbital and ossified suborbital tubules with spines (char. 3520: 0 → 1), convergent in *Tatia caxiuanensis*, *Liosomadoras*, *Trachycorystes trachycorystes* and *Spinipeterus*; (3) trigeminofacial foramen ventrally exposed (char. 3581: 1 → 0), convergent in Auchenipterini (except *Auchenipterus ambyiacus* and *Auchenipterus brachyurus*), *Tympanopleura cryptica*, *Tympanopleura piperata*, *Trachelyichthys decaradiatus*, *Trachelyopterus amblops* and Centromochlinae (except *Glanidium*); (4) distal portion of premaxilla extended (char. 3587: 0 → 1), convergent in Ageneiosini, *Centromochlus existimatus* and *Duringlanis perugiae*; (5) premaxillary teeth straight (char. 3589: 0 → 1), convergent in *Entomocorus*, *Gelanoglanis*, *Gephyromochlus*, *Glanidium cesarpinto*, *Liosomadoras oncinus*, *Tocantinsia*, *Trachycorystes trachycorystes*, *Spinipeterus* and some species of *Tatia*; (6) anterior process on pharyngobranchial tooth-plate absent (char. 3653: 0 → 1), convergent in *Ageneiosus*, *Tympanopleura*, *Achenipterichthys longimanus*, *Achenipterichthys punctatus*, *Epapterus*, *Pseudepapterus*, *Auchenipterus nuchalis*, *Auchenipterus osteomystax*, *Auchenipterus nigripinnis*, *Balroglanis*, *Trachycorystes trachycorystes*, clade 60 of *Tatia* and *Tatia* sp. 1; (7) two rows of serrations on anterior margin of dorsal-fin spine (char. 3690: 0 → 1), convergent in *Trachycorystes trachycorystes*; (8) serrations absent on posterior margin of dorsal-fin spine (char. 3693: 0 → 1), convergent in most *Ageneiosus*, *Asterophysus*, *Epapterus*, *Duringlanis*

perugiae, *Gelanoglanis travieso*, *Glanidium cesarpinto*, *Pseudepapterus*, *Pseudotatia*, *Tatia* (except *Tatia intermedia*), *Tocantinsia*, *Trachelyopterus amblops*, *Trachelyopterus insignis*, *Trachycorystes trachycorystes* and *Spinipeterus*; (9) contralateral anteromedial processes of basipterygium sutured to each other only on anterior portion (char. 3723: 0 → 2), convergent in *Centromochlus*, *Gelanoglanis*, *Entomocorus*, *Gephyromochlus*, *Tatia* (except *Tatia musaica* and *Tatia meesi*), *Trachelyopterus albicrux*, *Trachelyopterus insignis*, *Trachelyopterus teaguei* and *Trachelyopterus striatulus*; and (10) basal process of pelvic-fin rays posteromedially oriented (char. 3732: 1 → 0), convergent in several auchenipterids.

Comparisons: *Trachelyopterichthys* is a genus of medium- to large-sized body, which is distinguished from all auchenipterids, except *Trachelyichthys*, *Epapterus* and *Trachelyopterus coriaceus*, by lacking an adipose fin (vs. adipose fin present). It is also distinguished from all Auchenipterinae, except *Trachycorystes trachycorystes*, by having two rows of serration on the anterior margin of the dorsal-fin spine (vs. one row, or three in *Liosomadoras* and *Spinipeterus*) and, except for *Liosomadoras*, *Trachycorystes trachycorystes* and *Spinipeterus*, by having antorbital and ossified suborbital tubules with spines (vs. such bones devoid of spines). It is further diagnosed from remaining Auchenipterinae, except *Pseudepapterus hasemani* and *Trachelyopterus* (but not *Trachelyopterus amblops*, *Trachelyopterus coriaceus* and *Trachelyopterus galeatus*), by having the branched dorsal-fin rays supported by four pterygiophores (vs. branched dorsal-fin rays supported by two, three, five or six pterygiophores). It further differs from *Trachelyichthys* by having the interopercle large, plate shaped (vs. interopercle thin and elongated), the posterior process of the epioccipital forming a simple spine (vs. posterior process of epioccipital bifurcated) and, except for *Trachelyichthys* sp. 1, by having 39–55 total anal-fin rays (vs. 31–38 total anal-fin rays).

GENUS *TRACHELYICHTHYS* MEES, 1974 (CLADE 80)

Trachelyichthys Mees, 1974: 111 (type species: *Trachelyichthys decaradiatus* Mees, 1974; type by original designation and monotypy. Gender masculine).

Included species: *Trachelyichthys decaradiatus* Mees, 1974, *Trachelyichthys exilis* Greenfield & Glodek, 1977 and *Trachelyichthys* sp. 1 Calegari, Akama & Ferraris, undescribed.

Diagnosis: *Trachelyichthys* is diagnosed by 14 morphological synapomorphies. **Non-exclusive:** (1) outer pair of mental barbels long, surpassing

posterior margin of coracoid process (char. 3509: 0 → 1), convergent in *Auchenipterus*, *Epapterus*, *Pseudepapterus*, *Pseudauchenipterus nodosus*, *Trachelyopterus coriaceus*, *Trachelyopterus striatulus*, *Trachelyopterus porosus* and *Trachelyopterus* aff. *T. porosus*; (2) anterior fontanel rounded (char. 3542: 2 → 1), convergent in *Gelanoglanis pan*, *Spinipterus* and some species of *Tatia*; (3) dorsal margin of lateral ethmoid not exposed on dorsal surface of cranium (char. 3546: 0 → 2), convergent in *Centromochlus*, *Duringlanis*, *Gelanoglanis*, *Glanidium cesarpintoi*, *Glanidium* sp. 2 RS, *Pseudauchenipterus*, *Liosomadoras*, *Tatia* (except *Tatia intermedia*), *Tetranematchthys*, *Trachelyopterus lucenai* and *Trachelyopterus* cf. *Trachelyopterus galeatus*; (4) lateral margin of frontal not participating in orbital margin (char. 3553: 1 → 0), convergent in *Entomocorus*, *Tocantinsia*, *Trachycorystes trachycorystes* and *Centromochlinae*; (5) posterior process of epioccipital bifurcated (char. 3563: 0 → 1), convergent in *Auchenipterus*, *Epapterus*, *Pseudepapterus*, *Tetranematchthys* and *Trachelyopterus*; (6) posterior process of epioccipital and parapophyses of compound centrum connected by suture (char. 3566: 0 → 1), convergent in *Ageneiosini*, *Auchenipterus*, *Epapterus*, *Pseudepapterus* and *Trachelyopterus coriaceus*; (7) coronomeckelian bone separated from anguloarticular (char. 3597: 1 → 0), convergent in *Centromochlinae* (except *Centromochlus*, *Glanidium catharinensis*, *Glanidium ribeiroi*, *Glanidium* sp. 2 RS), *Pseudauchenipterus jequitinhonhae*, *Pseudauchenipterus nodosus* and *Pseudepapterus*; (8) adductor crest of hyomandibula absent or indistinguishable (char. 3616: 1 → 0), convergent in several auchenipterids; (9) suprapreopercle elongate, tubular in shape, much longer than wide (char. 3624: 0 → 1), convergent in several auchenipterids; (10) second hypobranchial cartilaginous (char. 3646: 0 → 1), exclusive in *Auchenipterinae*, convergent in *Gelanoglanis stroudi* and *Gelanoglanis travieso*; (11) postzygapophysis of compound centrum extended up to seventh vertebra (char. 3666: 4 → 3), convergent in *Tympanopleura*, *Auchenipterus*, *Balroglanis macracanthus*, *Duringlanis romani*, *Entomocorus*, *Pseudauchenipterus* and *Trachelyopterus teaguei*; (12) compound centrum including up to seventh vertebra (char. 3667: 4 → 3), convergent in *Centromochlinae* (except *Centromochlus*, *Ferrarissoaresia*, *Glanidium catharinensis* and *Glanidium cesarpintoi*), *Auchenipterini* (except *Pseudepapterus*), *Trachelyopterus albicrux* and *Trachelyopterus teaguei*; (13) posterior nuchal plate narrower than base of dorsal-fin spine (char. 3673: 1 → 0), convergent in *Ageneiosini*, *Auchenipterus*, *Gelanoglanis*, *Entomocorus*, *Gephyromochlus*, *Glanidium cesarpintoi*, *Liosomadoras*, *Pseudepapterus*, *Trachelyopterina* and

some species of *Tatia*; and (14) distal vesicle present on anterior margin of anal-fin rays in mature males (char. 3744: 0 → 1), convergent in *Asterophysus*, *Pseudauchenipterus* and *Pseudepapterus*.

Comparisons: *Trachelyichthys* is distinguished from remaining *Auchenipteridae*, except *Ageneiosini*, *Trachelyopterichthys*, *Auchenipterus*, *Epapterus* and *Pseudepapterus* by the anal fin being elongated, measuring at least half SL (vs. anal fin short to moderate, never surpassing one-third of SL) and, except for *Trachelyopterichthys*, *Epapterus* and *Trachelyopterus coriaceus*, by the absence of an adipose fin (vs. adipose fin present). It is further distinguished from all auchenipterines, except *Spinipterus*, by having the anterior fontanel rounded (vs. elliptical or elongated). It differs from *Trachelyopterichthys* by having the outer pair of mental barbels long, surpassing the posterior margin of the coracoid process (vs. outer pair of mental barbels never reaching posterior process of coracoid process), the posterior margin of the dorsal-fin spine bearing serration (vs. posterior margin of dorsal-fin spine smooth, lacking serration); interopercle thin and elongated (vs. interopercle large, plate shaped) and antorbital smooth, without any spine (vs. antorbital bearing spines). Finally, it differs from *Epapterus* by nuptial males having the anal-fin rays continuously distributed, without space between anterior modified and remaining rays (vs. anal fin with a space between modified anterior rays and remaining rays) and five branched dorsal-fin rays (vs. three branched dorsal-fin rays).

SUBTRIBE TRACHELYOPTERINA BLEEKER, 1858
(CLADE 82)

Trachelyopterini [*Trachelyopterina*] [Bleeker, 1858a](#): 40 (type genus: *Trachelyopterus Valenciennes*, 1840. Also in [Bleeker, 1858b](#): 49, 250, 257).

Included genera: *Spinipterus* Akama & Ferraris, 2011 and *Trachelyopterus Valenciennes*, 1840.

Diagnosis: *Trachelyopterina* is diagnosed by 26 molecular and two morphological synapomorphies. **Non-exclusive:** (1) coronoid process of anguloarticular deeper than dentary (char. 3601: 0 → 1), convergent in *Auchenipterus*; and (2) posterior process of third epibranchial elongated, approximately the same length as its mesial portion (char. 3648: 0 → 1), reversed in *Trachelyopterus porosus*, *Trachelyopterus* aff. *T. porosus* and *Trachelyopterus amblops*, convergent in *Auchenipterini* (except *Entomocorus* and *Pseudauchenipterus affinis*), *Trachycorystes trachycorystes*, *Trachelyichthys* (except *Trachelyichthys* sp.1), *Auchenipterichthys thoracatus*, *Auchenipterichthys*

longimanus, *Ageneiosus vittatus*, *Tympanopleura atronasmus*, *Pseudotatia* and *Gelanoglanis*.

GENUS *SPINIPTERUS* AKAMA & FERRARIS, 2011
(CLADE 83)

Spinipterus Akama & Ferraris, 2011: 53 (type species: *Spinipterus acsi* Akama & Ferraris, 2011; type by original designation and monotypy. Gender masculine).

Included species: *Spinipterus acsi* Akama & Ferraris, 2011, *Spinipterus* sp. 'oncinha' Rossoni *et al.*, undescribed.

Diagnosis: *Spinipterus* is diagnosed by three molecular and 13 morphological synapomorphies. **Exclusive:** (1) serration on dorsal margin of pectoral-fin spine present (char. 3705: 0 → 1). **Non-exclusive:** (2) dorsal projection of antorbital absent (char. 3515: 0 → 1), convergent in clade 98 of Auchenipterini; (3) spines present on antorbital and ossified suborbital tubules (char. 3520: 0 → 1), convergent in *Liosomadoras*, *Tatia caxiuanensis*, *Trachelyopterichthys* and *Trachycorystes trachycorystes*; (4) anterior fontanel restricted to frontals (char. 3541: 0 → 1), exclusive in Auchenipterinae, convergent in *Centromochlus heckelii*, *Duringlanis perugiae*, *Tatia simplex*, *Tatia* aff. *T. simplex* and *Gelanoglanis pan*; (5) anterior fontanel rounded (char. 3542: 0 → 1), convergent in small body-sized *Tatia* of clade 50, *Tatia brunnea*, *Tatia simplex*, *Gelanoglanis pan* and *Trachelyichthys*; (6) lateroposterior portion of sphenotic distinctly concave (char. 3552: 0 → 2), convergent in Auchenipterini, some *Ageneiosini*, *Trachelyopterichthys*, *Tatia reticulata* and *Trachelyichthys exilis*; (7) posterior process of posttemporal–supracleithrum posterodorsally oriented (char. 3561: 0 → 1), convergent in Centromochlinae (except *Glanidium catharinensis*, *Glanidium* sp. 1 RS and *Glanidium* sp. 2 RS), *Auchenipterichthys*, *Entomocorus*, *Epapterus*, *Pseudauchenipterus nodosus*, *Trachelyichthys*, *Trachelyopterus amblops*, *Trachelyopterus insignis*, *Trachelyopterus* cf. *T. galeatus*, some species of *Ageneiosus* and *Tympanopleura*; (8) transcapular process at angle of ~45° relative to body axis (char. 3570: 0 → 1), convergent in Auchenipterini, *Liosomadoras*, *Trachelyichthys* (except *Trachelyichthys decaradiatus*), *Tatia intermedia*, *Trachelyopterus lucenai*, *Trachelyopterus* cf. *T. galeatus* and *Trachycorystes trachycorystes*; (9) premaxillary teeth straight (char. 3589: 0 → 1), convergent in *Entomocorus*, *Gelanoglanis*, *Trachelyopterichthys*, *Gephyromochlus*, some species of *Tatia*, *Liosomadoras oncinus*, *Glanidium cesarpintoi*, *Tocantinsia* and *Trachycorystes trachycorystes*; (10) four free pterygiophores on dorsal fin (char. 3675: 2 → 3), convergent in *Gelanoglanini*, *Glanidium cesarpintoi*, *Pseudepapterus hasemani*, *Tatia* (except *Tatia brunnea* and *Tatia musaica*,

Trachelyichthys, *Trachelyopterichthys* and some species of *Trachelyopterus*; (11) dorsal-fin spine short, less than one-sixth of SL (char. 3685: 0 → 1), convergent in *Asterophysus*, *Epapterus* and *Pseudepapterus*; (12) three rows of serration on anterior margin of dorsal-fin spine (char. 3690: 0 → 2), convergent in *Liosomadoras*; and (13) posterior margin of dorsal-fin spine smooth, without serration (char. 3693: 0 → 1), convergent in *Asterophysus*, *Duringlanis perugiae*, *Epapterus*, *Gelanoglanis travieso*, *Glanidium cesarpintoi*, *Pseudepapterus*, *Pseudotatia*, *Tatia* (except *Tatia intermedia*), *Tocantinsia*, *Trachelyopterichthys*, *Trachelyopterus amblops*, *Trachelyopterus insignis* and *Trachycorystes trachycorystes*.

Comparisons: *Spinipterus* is somewhat similar externally to *Trachelyopterus* but of a smaller size and bearing distinctive features within the family. It can be diagnosed from remaining Auchenipteridae by having serrations on the dorsal and ventral margins of the pectoral-fin spine, exclusive in the family (vs. serrae in both dorsal and ventral margins of pectoral-fin spine present) and, except for *Liosomadoras*, by having three rows of serration on the anterior margin of the dorsal-fin spine (vs. one; or two in *Trachelyopterichthys* and *Trachycorystes trachycorystes*). It is further distinguished from remaining auchenipterines, except *Liosomadoras*, *Trachelyopterichthys* and *Trachycorystes trachycorystes*, by having spines on the antorbital and ossified suborbital tubules; and, except *Entomocorus* and *Trachelyopterus*, by having fewer branched pelvic-fin rays, four or five (vs. more numerous branched rays on the pelvic fin, six to 16).

Remarks: *Spinipterus* was described based only on the holotype from Peru, but an additional specimen of *Spinipterus acsi* was found recently in a distinct locality, the Juruá River basin in Brazil (Calegari *et al.*, 2018). Based on the examination of both specimens and the CT scan images of the holotype, the configuration of the serration rows on the dorsal and pectoral-fin spines was analysed, revealing distinctive features unique to this genus within Auchenipteridae. Although Akama & Ferraris (2011) have reported the presence of four rows of serration on the dorsal-fin spine, *Spinipterus acsi* has three rows of serration along the anterior and anterolateral margins of the spine, with one medial row and two others at an angle of 45° relative to the spine axis (see Calegari *et al.*, 2018: fig. 4).

GENUS *TRACHELYOPTERUS* VALENCIENNES, 1840
(CLADE 84)

Trachelyopterus Valenciennes, in Cuvier & Valenciennes, 1840: 220 (type species: *Trachelyopterus*

coriaceus Valenciennes, 1840; type by monotypy. Gender masculine).

Included species: *Trachelyopterus albicrux* (Berg, 1901), *Trachelyopterus amblops* (Meek & Hildebrand, 1913), **Trachelyopterus ceratophysus* (Kner, 1857), *Trachelyopterus coriaceus* Valenciennes, 1840, **Trachelyopterus cratensis* (Miranda Ribeiro, 1937), **Trachelyopterus fisheri* (Eigenmann, 1916), *Trachelyopterus galeatus* (Linnaeus, 1766), *Trachelyopterus insignis* (Steindachner, 1878), **Trachelyopterus lacustris* (Lütken, 1874), **Trachelyopterus leopardinus* (Borodin, 1927), *Trachelyopterus lucenai* Bertoletti et al., 1995, **Trachelyopterus peloichthys* (Schultz, 1944), *Trachelyopterus porosus* (Eigenmann & Eigenmann, 1888), *Trachelyopterus striatulus* (Steindachner, 1877) and *Trachelyopterus teaguei* (Devincenzi, 1942).

Diagnosis: *Trachelyopterus* is diagnosed by 20 molecular and five morphological synapomorphies. **Non-exclusive:** (1) posterior process of epioccipital bifurcated (char. 3563: 3 → 1), convergent in *Auchenipterus*, *Epapterus*, *Pseudauchenipterus*, *Tetranematchthys* and *Trachelyichthys*; (2) posterodorsal process of hyomandibula present, well developed (char. 3613: 0 → 2), convergent in *Auchenipterichthys* (except *Auchenipterichthys punctatus*), *Balroglanis schultzi*, *Glanidium*, *Liosomadoras*, *Pseudotatia*, most species of *Tatia* and *Ageneiosus*, *Tympanopleura rondoni* and *Trachycorystes trachycorystes*; (3) os suspensorium moderated in size (char. 3655: 1 → 0), reversed in *Trachelyopterus* aff. *T. porosus*, convergent in *Auchenipterus ambyacus*, *Auchenipterus nuchalis*, *Auchenipterichthyna*, *Balroglanis*, *Duringlanis romani*, *Centromochlus*, *Glanidium*, *Entomocorus*, *Epapterus*, *Pseudauchenipterus*, *Gephyromochlus*, most species of *Tatia* and *Trachycorystes menezesi*; (4) dorsal-fin spine of nuptial males sloping anteriorly when erect, forming angle of < 90° relative to head (char. 3688: 0 → 1), convergent in Ageneiosini and clade 90 of Auchenipterini; and (5) basal process of pelvic-fin rays posteromedially oriented (char. 3732: 1 → 0), reversed in *Trachelyopterus insignis*, convergent in Ageneiosini, Auchenipterini (except *Entomocorus*), *Glanidium*, *Gelanoglanis*, *Trachelyopterichthys* and *Trachycorystes*.

Comparisons: Species of *Trachelyopterus* are predators, relatively homogeneous regarding external morphology and with brown smudge coloration, usually being difficult to identify without access to internal characters of the skeleton. However, the genus can be distinguished from remaining auchenipterines, except *Asterophysus*, by having a prognathous lower

jaw, which is slightly outward in comparison to the premaxilla (vs. lower and upper jaws ending at the same vertical line); and, except *Entomocorus* and *Spinipterus*, by having fewer branched pelvic-fin rays, five (vs. more branched rays on pelvic-fin, six to 16). It further differs from auchenipterines, except Trachelyopterini (but not *Tocantinsia*), *Epapterus*, *Liosomadoras*, *Tetranematchthys*, *Ageneiosus inermis* and *Ageneiosus vittatus*, by having a truncated caudal fin (vs. bifurcated caudal fin); and, except for *Auchenipterus*, *Epapterus*, *Pseudauchenipterus*, *Tetranematchthys* and *Trachelyichthys*, by having the posterior process of the epioccipital bifurcated (vs. posterior process of epioccipital as a simple spine, laminar, or short and pointed) and from *Tocantinsia*, *Asterophysus* and *Liosomadoras* by the total number anal-fin rays, 18–30 (vs. 12–14 total anal-fin rays; 12 in *Tocantinsia*; 13 or 14 in *Asterophysus*; 12 or 13 in *Liosomadoras*).

TRIBE ASTEROPHYSINI BLEEKER, 1862

Astrophysini [Asterophysini] Bleeker, 1862 (in Bleeker, 1862–63): 7 (type genus: *Asterophysus* Kner, 1857).

Included genus: *Asterophysus* Kner, 1857.

Diagnosis: Asterophysini is diagnosed by 23 morphological autapomorphies. **Exclusive:** (1) hyomandibula articulated to neurocranium via prootic and sphenotic (char. 3619: 1 → 2); (2) symphysis of pectoral girdle barely in contact with each other, only anterior tip of the pectoral girdle in contact (char. 3619: 1 → 2). **Non-exclusive:** (3) ventral projection of antorbital absent (char. 3696: 0 → 1), exclusive within Auchenipterinae, convergent in *Gelanoglanis*; (4) fenestra present between parieto-supraoccipital, pterotic and sphenotic (char. 3554: 0 → 1), convergent in *Auchenipterus brevior*, *Auchenipterus dentatus*, *Auchenipterus fordicei*, *Trachelyopterus amblops* and *Trachelyopterus coriaceus*; (5) ascending process of Meckel's cartilage absent (char. 3598: 0 → 1), exclusive within Auchenipterinae, convergent in *Centromochlus*; (6) coronoid process of mandible absent (char. 3600: 0 → 1), convergent in *Centromochlus*; (7) posterodorsal portion of dentary straight (char. 3603: 0 → 1), convergent in *Centromochlus*; (8) symphysis of dentary with ventral process (char. 3606: 0 → 1), convergent in *Tympanopleura rondoni*, *Tympanopleura brevis*, *Ageneiosus dentatus*, *Ageneiosus intrusus*, *Auchenipterus*, *Pseudauchenipterus* (except *Pseudauchenipterus flavescens*) and *Trachycorystes trachycorystes*; (9) symphysis of dentary dorsally projected (char. 3607: 0 → 1), convergent in *Tocantinsia*; (10) gill filaments not ossified (char. 3641: 1 → 0), convergent in *Auchenipterus brevior*, *Balroglanis* (except *Balroglanis carolae*), *Duringlanis romani* and *Gelanoglanis*; (11) second and third

basibranchials reduced (char. 3642: 0 → 1), convergent in *Ageneiosus*, *Tympanopleura* and *Gelanoglanis*; (12) first hypobranchial elongate, cylindrical (char. 3645: 1, 2 → 3), exclusive within Auchenipterinae, convergent in *Gelanoglanis*; (13) anterior process of pharyngobranchial tooth-plate absent (char. 3654: 0 → 1), convergent in *Ageneiosus*, *Tympanopleura*, *Pseudepapterus*, *Epapterus*, *Auchenipterichthys longimanus*, *Auchenipterichthys punctatus*, *Auchenipterus nigripinnis*, *Auchenipterus nuchalis*, *Auchenipterus osteomystax*, *Duringlanis*, clade 60 of *Tatia*, *Tatia* sp. 1, *Trachelyopterichthys* and *Trachycorystes trachycorystes*; (14) posterior nuchal plate broad, approximately the same width or wider than the base of the dorsal-fin spine (char. 3673: 0 → 1), convergent in *Auchenipterichthys*, *Epapterus*, *Pseudauchenipterus*, *Glanidium* (except *Glanidium cesarpintoi*), *Balroglanis* (except *Balroglanis carolae*), *Duringlanis*, some species of *Tatia*, *Trachelyopterichthys* and *Trachycorystes*; (15) dorsal-fin spine rudimentary, less than one-sixth of SL (char. 3685: 0 → 1), convergent in *Epapterus*, *Pseudepapterus* and *Spinapterus*; (16) irregular serrations at proximal portion of anterior margin of dorsal-fin spine (char. 3691: 0 → 1), convergent in *Auchenipterichthys* and *Trachelyichthys*; (17) serration absent on posterior margin of dorsal-fin spine (char. 3693: 0 → 1), convergent in *Ageneiosus* (except *Ageneiosus dentatus*), *Pseudotatia*, *Epapterus*, *Duringlanis perugiae*, *Gelanoglanis travieso*, *Glanidium cesarpintoi*, *Pseudepapterus*, *Tatia* (except *Tatia intermedia*), *Tocantinsia*, *Trachelyopterichthys*, *Trachelyopterus amblops*, *Trachelyopterus insignis*, *Trachycorystes trachycorystes* and *Spinapterus*; (18) serrations on anterior margin of pectoral-fin spine antrorse (char. 3703: 2 → 0), exclusive in Auchenipterinae, convergent in *Ferrarissoaresia* and *Balroglanis carolae*; (19) scapulo-coracoids conspicuously interdigitated up to middle of coracoids or near to the posterior border (char. 3714: 1 → 2), convergent in *Balroglanis macracanthus*, *Gephyromochlus*, *Pseudepapterus*, *Gelanoglanis* and some species of *Tatia*; (20) pelvic girdle positioned within anterior half of body length (char. 3720: 0 → 1), convergent in *Epapterus*, *Pseudepapterus*, *Trachelyichthys* and *Trachelyopterichthys*; (21) posterior portion of basipterygium long, with process developed as a wing (char. 3729: 0 → 1), convergent in *Ageneiosus*, *Tympanopleura*, *Trachelyopterus* and *Trachycorystes*; (22) distal vesicles present on anterior anal-fin rays of nuptial males (char. 3744: 0 → 1), convergent in *Pseudepapterus*; and (23) hypurapophysis of type B (Lundberg & Baskin, 1969) (char. 3747: 2 → 1), convergent in several auchenipterids.

GENUS ASTEROPHYSUS KNER, 1857

Asterophysus Kner, 1857: 402 (type species: *Asterophysus batrachus* Kner, 1857; type by monotypy. Gender masculine).

Included species: *Asterophysus batrachus* Kner, 1857.

Diagnosis: Same as for tribe Asterophysini.

Comparisons: *Asterophysus* is a monotypic genus with uniform dark brown to black body coloration, known as a voracious predator, and is easily distinguished from other auchenipterids by the flexibility of the jaws and hyoid arch, with the ability to open its mouth to a size that is greater than its body depth (vs. mouth opening smaller than body depth), and except for *Tocantinsia*, by having the symphysis of the dentary dorsally projected (vs. symphysis of dentary straight). It is also distinguished from other auchenipterids, except *Auchenipterichthys* and *Trachelyichthys*, by having additional irregular serrations in the proximal portion of the anterior margin of the dorsal-fin spine (vs. irregular serrations absent) and, except for *Epapterus*, *Pseudepapterus* and *Spinapterus*, by having the dorsal-fin spine rudimentary, less than one-sixth of SL (vs. moderate, approximately one-third of SL). It is further distinguished from all auchenipterines, except *Trachycorystes*, *Tocantinsia* and *Trachelyopterus*, by having prognathism of the lower jaw, which is slightly projected outward in comparison to the premaxilla (vs. lower and upper jaws ending at same vertical line), and from all auchenipterines, except for *Pseudauchenipterus*, *Pseudepapterus* and *Trachelyichthys*, by nuptial males having distal vesicles on the anterior anal-fin rays to store sperm (vs. vesicles on anal fin absent). *Asterophysus* is further distinguished from *Tocantinsia* by having the dorsal-fin origin approximately along a vertical line from the pectoral-fin origin (vs. dorsal-fin origin posteriorly displaced relative to the pectoral-fin origin, at a distance approximately equivalent to the length of the dorsal-fin spine), posterior process of post-temporal suprachleitrum not reaching the vertical line from dorsal-fin origin (vs. posterior process of post-temporal suprachleitrum surpassing the vertical line from the dorsal-fin origin), and the mouth gape far surpassing the eye (vs. mouth gape reaching the eye, but never surpassing it).

TRIBE AUCHENIPTERINI BLEEKER, 1862 (CLADE 92)

Auchenipterini Bleeker, 1862 (in Bleeker, 1862–63): 14 (type genus: *Auchenipterus* Valenciennes, 1840).

Included genera: *Auchenipterus* Valenciennes, 1840, *Entomocorus* Eigenmann, 1917, *Epapterus* Cope, 1878, *Pseudauchenipterus* Bleeker, 1862 and *Pseudepapterus* Steindachner, 1915.

Diagnosis: Auchenipterini is diagnosed by six molecular and nine morphological synapomorphies.

Exclusive: (1) first hypobranchial discoid (char. 3645: 1, 2 → 0); (2) posterior process of scapulo-coracoid twisted, forming deep concavity (char. 3717: 0 → 1), reversed in *Auchenipterus*, *Epapterus*, *Pseudauchenipterus jequitinhonhae* and *Pseudauchenipterus nodosus*; and (3) distal margin of posterior process of the scapulo-coracoid pointed and thin (char. 3718: 0 → 1), reversed in *Pseudauchenipterus jequitinhonhae* and *Pseudauchenipterus nodosus*.

Non-exclusive: (4) five ossified suborbital tubules in adult (char. 3519: 3 → 1), reversed in *Auchenipterus* and *Entomocorus*, convergent in *Centromochlus*, *Balroglanis*, *Glanidium*, some species of *Tatia*, *Trachelyichthys*, *Trachelyopterus insignis* and *Trachelyopterus coriaceus*; (5) trigeminofacial foramen exposed (char. 3581: 1 → 0), reversed in *Auchenipterus ambyiacus* and *Auchenipterus brachyurus*, convergent in Centromochlinae (except *Glanidium*), *Tympanopleura piperata*, *Tympanopleura cryptica*, *Trachelyichthys decaradiatus*, *Trachelyopterichthys* and *Trachelyopterus amblops*; (6) distal portion of posterior process of third epibranchial pointed (char. 3649: 0 → 1), reversed in *Auchenipterus* (except *Auchenipterus ambyiacus* and *Auchenipterus brachyurus*), convergent in several auchenipterids; (7) os suspensorium moderate in size (char. 3655: 1 → 0), reversed in *Auchenipterus* (except *Auchenipterus nuchalis* and *Auchenipterus ambyiacus*) and *Pseudepapterus*, convergent in several auchenipterids; (8) postzygapophysis of compound centrum extended up to seventh vertebra (char. 3666: 2 → 3), reversed in *Epapterus dispilurus* and *Pseudepapterus*, convergent in *Tympanopleura* and *Trachelyichthys*; and (9) compound centrum including up to seventh vertebra (char. 3667: 2 → 3), reversed in *Pseudepapterus*, convergent in Centromochlinae (except *Gelanoglanis*, *Glanidium cesarpintoii* and *Glanidium catharinensis*), *Trachelyichthys*, *Trachelyopterus teaguei* and *Trachelyopterus albicrux*.

GENUS *PSEUDAUCHENIPTERUS* BLEEKER, 1862
(CLADE 93)

Pseudauchenipterus Bleeker, 1862 (in [Bleeker, 1862–63](#)): 6 (type species: *Silurus nodosus* Bloch, 1794; type by original designation. Gender masculine).

Included species: *Pseudauchenipterus affinis* Steindachner, 1877, *Pseudauchenipterus flavescens* Eigenmann & Eigenmann, 1888, *Pseudauchenipterus jequitinhonhae* (Steindachner, 1877) and *Pseudauchenipterus nodosus* (Bloch, 1794).

Diagnosis: *Pseudauchenipterus* is diagnosed by nine morphological synapomorphies. **Non-exclusive:** (1) papilla-like dermal tubercles present on tympanic

area (char. 3497: 0 → 1), convergent in *Ageneiosus pardalis*; (2) fenestra between lateral ethmoid and frontal present (char. 3550: 1 → 0), convergent in *Trachycorystes trachycorystes*; (3) transcapular process transverse to body axis (char. 3570: 1 → 0), convergent in *Lisomadoras oncinus*, *Auchenipterichthys*, Centromochlinae (except *Tatia intermedia*), *Trachelyopterichthys*, *Trachelyichthys decaradiatus*, *Trachelyopterus* (except *Trachelyopterus lucenai* and *Trachelyopterus* aff. *T. galeatus*) and *Trachycorystes menezesi*; (4) coronoid process of anguloarticular developed as large laminar process (char. 3602: 0 → 1), convergent in *Auchenipterichthys*, *Balroglanis*, *Duringlanis*, *Gephyromochlus*, *Gelanoglanis*, *Pseudotatia*, some species of *Tatia* and *Trachelyichthys*; (5) levator operculi crest of hyomandibula absent (char. 3617: 1 → 0), convergent in several auchenipterids; (6) interopercle short, ovoid (char. 3626: 1 → 2), convergent in Centromochlinae (except *Gelanoglanis*, *Tatia* sp. 1 and *Tatia* sp. 3) and *Liosomadoras*; (7) middle nuchal plate and parieto-supraoccipital separated, not in contact (char. 3672: 1 → 0), convergent in *Auchenipterus*, *Trachelyopterini*, *Liosomadoras*, *Centromochlus*, *Duringlanis perugiae*, *Glanidium* (except *Glanidium ribeiroi*), *Tatia* (except *Tatia musaica*, *Tatia meesi* and *Tatia* sp. 2); (8) posterior nuchal plate broad, approximately of same width or wider than base of dorsal-fin spine (char. 3673: 0 → 1), convergent in *Auchenipterichthys*, *Epapterus*, *Asterophysus*, *Glanidium* (except *Glanidium cesarpintoii*), *Balroglanis* (except *Balroglanis carolae*), *Duringlanis*, some species of *Tatia*, *Trachelyopterichthys* and *Trachycorystes*; and (9) ventral bony projection present in last pterygiophore of dorsal fin (char. 3679: 1 → 0), convergent in *Pseudepapterus cucuhyensis* and *Tetranematichthys wallacei*.

Comparisons: *Pseudauchenipterus* is distinguished from remaining auchenipterids, except *Ageneiosus pardalis*, by having papilla-like dermal tubercles on the tympanic area and, except *Liosomadoras*, *Auchenipterus* and *Trachelyopterini*, by having the middle nuchal plate and the parieto-supraoccipital separated, not in contact (vs. middle nuchal and parieto-supraoccipital sutured to each other). It further differs from all auchenipterines by the number of branched pelvic-fin rays, seven (vs. six in *Liosomadoras*, *Tocantinsia*, *Ageneiosus*, *Tympanopleura* and *Tetranematichthys*, five in *Entomocorus*, *Trachelyopterus* and *Spinipterus*, eight or nine in *Trachycorystes* and *Auchenipterichthys*, nine in *Asterophysus*, nine to 14 in *Pseudepapterus*, ten or 11 in *Trachelyichthys*, 10–14 in *Auchenipterus* and *Trachelyopterichthys*, and 14–16 in *Epapterus*) and, except for *Pseudepapterus*, *Epapterus*, *Auchenipterus*

(but not *Auchenipterus fordicei*) and some species of *Ageneiosus* (*Ageneiosus vittatus*, *Ageneiosus inermis*, *Ageneiosus militaris* and *Ageneiosus dentatus*) by having the anterior margin of the pectoral-fin spine smooth, without serration (vs. anterior margin of pectoral-fin spine serrated) and, except for *Pseudepapterus* and *Ageneiosini*, by the possession of an anterior nuchal plate (vs. anterior nuchal plate absent). It differs from the remaining auchenipterines, except *Ageneiosus* and *Tympanopleura*, and remaining Auchenipterini (except *Entomocorus*) by having the lateral line sinusoidal along its entire length (vs. lateral line straight, or sinusoidal in the anterior portion and straight in the posterior half) and, except for *Asterophysus*, *Liosomadoras*, *Tetranematichthys*, *Trachelyichthys* and *Trachelyopterus* (but not *Trachelyopterus galeatus* and *Trachelyopterus lucenai*), by having the dorsal margin of the lateral ethmoid not exposed on the dorsal surface of the head (vs. dorsal margin of lateral ethmoid exposed on dorsal surface of head).

GENUS *ENTOMOCORUS* EIGENMANN, 1917 (CLADE 97)

Entomocorus Eigenmann, 1917: 403 (type species: *Entomocorus benjamini* Eigenmann, 1917; type by monotypy. Gender masculine).

Included species: *Entomocorus benjamini* Eigenmann, 1917, *Entomocorus gameroi* Mago-Leccia, 1984, **Entomocorus melaphareus* Akama & Ferraris, 2003 and *Entomocorus radiosus* Reis & Borges, 2006.

Diagnosis: *Entomocorus* is diagnosed by 41 molecular and 19 morphological synapomorphies. **Exclusive:** (1) accessory dermal ossification present between frontal, sphenotic and parieto-supraoccipital (char. 3559: 0 → 1); and (2) first unbranched ray of pelvic fin in nuptial males larger than in females and non-nuptial males (char. 3721: 0 → 1). **Non-exclusive:** (3) extension present of anterior cartilage of lateral ethmoid (char. 3547: 1 → 0), convergent in Trachelyopterini, Centromochlinae (except *Gelanoglanis pan* and *Gelanoglanis varii*), *Liosomadoras* and *Epapterus*; (4) lateral margin of frontal participating of orbital margin (char. 3553: 1 → 0), convergent in Centromochlinae, *Tocantinsia*, *Trachelyichthys* and *Trachycorystes trachycorystes*; (5) posterior process of posttemporal-supracleithrum posterodorsally oriented (char. 3561: 0 → 1), convergent in Centromochlinae (except *Glanidium catharinensis*, *Glanidium* sp. 1 RS and *Glanidium* sp. 2 RS), *Auchenipterichthys*, *Spinipterus*, *Epapterus*, *Pseudauchenipterus nodosus*, *Trachelyichthys*, *Trachelyopterus amblops*, *Trachelyopterus insignis*, *Trachelyopterus* cf. *Trachelyopterus galeatus*, some species of *Ageneiosus* and *Tympanopleura*; (6) posterior

process of epioccipital forming simple spine (char. 3563: 1 → 0), convergent in *Asterophysus*, *Auchenipterichthys*, *Balroglanis*, *Gelanoglanis* and *Trachelyopterichthys*; (7) premaxilla almost straight (char. 3584: 1 → 0), convergent in *Auchenipterichthys*, *Gelanoglanis*, *Glanidium catharinensis* and *Glanidium cesarpintoi*; (8) premaxillary teeth straight (char. 3589: 0 → 1), convergent in several auchenipterids; (9) ascending process of Meckel's cartilage extended (char. 3599: 0 → 1), convergent in *Tympanopleura*, *Ageneiosus* and *Auchenipterichthys* (except *Auchenipterichthys thoracatus*); (10) cartilage of posterior condyle of the autopalatine small (char. 3609: 0 → 1), convergent in *Ageneiosus*, *Tympanopleura*, *Auchenipterus*, *Gephyromochlus* and some species of *Tatia*; (11) posteriormost pterygiophore of dorsal fin not supporting ray (char. 3677: 0 → 1), most Centromochlinae, *Trachelyichthys* sp. 1 and *Trachelyopterus coriaceus*; (12) posterior bony projection absent on last pterygiophore of dorsal fin (char. 3680: 1 → 0), convergent in *Auchenipterichthys punctatus*, *Balroglanis*, *Gelanoglanis*, *Glanidium*, *Liosomadoras*, *Pseudotatia*, some species of *Tatia*, *Trachelyichthys*, *Trachycorystes* and *Spinipterus*; (13) pectoral girdle elongate, at least half the width of the pectoral girdle (char. 3695: 0 → 2), convergent in *Auchenipterichthys*, Trachelyopterina and Centromochlinae (except *Glanidium catharinensis*); (14) anterior margin of pectoral-fin spine with retrorse serrations (char. 3703: 2 → 1), convergent in *Auchenipterichthys*, *Trachelyichthys* (except *Trachelyichthys* sp. 1), most species of *Trachelyopterus* and *Trachycorystes menezesi*; (15) basipterygium with anterolateral process much longer than anteromedial (char. 3725: 0 → 1), convergent in Centromochlinae (except *Ferrarissoaresia* and *Glanidium*), Trachelyopterini (except *Trachelyopterus amblops* and *Trachelyopterus coriaceus*); (16) short cartilage on lateral process of basipterygium (char. 3727: 1 → 0), convergent in *Epapterus*, *Glanidium*, *Tetranematichthys*, *Trachelyichthys* sp. 1 and *Trachelyopterichthys*; (17) basal process of pelvic-fin rays oriented posteromedially in dorsal view (char. 3732: 0 → 1), convergent in *Auchenipterichthys*, Centromochlinae (except *Gelanoglanis* and *Glanidium*), *Liosomadoras oncinus*, *Tocantinsia*, *Trachelyichthys*, *Trachelyopterus insignis* and *Spinipterus* sp. 'oncinha'; (18) genital tube anterior to anal-fin rays and apart from anal-fin base (char. 3735: 0 → 1), exclusive in Auchenipterinae, convergent in Centromochlinae; and (19) proximal portion of fifth hypural not contacting confluence between third and fourth hypurals and epineural (char. 3752: 1 → 0), convergent in *Duringlanis*, *Balroglanis*, some species of *Tatia*, *Liosomadoras oncinus*, *Pseudotatia*, *Glanidium* and *Gephyromochlus*.

Comparisons: *Entomocorus* is a remarkably morphologically distinctive small body-sized

genus within the family, with reproductive males developing conspicuous sexually dimorphic features. It is distinguished from the remaining auchenipterids by the unique features of an accessory dermal ossification between the frontal, sphenotic and parieto-supraoccipital (vs. accessory ossification absent) and by having the first unbranched pelvic-fin ray in nuptial males longer than in females and non-nuptial males (vs. sexual dimorphism absent in the pelvic-fin rays). It is further distinguished from all auchenipterines by males having the genital tube positioned anterior to the anal-fin rays and apart from the anal-fin base (vs. genital tube positioned at the base of the anal fin and united by skin to the anterior anal-fin rays) and, except for *Trachelyopterus* and *Spinipterus*, by the number of branched pelvic-fin rays, five (vs. six in *Liosomadoras*, *Tocantinsia*, *Ageneiosus*, *Tympanopleura* and *Tetranematichthys*, seven in *Pseudauchenipterus*, eight or nine in *Trachycorystes* and *Auchenipterichthys*, nine in *Asterophysus*, nine to 14 in *Pseudepapterus*, ten or 11 in *Trachelyichthys*, ten to 14 in *Auchenipterus* and *Trachelyopterichthys*, and 14–16 in *Epapterus*), except for *Asterophysus*, *Auchenipterichthys* and *Trachelyopterichthys*, by the posterior process of the epioccipital as a simple spine (vs. posterior process of the epioccipital small and pointed, laminar or bifurcated) and, except for *Trachelyichthys* sp. 1 and *Trachelyopterus coriaceus*, by having the posteriormost pterygiophore of the dorsal fin not supporting any ray (vs. posteriormost pterygiophore of dorsal fin supporting one or two rays).

GENUS *PSEUDEPAPTERUS* STEINDACHNER, 1915

(CLADE 99)

Pseudepapterus Steindachner, 1915: 199 (type species: *Auchenipterus (Pseudepapterus) hasemani* Steindachner, 1915; type by monotypy. Gender masculine).

Included species: *Pseudepapterus cucuhyensis* Böhlke, 1951, **Pseudepapterus gracilis* Ferraris & Vari, 2000 and *Pseudepapterus hasemani* (Steindachner, 1915).

Diagnosis: *Pseudepapterus* is diagnosed by 12 molecular and 17 morphological synapomorphies. **Exclusive:** (1) premaxilla extremely reduced in size (char. 3582: 0 → 1); and (2) cartilage of lateral process of basipterygium fused to main body of basipterygium (char. 3728: 0 → 1). **Non-exclusive:** (3) anteromedial portion of mesethmoid not contacting premaxilla (char. 3534: 0 → 1), convergent in *Ageneiosini* and *Gelanoglanis*; (4) posterior margin of cranial fontanel with longitudinal sulcus (char. 3544: 0 → 1), convergent in *Ageneiosus* and *Tympanopleura rondoni*; (5) posterior process of epioccipital laminar (char. 3563:

1 → 2), convergent in *Ageneiosus* and *Tympanopleura*; (6) coronomeckelian bone conspicuously separated from anguloarticular (char. 3597: 1 → 0), convergent in *Trachelyichthys*, *Pseudauchenipterus jequitinhonhae*, *Pseudauchenipterus nodosus* and *Centromochlinae* (except *Glanidium catharinensis*, *Glanidium ribeiroi* and *Glanidium* sp. 2 RS); (7) suprapreopercle short, approximately quadrangular to rectangular, with its length never surpassing twice the width (char. 3624: 1 → 0), convergent in several auchenipterids; (8) os suspensorium reduced in size (char. 3655: 0 → 1), convergent in several auchenipterids; (9) os suspensorium rounded or angled (char. 3656: 0 → 1), convergent in *Auchenipterus* (except *Auchenipterus ambyiacus* and *Auchenipterus nuchalis*), *Tatia reticulata*, *Tatia gyrina*, *Tatia* sp. 2, *Gelanoglanis*, *Asterophysus*, *Liosomadoras*, *Tetranematichthys*, *Trachelyichthys decaradiatus*, *Trachelyopterichthys anduzei*, *Trachycorystes trachycorystes* and *Trachelyopterus* aff. *T. porosus*; (10) Müllerian ramus reduced, not surpassing half the length of the transcapular process (char. 3661: 0 → 1), convergent in *Ageneiosus* and *Gelanoglanis*; (11) postzygapophysis of compound centrum extended up to sixth vertebra (char. 3666: 3 → 2), convergent in *Ageneiosus*, *Asterophysus*, *Centromochlinae* (except *Balroglanis macracanthus*), *Liosomadoras* and *Tetranematichthys*; (12) compound centrum including up to sixth vertebra (char. 3667: 3 → 2), convergent in *Asterophysini*, *Auchenipterini* and *Ageneiosini* (except *Ageneiosus militaris*, *Tympanopleura cryptica* and *Tympanopleura brevis*), *Glanidium cesarpintoi*, *Glanidium catharinensis* and *Liosomadoras*; (13) anterior nuchal plate absent (char. 3670: 0 → 1), convergent in *Ageneiosini*, *Balroglanis*, *Duringlanis romani*, *Tatia musaica*, *Tatia meesi*, clade 60 of *Tatia* and *Gelanoglanini*; (14) ventral process of dorsal-fin spinelet short, reaching ventrally up to 20% of pterygiophore height (char. 3682: 1 → 0), convergent in *Entomocorus gameroi*; (15) posterior process of cleithrum small, not surpassing base of branched pectoral-fin rays (char. 3711: 1 → 0), *Tympanopleura brevis*, *Tympanopleura rondoni*, *Asterophysus* and *Tetranematichthys*; (16) suture of scapulo-coracoids conspicuously interdigitated up to middle of coracoids or near to its posterior border (char. 3714: 1 → 2), convergent in *Asterophysus*, *Gelanoglanini*, *Gephyromochlus*, *Pseudepapterus* and some species of *Tatia*; and (17) distal vesicles present on anterior anal-fin rays of nuptial males (char. 3744: 0 → 1), convergent in *Trachelyichthys* and *Asterophysus*.

Comparisons: *Pseudepapterus* is a genus comprising small body-sized species and is distinctive within auchenipterids by the reduced size of the dorsal fin and premaxilla. It is distinguished from all other

auchenipterids by the premaxilla being extremely reduced in size (vs. premaxilla well developed) and, except *Epapterus*, by the absence of premaxillary teeth (vs. premaxillary teeth present). It is further distinguished from other aucheniapterids, except for *Asterophysus*, *Pseudauchenipterus* and *Trachelyichthys*, by having distal vesicles present on the anterior anal-fin rays of nuptial males (vs. distal vesicles absent in anterior anal-fin rays of nuptial males); except for *Ageneiosus* and *Tympanopleura rondoni*, by the posterior margin of the cranial fontanel with a longitudinal sulcus (vs. longitudinal sulcus absent on cranial fontanel); and, except *Auchenipterus* and *Epapterus*, by having a consistent skin membrane joining the proximal half of the contralateral innermost pelvic-fin ray (vs. contralateral innermost pelvic-fin rays separated from each other). It differs from all other aucheniapterines, except *Ageneiosus* and *Tympanopleura*, by the laminar posterior process of the epioccipital (vs. posterior process of epioccipital bifurcated, as a simple spine, or pointed); except for *Ageneiosini*, by the absence of an anterior nuchal plate (vs. anterior nuchal plate present); and, except for *Spinipterus* and *Asterophysus*, by having the dorsal-fin spine short, less than one-sixth of SL (vs. dorsal-fin spine moderate, shorter than one-third of SL, or long, greater than one-third of SL). It is further distinguished from other aucheniapterines, except *Asterophysus*, *Auchenipterus*, *Epapterus*, *Trachelyichthys* and *Trachelyopterichthys*, by having the pectoral-fin girdle within the anterior half of the body length (vs. pectoral-fin girdle approximately at the halfway point of the body).

GENUS *EPAPTERUS* COPE, 1878 (CLADE 101)

Epapterus Cope, 1878: 677 (type species: *Epapterus dispilurus* Cope, 1878; type by monotypy. Gender masculine).

Included species: *Epapterus blohmi* Vari, Jewett, Taphorn & Gilbert, 1984 and *Epapterus dispilurus* Cope, 1878.

Diagnosis: *Epapterus* is diagnosed by 11 morphological synapomorphies. **Exclusive:** (1) two free pterygiophores on dorsal fin (char. 3775: 2 → 5); and (2) anal fin of nuptial males with space between modified anterior rays and remaining rays (char. 3745: 0 → 1). **Non-exclusive:** (3) adipose fin absent (char. 3493: 0 → 1), convergent in *Trachelyichthys*, *Trachelyopterichthys* and *Trachelyopterus coriaceus*; (4) projection of the anterior cartilage on anterior margin of lateral ethmoid absent (char. 3547: 1 → 0), convergent in several aucheniapterids; (5) posterior process of posttemporal–supracleithrum posterodorsally oriented (char. 3561: 0 → 1), convergent in several aucheniapterids; (6) adductor crest of hyomandibula well developed (char. 3616: 0 → 1),

convergent in *Auchenipterichthys*, *Glanidium* (except *Glanidium* sp. 1RS), *Liosomadoras*, *Pseudauchenipterus jequitinhonhae*, *Trachelyopterus* (except some species of *Trachelyopterus*), *Tatia boemia*, *Tatia* sp. 4 and *Tetranematichthys*; (7) levator operculi crest of hyomandibula absent (char. 3617: 1 → 0), convergent in several aucheniapterids; (8) posterior projection of urohyal lamina (char. 3629: 0 → 1), convergent in *Tympanopleura brevior*, *Tympanopleura cryptica*, *Pseudepapterus cucuhyensis* and *Tetranematichthys*; (9) posterior nuchal plate broad, having the same width or wider than the base of the dorsal-fin spine (char. 3673: 0 → 1), convergent in some aucheniapterids; (10) extension on cartilage of lateral process of basipterygium short (char. 3727: 1 → 0), convergent in *Entomocorus*, *Glanidium*, *Tetranematichthys*, *Trachelyichthys* and *Trachelyopterichthys*; and (11) caudal fin truncated (char. 3746: 0 → 1), convergent in *Ageneiosus inermis*, *Ageneiosus vittatus*, *Tetranematichthys*, *Trachelyopterini* and *Liosomadoras*.

Comparisons: *Epapterus* is a genus of small body-sized species, with distinctive features within the family related to the reduced dorsal fin and premaxilla and to the anal fin of nuptial males. *Epapterus* is diagnosed from remaining aucheniapterids by nuptial males having the anal fin with a space between modified anterior rays and the remaining rays (vs. all anal-fin rays contiguous, without space between rays) and by having three soft, branched dorsal-fin rays (vs. four, five, six or seven). It is further distinguished from all aucheniapterines, except *Pseudepapterus*, by the absence of premaxillary teeth (vs. premaxillary teeth present); except for *Auchenipterus* and *Pseudepapterus*, by having a thick continuous skin membrane joining the proximal half of the contralateral innermost pelvic-fin rays (vs. contralateral innermost pelvic-fin rays separated from each other); and, except for *Trachelyichthys*, *Trachelyopterichthys* and *Trachelyopterus coriaceus*, by the absence of an adipose fin (vs. adipose fin present). It differs from most aucheniapterines, except *Ageneiosus inermis*, *Ageneiosus vittatus*, *Tetranematichthys*, *Trachelyopterini* and *Liosomadoras*, by the caudal fin being truncated (vs. caudal fin bifurcated) and, except for *Asterophysus*, *Auchenipterus*, *Epapterus*, *Trachelyichthys* and *Trachelyopterichthys*, by having the pectoral-fin girdle within the anterior half of the body length (vs. pectoral-fin girdle approximately at the halfway point of SL).

GENUS *AUCHENIPTERUS* VALENCIENNES, 1840 (CLADE 102)

Auchenipterus Valenciennes, in Cuvier & Valenciennes (1840): 207 (type species: *Hypophthalmus nuchalis* Spix & Agassiz, 1829; type by subsequent designation

by Bleeker, 1862 (in Bleeker, 1862–63): 15. Gender masculine).

Included species: *Auchenipterus ambyiacus* Fowler, 1915, *Auchenipterus brachyurus* (Cope, 1878), *Auchenipterus brevior* Eigenmann, 1912, **Auchenipterus britskii* Ferraris & Vari, 1999, *Auchenipterus demerarae* Eigenmann, 1912, *Auchenipterus dentatus* Valenciennes, 1840, *Auchenipterus fordicei* Eigenmann & Eigenmann, 1888, **Auchenipterus menezesi* Ferraris & Vari, 1999, *Auchenipterus nigripinnis* (Boulenger, 1895), *Auchenipterus nuchalis* (Spix & Agassiz, 1829) and *Auchenipterus osteomystax* (Miranda Ribeiro, 1918).

Diagnosis: *Auchenipterus* is diagnosed by nine morphological synapomorphies. **Exclusive:** (1) distal portion of first anal-fin unbranched ray ornamented with rounded hooks in nuptial males (char. 3742: 0 → 1). **Non-exclusive:** (2) anterior portion of nasal bifurcated (char. 3513: 0 → 1), convergent in *Ageneiosini*, *Trachelyopterus insignis* and *Trachycorystes trachycorystes*; (3) four ossified suborbital tubules in adult (char. 3519: 1 → 2), convergent in *Ageneiosus dentatus*, *Ageneiosus vittatus*, *Entomocorus*, *Auchenipterichthys*, *Trachelyopterus albicrux*, *Trachelyopterus porosus* and *Trachycorystes* aff. *Trachelyopterus porosus* and *Trachycorystes*; (4) anterior cranial fontanel elliptical (char. 3542: 0 → 2), convergent in several auchenipterids; (5) ventral process present on dentary symphysis (char. 3606: 0 → 1), convergent in *Ageneiosus lineatus*, *Tympanopleura brevis*, *Tympanopleura rondoni*, *Asterophysus*, *Pseudauchenipterus* (except *Pseudauchenipterus flavescens*) and *Trachycorystes trachycorystes*; (6) cartilage of posterior condyle of autopalatine small (char. 3609: 0 → 1), convergent in *Entomocorus*, *Ageneiosus*, *Tympanopleura*, some species of *Tatia* and *Gephyromochlus*; (7) parapophysis of fifth vertebra moderate in size, approximately the same size as sixth vertebra (char. 3665: 0 → 1), convergent in *Centromochlinae* (except *Centromochlus*, *Gephyromochlus*, *Glanidium catharinensis*, *Balroglanis carolae*, *Tatia creutzbergi* and *Tatia intermedia*), *Liosomadoras*, *Tocantinsia*, *Trachelyichthys* (except *Trachelyichthys exilis*) and *Spinipterus*; (8) middle nuchal plate not in contact with parieto-supraoccipital (char. 3672: 1 → 0), convergent in *Pseudauchenipterus*, *Trachelyopterini*, *Centromochlus*, *Duringlanis perugiae*, *Glanidium* (except *Glanidium ribeiroi*), *Tatia* (except *Tatia musaica*, *Tatia meesi* and *Tatia* sp. 2) and *Liosomadoras*; and (9) last proximal radial of anal fin laminar (char. 3741: 1 → 0), convergent in *Auchenipterichthys*, *Tocantinsia*, *Ageneiosus* (except *Ageneiosus lineatus*, *Ageneiosus*

pardalis and *Ageneiosus inermis*), *Tympanopleura rondoni* and *Tympanopleura cryptica*.

Comparisons: *Auchenipterus* is distinguished from all auchenipterines, except *Trachelyichthys* and *Pseudepapterus*, by the number of branched pelvic-fin rays, ten to 14 (vs. less branched pelvic-fin rays in remaining auchenipterines, except 14–16 in *Epapterus*) and, except for *Trachelyichthys exilis* and *Trachelyichthys* sp. 1, by having the posteriormost pterygiophore of dorsal fin supporting two separate rays (vs. posteriormost pterygiophores of dorsal fin, ultimate and in some cases the penultimate, supporting only a single ray). Except for *Auchenipterus fordicei*, the genus is also distinguished from auchenipterines, except *Pseudauchenipterus*, *Pseudepapterus*, *Epapterus*, *Ageneiosus vittatus*, *Ageneiosus inermis*, *Ageneiosus dentatus* and *Ageneiosus militaris*, by the absence of serrations on the anterior margin of the pectoral-fin spine (vs. anterior margin of pectoral-fin spine serrated); except for *Epapterus* and *Pseudepapterus*, by having a consistent skin membrane joining the proximal half of the contralateral innermost pelvic-fin rays (vs. contralateral innermost pelvic-fin rays separated from each other); except for *Asterophysus*, *Pseudepapterus*, *Epapterus*, *Trachelyichthys* and *Trachelyopterichthys*, by having the pelvic-fin girdle within the anterior half of the body length (vs. pelvic-fin girdle approximately at the halfway point of the body); and except for *Pseudauchenipterus*, *Trachelyopterini* and *Liosomadoras*, by the absence of contact between the middle nuchal plate and parieto-supraoccipital (vs. middle nuchal plate and parieto-supraoccipital in contact with each other).

TRIBE AGENEIOSINI BLEEKER, 1862 (CLADE 107)

Ageneiosi Bleeker, 1862 (in Bleeker, 1862–63): 14 (type genus: *Ageneiosus* La Cepède, 1803).

Included genera: *Ageneiosus* La Cepède, 1803, *Tetranematichthys* Bleeker, 1858 and *Tympanopleura* Eigenmann, 1912.

Diagnosis: *Ageneiosini* is diagnosed by 13 molecular and 19 morphological synapomorphies. **Exclusive:** (1) maxillary barbel short, not surpassing anterior margin of orbit (char. 3499: 0 → 1); (2) mesethmoid expanded anterolaterally, with notch on anterior and posterior portions (char. 3532: 1 → 0); (3) anterolateral process of sphenotic present (char. 3551: 0 → 1); (4) sesamoid bone 1 large, plate-like (char. 3621: 1 → 2); (5) posterior projection of urohyal bifurcated in ventral view (char. 3630: 0 → 1), reversed in *Tympanopleura brevis* and *Tympanopleura cryptica*; (6) ventral connection between posterior portion of ventral hypohyal and anterior ceratohyal via

bony suture (char. 3634: 0 → 1); and (7) medial portion of first epibranchial enlarged, wider than lateral portion (char. 3647: 1 → 0), reversed in *Tympanopleura brevis* and *Tympanopleura cryptica*. **Non-exclusive:** (8) anterior portion of nasal bifurcated (char. 3513: 0 → 1), convergent in *Auchenipterus*, *Trachelyopterus insignis* and *Trachycorystes trachycorystes*; (9) antorbital not participating on orbital margin (char. 3514: 1 → 0), convergent in *Trachelyopterus insignis* and *Gelanoglanis*; (10) anteromedial portion of mesethmoid not contacting premaxilla (char. 3534: 0 → 1), reversed in *Tympanopleura cryptica*, convergent in *Gelanoglanis* and *Pseudepapterus*; (11) posterior process of epioccipital connected by suture to parapophysis of compound centrum (char. 3566: 0 → 1), convergent in *Auchenipterus*, *Epapterus*, *Pseudepapterus*, *Trachelyichthys* and *Trachelyopterus coriaceus*; (12) distal portion of premaxilla extended (char. 3586: 0 → 1), convergent in *Auchenipterus*, *Epapterus*, *Gelanoglanis* and *Pseudepapterus cucuhyensis*; (13) process present on posteromesial portion of distal extension of premaxilla (char. 3587: 0 → 1), convergent in *Centromochlus existimatus* and *Trachelyopterichthys*; (14) spines present on maxilla of nuptial males (char. 3594: 0 → 1), reversed in *Ageneiosus ucayalensis*, convergent in *Trachelyopterus insignis*; (15) hyomandibula not contacting metapterygoid (char. 3620: 0 → 1), convergent in *Centromochlus*, *Gelanoglanis* and *Tatia*; (16) posterior projection of urohyal short, approximately the same length as the main body of the urohyal in ventral view (char. 3628: 1 → 0), convergent in *Auchenipterichthys longimanus*, *Auchenipterus*, *Centromochlus*, *Epapterus* and *Pseudepapterus*; (17) anterior nuchal plate absent (char. 3670: 0 → 1), convergent in *Gelanoglanis*, *Duringlanis romani*, *Pseudepapterus* and clade 58 of *Tatia*; (18) dorsal-fin spine of nuptial males strongly arched (char. 3687: 0 → 1), convergent in *Trachelyopterus amblops*, *Trachelyopterus insignis* and *Trachelyopterus teaguei*; and (19) anal fin elongated, at least half of body length (char. 3740: 0 → 2), convergent in *Auchenipterus*, *Epapterus*, *Pseudepapterus*, *Trachelyichthys* and *Trachelyopterichthys*.

GENUS *TETRANEMATICHTHYS* BLEEKER, 1858

Tetranematichtys Bleeker, 1858b: 357, 359 (type species: *Ageneiosus quadrifilis* Kner, 1857; type by monotypy. Gender masculine).

Included species: **Tetranematichtys barthemii* Peixoto & Wosiacki, 2010, **Tetranematichtys quadrifilis* (Kner, 1857) and *Tetranematichtys wallacei* Vari & Ferraris, 2006.

Diagnosis: *Tetranematichtys* is diagnosed by 114 molecular and 14 morphological autapomorphies.

Exclusive: (1) laterodorsal projections present on posterior portion of urohyal (char. 3631: 0 → 1); and (2) ornamentation on mental barbel present (char. 3507: 0 → 1); because this character was codified as inapplicable for *Ageneiosus* and *Tympanopleura*, which completely lack mental barbels, it was optimized as ambiguous for these genera and not listed as autapomorphic for *Tetranematichtys*. **Non-exclusive:** (3) mesethmoid elongated, approximately two times its width, or longer (char. 3533: 1 → 0), convergent in *Auchenipterus*, *Epapterus*, *Entomocorus*, *Gelanoglanis* and *Pseudepapterus*; (4) epioccipital partially exposed, only anterior portion participating of cephalic shield (char. 3555: 1 → 0), convergent in *Epapterus* and *Auchenipterus*; (5) posterodorsal process of hyomandibula small, weakly developed (char. 3613: 0 → 1), convergent in several auchenipterids; (6) levator operculi crest on hyomandibula absent (char. 3617: 1 → 0), convergent in several auchenipterids; (7) posterior projection of urohyal laminar in ventral view (char. 3629: 0 → 1), convergent in *Tympanopleura brevis*, *Tympanopleura cryptica*, *Epapterus* and *Pseudepapterus cucuhyensis*; (8) spines present on gill rakers (char. 3640: 0 → 1), convergent in *Tympanopleura atronatus*, *Tympanopleura brevis*, *Ageneiosus ucayalensis* and *Ageneiosus intrusus*; (9) accessory cartilage present on third and fourth basibranchials (char. 3644: 0 → 1), convergent in *Ageneiosus dentatus*, *Ageneiosus intrusus*, *Ageneiosus vittatus*, *Ageneiosus uranophthalmus*, *Auchenipterus fordicei*, *Auchenipterichthys*, *Centromochlus perugiae*, *Pseudauchenipterus flavescens*, *Pseudepapterus hasemani*, *Trachelyichthys* and *Trachelyopterichthys taeniatus*; (10) ventral bony projection in last pterygiophore of dorsal fin (char. 3679: 1 → 0), convergent in *Pseudauchenipterus* and *Pseudepapterus cucuhyensis*; (11) cartilage of lateral process of basipterygium short (char. 3727: 1 → 0), convergent in *Epapterus*, *Glanidium*, *Trachelyopterichthys* and *Trachelyichthys* sp. 1; (12) caudal fin truncated (char. 3746: 0 → 1), convergent in *Ageneiosus inermis*, *Ageneiosus vittatus*, *Auchenipterichthys*, *Epapterus*, *Liosomadoras* and *Trachelyopterini* (except *Tocantinsia*); (13) hypurapophysis of type B (Lundberg & Baskin, 1969) (char. 3747: 2 → 1), convergent in several auchenipterids; (14) first ventral unbranched caudal-fin ray articulated on antepenultimate haemal spine (char. 3749: 1 → 3), convergent in *Trachelyopterus striatulus*, *Trachelyopterus porosus* and *Trachelyopterus* aff. *T. porosus*; and (15) caudal skeleton posteroventrally oriented (char. 3753: 0 → 1), convergent in *Trachelyichthys*, *Trachelyopterichthys* and *Trachycorystes trachycorystes*.

Comparisons: *Tetranematichtys* is a robust, medium body-sized genus known for nuptial males developing

conspicuous sexually dimorphic features related to the dorsal-fin spine and maxillary barbel. This genus is distinguished from all auchenipterids by the digitiform ornamentation on the mental barbel (vs. mental barbel smooth, not bearing any ornamentation). It further differs from auchenipterids, except *Tympanopleura* and *Ageneiosus*, by having the predorsal region deeply arched, forming a sloped nuchal shield (vs. approximately straight in relationship to the dorsal fin region, or slightly arched, but never forming a deep slope) and by the short maxillary barbel, not surpassing the anterior margin of the orbit (vs. long maxillary barbel, extending beyond the anterior margin of the orbit). It is distinguished from all Auchenipterids, except *Gelanoglanis*, by the presence of one pair of mental barbels (vs. mental barbel absent in *Tympanopleura* and *Ageneiosus*, or two pairs present in remaining genera). It is distinguished from other auchenipterines, except *Pseudepapterus*, by the absence of an anterior nuchal plate (vs. anterior nuchal plate present); and, except for *Trachelyichthys*, *Trachelyopterichthys* and *Trachycorystes trachycorystes*, by having the caudal skeleton posteroventrally oriented, usually forming a subtle sloping in dorsal profile of the caudal-fin origin (vs. caudal skeleton posteriorly oriented).

GENUS *TYMPANOPLEURA* EIGENMANN, 1912
(CLADE 109)

Tympanopleura Eigenmann, 1912: 203 (type species: *Tympanopleura piperata* Eigenmann, 1912; type by original designation. Gender feminine).

Included species: *Tympanopleura atronasus* (Eigenmann & Eigenmann, 1888), *Tympanopleura brevis* (Steindachner, 1881), *Tympanopleura cryptica* Walsh, Ribeiro & Py-Daniel 2015, *Tympanopleura longipinna* Walsh, Ribeiro & Py-Daniel 2015, *Tympanopleura piperata* Eigenmann, 1912, *Tympanopleura rondoni* (Miranda Ribeiro, 1914) and *Tympanopleura* sp. 1 Ribeiro *et al.*, undescribed.

Diagnosis: *Tympanopleura* is diagnosed by six molecular and three morphological synapomorphies. **Non-exclusive:** (1) eye very large, occupying almost entire head depth (char. 3491: 0 → 1), convergent in *Auchenipterus*, *Pseudepapterus cucuhyensis*, *Epapterus*, *Entomocorus*, *Centromochlus* and *Balroglanis* (except *Balroglanis carolae*); (2) upper gill rakers conical (char. 3639: 1 → 0), convergent in *Auchenipterichthys*, *Centromochlinae* (except *Gelanoglanis*), *Liosomadoras oncinus* and *Trachelyopterina*; and (3) postzygapophysis of compound centrum extended up to seventh vertebra (char. 3666: 4 → 3), convergent in *Auchenipterus*, *Balroglanis macracanthus*, *Duringlanis romani*,

Entomocorus, *Pseudauchenipterus*, *Trachelyichthys* and *Trachelyopterus teaguei*.

Additional diagnosis: *Tympanopleura* differs from *Ageneiosus* by having a smaller adult body size; more gently rounded anterior profile of the head, and less protruded upper jaw, which is reflected by a shorter relative preorbital distance; large, cordiform gas bladder that is unencapsulated in bone; and prominent pseudotympanum, visible externally. *Tympanopleura* (except *Tympanopleura piperata*) also differs from *Ageneiosus* by having paired posterior diverticula on the gas bladder (Walsh *et al.*, 2015).

Comparisons: *Tympanopleura* is a small body-sized *Ageneiosini* that is distinguished from other auchenipterines, except *Ageneiosus*, by having the eye ventrolaterally positioned, in such a way that it is visible in both ventral and dorsal views (vs. eye not visible in ventral view), mouth subterminal, upper jaw extended well anteriorly to the lower jaw (vs. mouth terminal, both upper and lower jaws extended anteriorly at the same vertical line) and absence of mental barbels (vs. two pairs of mental barbels present, one pair in *Tetranematichthys* and *Gelanoglanis*). It is further distinguished from all auchenipterines, except *Ageneiosus* and *Tetranematichthys*, by the short maxillary barbel, not surpassing the anterior margin of the orbit (vs. long maxillary barbel, extending beyond the anterior margin of the orbit). It is distinguished from *Ageneiosus* by lacking a longitudinal sulcus on the posterior margin of the anterior cranial fontanel (except *Tympanopleura rondoni*; vs. longitudinal sulcus present on posterior margin of the anterior cranial fontanel); prominent pseudotympanum, conspicuously visible externally (vs. not visible externally, or very little visible externally); except for *Ageneiosus vittatus* and *Ageneiosus dentatus*, by having the posterior margin of dorsal-fin spine serrated (vs. posterior margin of dorsal-fin spine smooth); and the Müllerian ramus large, surpassing the line through the suture in the posterolateral margin of the transcapular process (vs. reduced, not surpassing half the length of the transcapular process).

GENUS *AGENEIOSUS* LA CEPÈDE, 1803 (CLADE 115)

Ageneiosus La Cèpède, 1803: 132 (type species: *Ageneiosus armatus* La Cèpède, 1803; type by subsequent designation by Eigenmann & Eigenmann, 1890: 299. Gender masculine).

Included species: *Ageneiosus akamai* Ribeiro, Py-Daniel & Walsh, 2017, **Ageneiosus apiaka* Ribeiro, Py-Daniel & Walsh, 2017, *Ageneiosus dentatus* Kner, 1857, *Ageneiosus inermis* (Linnaeus, 1766), *Ageneiosus*

intrusus Ribeiro, Py-Daniel & Walsh, 2017, *Ageneiosus lineatus* Ribeiro, Py-Daniel & Walsh, 2017, **Ageneiosus magoi* Castillo & Brull, 1989, *Ageneiosus militaris* Valenciennes, 1836, *Ageneiosus pardalis* Lütken, 1874, *Ageneiosus polystictus* Steindachner, 1915, *Ageneiosus ucayalensis* Castelnau, 1855, *Ageneiosus uranophthalmus* Ribeiro & Py-Daniel, 2010 and *Ageneiosus vittatus* Steindachner, 1908.

Diagnosis: *Ageneiosus* is diagnosed by six morphological synapomorphies. **Non-exclusive:** (1) bones of cephalic shield trabeculated (char. 3531: 0 → 1), convergent in *Tympanopleura atronasus* and *Tympanopleura rondoni*; (2) epioccipital not exposed, not participating of cephalic shield (char. 3555: 1 → 2), convergent in *Pseudepapterus*; (3) bony expansion present on posteromedial portion of premaxilla (char. 3585: 0 → 1), reversed in *Ageneiosus uranophthalmus* and *Ageneiosus intrusus*, convergent in *Auchenipterus fordicei* and *Trachycorystes*; (4) coronoid process of anguloarticular developed as a large and laminar process (char. 3602: 0 → 1), convergent in *Tympanopleura rondoni*, *Tympanopleura atronasus*, *Auchenipterichthys*, *Pseudauchenipterus*, *Trachelyichthys*, *Gephyromochlus*, *Pseudotatia*, *Duringlanis*, *Balroglanis* and most species of *Tatia*; (5) Müllerian ramus reduced, not surpassing half the length of the transcapular process (char. 3661: 0 → 1), convergent in *Asterophysus*, *Gelanoglanis* and *Pseudepapterus*; and (6) serrations absent on posterior margin of dorsal-fin spine (char. 3693: 0 → 1), reversed in *Ageneiosus dentatus* and *Ageneiosus vittatus*, convergent in *Asterophysus*, *Duringlanis perugiae*, *Epapterus*, *Gelanoglanis travieso*, *Pseudepapterus*, *Tatia* (except *Tatia intermedia* and *Tatia simplex*), *Tocantinsia*, *Trachelyopterichthys*, *Spinipterus*, *Trachycorystes trachycorystes*, *Trachelyopterus insignis* and *Trachelyopterus amblops*.

Additional diagnosis: Posterior diverticula on gas bladder absent; epaxial muscles almost completely covering tympanic region in adults, except *Ageneiosus pardalis*.

Comparisons: *Ageneiosus* is a large body-sized Ageneiosini that is distinguished from other auchenipterids, except *Tympanopleura*, by having the snout strongly depressed, resembling a duck's beak (vs. snout only slightly depressed, or laterally compressed in *Gelanoglanis*), with the eye ventrolaterally positioned, in such a way that it is as visible in ventral and dorsal views (vs. eye not visible in ventral view), mouth subterminal, upper jaw extended well anteriorly to the lower jaw (vs. mouth terminal, both upper and lower jaws extended anteriorly to the same vertical line), and absence of mental barbels

(vs. two pairs of mental barbels present, but one pair in *Tetranematichthys* and *Gelanoglanis*). It is further distinguished from all auchenipterines, except *Tympanopleura* and *Tetranematichthys*, by the short maxillary barbel, not surpassing the anterior margin of the orbit (vs. long maxillary barbel, extending beyond the anterior margin of the orbit) and, except for *Pseudepapterus*, the epioccipital not exposed, not participating in the cephalic shield (vs. epioccipital exposed on the dorsal surface of head). It is distinguished from *Tympanopleura* by a longitudinal sulcus on the posterior margin of the anterior cranial fontanel (vs. longitudinal sulcus absent, except in *Tympanopleura rondoni*); pseudotympanum not visible externally, or very little visible externally (vs. prominent pseudotympanum, conspicuously visible externally); posterior margin of the dorsal-fin spine smooth, not serrated, except for *Ageneiosus vittatus* and *Ageneiosus dentatus* (vs. posterior margin of dorsal-fin spine serrated); and Müllerian ramus reduced, not surpassing half the length of the transcapular process (vs. Müllerian ramus large, surpassing the suture in the posterolateral margin of the transcapular process).

Remarks: The condition of an ossified gas bladder was suggested by Ribeiro *et al.* (2017) as diagnostic for *Ageneiosus*. The present hypothesis, however, has not recovered this feature as synapomorphic for the genus, because the gas bladder of *Tympanopleura cryptica* and *Tympanopleura piperata* are ossified but that of *Ageneiosus lineatus* is unossified, a condition also shared with *Ageneiosus pardalis*, not observed in this study but reported by Ribeiro *et al.* (2017).

DISCUSSION

MONOPHYLY OF AUCHENIPTERIDAE AND DORADOIDEA

The analyses result in a well-supported phylogenetic hypothesis that provides a historical framework for a discussion of auchenipterid relationships and the unveiling of some phenotypic features that possibly led to the evolution of the family and its diversity.

The newly reconstructed phylogeny of the Auchenipteridae recovers the monophyly of the family, which was strongly supported by several previous studies (Ferraris, 1988; Royero, 1999; Akama, 2004; Ribeiro, 2011; Birindelli, 2014). Moreover, the hypothesis discloses new arrangements in the classification of the family compared with previous studies, mainly by the investigation of new molecular data and a comprehensive taxonomic sampling. Two major lineages are recognized in Auchenipteridae: the subfamilies Centromochlinae and Auchenipterinae, agreeing with the current classification, except for the transfer of *Pseudotatia* to Centromochlinae. However,

KEY TO THE GENERA OF AUCHENIPTERIDAE

- 1a. Head strongly compressed, mouth sinuous *Gelanoglanis*
 1b. Head depressed at some level, mouth straight 2
 2a. Maxillary barbel short, not surpassing anterior margin of orbit; mental barbels absent or, if present, one pair 3
 2b. Maxillary barbel long, extending beyond anterior margin of orbit; two pairs of mental barbels 5
 3a. One pair of mental barbels; eye dorsolateral, not visible in ventral view *Tetranematichthys*
 3b. Mental barbels absent; eye ventrolateral, visible in ventral view 4
 4a. Pseudotympanum not visible or almost not visible externally; posterior margin of dorsal-fin spine smooth, not serrated (except *Ageneiosus vittatus* and *Ageneiosus dentatus*) *Ageneiosus*
 4b. Pseudotympanum conspicuous and clearly visible externally; posterior margin of dorsal-fin spine serrated *Tympanopleura*
 5a. Caudal fin truncated 6
 5b. Caudal fin bifurcated 13
 6a. Lower jaw prognate, slightly outward projected in comparison to upper jaw 7
 6b. Lower and upper jaws ending on same vertical line 8
 7a. Branched pelvic-fin rays, eight or nine *Trachycorystes trachycorystes*
 7b. Branched pelvic-fin rays, five *Trachelyopterus*
 8a. Antorbital and suborbital ossified tubules spiny 9
 8b. Antorbital and suborbital ossified tubules smooth, lacking spines 11
 9a. Two rows of serrae on anterior margin of dorsal-fin spine; body very elongated, anal fin with 39–58 total rays *Trachelyopterichthys*
 9b. Three rows of serrae on anterior margin of dorsal-fin spine; body moderately elongated, anal fin with 13–20 total rays 10
 10a. Four rows of serrae on pectoral-fin spine (anterior, posterior, dorsal and ventral); posterior margin of dorsal-fin spine serrated *Spinipterus*
 10b. Two rows of serrae on pectoral-fin spine (anterior and posterior); posterior margin of dorsal-fin spine smooth, not serrated *Liosomadoras*
 11a. Adipose fin present *Auchenipterichthys*
 11b. Adipose fin absent 12
 12a. Dorsal fin rudimentary, with spine poorly developed and two or three branched rays; premaxillary teeth absent; base of inner mental barbel anterior to outer *Epapterus*
 12b. Dorsal fin and spine well developed with four or five branched rays; premaxillary teeth present; base of both inner and outer barbels adjacent *Trachelyichthys*
 13a. Mental barbel short, not reaching pectoral-fin origin 21
 13b. Mental barbel long, surpassing pectoral-fin origin 14
 14a. Anal fin short, up to ten total rays *Ferrarissoaresia*
 14b. Anal fin long, 12 or more total rays 15
 15a. Branched pelvic-fin rays, 10–14 16
 15b. Branched pelvic-fin rays, five to nine 17
 16a. Premaxillary teeth absent; dorsal-fin spine rudimentary, and three to five branched rays (rarely six in *Pseudepapterus hasemani*) *Pseudepapterus*
 16b. Premaxillary teeth present; dorsal-fin spine well developed, and six or seven branched rays *Auchenipterus*
 17a. Midline of abdomen between pelvic and anal fins compressed and forming fleshy keel; branched pelvic-fin rays, five *Entomocorus*
 17b. Midline of abdomen between pelvic and anal fins not compressed, flat to rounded, not forming fleshy keel; branched pelvic-fin rays, six to nine 18
 18a. Anterior margin of pectoral-fin spine smooth, not serrated *Pseudauchenipterus*
 18b. Anterior margin of pectoral-fin spine serrated 19
 19a. Mouth gape far surpassing eye; dorsal-fin origin at or slightly posterior to vertical from pectoral-fin origin *Asterophysus*
 19b. Mouth gape reaching eye, but never surpassing; dorsal-fin origin displaced posteriorly from pectoral-fin origin, approximately one dorsal-fin spine in length 20

| | |
|---|--------------------------------|
| 20a. Branched anal-fin rays, 12; branched pelvic-fin rays, six; head as deep as wide | <i>Tocantinsia</i> |
| 20b. Branched anal-fin rays, 19–22; branched pelvic-fin rays, eight; head depressed, wider than deep | <i>Trachycorystes menezesi</i> |
| 21a. Eye not visible or barely visible in ventral view | 22 |
| 21b. Eye clearly visible in ventral view | 25 |
| 22a. Total anal-fin rays, 15–17; branched dorsal-fin rays, six | <i>Pseudotatia</i> |
| 22b. Total anal-fin rays, seven to 14; branched dorsal-fin rays, four or five (but six in <i>Glanidium ribeiroi</i>) | 23 |
| 23a. Anterior margin of pectoral-fin spine smooth, not serrated; branched pectoral-fin rays, six | <i>Gephyromochlus</i> |
| 23b. Anterior margin of pectoral-fin spine serrated; branched pectoral-fin rays, four or five | 24 |
| 24a. Dorsal-fin spine long, subequal to anterior branched rays or slightly shorter, but never half its length; skin covering head thin, leaving cranial bones visible and distinguishable; branched anal-fin rays, six to eight | <i>Tatia</i> |
| 24b. Dorsal-fin spine short, approximately half the length of anterior branched rays; skin covering head thick, leaving cranial bones concealed; branched anal-fin rays, eight or nine (eight in <i>Glanidium botocudo</i> and <i>Glanidium albescens</i>) | <i>Glanidium</i> |
| 25a. Maxillary barbel inserted laterally in the head, proximal portion not visible ventrally; lower and upper jaws with similar width, positioning labial skin flap laterally to vertical from anterior naris (Fig. 1B); lateral margins of mandibulae diverging laterally; origin of outer mental barbel positioned further laterally relative to inner, spaced from latter by more than barbel-base size (Fig. 1D)..... | <i>Duringlanis</i> |
| 25b. Maxillary barbel inserted ventrally in the head, proximal portion visible ventrally; lower jaw narrower than upper jaw, positioning labial skin flap at vertical from anterior naris (Fig. 1C); lateral margins of mandibulae running approximately in parallel; origin of outer mental barbel almost aligned to a vertical passing by origin of inner one (Fig. 1A)..... | 26 |
| 26a. Anterior margin of pectoral-fin spine smooth; posterior naris positioned anterior to eye; outer and inner mental barbels subequal in length (Fig. 1A) | <i>Centromochlus</i> |
| 26b. Anterior margin of pectoral-fin spine serrated; posterior naris positioned dorsally to eye; outer mental barbel distinctly longer than inner (Fig. 1C) | <i>Balroglanis</i> |

interrelationships of the auchenipterid genera in each of these subfamilies differ substantially from all previous hypotheses (Ferraris, 1988; Curran, 1989; Walsh, 1990; Soares-Porto, 1998; Royero, 1999; Akama, 2004; Ribeiro, 2011; Birindelli, 2014). Overall, this nearly complete taxonomic sampling, compared with previous studies, was adequate to test internal topology of the groups consistently and to gain a general perspective on infrageneric relationships. The new classification scheme proposes nine tribes based on the monophyly of the major groups of both subfamilies: Centromochlinae represented by four tribes and Auchenipterinae by five. Despite the existence of older names available in the literature for some of the groups proposed here, their composition differs greatly (see more details about the subfamilies in the subsection of the Discussion).

Based on the MP hypothesis, and in agreement with previous propositions (Ferraris, 1988; Royero, 1999; Akama, 2004; Birindelli, 2014), Auchenipteridae is a well-supported family, with 20 molecular and 14 morphological synapomorphies (Figs 13, 14). Among synapomorphies, the several features related to sexual dimorphism have been demonstrated to be highly informative and, consequently, helpful to

diagnose the group among catfishes, given that they represent unreversed exclusive synapomorphies. In addition, several other exclusive and non-exclusive synapomorphies also support the family, with some of them representing new discoveries.

The monophyly of Doradoidea (Auchenipteridae + Doradidae) is highly corroborated in this and previous studies (de Pinna, 1998; Britto, 2002; Diogo, 2004; Sullivan *et al.*, 2008; Birindelli, 2014), although the relationships of this superfamily with remaining catfish families remain controversial between molecular and morphological phylogenies. For the first time recovered under a total evidence approach, through both MP and Bayesian information analyses (Figs 13, 14; and Supporting Information, Appendix S4, respectively), Aspredinidae resolves as a sister group to Doradoidea, corroborating previous multilocus molecular and genomic phylogenies (Sullivan *et al.*, 2006, 2008; Arcila *et al.*, 2017; Betancur-R *et al.*, 2017), and in disagreement with previous morphological hypotheses, which suggested the African Mochokidae as sister to the Neotropical Doradoidea. Furthermore, the molecular-only hypothesis (Supporting Information, Appendix S5) also corroborates Aspredinidae as the sister to Doradoidea, whereas in the morphology-only

hypothesis the closest relationships to Doradoidea are unresolved, which somehow does not corroborate other morphological hypotheses (Supporting Information, Appendix S6).

Doradoidei [Aspredinidae (Auchenipteridae, Doradidae)], as herein defined, is demonstrated to be monophyletic based on 29 molecular and four morphological synapomorphies: (1) anterior fontanel elliptic (char. 3542: 0 → 2; exclusive for the clade, but reversed in some doradoids); (2) proximal extremity of pleural ribs twisted (char. 3669: 0 → 1, exclusive for the clade but reversed in some doradoids); (3) hyomandibula articulated to the neurocranium via sphenotic and pterotic (char. 3619: 0 → 1; convergent in *Pimelodus* examined); and (4) compound centrum including up to fifth vertebra (char. 3667: 2 → 1; this feature is highly homoplastic within the group, with many transformations along the tree). The morphological similarities of the Weberian apparatus of Mochokidae and Doradoidea were not optimized as synapomorphies, as previous morphological phylogenies suggested. Beyond that, Mochokidae have recently been proposed to be closely related to the African Claroteidae, and this clade to the Asian Pangasiidae by genomic studies (Arcila *et al.*, 2017; Betancur-R *et al.*, 2017).

Interestingly, the recent evolutionary history consolidated in genomic-based phylogenies (Arcila *et al.*, 2017; Betancur-R *et al.*, 2017) reported four major divergence events in Siluroidei, a basal clade of the Cetopsidae succeeded by a separated Siluridae sister taxa of two large groups, a Neotropical catfish clade and a second clade formed by non-Neotropical fish families. The genomic-based phylogenies have, by all means, recovered as monophyletic a group formed exclusively by Neotropical families, contrary to all past phylogenies that have recovered lineages of Neotropical catfishes clustering with lineages including at least some non-Neotropical members (de Pinna, 1998; Britto, 2002; Diogo, 2004; Sullivan *et al.*, 2006, 2008).

A REDESIGNED CENTROMOCHLINAЕ AND ITS DIVERSITY

The subfamily Centromochlinae is monophyletic, here diagnosed by 28 molecular and eight morphological synapomorphies, corroborating previous results of Ferraris (1988), Royero (1999) and Birindelli (2014), except for the inclusion of *Pseudotatia*. Some of the exclusive synapomorphies are traits related to the sexually dimorphic anal fin of nuptial males and, once again, reflect the importance of the reproductive system and related behaviour of the centromochline evolutionary scenario.

The broad taxonomic sampling and encompassing dataset of the present study support the first largely robust topology for Centromochlinae. The intrarelationships of the subfamily, and particularly the intrageneric relationships, are fully resolved (with the exception of some internal relationships of *Tatia* and *Gelanoglanis*). Thus, a new classification scheme is proposed for the Centromochlinae, with four major clades that represent distinct tribes (Fig. 13): Gelanoglanini (*Ferrarissoaresia* and *Gelanoglanis*), Pseudotatiini (*Pseudotatia*), Centromochlini (*Centromochlus*, *Duringlanis* and *Gephyromochlus*) and Glandiini (*Balroglanis*, *Glandidium* and *Tatia*). This phylogenetic arrangement differs significantly from the currently accepted taxonomy, in which only two of the genera, *Gelanoglanis* and *Pseudotatia*, remain with the same composition, because *Centromochlus*, *Glandidium* and *Tatia* were each found to be non-monophyletic.

Notably, *Centromochlus* and *Tatia* have already been informally recognized as non-monophyletic (Ferraris, 1988), representing the most complex genera in the family. The high amount of historical homoplasy in this subfamily, primarily caused by many descriptions and reallocations of species of *Tatia* in *Centromochlus*, has hindered the taxonomic limits and recognition of these groups. *Centromochlus*, as currently recognized, is recovered as polyphyletic. The typical morphology of a long pectoral-fin spine, eye ventrally displaced and elongated body, shared by *Centromochlus heckelii* and *Centromochlus existimatus*, had already indicated the possibility of more than one group in the genus. This hypothesis is corroborated in the present study, resulting in the recognition of four distinct lineages in *Centromochlus s.l.*, bringing together one species previously assigned to *Tatia* (*Tatia carolae*). Thus, *Centromochlus s.s.* is herein restricted to a clade comprising *Centromochlus heckelii* and *Centromochlus existimatus*. Interestingly, Ferraris (1988) and Mees (1974) have already restricted *Centromochlus* to these two species. Nonetheless, Soares-Porto (1998), in a phylogenetic study of the Centromochlinae, expanded *Centromochlus* to include several *Tatia* species, a genus previously composed of two easily distinguishable forms. An interesting feature suggested by her as synapomorphic for *Centromochlus* is the absence of the anterior nuchal plate. Contrary to that observation, the presence of an anterior nuchal plate was recovered as a synapomorphy for the species herein assigned to *Centromochlus*, a condition convergent in *Tatia*, a genus not the closest related. This transition is marked, in fact, by the lack of the anterior nuchal plate as an independent loss in *Ferrarissoaresia*, *Duringlanis* (except for *Duringlanis perugiae*), *Balroglanis* (except for *Balroglanis carolae*) and *Gephyromochlus*.

To maintain a monophyletic classification of Centromochlinae, three available names previously proposed by Grant (2015) as subgenera of *Centromochlus* were elevated to genus rank. *Ferrarissoaresia*, a very distinctive form with small, dorsally positioned eyes, short and deep body and long outer mental barbel, is composed of *Ferrarissoaresia meridionalis* from the upper Tapajós River, and provisionally includes *Ferrarissoaresia ferrarisi* from the Tocantins River basin.

The second name elevated to genus is *Duringlanis*, comprising the species *Duringlanis romani*, *Duringlanis perugiae* and, provisionally, *Duringlanis altae*, with a short and deep body, from the coastal rivers of Venezuela, with the last two coming from the upper Amazon basin. The validity of *Duringlanis* is justified by the significant genetic and morphological differentiation from *Centromochlus* s.s. Interestingly, Royero (1999) also recognized a clade including *Tatia romani* separated from *Centromochlus* s.s. and *Tatia*, which was posteriorly proposed by Grant (2015) as part of a subgenus of *Centromochlus*. Reinforcing this result, Ferraris (1988) also recognized *Duringlanis perugiae* plus *Duringlanis altae* as a distinct genus (his Genus A), sister group of *Centromochlus*, exactly reflecting the relationship recovered herein.

Balroglanis is the third name elevated to genus, encompassing species with larger body size, more closely related to *Tatia* and *Glanidium*. *Balroglanis schultzi*, *Balroglanis macracanthus* and *Balroglanis carolae* are distributed in the Xingu, Negro and Cuyuni river basins, respectively. This group includes species superficially similar to *Centromochlus* s.s., with larger eyes positioned ventrolaterally on the head, body elongated, and dorsal and pectoral fins with strong spines. The elevation of this clade to genus rank is justified by its isolated position in the centromochline radiation.

Tatia is the most diverse genus in Centromochlinae and, although the present hypothesis has not recovered fully intrageneric relationships, the monophyly is supported by 13 molecular and three morphological synapomorphies. Furthermore, *Centromochlus simplex*, *Centromochlus reticulatus* and *Centromochlus orca* share the synapomorphies for the clade and are reallocated in *Tatia*. An interesting subclade recovered in *Tatia* is that comprising the small body-sized species, including *Tatia gyrina*, *Tatia creutzbergi* and two new species. This evolutionary scenario could be indicating that one diversification event gave rise to two groups in *Tatia*, one formed by smaller-bodied species and other composed of the larger-sized forms.

Pursuant to the results, the monotypic genus *Pseudotatia* was recovered as a distinctive lineage nested in Centromochlinae, sister to Centromochlini

plus Glanidiini in the MP analysis, but sister to Glanidiini in the BI analysis. *Pseudotatia* has been recognized as a member of Auchenipterinae by previous authors (Ferraris, 1988; Royero, 1999; Birindelli, 2014), but Curran (1989) recovered *Pseudotatia* closely related to *Centromochlus* and *Glanidium*. However, the genus shares most of the synapomorphies of Centromochlinae.

Glanidium s.s. (i.e. except *Glanidium leopardum*) was recovered as monophyletic and sister to *Tatia*, corroborating the hypothesis of Ferraris (1988). Owing to the highly confusing taxonomic history of the genus, only specimens from the type locality of each taxa were included, which rendered the inclusion of all species impossible. *Glanidium leopardum* is here removed from *Glanidium* and assigned to the previously available *Gephyromochlus* Hoedman, 1961, originally proposed as a subgenus of *Centromochlus*, and posteriorly synonymized with *Glanidium* by Mees (1974: 93). *Gephyromochlus* is an independent lineage supported by 71 molecular and ten morphological autapomorphies. The BI also recovered *Gephyromochlus* as separated from *Glanidium*, and the genus was positioned as sister to all Centromochlinae (except *Entomocorus*), instead of as a member of Centromochlini.

The hypotheses based on both MP and BI of the combined datasets recognized *Gelanoglanis* as monophyletic and not deeply nested in *Tatia* or *Centromochlus* as previously found by Soares-Porto (1998) and Royero (1999). Unprecedentedly, the BI analysis hypothesized *Entomocorus* as a member of Centromochlinae in contrast to MP. This result is discussed further below.

LINEAGES AND RELATIONSHIPS OF AUCHENIPTERINAE

Auchenipterinae is recognized here as a monophyletic auchenipterid subfamily, as reported by previous authors (Ferraris, 1988; Akama, 2004; Ribeiro, 2011; Birindelli, 2014), except for the exclusion of *Pseudotatia* (Fig. 13) and the inclusion of the former Ageneiosidae (*Ageneiosus*, *Tympanopleura* and *Tetranematichthys*) deeply nested in the subfamily, considered as a separate family by Britski (1972), Curran (1989) and Walsh (1990).

The new classification proposal formally recognizes, for the first time, five tribes in Auchenipterinae: Ageneiosini, Asterophysini, Liosomadoradini, Trachelyopterini and Auchenipterini (the latter two informally proposed by Ribeiro, 2011). This hypothesis clearly reflects the distinct morphological and genetic groups found in Auchenipterinae and represents an advance in the phylogenetic knowledge by taxonomically recognizing monophyletic units. The subdivision of Auchenipterinae into more numerous

groups was proposed by previous authors (Bleeker, 1862–63; Miranda Ribeiro, 1911; Ribeiro, 2011) and, except for Ribeiro (2011), those hypotheses were not based on a phylogeny. Bleeker (1862–63) separated Auchenipterinae into many subgroups, some of them recognized herein, in spite of the different composition. Liosomadoradini is recognized herein as a monotypic tribe comprising *Liosomadoras oncinus* and *Liosomadoras morrowi*, supported by a high degree of molecular differentiation (68 autapomorphies of *Liosomadoras oncinus*, because genetic data for *Liosomadoras morrowi* were not available) and seven morphological synapomorphies, as detailed in the Diagnosis. Liosomadoradini was recovered as sister group to all remaining Auchenipterinae, a hypothesis never advanced before. In contrast, Birindelli (2014) recovered *Tocantinsia* as sister to all remaining Auchenipterinae, and *Asterophysus* as sister taxon to *Liosomadoras*. The BI analysis, on the contrary, found Auchenipterini (with exclusion of *Pseudauchenipterus*) to be sister to all auchenipterines and then Liosomadoradini to be sister to remaining tribes.

The Trachelyopterini includes three subtribes with the following composition: Trachelyopterina (*Spinipterus* and *Trachelyopterus*), Trachycorystina (*Tocantinsia* and *Trachycorystes*) and Auchenipterichthyina (*Auchenipterichthys*, *Trachelyichthys* and *Trachelyopterichthys*). The composition of Trachelyopterini is similar to a clade found by Akama (2004), except for the inclusion of *Liosomadoras* in his hypothesis, and also found by Birindelli (2014), except for the exclusion of *Spinipterus*, which was found to be more closely related to the Ageneiosini plus Auchenipterini. The position of *Spinipterus* far from the Trachelyopterini in Birindelli's (2014) hypothesis is probably because of the missing data, because until recently, *Spinipterus acsi* was known only by the holotype, and he was unable to verify most of the characters. In the present study, an undescribed species was also included (*Spinipterus* sp. 'oncinha'), and the holotype of *Spinipterus acsi* was studied via high-resolution computed microtomography, which allowed the verification of many characters and resulted in the recovery of a well-supported closest relationship of this genus with *Trachelyopterus*. The present results also corroborate the relationship of *Auchenipterichthys* as sister to the clade formed by *Trachelyichthys* plus *Trachelyopterichthys*, as previously recovered by Akama (2004).

A second major clade in Auchenipterinae encompasses three subclades, which are classified as the tribes Asterophysini, Auchenipterini and Ageneiosini. The Asterophysini is represented by *Asterophysus batrachus*, a very distinctive species

diagnosed by 23 morphological autapomorphies. In the present study, Asterophysini is sister to Auchenipterini plus Ageneiosini. Conversely, Akama (2004) recovered *Asterophysus* as sister group of all remaining Auchenipterinae.

The close relationships between *Entomocorus*, *Pseudepapterus*, *Epapterus* and *Auchenipterus* are in agreement with Ferraris (1988) and Royero (1999), despite the lack of *Pseudepapterus* in their studies, Akama (2004, *Epapterus* not included), Ribeiro (2011) and Birindelli (2014). The present hypothesis corroborates the monophyly of this clade, with the addition of *Pseudauchenipterus* that together comprise the tribe Auchenipterini. Notwithstanding, Auchenipterini is more closely related to the clade formed by *Ageneiosus*, *Tympanopleura* and *Tetranematichthys*, here classified as Ageneiosini. This large group, Auchenipterini + Ageneiosini, was also recovered by Ferraris (1988), Akama (2004), Ribeiro (2011) and Birindelli (2014) and is highly supported under MP based on the combined datasets. However, in the BI analysis, the clade formed by *Pseudepapterus*, *Epapterus* and *Auchenipterus* was recovered as sister to the remaining Auchenipterinae (Supporting Information, Appendix S4). Additionally, the BI total evidence analysis hypothesized *Entomocorus* as a member of the Centromochlinae, in addition to the BI hypothesis based on the molecular data alone (Supporting Information, Appendix S5), indicating that the genotypic data are responsible for shaping this relationship. Furthermore, Birindelli (2014) noted that *Entomocorus* shares several synapomorphies with *Epapterus*, *Pseudepapterus* and *Auchenipterus*, but at the same time also shares many features present only in the Centromochlinae. The present analysis corroborates this observation, and the results under different phylogenetic approaches seem to reflect the ambiguous characters of *Entomocorus*. Considering morphological features, *Entomocorus* undoubtedly has the cranium elongated, the premaxilla reduced and the dorsal-fin spine of nuptial males longer than that of females and non-nuptial males, typical of the Auchenipterinae, which involves many derived conditions. In contrast, *Entomocorus* is the only Auchenipterinae that has the genital tube positioned anterior to the anal-fin base and separated from the first anal-fin rays, typical of the Centromochlinae. Thus, the position of *Entomocorus* recovered as Centromochlinae in the BI could be an artefact of a high genetic homoplasy between these groups rather than a likely scenario of sharing of a common ancestor.

The Ageneiosini have been recognized historically as monophyletic, being considered as a separate family in the past. This tribe has a high Bremer support and shares several synapomorphies. *Tympanopleura* was recently

resurrected and forms a monophyletic unit recovered as sister to *Ageneiosus* in the total evidence analysis. Hypotheses based only on molecular or morphological data did not support both as monophyletic genera. In the molecular tree (Supporting Information, Appendix S5), the basal position of *Ageneiosus militaris* results in a nested *Tympanopleura*, but each of the genera form separated clades. In the morphological tree (Supporting Information, Appendix S6), *Ageneiosus* is recovered as monophyletic, but *Tympanopleura* is scaled in different levels owing to high homoplasy and/or lack of species included in this analysis.

A comparison of the different approaches reveals results of the BI molecular-based hypothesis largely in agreement with the BI total evidence hypothesis. Exceptions are the absence of *Pseudotatia* (no DNA available), the position of *Tetranematichthys* as sister to Auchenipterichthyina and the close relationship of *Pseudauchenipterus* and Trachycorystina. These latter relationships are probably biased owing to the lack of *Asterophysus* in the molecular analysis, once *Pseudauchenipterus* and *Asterophysus* are recovered as sister taxa in BI total evidence. In contrast, MP total evidence (Fig. 14) incorporates important changes found in the morphology-based hypothesis, mainly on the relationships of the Auchenipterinae. These changes include bringing *Pseudauchenipterus* to the Auchenipterini along with *Entomocus*, *Pseudepapterus*, *Epapterus* and *Auchenipterus*, and positioning this tribe closest to the Ageneiosini, rather than in a basal position in the subfamily, as recovered in BI total evidence and BI molecular trees. Despite the lack of resolution in the interrelationships of the genera of Centromochlinae in the MP morphology-based analysis, all new generic ranks remain supported, except the composition of *Duringlanis*, which includes *Centromochlus simplex*, *Centromochlus reticulatus* and *Centromochlus meesi* and excludes *Centromochlus romani*, found as *incertae sedis*.

Nevertheless, the signal of the different datasets allows to evince the contribution of the molecular data to the reconstruction of the evolutionary history of auchenipterids, mostly in the definition of genera, and species relationships of some of them, whereas morphological data seemed to contribute to the reconstruction of the interrelationships among genera and the position of higher-level groups.

The evolutionary process involves changes in both the genome and the phenotypic traits of species. Therefore, the phylogenetic topologies reconstructed here show the value of morphological evidence undoubtedly supporting or contributing to the resolution of many of the clades herein recognized, revealing the importance of the inclusion of both phenotypic and molecular data in a combined approach. Notably, the combination of

evidence from different sources increases the resolution and stability mainly of the deep nodes of the tree, because together they can reconstruct the evolutionary history of groups at different levels, and yet enable a more comprehensive taxonomic sampling for those groups with incomplete datasets.

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REFERENCES

- Akama A. 2004.** *Revisão sistemática dos gêneros Parauchenipterus Bleeker, 1862 e Trachelyopterus Valenciennes, 1840 (Siluriformes, Auchenipteridae)*. Unpublished D. Phil. Dissertation, Universidade de São Paulo.
- Akama A, Ferraris CJ Jr. 2003.** *Entomocorus melaphareus*, a new species of auchenipterid catfish (Osteichthyes: Siluriformes) from the lower and middle reaches of the Amazon River. *Neotropical Ichthyology* **1**: 77–82.
- Akama A, Ferraris CJ Jr. 2011.** *Spinipterus*, a new genus of small, spiny catfish (Siluriformes: Auchenipteridae) from the Peruvian Amazon. *Zootaxa* **2992**: 52–60.
- Albert JS, Reis RE. 2011.** Introduction to Neotropical freshwaters. In: Albert JS, Reis RE, eds. *Historical biogeography of neotropical freshwater fishes*. Berkeley: University of California Press, 3–19.
- Alexander RM. 1965.** Structure and function in the catfish. *Journal of Zoology* **148**: 88–152.
- Altekar GS, Dwarkadas JP, Huelsenbeck JP, Ronquist F. 2004.** Parallel Metropolis-coupled Markov chain Monte Carlo for Bayesian phylogenetic inference. *Bioinformatics* **20**: 407–415.
- Arce HM, Reis RE, Geneva AJ, Sabaj-Pérez MH. 2013.** Molecular phylogeny of thorny catfishes (Siluriformes: Doradidae). *Molecular Phylogenetics and Evolution* **67**: 560–577.
- Arcila D, Ortí G, Vari RP, Armbruster JW, Stiassny MLJ, Ko KD, Sabaj MH, Lundberg J, Revell LJ, Betancur-RR. 2017.** Genome-wide interrogation advances resolution of recalcitrant groups in the tree of life. *Nature: Ecology & Evolution* **1**: 0020.
- Arratia G. 1987.** Description of the primitive family Diplomystidae (Siluriformes, Teleostei, Pisces): morphology, taxonomy and phylogenetic implications. *Bonner Zoologische Monographien* **24**: 1–120.
- Arratia G. 1990.** Development and diversity of the suspensorium of Trichomycterids and comparison with Loricarioids (Teleostei: Siluriformes). *Journal of Morphology* **205**: 193–218.
- Arratia G. 1992.** Development and variation of the suspensorium of primitive catfishes (Teleostei: Ostariophysi) and their phylogenetic relationships. *Bonner Zoologische Monographien* **32**: 1–149.
- Arratia G. 2003a.** Catfish head skeleton, an overview. In: Arratia G, Kapoor BG, Chardon M, Diogo R, eds. *Catfishes*. Enfield: Science Publishers Inc., 3–46.
- Arratia G. 2003b.** The siluriform postcranial skeleton, an overview. In: Arratia G, Kapoor BG, Chardon M, Diogo R, eds. *Catfishes*. Enfield: Science Publishers Inc., 121–158.
- Arratia G, Gayet M. 1995.** Sensory canals and related bones of tertiary Siluriform crania from Bolivia and North America and comparison with recent forms. *Journal of Vertebrate Paleontology* **15**: 482–505.
- Arratia G, Huaquin L. 1995.** Morphology of the lateral line system and of the skin of Diplomystid and certain primitive Loricarioid catfishes and systematic and ecological considerations. *Bonner Zoologische Monographien* **36**: 1–109.
- Arratia G, Schultze HP. 1991.** Paleoquadrate and its ossifications: development and homology within Osteichthyan. *Journal of Morphology* **208**: 1–81.
- Arroyave J, Stiassny MLJ. 2011.** Phylogenetic relationships and the temporal context for the diversification of African characins of the family Alestidae (Ostariophysi: Characiformes): Evidence from DNA sequence data. *Molecular Phylogenetics and Evolution* **60**: 385–397.
- Berg C. 1901.** Comunicaciones ictiológicas, IV. *Comunicaciones del Museo Nacional de Buenos Aires* **1**: 293–311.
- Berg LS. 1940.** Classification of fishes, both recent and fossil. *Trudy Instituta Zoologii / Akademiia Nauk, Azerbaidzhanskoi SSR* **5**: 87–517.
- Bertoletti JJ, Pezzi SJF, Pereira EHL. 1995.** A new species of the catfish genus *Trachelyopterus* (Siluriformes, Auchenipteridae) from southern Brazil. *Revue Française d'Aquariologie et Herpetologie* **22**: 71–74.
- Betancur-RR. 2009.** Molecular phylogenetics and evolutionary history of ariid catfishes revisited: a comprehensive sampling. *BMC Evolutionary Biology* **9**: 175.
- Betancur-R R, Armbruster JW. 2009.** Molecular clocks provide new insights into the evolutionary history of Galeichthyine sea catfishes. *Evolution* **63**: 1232–1243.
- Betancur RR, Wiley EO, Arratia G, Arturo A, Bailly N, Miya M, Lecointre G, Orti G. 2017.** Phylogenetic classification of bony fishes. *BMC Evolutionary Biology* **12**: 162.
- Birindelli JLO. 2014.** Phylogenetic relationships of the South American Doradoidea (Ostariophysi: Siluriformes). *Neotropical Ichthyology* **12**: 451–564.
- Birindelli JLO, Jansen Z. 2012.** Systematics of the jaguar catfish genus *Liosomadoras* Fowler, 1940 (Auchenipteridae: Siluriformes). *Neotropical Ichthyology* **10**: 1–11.
- Bleeker P. 1858a.** De heer Bleeker brengt nog ter tafel het eerste deel van eene ichthyologiae Archipelagi Indici Prodromus. *Natuurkundig Tijdschrift voor Nederlandsch Indië* **16**: 38–41.

- Bleeker P. 1858b.** De Visschen van den Indischen Archipel. Beschreven en toegelicht. Siluri. *Acta Societatis Regiae Scientiarum Indo-Néerlandicae* **4**: 1–370.
- Bleeker P. 1862–1863.** *Atlas ichthyologique des Indes Orientales Néerlandaises. Siluroïdes, Chacoïdes et Hétérobranchoïdes. Tome II.* Amsterdam: Publié sous les auspices du Gouvernement colonial néerlandais, 1–112.
- Bloch ME. 1794.** *Naturgeschichte der ausländischen Fische*, Vol. 8. Berlin: iv + 174 p., pls. 361–396.
- Bloch ME, Schneider JG. 1801.** *Systema ichthyologiae iconibus cx illustratum.* Saxo: Sumtibus Austoris Impressum et Bibliopolio Sanderiano Commissum.
- Bockmann FA. 1994.** Description of *Mastiglanis asopos*, a new pimelodid catfish from Northern Brazil, with comments on phylogenetic relationships inside the subfamily Rhamdiinae (Siluriformes: Pimelodidae). *Proceedings of the Biological Society of Washington* **107**: 760–777.
- Bockmann FA. 1998.** *Análise filogenética da família Heptapteridae (Teleostei, Ostariophysi, Siluriformes) e redefinição de seus gêneros.* Unpublished D. Phil. Thesis, Universidade de São Paulo.
- Boeseman M. 1953.** Scientific results of the Surinam Expedition 1948–1949. Part II. *Zoology* no. 2: the Fishes (I). *Zoologische Mededelingen* **32**: 1–24.
- Böhlke JE. 1951.** Description of a new auchenipterid catfish of the genus *Pseudepapterus* from the Amazon Basin. *Stanford Ichthyological Bulletin* **4**: 38–40.
- Böhlke JE. 1980.** *Gelanoglanis stroudi*: a new catfish from the Rio Meta system in Colombia (Siluriformes, Doradidae, Auchenipterinae). *Proceedings of the Academy of Natural Sciences of Philadelphia* **132**: 150–155.
- Boulenger GA. 1895.** Abstract of a report on a large collection of fishes formed by Dr. C. Ternetz in Matto Grosso and Paraguay, with descriptions of new species. *Proceedings of the Zoological Society of London* **1895**: 523–529.
- Bremer K. 1988.** The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution; international journal of organic evolution* **42**: 795–803.
- Britski HA. 1972.** *Sistemática e evolução dos Auchenipteridae e Ageneiosidae (Teleostei, Siluriformes).* Unpublished D. Phil. Thesis, Universidade de São Paulo.
- Britski HA, Akama A. 2011.** New species of *Trachycorystes* Bleeker, with comments on other species of the genus (Ostariophysi: Siluriformes: Auchenipteridae). *Neotropical Ichthyology* **9**: 273–280.
- Britto MR. 2002.** *Análise filogenética da ordem Siluriformes com ênfase nas relações da superfamília Loricarioidea (Teleostei: Ostariophysi).* Unpublished D. Phil. Thesis, Universidade de São Paulo.
- Burgess WE. 1989.** *An atlas of freshwater and marine catfishes. A preliminary survey of the Siluriformes.* Neptune City: TFH.
- Calegari B, Reis RE. 2016.** New species of the miniature genus *Gelanoglanis* (Siluriformes: Auchenipteridae) from the Tocantins River basin (Brazil) and osteological description of *G. nanonotocolus*. *Journal of Fish Biology* **90**: 1702–1716.
- Calegari BB, Akama A, Reis R. 2018.** First record of the driftwood catfish *Spinipterus acsi* Akama & Ferraris, 2011 (Siluriformes, Auchenipteridae) for Brazil, Juruá River, Amazon basin. *Check List* **14**: 693–697.
- Calegari BB, Reis R, Vari RP. 2014.** Miniature catfishes of the genus *Gelanoglanis* (Siluriformes: Auchenipteridae): monophyly and the description of a new species from the upper rio Tapajós basin, Brazil. *Neotropical Ichthyology* **12**: 699–706.
- Carvalho TP, Arce HM, Reis RE, Sabaj MH. 2018.** Molecular phylogeny of Banjo catfishes (Ostariophysi: Siluriformes: Aspredinidae): A continental radiation in South American freshwaters. *Molecular Phylogenetics and Evolution* **127**: 459–467.
- Castillo GO, Brull GO. 1989.** *Ageneiosus magoi* una nueva especie de bagre ageneiosido (Teleostei, Siluriformes) para Venezuela y algunas notas sobre su historia natural. *Acta Biologica Venezuelica* **12**: 72–87.
- La Cèpede BGE. 1803.** *Histoire naturelle des poisons*, Vol. 5. Paris: Plasson.
- Chardon M. 1968.** Anatomie comparée de l'appareil de Weber et structures connexes chez les Siluriformes. *Annales de Musée Royal de l'Afrique Central sér. 8, Sciences Zoologiques* **169**: 1–277.
- Cope ED. 1878.** Synopsis of the fishes of the Peruvian Amazon, obtained by Professor Orton during his expeditions of 1873 and 1877. *Proceedings of the American Philosophical Society* **17**: 673–701.
- Cramer CA, Bonatto SL, Reis RE. 2011.** Molecular phylogeny of the Neoplecostominae and Hypoptopomatinae (Siluriformes: Loricariidae) using multiple genes. *Molecular Phylogenetics and Evolution* **59**: 43–52.
- Curran DJ. 1989.** Phylogenetic relationships among the catfish genera of the family Auchenipteridae (Teleostei: Siluroidea). *Copeia* **1989**: 408–419.
- Cuvier G. 1817.** *Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée.* Paris: Deterville Tombo II.
- Cuvier G, Valenciennes A. 1840.** *Histoire naturelle des poissons. Tome Quinzième. Suite du Livre Dix-septième. Siluroïdes* Paris, Strasbourg: Chez P. & Levrault.
- Datovo A, Vari RP. 2014.** The adductor mandibulae muscle complex in lower teleostean fishes (Osteichthyes: Actinopterygii): comparative anatomy, synonymy and phylogenetic implications. *Zoological Journal of the Linnean Society* **171**: 554–622.
- Devincenzi GJ. 1942.** Ictiofauna del Rio Uruguay medio. *Anales del Museo Nacional de Historia Natural de Montevideo* **5**: 1–100.
- Diogo R, Oliveira C, Chardon M. 2001.** On the homologies of the skeletal components of catfish (Teleostei: Siluriformes) suspensorium. *Belgian Journal of Zoology* **131**: 155–171.
- Diogo R. 2003.** Higher-level phylogeny of Siluriformes - An Overview. chap.12: 353–384 p. In: Arratia G, Kapoor BG, Chardon M, Diogo R, eds. *Catfishes*. Enfield: Science Publishers Inc., 353–384.
- Diogo R. 2004.** *Morphological evolution, adaptations, homoplasies, constraints and evolutionary trends: catfishes as a case study on general phylogeny and macroevolution.* Enfield: Science Publisher Inc.

- Eigenmann CH. 1912.** The freshwater fishes of British Guiana, including a study of the ecological grouping of species, and the relation of the fauna of the plateau to that of the lowlands. *Memoirs of the Carnegie Museum* **5**: 1–578.
- Eigenmann CH. 1917.** New and rare species of South American Siluridae in the Carnegie Museum. *Annals of the Carnegie Museum* **11**: 398–404.
- Eigenmann CH. 1925.** A review of the Doradidae, a family of South American nematognathi or catfishes. *Transactions of the American Philosophical Society* **22**: 280–365.
- Eigenmann CH, Allen WR. 1942.** *Fishes of Western South America. I. The Intercordilleran and Amazonian lowlands of Peru. II. The high pampas of Peru, Bolivia, and northern Chile. With a revision of the Peruvian Gymnotidae and, of the genus Orestias.* Lexington: The University of Kentucky.
- Eigenmann CH, Eigenmann RS. 1888.** Preliminary notes on South American Nematognathi, I. *Proceedings of the California Academy of Sciences* **2**: 119–172.
- Eigenmann CH, Eigenmann RS. 1890.** A revision of the South American Nematognathi or Catfishes. *Occasional Papers of California Academy of Sciences* **1**: 1–508.
- Felsenstein J. 1985.** Phylogenies and the comparative method. *The American Naturalist* **125**: 1–15.
- Ferraris CJ Jr. 1988.** *The Auchenipteridae: putative monophyly and systematics, with a classification of the neotropical doradoid catfishes (Ostariophysi: Siluriformes).* Unpublished D. Phil. Thesis, City University of New York.
- Ferraris CJ Jr. 2007.** Checklist of catfishes, recent and fossil (Osteichthyes: Siluriformes), and catalogue of siluriform primary types. *Zootaxa* **1418**: 1–628.
- Ferraris CJ Jr, Fernandez J. 1987.** *Trachelyopterichthys anduzei*, a new species of auchenipterid catfish from the upper Río Orinoco of Venezuela with notes on *T. taeniatus* (Kner). *Proceedings of the Biological Society of Washington* **100**: 257–261.
- Ferraris CJ Jr, Vari RP. 1999.** The South American catfish genus *Auchenipterus* Valenciennes, 1840 (Ostariophysi: Siluriformes: Auchenipteridae): monophyly and relationships, with a revisionary study. *Zoological Journal of the Linnean Society* **126**: 387–450.
- Ferraris CJ Jr, Vari RP. 2000.** The deep-water South American catfish genus *Pseudepapterus* (Ostariophysi: Auchenipteridae). *Ichthyological Exploration of Freshwaters* **11**: 97–112.
- Ferraris CJ Jr, Vari RP, Raredon SJ. 2005.** Catfishes of the genus *Auchenipterichthys* (Osteichthyes: Siluriformes: Auchenipteridae). *Neotropical Ichthyology* **3**: 89–106.
- Fink SV, Fink WL. 1981.** Interrelationships of the ostariophysian fishes (Teleostei). *Zoological Journal of the Linnean Society* **72**: 297–353.
- Fink SV, Fink WL. 1996.** Interrelationship of the Ostariophysian fishes (Teleostei). In: Stiassny MLJ, Parenti LR, Johnson GD, eds. *Interrelationships of the fishes.* San Diego: Academic Press, 209–249.
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994.** DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**: 294–299.
- Fowler HW. 1915.** Notes on nematognathous fishes. *Proceedings of the Academy of Natural Sciences of Philadelphia* **67**: 203–243.
- Fowler HW. 1940.** A collection of fishes obtained by Mr. William C. Morrow in the Ucayali River Basin, Peru. *Proceedings of the Academy of Natural Sciences of Philadelphia* **91**: 219–289.
- Fowler HW. 1951.** Os peixes de água doce do Brasil. *Arquivos de Zoologia do Estado de São Paulo* **6**: 405–625.
- Freitas TMS, Almeida VHC, Valente RM, Montag LFA. 2011.** Feeding ecology of *Auchenipterichthys longimanus* (Siluriformes: Auchenipteridae) in a riparian flooded forest of eastern Amazônia, Brazil. *Neotropical Ichthyology* **9**: 629–636.
- Fricke R, Eschmeyer WN, Fong JD. 2019.** *Species of fishes by family/subfamily.* On-line version. Available at: <http://research.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp>
- Friel J. 1994.** *A phylogenetic study of the Neotropical banjo catfishes (Teleostei: Siluriformes: Aspredinidae).* Unpublished Ph.D. Thesis, Duke University.
- Friel J. 2008.** *Pseudobunocephalus*, a new genus of banjo catfish with the description of a new species from the Orinoco River system of Colombia and Venezuela (Siluriformes: Aspredinidae). *Neotropical Ichthyology* **6**: 293–300.
- Goloboff PA, Farris J, Nixon K. 2003.** *T.N.T.: tree analysis using new technology. Program and documentation.* Available at: <http://www.zmuc.dk/public/phylogeny/tnt>
- Goloboff PA, Farris J, Nixon K. 2008.** TNT, a free program for phylogenetic analysis. *Cladistics* **24**: 774–786.
- Gosline WA. 1945.** Catálogo dos nematognatos de água doce da América do Sul e Central. *Boletim do Museu Nacional do Rio de Janeiro* **33**: 1–138.
- Gosline WA. 1975.** The palatine-maxillary mechanism in catfishes, with comments on the evolution and zoogeography of modern siluroids. *Occasional Papers of the California Academy of Sciences* **120**: 1–31.
- Goulding M. 1980.** *The fishes and the forest, explorations in Amazonian natural history.* Berkeley: University of California Press.
- Grande L. 1987.** Redescription of *Hypsidoris farsonensis* (Teleostei: Siluriformes), with a reassessment of its phylogenetic relationships. *Journal of Vertebrate Paleontology* **7**: 24–54.
- Grant S. 2015.** Four new subgenera of *Centromochlus* Kner, 1858 with comments on the boundaries of some related genera (Siluriformes: Auchenipteridae: Centromochlinae). *Ichthyofile* **3**: 1–16.
- Greenfield DW, Glodek GS. 1977.** *Trachelyichthys exilis*, a new species of catfish (Pisces: Auchenipteridae) from Peru. *Fieldiana: Zoology* **72**: 47–58.
- Greenwood PH, Rosen DE, Weitzman SH, Myers GS. 1966.** Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History* **131**: 339–456.
- Guindon S, Gascuel O. 2003.** A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* **52**: 696–704.

- Günther A. 1864.** *Catalogue of fishes in the British Museum*. London: Trustees of the British Museum.
- Hardman M. 2002.** *The phylogenetic relationships among extant catfishes, with special reference to Ictaluridae (Otophysi: Siluriformes)*. Unpublished D. Phil. Thesis, University of Illinois at Urbana-Champaign.
- Hardman M. 2004.** The phylogenetic relationships among *Noturus* catfishes (Siluriformes: Ictaluridae) as inferred from mitochondrial gene cytochrome *b* and nuclear recombination activating gene 2. *Molecular Phylogenetics and Evolution* **30**: 395–408.
- Hardman M. 2005.** The phylogenetic relationships among nondiplomystid catfishes as inferred from mitochondrial cytochrome *b* sequences; the search for the ictalurid sister taxon (Otophysi: Siluriformes). *Molecular Phylogenetics and Evolution* **37**: 700–720.
- Haseman JD. 1911.** Descriptions of some new species of fishes and miscellaneous notes on others obtained during the expedition of the Carnegie Museum to central South America. *Annals of the Carnegie Museum* **7**: 315–328.
- Hennig W. 1950.** *Grundzüge einer Theorie der phylogenetischen Systematik*. Berlin: Deutsche Zentralverlag.
- Hennig W. 1966.** *Phylogenetic systematics*. Urbana: University of Illinois Press.
- Higuchi H. 1992.** *A phylogeny of the South American thorny catfishes (Osteichthyes; Siluriformes; Doradidae)*. Unpublished D. Phil. Thesis, Harvard University.
- Higuchi H, Birindelli JLO, Sousa LM, Britski HA. 2007.** *Merodoras nheco*, new genus and species of doradid from Pantanal Matogrossense, with nomination of the new subfamily Astrodoradinae (Siluriformes, Doradidae). *Zootaxa* **1446**: 31–42.
- Hoedeman JJ. 1961.** Notes on the ichthyology of Surinam and other Guianas. 8. Additional records of siluriform fishes. *Bulletin of Aquatic Biology* **2**: 129–139.
- Howes GJ, Teugels GG. 1989.** Observations on the ontogeny and homology of the pterygoid bones in *Corydoras paleatus* and some other catfish. *Journal of Zoology* **219**: 441–456.
- Huelsenbeck JP, Ronquist F. 2001.** MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**: 754–755.
- von Ihering R. 1928.** *Glanidium cesarpinto* n. sp. de Peixe de couro (fam. Siluridae sub-fam. Auchenipterinae). *Boletim Biológico* **12**: 46–49.
- von Ihering R. 1930.** Notas ecológicas referentes a peixes d'água doce do Estado de S. Paulo e descrição de 4 espécies novas. *Archivos do Instituto Biológico* **3**: 93–103.
- von Ihering R. 1937.** Oviclaval fertilization in South American catfish, *Trachycorystes*. *Copeia* **1937**: 201–205.
- Ivanova NV, Zenlack TS, Hanner RH, Hebert PDN. 2007.** Universal primer cocktails for fish DNA barcoding. *Molecular Ecology Notes* **7**: 544–548.
- Jordan DS. 1920.** The genera of fishes, part IV, from 1881 to 1920, thirty-nine years, with the accepted type of each. A contribution to the stability of scientific nomenclature. *Leland Stanford Jr. University Publications, University series* **43**: 411–576.
- Jordan DS. 1929.** *Manual of the vertebrate animals of the northeastern United States inclusive of marine species, 13th edn*. New York: World Book Co.
- Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Mentjies P, Drummond A. 2012.** Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28**: 1647–1649.
- Kindred JE. 1919.** The skull of *Amiurus*. *Illinois Biological Monographs* **5**: 1–120.
- Kner R. 1857.** Ichthyologische Beiträge. II Abtheilung. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftlichen Classe* **26**: 373–448.
- Kner R. 1858.** Kritische Bemerkungen über Castelnau's Siluroiden. *Archiv für Naturgeschichte* **24**: 344–350.
- Koch WR, Reis RE. 1996.** *Tatia boemia*, a new species of auchenipterid catfish (Teleostei: Siluriformes) from the rio Uruguai drainage, southern Brazil. *Ichthyological Exploration of Freshwaters* **7**: 85–90.
- Lacépède BGE. 1803.** *Histoire naturelle des poissons*. Vol. 5. Paris: Plasson.
- Lanfear R, Calcott B, Ho SYW, Guindon S. 2012.** PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biological Evolution* **29**: 1695–1701.
- Lavoué S, Sullivan JP. 2004.** Simultaneous analysis of five molecular markers provides a well-supported phylogenetic hypothesis for the living bony-tongue fishes (Osteoglossomorpha: Teleostei). *Molecular Phylogenetics and Evolution* **33**: 171–185.
- Lewis PO. 2001.** A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology* **50**: 913–925.
- Li C, Ortí G, Zhang G, Lu G. 2007.** A practical approach to phylogenomics: the phylogeny of ray-finned fish (Actinopterygii) as a case study. *BMC Evolutionary Biology* **7**: 44.
- Lindberg GU. 1971.** *Fishes of the world. A key to families and a checklist*. New York: Halsted Press.
- Linnaeus C. 1766.** *Systema Naturae, 12th edn*. Stockholm: L. Salvius.
- Liu K, Raghavan S, Nelesen S, Linder CR, Warnow T. 2009.** Rapid and Accurate Large-Scale Coestimation of Sequence Alignments and Phylogenetic Trees. *Science* **324**: 1561–1564.
- López JA, Chen W, Ortí G. 2004.** Esociform phylogeny. *Copeia* **2004**: 449–464.
- Lovejoy N, Collette BB. 2001.** Phylogenetic relationships of New World needle fishes (Teleostei: Belontiidae) and the biogeography of transitions between marine and freshwater habitats. *Copeia* **2001**: 324–338.
- Lovejoy N, Lester C, Crampton WGR, Marques FPL, Albert JS. 2010.** Phylogeny, biogeography, and electric signal evolution of Neotropical knifefishes of the genus *Gymnotus* (Osteichthyes: Gymnotidae). *Molecular Phylogenetics and Evolution* **54**: 278–290.

- Lundberg JG. 1970.** *The evolutionary history of North American catfishes, family Ictaluridae*. Unpublished Ph.D. Thesis, University of Michigan.
- Lundberg JG. 1993.** African-South American freshwater fish clades and continental drift: problems with a paradigm. In: Goldblatt, ed. *Biological relationships between Africa and South America*. New Haven: Yale University Press, 156–199.
- Lundberg JG, Baskin JN. 1969.** The caudal skeleton of the catfishes, order Siluriformes. *American Museum Novitates* **2398**: 1–49.
- Lundberg JG, Mago-Leccia F. 1986.** A Review of *Rhabdolichops* (Gymnotiformes, Sternopygidae), a Genus of South American Freshwater Fishes, with Descriptions of Four New Species. *Proceedings of the Academy of Natural Sciences of Philadelphia* **138**: 53–85.
- Lundberg JG, Mago-Leccia F, Nass P. 1991.** *Exallodontus aguanai*, a new genus and species of Pimelodidae (Pisces: Siluriformes) from deep river channels of South America, and delimitation of the subfamily Pimelodidae. *Proceedings of the Biological Society of Washington* **104**: 840–869.
- Lundberg JG, Sullivan JP, Hardman M. 2011.** Phylogenetics of the South American catfish family Pimelodidae (Teleostei: Siluriformes) using nuclear and mitochondrial gene sequences. *Proceedings of the Academy of Natural Sciences of Philadelphia* **161**: 153–189.
- Lütken CF. 1874.** Siluridae novae Brasiliae centralis a clarissimo J. Reinhardt in provincia Minae-geraës circa oppidulum Lagoa Santa, præcipue in flumine Rio das Velhas et affluentibus collectae, secundum characteres essentialia breviter descriptæ a Chr. Lütken. *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandling og dets Medlemmers Arbejder i Aaret* **1874**: 29–36.
- Maddison WP, Maddison DR. 2017.** *Mesquite: a modular system for evolutionary analysis, Version 3.31*. Available at: <http://mesquiteproject.org>
- Mago-Leccia F. 1984.** *Entomocorus gameroi*, una nueva especie de bagre auquenipterido (Teleostei, Siluriformes) de Venezuela, incluyendo la descripción de su dimorfismo sexual secundario. *Acta Biologica Venezuelica* **11**: 215–236.
- Marceniuk AP, Menezes NA, Britto MR. 2012.** Phylogenetic analysis of the family Ariidae (Ostariophysi: Siluriformes), with a hypothesis on the monophyly and relationships of the genera. *Zoological Journal of the Linnean Society* **165**: 534–669.
- Meek SE, Hildebrand SF. 1913.** New species of fishes from Panama. *Zoological Series, Field Museum of Natural History* **10**: 77–91.
- Mees GF. 1974.** The Auchenipteridae and Pimelodidae of Suriname (Pisces, Nematognathi). *Zoologische Verhandelingen* **132**: 1–256.
- Mees GF. 1984.** A note on the genus *Tocantinsia* (Pisces, Nematognathi, Auchenipteridae). *Amazoniana* **9**: 31–34.
- Mees GF. 1988.** Notes on the genus *Tatia* (Pisces, Nematognathi, Auchenipteridae). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen (Series C)* **91**: 405–414.
- Menezes RS. 1949.** Alimentação do mandi bicudo, *Hassar affinis* (Steindachner), da bacia do Rio Parnaíba, Piauí (Actinopterygii, Doradidae, Doradinae). *Revista Brasileira de Biologia* **9**: 93–96.
- Miller MA, Pfeiffer W, Schwartz T. 2010.** Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*. New Orleans: 1–8.
- Miranda Ribeiro A. 1911.** Fauna brasiliensis. Peixes IV(a). Eleutherobranchios Aspirophoros. *Archivos do Museu Nacional do Rio de Janeiro* **16**: 1–504.
- Miranda Ribeiro A. 1937.** Sobre uma coleção de vertebrados do nordeste brasileiro. Primeira parte: peixes e batrachios. *O Campo, Rio de Janeiro* **1**: 54–56.
- Miranda Ribeiro P. 1968.** Apontamentos ictiológicos IV. *Boletim do Museu Nacional do Rio de Janeiro, Nova Série, Zoologia* **262**: 1–7.
- Mo T. 1991.** *Anatomy, relationships and systematics of the Bagridae (Teleostei: Siluroidei), with a hypothesis of Siluroid phylogeny. Theses Zoologicae* **17**. Königstein: Koeltz Scientific Books.
- Müller J. 1842a.** Über die Schwimmblase der Fische, mit Bezug auf einige neue Fischgattungen. *Königlichen Preussische Akademie des Wissenschaften zu Berlin* **1842**: 202–210.
- Müller J. 1842b.** Beobachtungen über die Schwimmblase der Fische, mit Bezug auf einige neue Fischgattungen. *Archiv für Anatomie, Physiologie und Wissenschaftliche Medicin* **1842**: 307–329.
- Müller J, Troschel FH. 1849.** *Horae Ichthyologicae: Beschreibung und Abbildung neuer Fische, drittes Heft*. Berlin: Veit & Co.
- Nakatani K, Agostinho AA, Baumgartner G, Bialecki A, Sanches PV, Makrakis MC, Pavanelli CS. 2001.** *Ovos e larvas de peixes de água doce: desenvolvimento e manual de identificação, 1st edn*. Maringá: EDUEM.
- Nylander JAA, Ronquist F, Huelsenbeck JP, Nieves JLA. 2004.** Bayesian phylogenetic analysis of combined data. *Systematic Biology* **53**: 47–67.
- Palumbi SR, Martin A, Romano S, Mcmillan WO, Stice L, Grabowski G. 1991.** *The simple fool's guide to PCR*. Honolulu: University of Hawaii Press.
- Pastana MNL. 2014.** *Canais e poros do sistema látero-sensorial cefálico de Characiformes (Ostariophysi): anatomia e seu significado filogenético*. Unpublished PhD Dissertation, Universidade de São Paulo.
- Pavanelli CS, Bifi AG. 2009.** A new *Tatia* (Ostariophysi: Siluriformes: Auchenipteridae) from the rio Iguaçu basin, Paraná State, Brazil. *Neotropical Ichthyology* **7**: 199–204.
- Peixoto LAW, Wosiacki BW. 2010.** Description of a new species of *Tetranematichthys* (Siluriformes: Auchenipteridae) from the lower Amazon basin, Brazil. *Neotropical Ichthyology* **8**: 69–76.
- Pereira LHG, Maia GMG, Hanner R, Foresti F, Oliveira C. 2011.** DNA barcodes discriminate freshwater fishes from the Paraíba do Sul River Basin, São Paulo, Brazil. *Mitochondrial DNA* **22**: 71–79.

- Pereira LHG, Hanner R, Foresti F, Oliveira C. 2013.** Can DNA barcoding accurately discriminate megadiverse Neotropical freshwater fish fauna?. *Biomed Central Genetics* **14**: 20.
- de Pinna MCC. 1993.** *Higher-level phylogeny of Siluriformes (Teleostei, Ostariophysii), with a new classification of the order.* Unpublished PhD Thesis, City University of New York.
- de Pinna MCC. 1996.** A phylogenetic analysis of the Asian catfish families Sisoridae, Akysidae, and Amblycipitidae, with a hypothesis on the relationships of Neotropical Aspredinidae (Teleostei, Ostariophysii). *Fieldiana: Zoology* **1478**: 1–83.
- de Pinna MCC. 1998.** Phylogenetic relationships of neotropical Siluriformes (Teleostei: Ostariophysii): historical overview and synthesis of hypotheses. In: Malabarba L, Reis R, Vari RP, Lucena C, Lucena L, eds. *Phylogeny and classification of neotropical fishes*. Porto Alegre: EdiPUCRS, 279–330.
- de Pinna MCC, Ferraris CJ Jr, Vari RP. 2007.** A phylogenetic study of the Neotropical catfish family Cetopsidae (Osteichthyes, Ostariophysii, Siluriformes), with a new classification. *Zoological Journal of Linnean Society* **150**: 755–813.
- Rafinesque CS. 1815.** *Analyse de la nature, ou tableau de l'univers et des corps organises*. Palermo.
- Rambaut A, Suchard MA, Xie D, Drummond AJ. 2014.** *Tracer v1.6*. Available at: <http://beast.bio.ed.ac.uk/Tracer>
- Regan CT. 1911.** The classification of the teleostean fishes of the order Ostariophysii. 2. Siluroidea. *Annals and Magazine of Natural History* **8**: 553–577.
- Reis RE, Albert JS, Di Dario F, Mincarone MM, Petry P, Rocha LA. 2016.** Fish biodiversity and conservation in South America. *Journal of Fish Biology* **89**: 12–47.
- Reis RE, Borges TAK. 2006.** The South American catfish genus *Entomocorus* (Ostariophysii: Siluriformes: Auchenipteridae), with the description of a new species from the Paraguay river basin. *Copeia* **2006**: 412–421.
- Reis RE, Kullander SO, Ferraris CJ Jr. 2003.** *Check list of the freshwater fishes of South and Central America*. Porto Alegre: EdiPUCRS.
- Rengifo B, Lujan NK, Taphorn D, Petry P. 2008.** A new species of *Gelanoglanis* (Siluriformes: Auchenipteridae) from the Marañon River (Amazon Basin), northeastern Perú. *Proceedings of the Academy of Natural Sciences of Philadelphia* **157**: 181–188.
- Ribeiro AO, Caires RA, Mariguela TC, Pereira LHG, Hanner R, Oliveira C. 2012.** DNA barcodes identify marine fishes of São Paulo State, Brazil. *Molecular Ecology Resources* **12**: 1012–1020.
- Ribeiro FRV. 2011.** *Sistemática do gênero Ageneiosus La Cépède (Siluriformes; Auchenipteridae)*. Unpublished PhD Dissertation, Instituto Nacional de Pesquisas da Amazônia.
- Ribeiro FRV, Py-Daniel LHR, Walsh SJ. 2017.** Taxonomic revision of the South American catfish genus *Ageneiosus* (Siluriformes: Auchenipteridae) with the description of four new species. *Journal of Fish Biology* **90**: 1388–1478.
- Ronquist F, Huelsenbeck JP. 2003.** MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.
- Rosen DE, Greenwood PH. 1970.** Origin of the Weberian apparatus and the relationships of the ostariophysan and gonorynchiform fishes. *American Museum Novitates* **2428**: 1–25.
- Rössel F. 1962.** *Centromochlus schultzi*, ein neues Wels aus Brasilien (Pisces, Teleostei, Auchenipteridae). *Senckenbergiana Biologica* **43**: 27–30.
- Royero R. 1987.** *Morfología de la aleta dorsal en los bagres (Teleostei: Siluriformes), con especial referencia a las familias amaricanas*. Unpublished PhD Dissertation, Universidad Central de Venezuela.
- Royero R. 1992.** *Tatia musaica*, una nueva especie de bagre auquenipterido (Siluriformes - Auchenipteridae) de la cuenca del Rio Orinoco, Territorio Federal Amazonas, Venezuela. *Acta Científica Venezolana* **43**: 300–306.
- Royero R. 1999.** *Studies on the systematics and phylogeny of the catfish family Auchenipteridae (Teleostei: Siluriformes)*. Unpublished PhD Thesis, University of Bristol.
- Sabaj MH. 2002.** *Taxonomy of the Neotropical thorny catfishes (Siluriformes: Doradidae) and revision of the genus Leptodoras*. Unpublished PhD Thesis, University of Illinois.
- Sarmiento-Soares LM, Cabeceira FG, Carvalho LN, Zuanon J, Akama A. 2013.** *Centromochlus meridionalis*, a new catfish species from the southern Amazonian limits, Mato Grosso State, Brazil (Siluriformes: Auchenipteridae). *Neotropical Ichthyology* **11**: 797–808.
- Sarmiento-Soares LM, Martins-Pinheiro RF. 2008.** A systematic revision of *Tatia* (Siluriformes: Auchenipteridae: Centromochlinae). *Neotropical Ichthyology* **6**: 495–542.
- Schaefer SA. 1987.** Osteology of *Hypostomus plecostomus* (Linnaeus), with a phylogenetic analysis of the loricariid subfamilies (Pisces: Siluroidei). *Contributions in Science of the Natural History Museum of Los Angeles County* **394**: 1–31.
- Schomburgk RH. 1841.** The natural history of fishes of Guiana. Part I. In: Jardine W, ed. *The Naturalists' library*, Vol. 3. Edinburgh: W. H. Lizars.
- Schultz LP. 1944.** The catfishes of Venezuela, with descriptions of thirty-eight new forms. *Proceedings of the United States National Museum* **94**: 173–338.
- Sereno PC. 2007.** Logical basis for morphological characters in phylogenetics. *Cladistics* **23**: 565–587.
- Soares-Porto LM. 1998.** Monophyly and interrelationships of the Centromochlinae (Siluriformes: Auchenipteridae). In: Malabarba LR, Reis RE, Vari RP, Lucena ZMS, Lucena CAS, eds. *Phylogeny and classification of neotropical fishes*. Porto Alegre: EdiPUCRS, 331–350.
- Soares-Porto LM. 2000.** A new species of *Centromochlus* (Siluriformes: Auchenipteridae) from the rio Negro drainage, Amazon basin, Brazil, with comments on its relationships. *Ichthyological Exploration of Freshwaters* **11**: 279–287.
- Soares-Porto LM, Walsh SJ, Nico LG, Netto JM. 1999.** A new species of *Gelanoglanis* from the Orinoco and Amazon river basin, with comments on miniaturization within the

- genus (Siluriformes: Auchenipteridae: Centromochlinae). *Ichthyological Exploration of Freshwaters* **10**: 63–72.
- Sousa LM. 2010.** *Revisão taxonômica e filogenia de Astrodoradinae (Siluriformes, Doradidae)*. Unpublished PhD Dissertation, Universidade de São Paulo.
- Spadella MA, Oliveira C, Quagio-Grassiotto I. 2006.** Spermiogenesis and introsperm ultrastructure of *Scoloplax distolothrix* (Ostariophysi: Siluriformes: Scoloplacidae). *Acta Zoologica* **87**: 341–48.
- Spadella MA, Oliveira C, Quagio-Grassiotto I. 2012.** Spermiogenesis and sperm ultrastructure in ten species of Loricariidae (Siluriformes, Teleostei). *Zoomorphology* **131**: 249–263.
- von Spix JB, Agassiz L. 1829–1831.** *Selecta genera et species piscium quos in itinere per Brasiliam annos MDCCCXVII–MDCCCXX Jussu et auspiciis Maximiliani Josephi I. colleget*. Munich: C. Wolf.
- Steindachner F. 1877.** Die Süßwasserfische des südöstlichen Brasilien, III. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftlichen Classe, Abt. 1. Botanik, Zoologie, Anatomie, Geologie und Paläontologie* **74**: 559–694.
- Steindachner F. 1878.** Zur Fischfauna des Magdalenen-Stromes. *Anzeiger der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften in Wien* **15**: 88–91.
- Steindachner F. 1881.** Beiträge zur Kenntniss der Flussfische Südamerika's. III. *Denkschriften der Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse* **44**: 1–17.
- Steindachner F. 1882.** Beiträge zur Kenntniss der Flussfische Südamerika's, IV. *Anzeiger der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftlichen Classe* **19**: 175–180.
- Steindachner F. 1915.** Beiträge zur Kenntnis der Flussfische Südamerikas, V. *Anzeiger der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftlichen Classe* **52**: 217–219.
- Sullivan JP, Lavoué S, Hopkins CD. 2000.** Molecular systematics of the African electric fishes (Mormyroidea: Teleostei) and a model for the evolution of their electric organs. *The Journal of Experimental Biology* **203**: 665–683.
- Sullivan JP, Lundberg JG, Hardman M. 2006.** A phylogenetic analysis of the major groups of catfishes (Teleostei: Siluriformes) using *rag1* and *rag2* nuclear gene sequences. *Molecular Phylogenetics and Evolution* **41**: 636–662.
- Sullivan JP, Peng Z, Lundberg JG, Peng J, He S. 2008.** Molecular evidence for diphyly of the Asian catfish family Amblycipitidae (Teleostei: Siluriformes) and exclusion of the South American Aspredinidae from Sisoroidea. *Proceedings of the Academy of Natural Sciences of Philadelphia* **157**: 51–65.
- Swofford DL, Maddison WP. 1987.** Reconstructing ancestral character states under Wagner parsimony. *Mathematical Biosciences* **87**: 199–229.
- Taylor R, Van Dyke CC. 1985.** Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium* **9**: 107–119.
- Valenciennes A. 1840.** Poissons; catalogue des principales espèces de poissons, rapportées de l'Amérique méridionale. In: d'Orbigny A, ed. *Voyage dans l'Amérique méridionale (le Brésil, la République Orientale de l'Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivie, la République du Pérou)*, Vol. 5. Paris: Bertrand et Levrault.
- Vari RP, Ferraris Jr CJ. 1998.** The neotropical catfish genus *Epapterus* Cope (Siluriformes: Auchenipteridae): a reappraisal. *Proceedings of the Biological Society of Washington* **111**: 9992–1007.
- Vari RP, Ferraris Jr CJ. 2006.** The catfish genus *Tetranematichthys* (Auchenipteridae). *Copeia* **2006**: 168–180.
- Vari RP, Ferraris CJ Jr. 2013.** Two new species of the catfish genus *Tatia* (Siluriformes: Auchenipteridae) from the Guiana Shield and a reevaluation of the limits of the genus. *Copeia* **2013**: 396–402.
- Vari RP, Jewett SL, Taphorn DC, Gilbert CR. 1984.** A new catfish of the genus *Epapterus* (Siluriformes: Auchenipteridae) from the Orinoco River basin. *Proceedings of the Biological Society of Washington* **97**: 462–472.
- Vigliotta TR. 2008.** A phylogenetic study of the African catfish family Mochokidae (Osteichthyes, Ostariophysi, Siluriformes), with a key to genera. *Proceedings of the Academy of Natural Sciences of Philadelphia* **157**: 73–136.
- Walsh SJ. 1990.** *A systematic revision of the Neotropical catfish family Ageneiosidae (Teleostei: Ostariophysi: Siluriformes)*. Unpublished PhD Thesis, University of Florida.
- Walsh SJ, Ribeiro FRV, Py-Daniel LHR. 2015.** Revision of *Tympanopleura* Eignmann (Siluriformes: Auchenipteridae) with description of two new species. *Neotropical Ichthyology* **13**: 1–46.
- Wiley EO. 1981.** *Phylogenetics: the theory and practice of phylogenetics systematics*. New York: John Wiley & Sons.
- Yu J, Holder MT, Sukumaran J, Mirarab S, Oaks J. SATé version gui 2.2.7.** Available at: <http://phylo.bio.ku.edu/software/sate/sate.html> (accessed Jul 2015).
- Zwickl D. 2006.** *Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion*. Unpublished PhD Thesis, University of Texas at Austin.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Material examined.

Appendix S2. Character state matrix of the 264 morphological characters for the 130 available taxa. Missing data are represented by '?', inapplicable data by '–' and polymorphisms by '&'.

Appendix S3. List of synapomorphies for each clade and autapomorphies for monotypic genera or those represented by single taxa. Clade numbers correspond to a strict consensus tree (Figs 13, 14) under Maximum Parsimony. Characters are numbered starting from zero (corresponding to the number shown in square brackets in the character description): molecular characters, 0–3489; morphological characters, 3490–3753. Character transitions with double states correspond to ambiguous optimizations.

Appendix S4. Phylogenetic estimate of relationships of Auchenipteridae based on Bayesian Inference analysis of the combined dataset of morphological and molecular characters. Clade numbers denote nodal posterior probabilities values. Black circles represent monophyletic groups and red circles polyphyletic assemblages compared with the Maximum Parsimony analysis.

Appendix S5. Molecular phylogenetic estimate of Auchenipteridae relationships based on Bayesian Inference of five combined genes (*coI*, 16S, *rag2*, *myh6* and *SH3PX3*). Clade numbers denote nodal posterior probability values in red (< 85%) and blue (≥ 85%).

Appendix S6. Maximum parsimony analysis of morphological data (264 characters). Strict consensus of 1195 maximally parsimonious trees (consistency index = 0.21; retention index = 0.76), with 1822 steps showing Auchenipteridae relationships. Goodman–Bremer index appears below branches.